Patterns of morphological variation and correlates of habitat use in Chameleons

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The lizard family Chameleonidae is one of the most distinctive taxa of all vertebrates. Nonetheless, despite great intrafamilial diversity, little research has been conducted on morphological variation among chameleons. As a first step in this direction, we took morphological measurements on the head, limbs, spines, and tail of 56 species. Our goals were to investigate whether morphological variation correlates with differences in ecology and to examine whether correlations exist among different aspects of morphology. Based on existing information, species were classified either as arboreal or terrestrial, the latter referring to species that are known to use the ground on a regular basis. This study confirms that considerable intrafamilial variation exists among chameleons and that these traits appear to be evolutionarily quite labile. Once the effects of size are removed, functionally related traits tend to covary; however, few correlations are observed between non-functionally related traits. Many differences in the lengths of the limbs and head elements were detected between terrestrial and arboreal species, but the functional and selective significance of these differences is not clear. Further research on chameleon behaviour and ecology is required to understand the factors contributing to chameleon morphological diversity.   © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, **76**, 91–103.

ADDITIONAL KEYWORDS: chameleon – ecological morphology – lizard – morphology.

INTRODUCTION

With their projectile tongues, zygodactylous feet, and prehensile tails, chameleons surely rank among the world's most remarkable vertebrates. Although distinctive in these attributes, the Chameleonidae also exhibits considerable morphological diversity among its approximately 100 species. This diversity is most apparent in body size – ranging from the minute dwarf chameleons in the genus *Brookesia* to the several orders of magnitude more massive giants such as *Calumma parsoni*, *Furcifer oustaleti*, and *Chamaeleo melleri* – and head ornamentation, which includes elaborate crests, horns, nasal appendages and other structures in many species. In addition, chameleons differ in a variety of other respects, including tail and limb length and presence of a dorsal crest (Nečas, 1999, provides a nice overview of chameleon variation).

Over the course of the last three decades, several studies have examined the ecological correlates of morphological diversity in a wide variety of lizards, including *Anolis*, *Tropidurus*, *Ctenotus*, sceloporines, lacertids and others (e.g. Jaksić, Núñez & Ojeda, 1980; Pianka, 1986; Scheibe, 1987; Pounds, 1988). These studies have found a great variety of ecomorphological correlations; the adaptive nature of many of these has been clarified by behavioural, functional, and phylogenetic information (Losos, 1990; Miles, 1994; Irschick *et al.*, 1997; Vitt *et al.*, 1997; Vanhooydonck & Van Damme, 1999; Melville & Swain, 2000; Vanhooydonck, Van Damme & Aerts, 2000; Zani, 2000; Kohlsdorf, Garland & Navas, 2001).

By contrast, the ecological morphology of chameleons has been little explored. In large part, this is probably a result of the surprisingly sparse information known about basic aspects of the ecology and behaviour of almost all chameleon species (Nečas, 1999, summarizes what is known). Our study is a preliminary effort to rectify this shortcoming and has two goals:

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1 To investigate whether morphological variation among chameleons correlates with differences in ecology; given the paucity of ecological and behavioural information on chameleons, a detailed analysis is not possible. Nonetheless, one avenue of ecological differentiation can be examined. On the one hand, despite their obvious adaptations for locomotion on narrow arboreal perches, such as zygodactylous feet and prehensile tails, a number of chameleon species spend a considerable amount of time on the ground (e.g. *Brookesia* species, *Chamaeleo namaquensis*). Other species, although more arboreal, still frequently can be observed moving on the ground. On the other hand, many species, as far is known (and the lack of information for many species must be kept in mind), rarely come to the ground. We crudely classified species as 'arboreal' or 'terrestrial' (meaning they were known to use the ground, not that they never used arboreal habitats) and asked whether the two groups differed morphologically. We predicted that limb and tail lengths should be related to locomotor behaviour, as it is in other lizard groups (e.g. anoles: Moermond, 1979; Pounds, 1988; Losos & Irschick, 1996; Irschick & Losos, 1998, 1999), and thus might vary between arboreal and terrestrial species. Head and spine dimensions are most likely used in intra- and interspecific communication (Rand, 1961; Nečas, 1999). Whether arboreal and terrestrial species differ in their social behaviour is unknown, but one might predict that different structural habitats select for different types of communication behaviours or social structures (e.g. Jarman, 1974; Lythgoe, 1979; Waser & Brown, 1984; Fleishman, 1992; Butler, Schoener and Losos, 2000), which might lead to the evolution of different morphological display structures.

2 To examine whether morphological character correlations exist. We examined four groups of morphological characters: limb elements, tail length, aspects of head shape (focusing on the crest), and dorsal spines. Because different morphological character complexes may be responding to different selective pressures (e.g. limbs for selection on locomotion, crests for selection on social behaviour), we predicted that variation among characters within a complex may be correlated, but variation in characters in different complexes may not be.

MATERIAL AND METHODS

Morphological measurements

Six external morphological measurements were taken on one or two adult individuals, usually males, of 56 species of chameleon in the genera *Bradypodion* (*Bra.*), *Brookesia* (*Bro.*), *Calumma* (*Ca.*), *Chamaeleo* (*Ch.*), and *Furcifer* (*F.*) (see Appendix 1): snout–vent length (SVL), tail length, and medial and lateral hand and foot pad length. Measurements of SVL and tail length were taken by placing a string along the dorsal side of the specimen and then measuring the string with a metric ruler. Hand and foot pad measurements were taken with calipers from the point at which the medial and lateral pads meet to the insertion of the claw on the longest digit within the pad. Because the hands and feet often were contorted, measurements were taken on both sides of the body and the larger of the two measurements retained for subsequent analysis.

Following these measurements, specimens were radiographed laterally. MORPHOSYS (Meacham & Duncan, 1990), a computer-based video imaging system, was used to measure skeletal elements from the radiographs. Four limb measurements were taken: humerus, ulna, femur, and tibia. All long bones were measured from the proximal point to the most distal point on the side that was flat against the plate. The length of the 5th, 10th, and 15th vertebral spines also were measured on their anterior sides.

Eight head measurements were taken from the radiographs to examine head shape (Fig. 1). Two measures of head height were taken: crest head height was measured by drawing a perpendicular line from the highest point on the crest (which is the highest point on a chameleon's head) to a line perpendicular to the maxilla; eye head height was similarly measured by drawing a perpendicular line from the highest point on the skull above the eye to the maxilla. Head length was measured by drawing a perpendicular line from the most anterior point of the mouth to the line described above connecting the top of the crest to the maxilla. Jaw length was the distance from the most anterior point of the mouth to the most distal point on the lower jaw. Four additional measurements
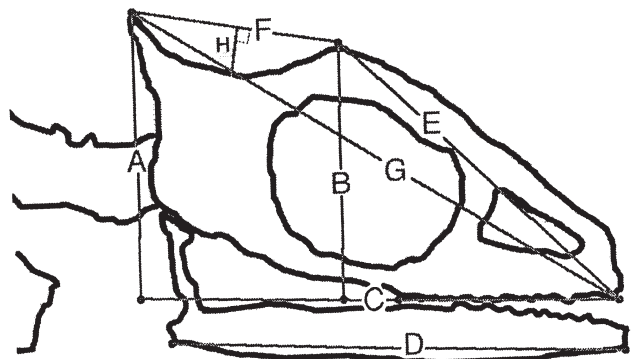

Figure 1. Head measurements taken from radiographs. A, crest head height; B, eye head height; C, head length; D, jaw length; E, eye–mouth length; F, crest–eye length; G, crest–mouth length; H, crest convexity.

were taken: crest–eye length was measured from the highest point on the crest to the highest point on the skull above the eye; eye–mouth length was the distance from the highest point on the skull above the eye to the most anterior point on the mouth; crest–mouth length was the distance from the most anterior point on the mouth to the highest point on the crest; and crest convexity (the extent to which the crest had a convex or concave shape) was the perpendicular distance from the crest to the midpoint of the line connecting the point on the skull above the eye to the point at the height of the crest. Because this value could be negative (if the crest was below the midpoint of the line, as was the case for some species), we added a constant number to all measurements for this variable so that values would be positive and thus ln-transformable.

Measurements were not taken if the specimen was not flat on the X-ray plate. All measurements were taken twice and averaged. If the values differed by more than 5%, a third measurement was taken. In such cases, measurements that were outliers and appeared to be mistakes were excluded; otherwise the three values were averaged.

STATISTICAL ANALYSES

To examine correlations among characters, principal components analyses (PCA) were conducted on a correlation matrix. Because all variables except one increase interspecifically with body size, a PCA was also conducted on size-adjusted variables (the one variable that doesn't scale with size, crest convexity, was not size-corrected for this analysis). To remove the effect of body size, data for all species for each variable were regressed against SVL; residuals from these regressions were then used in subsequent analyses. Interpretation of the loadings on PC analyses was clarified by examination of a matrix of pairwise Pearson correlation values amongst all variables.

Species were classified as terrestrial if they had been documented to use the ground (Appendix 1). Nečas (1999) was the primary literature source used to make this determination. All *Brookesia* were classified as terrestrial, even if specific literature references were unavailable. Of course, few chameleon species are entirely, or even primarily, terrestrial; nonetheless, many species (e.g. *Ch. dilepis*, *F. oustaleti*) will use the ground regularly to move between bushes or trees (Losos, unpubl. obs.). Thus, the distinction we examined is between species that use the ground regularly vs. those that are rarely, if at all, found on the ground. Obviously, much better data on behaviour and habitat use is required for a more detailed investigation of the morphological correlates of habitat use in chameleons.

The hypothesis that terrestrial and arboreal species differ morphologically was investigated in two ways. First, discriminant function analyses (DFA) were conducted. Separate analyses were conducted for appendicular and head variables. Spine measures were included with the head variables because both are likely to be involved in social behaviour. Secondly, each variable was examined separately using analyses of covariance (ANCOVA).

It is now widely recognized that phylogenetic information may be necessary for comparative statistical analyses (Felsenstein, 1985). Unfortunately, despite decades of work (e.g. Hillenius, 1986; Klaver & Böhme, 1986; Rieppel, 1987; Hofman, Maxson & Arntzen, 1991), phylogenetic relationships amongsts chameleons are still uncertain. For example, the most recent molecular systematic analysis of chameleon relationships (Townsend & Larson, in press) found only one of the five commonly recognized genera to be monophyletic (and even the monophyly of *Brookesia* was not supported strongly). Although several clades were supported strongly in this analysis (Fig. 2), the support for many nodes, particularly those deep in the phylogeny, was weak. For these reasons, we considered our knowledge of chameleon phylogeny too unreliable to be used explicitly in statistical comparative methods.

Nonetheless, for several reasons we believe that our statistical results are unlikely to be confounded by phylogeny. For phylogeny to be a confounding factor in a comparative study, closely related species must be more similar phenotypically than one would expect by chance. Conversely, if no such phylogenetic effect exists, then statistical analyses may not require information on phylogenetic relationships (Gittleman & Luh, 1994; Losos, 1999). We examined trait variation within and between four strongly supported clades in the study by Townsend & Larson (in press) to determine whether closely related species were particularly similar in phenotype. In Figure 3, we illustrate that no such phylogenetic effect exists for several characters (other characters exhibit similar patterns). The four clades overlap almost entirely in trait variation; many species are more similar phenotypically to species in other clades than they are to other species in their own clade. Indeed, no significant differences were found between the groups for any of these characters (ANOVA, not presented), contrary to what would be expected if a phylogenetic effect existed. Habitat use also is evolutionarily labile and not indicative of a phylogenetic effect; Figure 2 illustrates that at least six evolutionary transitions have occurred in habitat use. This lack of phylogenetic effect is also apparent in the DFA analyses reported below. Examination of the species misclassified in these analyses reveals
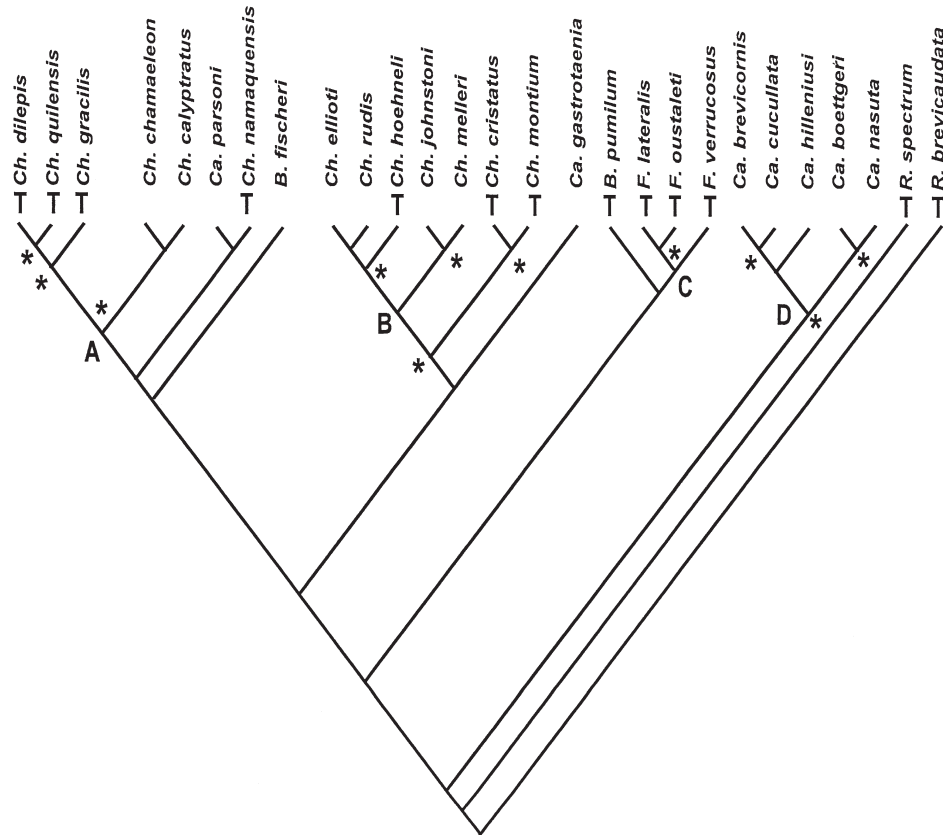
Figure 2. A phylogeny of the Chameleonidae based on DNA sequence data (Townsend & Larson, in press). Species included in that study, but for which we have no morphometric data, are not included. Asterisks indicate clades that are supported in more than 90% of the bootstrap runs. Letters at nodes refer to the four clades highlighted in Figure 3 and the 'T' indicates species classified as using terrestrial habitats. Raxworthy, Forstner & Nussbaum's (2002) recent phylogeny appeared too late to be used in this study, but their findings are generally consistent with those of Townsend & Larson (in press).

a miscellany of species that are not closely related, the opposite of what would be expected if phylogeny were confounding the analyses. As a final means of assessing whether phylogenetic effects confound our analyses, we excluded *Brookesia* and *Rhampholeon* from statistical analyses because these dwarf chameleon genera are each likely to be monophyletic and exhibit, at least for body size and habitat use (terrestrial vs. arboreal), relatively little phenotypic variation. In almost all cases, results were qualitatively unchanged.

RESULTS

The first two axes of the principal components analysis on non-size adjusted data account for 94.3% of the variation (Table 1). All variables load strongly and positively on the first axis, with the exception of crest convexity, which is the only variable loading strongly on the second axis. All variables were highly correlated with logsvl (Pearson $r > 0.85$, $N = 51$, $P \ll 0.001$, except crest convexity ($r = 0.23$, $N = 54$, $P < 0.10$).

In the PCA on size-adjusted values, the first five PC axes account for 84.8% of the variation (Table 2). Interpreting these axes is not altogether straightforward. The first axis suggests a positive correlation among all head, crest (except crest convexity), proximal limb (i.e. not including hand and foot pad measurements), and spine measurements. The second axis loads strongly and positively for foot and hand pad measurements and more weakly for a limb, tail, and spine vs. head contrast. The third axis is positive for tail, hand, foot, and some head measurements, and loads negatively for spine measurements. The fourth axis contrasts limb measurements vs. spine length and crest head height, and the fifth axis loads strongly for crest convexity.

Examination of Pearson correlation values between size-adjusted variables clarifies these relationships
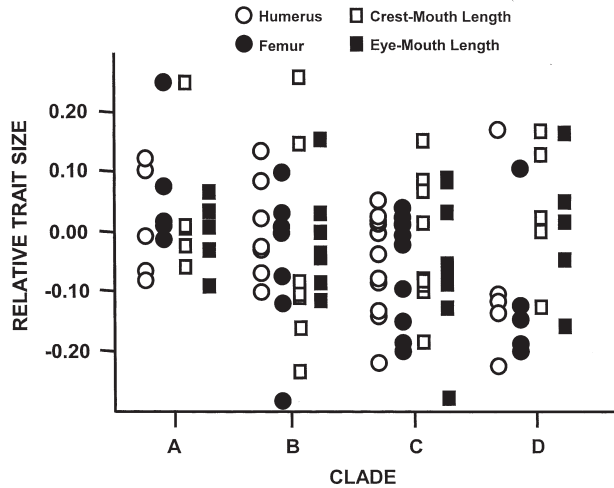
Figure 3. Range in trait variation within the four clades highlighted in Figure 2. Traits are size-adjusted. On the assumption that *Furcifer* is monophyletic (Townsend & Larson in press), several species of the genus *Furcifer* are included even though those species were not included in the molecular phylogeny presented in Figure 2.

(Appendix 2). Limb elements are highly correlated with each other ($r \geq 0.68$, $P \ll 0.001$); similarly, spine elements are also correlated with each other ($r > 0.85$, $P \ll 0.001$), as are hand and foot pad lengths ($r > 0.76$, $P \ll 0.001$). Head and crest elements are generally correlated with each other, although some more so than others ($r = 0.40$–0.91, $P < 0.002$). Correlations between character groups are generally lower. Tail length only shows significant correlations to hand and foot measurements. Crest convexity, which is significantly related only to some of the other crest measurements, is negatively related to the length of the 5th and 15th spines (these are the only significant negative correlations). Proximal limb elements are positively related to spine characters (0.29–0.49), but not as much to head and crest elements (0.09–0.54) or to hand and foot pad lengths (–0.04–0.34). Spine characters are generally not related to other characters except crest head height and eye head height, and hand and foot pad lengths are not related to any other characters.

LIMB ANALYSES

DFA can distinguish arboreal from terrestrial species using limb measurements regardless of whether raw or size-adjusted data were used and whether *Brookesia* and *Rhampholeon* were included or excluded. In the analysis on raw data including all species, the analysis was significant ($N = 55$, Wilks' $\lambda = 0.58$,

Table 1. PCA on non-size adjusted data

	Component loadings	
	1	2
SVL	0.988	−0.025
Tail	0.921	0.000
Crest–eye length	0.973	−0.133
Eye–mouth length	0.986	−0.017
Jaw length	0.982	−0.073
Eye head height	0.986	−0.019
Crest head height	0.964	−0.090
Crest–mouth length	0.985	−0.089
Head length	0.980	−0.065
Spine 5 length	0.934	0.204
Spine 10 length	0.895	0.198
Spine 15 length	0.913	0.220
Humerus	0.987	−0.001
Ulna	0.986	0.009
Femur	0.983	0.001
Tibia	0.983	0.004
Lateral hand pad length	0.966	0.044
Medial hand pad length	0.967	0.039
Lateral foot pad length	0.960	0.048
Medial foot pad length	0.978	0.015
Crest convexity	0.236	−0.946
Eigenvalue	18.7	1.1
% Variance explained	89.2	5.1

$P = 0.0009$) and 82% of the species were classified correctly. The misclassified arboreal species were *Ca. tigris*, *Ch. zeylanicus*, and *F. petteri* and the misclassified terrestrial species were *Ch. affinis*, *Ch. dilepis*, *Ch. montium*, *Ch. oweni*, *F. oustaleti*, *F. pardalis*, *F. verrucosus*, and *R. marshalli*. When *Brookesia* and *Rhampholeon* are excluded, results are significant ($N = 42$, Wilks' $\lambda = 0.57$, $P = 0.001$) and 79% are classified correctly; misclassified arboreal species are *Bra. fischeri*, *Ca. cucullata*, *Ca. tigris*, *Ch. calyptratus*, *Ch. zeylanicus*, and *F. minor*; misclassified terrestrial species are *Ch. affinis*, *Ch. oweni*, *Ch. montium*, and *F. oustaleti*. With size-adjusted data, results are similar. When all species are included, the analysis is significant ($N = 55$, Wilks' $\lambda = 0.67$, $P = 0.011$) and 75% of the species are classified correctly. Misclassified arboreal species are *Bra. fischeri*, *Ca. tigris*, *Ch. calyptratus*, Ch. *zeylanicus*, *F. bifidus*, *F. minor*, *F. petteri*, and *F. rhinoceratus*. Misclassified terrestrial species are *Bro. betschi*, *Ch. affinis*, *F. pardalis*, *R. brevicaudatus*, *R. marshalli* and *R. platyceps*. When the *Brookesia* and *Rhampholeon* are excluded, the DFA is significant ($N = 42$, Wilks' $\lambda = 0.55$, $P = 0.007$) and 81% of the species are classified correctly. Misclassified

Table 2. PCA on residual values

Component Loadings	1	2	3	4	5
Tail	−0.134	0.385	0.507	0.034	−0.034
Humerus	0.674	0.361	−0.243	−0.394	0.186
Ulna	0.696	0.305	−0.308	−0.404	0.070
Femur	0.671	0.229	−0.280	−0.552	0.002
Tibia	0.716	0.157	−0.278	−0.486	−0.106
Spine 5 length	0.542	0.446	−0.519	0.407	0.053
Spine 10 length	0.599	0.291	−0.474	0.477	0.046
Spine 15 length	0.532	0.319	−0.505	0.497	−0.060
Lateral hand pad length	0.105	0.766	0.531	0.028	−0.060
Medial hand pad length	0.163	0.774	0.421	0.001	0.079
Lateral foot pad length	0.078	0.732	0.595	0.129	−0.025
Medial foot pad length	0.251	0.732	0.479	−0.063	0.134
Head length	0.627	−0.460	0.484	−0.008	−0.297
Jaw length	0.756	−0.415	0.324	−0.047	−0.183
Crest–eye length	0.667	−0.429	0.402	0.123	0.253
Crest–mouth length	0.767	−0.437	0.420	0.140	0.034
Eye–mouth length	0.744	−0.311	0.228	0.009	−0.448
Crest head height	0.685	−0.191	0.133	0.406	0.402
Eye head height	0.813	−0.126	−0.037	0.091	−0.004
crest convexity	0.031	−0.427	0.210	−0.204	0.755
Eigenvalue	6.65	4.2	3.2	1.8	1.2
% Variance Explained	33.2	20.9	15.8	8.9	6.0

arboreal species are *Ca. cucullata*, *Ca. gastrotaenia*, *Ca. tigris*, *Ch. calyptratus*, *Ch. zeylanicus* and *F. minor*. Misclassified terrestrial species are *Ch. affinis* and *F. oustaleti*.

Univariate analysis of the limb and foot elements clarifies the differences between arboreal and terrestrial species. For the proximal limb elements, *Brookesia* and *Rhampholeon* have longer limb elements than other chameleons of comparable size, all of which are arboreal. Among other chameleons (i.e. *Chamaeleo*, *Calumma*, and *Furcifer*), terrestrial species seem to have longer limbs at smaller sizes, but this relationship reverses at larger sizes (Fig. 4). *Brookesia* has relatively short hand and foot pads compared to other chameleons; *Rhampholeon* appears to have slightly longer relative foot element lengths, but the relationship between foot element length and SVL among *Rhampholeon* species is surprisingly flat. Among the other species, terrestrial and arboreal species do not differ at smaller sizes, but arboreal species have longer hand and foot pads at larger sizes (Fig. 5).

These impressions are confirmed by ANCOVA with SVL as the covariate: when *Brookesia* and *Rhampholeon* are excluded, significant differences in slope are found for all variables ($N = 42$ or 43, $F = 5.19$–10.86, $P = 0.002$–0.028); When those genera are included, all variables exhibit significant or nearly significant differences between arboreal and terrestrial species, but the results are more complicated. A difference in slopes still exists for femur and humerus ($N = 55$–56, $F > 7.20$, $P \leq 0.01$) and nearly exists for medial hand pad length ($N = 56$, $F = 3.73$, $P = 0.059$; no significant difference in intercepts exists for this variable, $F = 2.19$, $P = 0.15$) and ulna ($N = 56$, $F = 2.84$, $P = 0.098$; intercepts not significantly different, $F = 1.16$, $P = 0.29$). Several other variables (tibia, lateral hand and foot pad lengths) do not differ in slopes ($P > 0.15$), but are significantly different in intercepts ($N = 55$–56, $F > 5.40$, $P < 0.025$) or are nearly so (medial foot pad length, $N = 56$, $F = 3.20$, $P = 0.08$).

All limb elements increase with positive allometry relative to body size (slope coefficient $= 1.02$–1.12). When the species are divided into small chameleons (*Brookesia* and *Rhampholeon*) and other terrestrial and arboreal species, the other arboreal species also displayed positive allometry, the other terrestrial species displayed negative allometry, and *Brookesia* and *Rhampholeon* displayed positive allometry for all traits except lateral foot pad length and medial hand pad length.
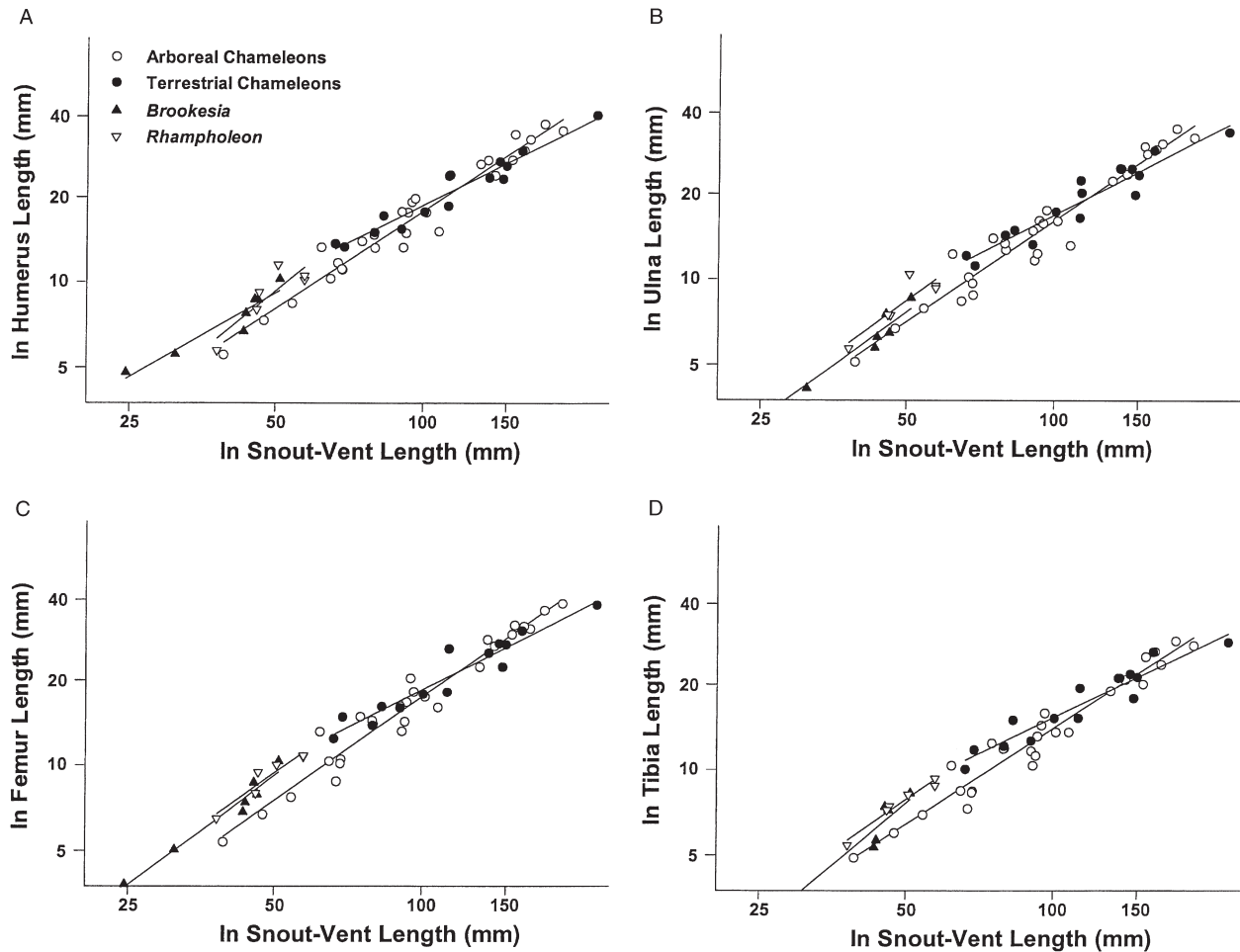
Figure 4. Variation in limb elements relative to overall size. A, Humerus; B, ulna; C, femur; D, tibia.

TAIL LENGTH

Arboreal and terrestrial species differ in relative tail length when *Brookesia* and *Rhampholeon* are included ($N = 56$, difference in slopes, $F = 2.47$, $P = 0.12$; difference in intercepts, $F = 7.66$, $P = 0.008$), but not when they are excluded ($N = 43$, difference in slopes, $F = 1.25$, $P = 0.27$; difference in intercepts, $F = 0.37$, $P = 0.55$).

CRESTS, SPINES AND HEAD LENGTH

Arboreal and terrestrial species can be distinguished on the basis of residual crest and spine variables (DFA, $n = 52$, Wilks' $\lambda = 0.63$, $P = 0.02$); 75% of species were classified correctly (species misclassified, arboreal: *Ch. bitaeniatus, Ca. cucullata, Bra. fischeri, Ca. parsoni, Ch. tigris, Ch. zeylanicus, F. petteri*; terrestrial: *Ch. affinis, Ch. montium, Ch. senegalensis, R. kerstenii, R. marshalli, R. spectrum*). Examination of the discriminant function indicates that the most important variables in distinguishing the two groups are crest–eye

length, crest–mouth length, and eye–mouth length (Table 3). When *Brookesia* and *Rhampholeon* are excluded, the DFA is marginally non-significant ($N = 40$, Wilks' $\lambda = 0.60$, $P = 0.09$; 60% of species classified correctly; misclassified species for the most part the same as in the previous analysis) with the same variables playing an important role in the discriminant function (Table 3). Because spine characters appear not to be important in distinguishing terrestrial from arboreal species, we re-ran this analysis including only head characters. The DFA again was significant ($N = 42$, Wilks' $\lambda = 0.63$, $P = 0.02$); and 76% of species were classified correctly (species misclassified, arboreal: *Bra. fischeri, Ca. cucullata, Ca. parsoni, Ch. bitaeniatus, Ch. laevigatus, Ch. rudis, Ch. zeylanicus, F. bifidus*; terrestrial: *Bra. pumilum, Ch. montium*) and the same variables drove the discriminant function.

ANCOVAS on each variable illustrate the differences between arboreal and terrestrial species (all species included in these analyses). In all cases, the
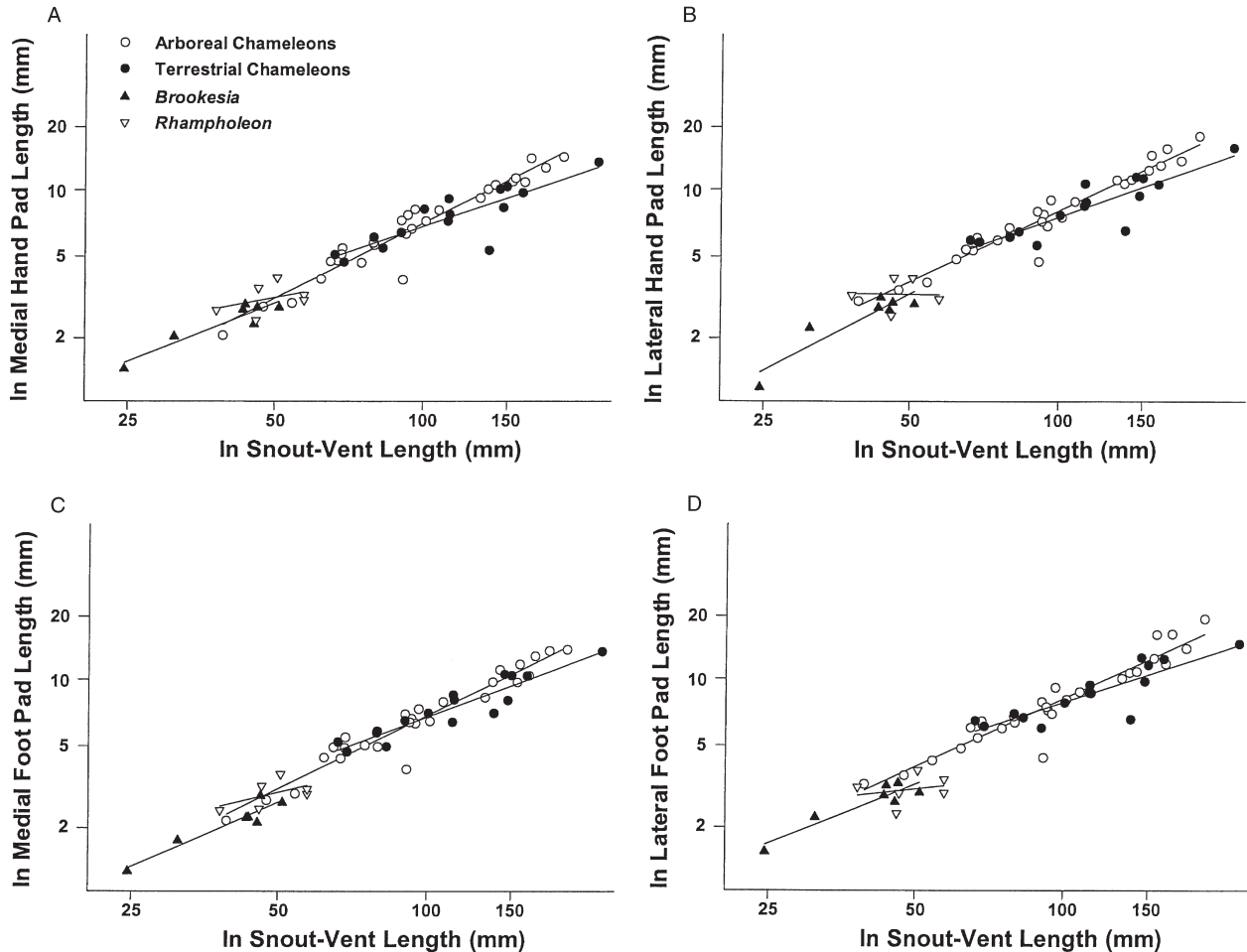
Figure 5. Variation in foot and hand pad lengths relative to overall size. A, Medial hand pad length; B, lateral hand pad length; C, Medial foot pad length; D, lateral foot pad length.

hypothesis of slope heterogeneity could not be rejected ($N = 54$–56, $F < 2.26$, $P > 0.13$). Several variables exhibited significant differences in intercepts, with terrestrial species having larger head and crest dimensions (although this difference seems to disappear at larger sizes; Fig. 6): head length, eye–mouth length, crest–mouth length, crest–eye length, eye–head height ($N = 54$, $F > 4.17$, $P < 0.05$); whereas other variables were non-significant, although crest convexity and 10th and 15th spine lengths were nearly significant ($N = 56$, $F > 3.04$, $P < 0.09$). Results were generally the same when *Brookesia* and *Rhampholeon* were excluded, although probability levels were generally less significant (results not shown).

DISCUSSION

Our data reveal substantial variation among chameleon species in head morphology, limb and tail length, and dorsal crest development. Almost all vari-

ables increase interspecifically with body size; when size effects are removed, two patterns are evident. First, all traits within a functional group are correlated, but few correlations occur between traits in different functional groups. For example, relative lengths of limb elements are highly correlated, but few significant correlations exist between limb and head elements. Second, terrestrial – defined as those species known to use the ground at least occasionally – and arboreal species differ in limb and head measurements.

That limb length is related to habitat use is not unexpected. Studies on a number of lizard clades have revealed relationships between habitat use and size-adjusted limb length (reviewed in Kohlsdorf *et al.*, 2001); among arboreal species, this relationship usually takes the form of a correlation between relative limb length and substrate diameter (Losos, 1990; Miles, 1994; Kohlsdorf *et al.*, 2001). What is surprising, however, is the form of the relationship in

Table 3. Discriminant functions

All species, all variables

Constant	−0.042
Crest–eye length	31.023
Crest–mouth length	−71.553
Eye–mouth length	38.146
Crest head height	6.307
Eye head height	−9.609
Crest convexity	3.567
Spine 5 length	1.325
Spine 10 length	0.497
Spine 15 length	−0.307
Head length	13.157

***Brookesia* and *Rhampholeon* excluded, all variables**

Constant	0.190
Crest–eye length	40.881
Crest–mouth length	−93.489
Eye–mouth length	45.814
Crest head height	9.466
Eye head height	−10.643
Crest convexity	3.009
Spine 5 length	1.258
Spine 10 length	−1.429
Spine 15 length	1.271
Head length	15.519

***Brookesia* and *Rhampholeon* excluded, crest variables**

Constant	0.221
Crest–eye length	38.554
Crest–mouth length	−85.815
Eye–mouth length	37.738
Crest head height	7.922
Eye head height	−5.214
Crest convexity	1.364
Head length	14.878

Figure 6. Variation in several aspects of head morphology. A, Head length; B, crest–eye length; C, crest–mouth length.

chameleons. Based on studies of other lizards, we expected that terrestrial species, using a broad surface, would have longer limbs than arboreal species. However, we found exactly the opposite: as a generality, chameleon species that use the ground have shorter limbs than arboreal species, at least for large species.

Why arboreal species have longer limbs than terrestrial species is unclear. Chameleons are fundamentally different from other lizards in their body plan and locomotor behaviour. For example, in chameleons the limbs are held more vertically under the body and movement is usually slow and often in a hesitating, back-and-forth pattern with little lateral undulation (Peterson, 1984). Given that chameleons run relatively infrequently, selection for maximal sprinting ability on broad surfaces may not have occurred. Moreover, the grasping feet, prehensile tail,
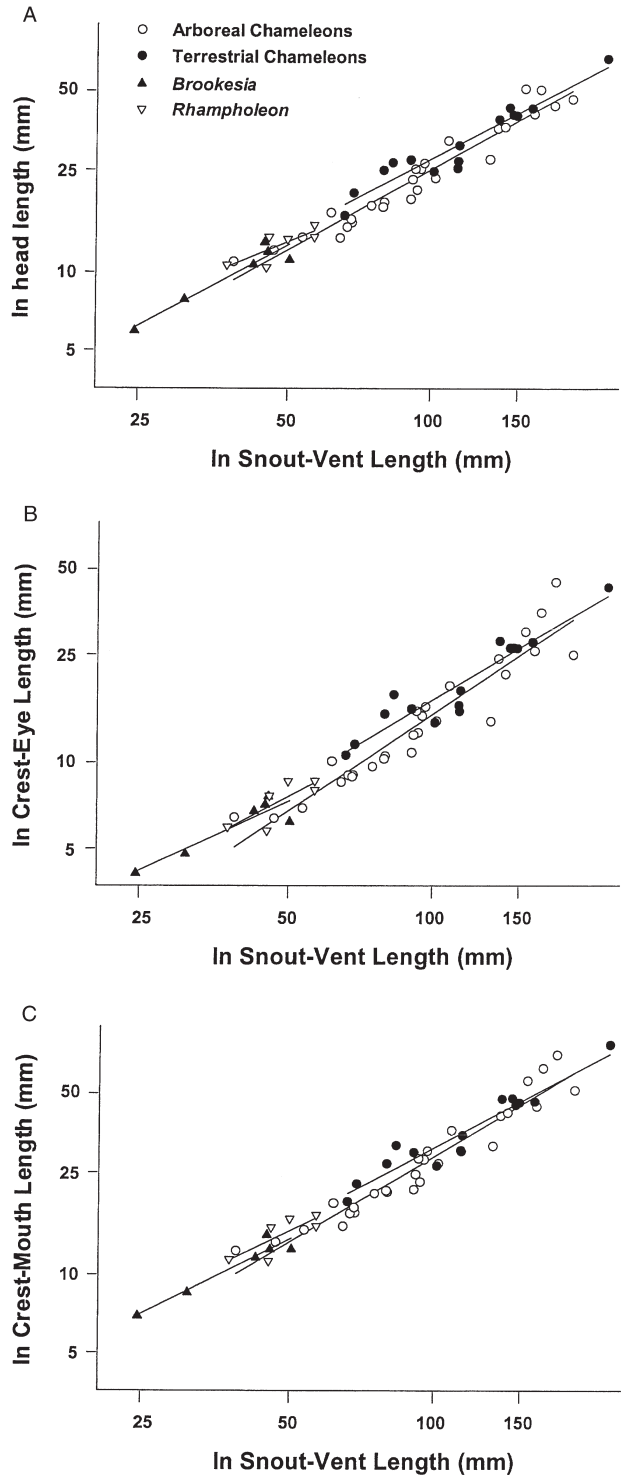
laterally compressed body and girdle mobility of chameleons all appear to be adaptations for moving with agility on narrow surfaces (Gans, 1967; Bellairs, 1969; Peterson, 1984; Losos, Walton & Bennett, 1993). As a result of these features, arboreal species may not need to have shorter limbs than their terrestrial counterparts. More research is needed on chameleon biomechanics to understand the morphological demands and functional consequences of moving on different surfaces (see Abu-Ghalyun *et al.*, 1988, and Losos *et al.*, 1993). Moreover, an implicit assumption in our reasoning was that terrestrial species, when using arboreal surfaces, would use broader surfaces than arboreal species, or at least that the demands of terrestrial movement were sufficient to select for different morphologies. No comparative information is available on the use of arboreal habitats among chameleon species. Given that so much attention has been paid to characterizing perch diameter use in other types of lizards (e.g. anoles, Rand, 1964, 1967; Schoener, 1968; Losos, 1990), the lack of such data for chameleons is all the more surprising. To understand the differences in limb morphology we have detected, more detailed field and biomechanical studies are needed.

The situation is no better for understanding the difference in head shape between terrestrial and arboreal chameleons. Previous researchers have commented on the remarkable variety of head ornaments in chameleons and have speculated that this variation is related to species recognition and sexual selection (Darwin, 1871; Rand, 1961; Nečas, 1999). Detailed studies of the behaviour of most species are lacking, which makes evaluation of this hypothesis difficult. Given this uncertainty, explanations for the effect of habitat use on head shape must remain speculative. In this vein, we present two possibilities. First, arboreal habitats may constrain the development of large head crests. Such a constraint could occur in two ways: either crests may impede movement through the clutter of an arboreal habitat or visibility may be constrained in an arboreal habitat, rendering ineffective the use of a crest as a communication signal. Secondly, and conversely, crests may be beneficial in terrestrial habitats, either if the opportunity there is greater for sexual selection, perhaps as a result of greater visibility (cf. Butler, Schoener & Losos, 2000), or because the likelihood of encountering other chameleon species is greater, thus increasing the need for species-recognition signals. None of these explanations is excessively convincing; more research is required on chameleon social and signalling behaviour before the hypotheses can be reasonably evaluated.

Chameleons also vary in a number of traits we did not examine. Most relevant to this study are the horns, ridges, and nasal appendages sported by many species (see Nečas, 1999). We would have liked to have included these traits, but the lack of homology even among different types and placements of horns, much less between horns and other appendages, made data collection problematic. Nonetheless, using data from Nečas (1999), we can compare the frequency of horns among arboreal and terrestrial species (lumping together species with 1–4 horns placed in various positions). Among the species in our study, 61% of arboreal species, but only 32% of terrestrial species, have horns (data from Nečas, 1999), a difference that is significant ($\chi^2 = 4.60$, $P = 0.032$). This difference is unlikely to be confounded by phylogeny, as the presence of horns varies even among closely related groups (e.g. Townsend & Larson in press). That terrestrial species have larger crests, but less frequently exhibit horns, is interesting; examination of our data suggests no relationship between horn presence and crest size, though more detailed analyses are needed.

Chameleons are also renowned for their variety of colours and patterns and their ability to change both. These traits are likely to have ecological relevance, an interesting topic for further study.

Examination of the relationships among characters indicates that functionally related traits covary to a large extent. A number of other studies have indicated that a similar relationship exists among limb elements in a variety of lizards (Losos, 1990; Miles, 1994; Melville & Swain, 2000; and, to a lesser extent, Vanhooydonck & Van Damme, 1999). Thus, species that have, for example, long femora also tend to have long ulnae and long hands. Head measurements are also correlated to each other, but this may result because the variables are not independent measures of crest size. A species with a large head crest height, such as *Ch. calyptratus*, would by necessity have large values for all measurements. Hence, the finding that measures are correlated may not tell us much [as an aside, we note that future studies of chameleon crest shape might profitably employ geometric morphometric methods (e.g. Adams & Rohlf, 2000); we did not use such methods here because the remainder of the variables we measured were linear and did not require such an approach, although all measurements could have been taken as landmarks]. However, the lack of a correlation between head and spine measurements (and seemingly between head measurements and horn presence) indicates that if both traits are related to communication, then they most likely have different communicative functions.

Obviously, our research has raised as many questions as it has answered and thus is only a preliminary examination of chameleon ecological morphology; much work remains to be done. Nonethe-

less, we have shown that substantial morphological variation exists among chameleons and that some of this variation is related to a crude measure of habitat use. Further interpretation, however, is stymied by our lack of knowledge about chameleon behaviour, ecology, and functional morphology.

We hope that the near future will see a blossoming in research on chameleon biology and that this study may highlight interesting patterns requiring further study.

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APPENDIX 1

Species included in the study and their classification as either terrestrial (i.e. known to use the ground) or arboreal.

Arboreal
Bradypodion fischeri Reichenow
Calumma boettgeri Boulenger
Ca. brevicornis Günther
Ca. cucullatus Gray
Ca. gastrotaenia Boulenger
Ca. hilleniusi Klusmeyer
Ca. malthe Günther
Ca. nasuta Duméril & Bibron
Ca. parsonii Cuvier
Ca. tigris Kuhl
Chamaeleo bitaeniatus Fischer
Ch. calyptratus Duméril & Bibron
Ch. chameleon Linnaeus
Ch. ellioti Günther
Ch. goetzei Tornier
Ch. ituriensis Schmidt
Ch. johnstoni Boulenger
Ch. laevigatus Gray
Ch. melleri Gray
Ch. rudis Boulenger
Ch. tempeli Tornier
Ch. zeylanicus Laurenti
Furcifer balteatus Duméril & Bibron
F. bifidus Brogniart
F. minor Günther
F. petteri Schmidt
F. rhinoceratus Gray
F. willsi Schmidt

Terrestrial
Bradypodion pumilum Gmelin
Brookesia ambreensis Raxworthy & Nussbaum
Bro. antakarana Raxworthy & Nussbaum
Bro. betschi Brygoo, Blanc & Domergue
Bro. ebenaui Boettger
Bro. minima Boettger
Bro. stumpffi Boettger
Bro. superciliaris Kuhl
Ch. affinis Rüppell
Ch. cristatus Stutchbury
Ch. dilepis Leach
Ch. gracilis Hallowell
Ch. höhnelii Steindachner
Ch. montium Buchholz
Ch. namaquensis Smith
Ch. oweni Gray
Ch. quilensis Bocage
Ch. senegalensis Daudin
Furcifer lateralis Gray
F. oustaleti Mocquard
F. pardalis Cuvier
F. verrucosus Cuvier
Rampholeon boulengeri Steindachner
R. brevicaudatus Matschie
R. kerstenii Peters
R. marshalli Boulenger
R. platyceps Günther
R. spectrum Buchholz

APPENDIX 2

Pearson correlation coefficients of size-adjusted values.

	Tail	Humerus	Ulna	Femur	Tibia	Spine 5 length	Spine 10 length
Tail	1.000						
Humerus	−0.060	1.000					
Ulna	−0.070	0.812	1.000				
Femur	−0.147	0.788	0.765	1.000			
Tibia	−0.112	0.680	0.803	0.882	1.000		
Spine 5 length	−0.192	0.468	0.492	0.411	0.409	1.000	
Spine 10 length	−0.206	0.416	0.430	0.365	0.403	0.893	1.000
Spine 15 length	−0.080	0.396	0.423	0.285	0.364	0.856	0.884
Lateral hand pad length	0.478	0.162	0.135	0.076	0.059	0.137	0.072
Medial hand pad length	0.282	0.301	0.172	0.157	0.056	0.233	0.115
Lateral foot pad length	0.594	0.126	0.052	−0.020	−0.036	0.103	0.027
Head length	−0.018	0.092	0.100	0.210	0.284	−0.116	0.047
Jaw length	−0.200	0.219	0.317	0.333	0.427	0.062	0.160
Crest–eye length	−0.033	0.208	0.151	0.202	0.227	0.025	0.146
crest–mouth length	−0.036	0.202	0.219	0.238	0.311	0.064	0.213
Eye–mouth length	−0.102	0.269	0.321	0.324	0.434	0.104	0.232
Crest head height	−0.048	0.272	0.290	0.172	0.186	0.400	0.462
Eye head height	−0.153	0.539	0.513	0.404	0.452	0.395	0.407
Crest convexity	−0.094	−0.005	−0.055	−0.042	−0.049	−0.323	−0.212
Medial foot pad length	0.342	0.335	0.249	0.242	0.163	0.210	0.130

	Spine 15 length	Lateral hand pad length	Medial hand pad length	Lateral foot pad length	Head length	Jaw length	Crest–eye length
Spine 15 length	1.000						
Lateral hand pad length	0.036	1.000					
Medial hand pad length	0.090	0.814	1.000				
Lateral foot pad length	0.071	0.896	0.765	1.000			
Head length	−0.034	−0.016	−0.067	0.002	1.000		
Jaw length	0.088	−0.026	−0.042	−0.049	0.871	1.000	
Crest–length	0.074	−0.105	−0.032	−0.018	0.765	0.720	1.000
Crest–mouth	0.114	−0.030	−0.055	0.007	0.883	0.868	0.912
Eye–mouth length	0.221	0.013	−0.042	−0.022	0.823	0.843	0.519
Crest head height	0.351	−0.006	−0.006	0.040	0.408	0.527	0.706
Eye head height	0.459	−0.066	0.080	−0.062	0.468	0.595	0.576
Crest convexity	−0.307	−0.210	−0.172	−0.211	0.115	0.186	0.378
Medial foot pad length	0.041	0.787	0.865	0.783	0.024	0.043	0.088

	Crest-mouth length	Eye-mouth length	Crest head height	Eye head height	Crest convexity	Medial foot length
Crest–mouth Length	1.000					
Eye–mouth length	0.771	1.000				
Crest head height	0.760	0.427	1.000			
Eye head height	0.617	0.697	0.600	1.000		
Crest convexity	0.271	−0.067	0.269	0.029	1.000	
Medial foot pad length	0.068	−0.006	0.104	0.080	−0.123	1.000