

Locomotor morphometry of the *Pachydactylus* radiation of lizards (Gekkota: Gekkonidae): a phylogenetically and ecologically informed analysis

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Abstract: The *Pachydactylus* radiation comprises a diverse group of African gekkonids that exploit a variety of microhabitats and exhibit both climbing and terrestrial locomotion. The phylogeny of this radiation is well supported, making it a promising candidate for the investigation of relationships between limb proportions, ecology, and behaviour. Skeletal and external measurements were recorded for an array of taxa and analyzed using principal components analysis (PCA). The results of the PCAs were further analyzed using phylogenetic statistical methods to ascertain whether climbing and terrestrial species and (or) clades within the radiation differed significantly from each other in limb proportions. Phylogenetically based comparisons revealed that although there is some differentiation between climbing and terrestrial species, this is not a general pattern but is primarily attributable to certain species and clades within the radiation that differ considerably from other members of the group. The results indicate that *Chondrodactylus angulifer* Peters, 1870 possesses shortened distal phalanges and that *Pachydactylus rangei* (Andersson, 1908), *P. austeni* Hewitt, 1923, and the *Rhoptropus* clade (particularly *R. afer* Peters, 1869) possess elongated limbs relative to the rest of the radiation. These differences correlate with aspects of the lifestyles of these species, such as increased terrestriality, a reduction or loss of the subdigital adhesive apparatus, digging behaviour, and a transition to diurnality.

Résumé : La radiation évolutive de *Pachydactylus* comprend un groupe diversifié de gekkonidés africains qui exploitent une variété de microhabitats et qui grimpent et se déplacent au sol. La phylogénie de cette radiation est bien appuyée, ce qui en fait un candidat prometteur pour l'étude des relations entre les proportions des membres, l'écologie et le comportement. Nous avons compilé des mesures squelettiques et externes pour une gamme de taxons et les avons examinées au moyen d'analyses en composantes principales (PCA). Les résultats des PCA ont été analysés plus avant à l'aide de méthodes statistiques phylogénétiques afin de déterminer si les espèces grimpeuses et terrestres et (ou) les clades au sein de la radiation diffèrent par les proportions de leurs membres. Les comparaisons basées sur la phylogénie montrent que, bien qu'il existe une différenciation entre les espèces grimpeuses et terrestres, il ne s'agit pas d'un pattern général, mais que la différenciation s'explique par certaines espèces et certains clades au sein de la radiation qui diffèrent considérablement des autres membres du groupe. Nos résultats indiquent que *Chondrodactylus angulifer* Peters, 1870 possède des phalanges distales raccourcies et que *Pachydactylus rangei* (Andersson, 1908), *Pachydactylus austeni* Hewitt, 1923 et le clade de *Rhoptropus* (particulièrement *R. afer* Peters, 1869) ont des membres allongés par comparaison au reste de la radiation. Ces différences sont en corrélation avec certains aspects du style de vie de ces espèces, tels qu'une adaptation plus grande à la vie terrestre, la réduction ou la perte de l'appareil adhésif subdigital, le comportement fouisseur et une transition à la vie diurne.

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Introduction

Ecomorphological theory suggests that there is a relationship between the morphology, ecology, and behaviour of organisms (Losos 1990a). Lizard locomotion has become a particular focus of ecomorphological studies because lizards

occupy a wide diversity of habitats that place different demands on the mechanics of the locomotor system (Aerts et al. 2000; Herrel et al. 2002). For example, the biomechanics of organisms that climb are purported to be different from those that are solely ground-dwelling (Zaaf and Van Damme 2001). Various investigators have attempted to correlate

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limb proportions and habitat use in lizards and have explored whether or not morphological characteristics are adaptations to the demands of the animals' microhabitats. Such studies have yielded a variety of conclusions.

The differing conclusions reached by ecomorphological studies of lizards may, in part, be the result of different approaches to measurement and analysis. For instance, the use of external measurements to investigate relationships between locomotor morphology and ecology has yielded inconsistent results. Strong correlations have been revealed in some lizard groups including the genera *Anolis* (Collette 1961; Moermond 1979; Pounds 1988; Losos 1990a, 1992; Powell and Russell 1992) and *Tropidurus* (Vitt et al. 1997; Kohlsdorf et al. 2001) and different populations of the phrynosomatid *Urosaurus ornatus* (Baird and Girard, 1852) (Herrel et al. 2001), but not in others such as *Liolaemus* species (Jaksić and Núñez 1979; Jaksić et al. 1980), lacertids (Vanhooydonck and Van Damme 1999), phrynosomatids (Herrel et al. 2002), and gekkonids (Zaaf and Van Damme 2001).

In contrast, studies employing skeletal measurements have revealed significant correlations between limb morphology and locomotor behaviour in the lizard genera *Sceloporus* (Lundelius 1957) and *Niveoscincus* (Melville and Swain 2000), the Chamaeleonidae (Bickel and Losos 2002), and the gekkonid genus *Rhoptropus* (Bauer et al. 1996). Thus, it may be that subtle differences in limb proportions can be detected only by the measurement of skeletal elements, an approach that permits more complete measurement of individual distal limb segments, such as metapodial and phalangeal elements, and measurement of the actual lever arms that are the fundamental components of the locomotor system (Russell and Bels 2001).

Results also conflict between studies that have considered phylogenetic relationships between species (Vanhooydonck and Van Damme 1999; Melville and Swain 2000; Kohlsdorf et al. 2001; Zaaf and Van Damme 2001; Bickel and Losos 2002; Herrel et al. 2002) and those that have not included such considerations (Lundelius 1957; Jaksić and Núñez 1979; Jaksić et al. 1980). This further complicates the problem by suggesting that correlations found in non-phylogenetically based studies may be misleading, and highlights the importance of considering phylogenetic information in order to properly interpret the results of comparative ecomorphological studies (Huey and Bennett 1987; Losos 1990b; Harvey and Purvis 1991; Garland and Losos 1994).

In the case of gekkonids, two phylogenetically based studies using different approaches to morphological measurement conflict regarding morphological differences between climbing and terrestrial taxa (Bauer et al. 1996; Zaaf and Van Damme 2001). These results may be contradictory for a variety of reasons other than different approaches to measurement. The investigation of the genus *Rhoptropus* (Bauer et al. 1996) focused on only five species and revealed significant locomotor differences between four climbing taxa and a single terrestrial species. The broader study of 29 species of gekkotans by Zaaf and Van Damme (2001) reported no statistical differences between the locomotor systems of terrestrial and climbing taxa. That study, however, was very broad in terms of choice of taxa, including examples from

taxa now allocated to three families (Eublepharidae, Diploctylidae, Gekkonidae) (Han et al. 2004) and taxa that are primitively padless, as well as taxa from seven lineages that are hypothesized to have independently evolved subdigital adhesive pads (Russell 1976, 2002). Furthermore, no lineages exhibiting secondary pad loss (Russell 1976) were included. Even when phylogeny is controlled for, the inclusion of species from disparate phylogenetic lineages (Russell and Bauer 2002; Han et al. 2004) can obscure the phylogenetic signal evident in more closely related clades. Such conflicting results may also result from the division of locomotor type into two general and broadly defined categories (terrestrial and climbing). Absolute size and the preferred locomotor habitat may also play a role in how individual species interact with their environment.

These considerations prompted us to investigate locomotor morphology in gekkotans by examining the *Pachydactylus* radiation, a geographically well-circumscribed and phylogenetically well-resolved clade (Bauer and Lamb 2005) displaying an array of habitat occupancy that is reasonably well understood as a result of extensive field-based observations. Until recently, this radiation included the nominal genera *Chondrodactylus*, *Colopus*, *Palmatogecko* (now including *Kaokogecko*; Kluge and Nussbaum 1995), *Pachydactylus*, *Rhoptropus*, and *Tarentola* (now including *Geckonia*; Carranza et al. 2002), which rendered *Pachydactylus* paraphyletic. Resolution of phylogenetic relationships within this group has led to a proposed change in classification that breaks the entire radiation into separate, monophyletic genera (Bauer and Lamb 2005). Primarily, this new classificatory scheme proposes the application of the name *Chondrodactylus* to all members of the large-bodied *Pachydactylus bibronii* clade, which includes the species formerly known as *P. bibronii* (Smith, 1846), *P. fitzsimonsi* Loveridge, 1947, and *P. turneri* (Gray, 1864) (Fig. 1) (Bauer and Lamb 2005). Additionally, *Palmatogecko* is subsumed under the generic name *Pachydactylus*, yielding a monophyletic genus of small-bodied species (Fig. 1) (Bauer and Lamb 2005). The new classification is employed herein.

The *Pachydactylus* radiation, with the exception of *Tarentola*, is endemic to the southern part of Africa and has experienced a long history of evolution in this region, marked by numerous climatic changes (Bauer 1999). In adapting to increasingly extreme desert environments (Harris et al. 1998) and shifting climatic regimes, the radiation has undergone extensive speciation (Bauer 1999), and the widely diverse species in this group are generally restricted to isolated microhabitats and demonstrate substrate specialization (Bauer et al. 1996).

The *Pachydactylus* radiation is descended from an ancestral stock that was primitively pad-bearing (Russell and Bauer 2002), contains taxa that may be broadly categorized as climbers or ground dwellers (Haacke 1976a; Russell 1976; Bauer 1999), and includes taxa that have secondarily reduced or lost the subdigital adhesive system (Russell 1976). Furthermore, one included taxon, the genus *Rhoptropus*, has become diurnal (Bauer et al. 1996; Autumn 1999) and consequently is exposed to a markedly different selective environment than its nocturnal relatives.

Fig. 1. Cladograms showing the relationships between members of the *Pachydactylus* radiation. These represent pruned versions of two equally parsimonious cladograms (a and b) with different branch lengths, generated by the maximum parsimony analysis of Bauer and Lamb (2005), and show only those taxa included in this study. The locomotor behaviour of each species (T, terrestrial; C, climbing), the clades compared for the phylogenetic analysis (1–7), and the natural groups within the radiation (Ta, *Tarentola*; R, *Rhoptropus*; C, *Chondrodactylus* (large-bodied), P, *Pachydactylus* (small-bodied)) are indicated alongside the species' names. Asterisks designate burrowing taxa. Crosses indicate taxa that previously rendered *Pachydactylus* paraphyletic and that are long-recognized as having many autapomorphies.

Terrestrial members of this radiation do not constitute a monophyletic assemblage (Fig. 1), and display the derived state (Lamb and Bauer 2005). Climbing members of the radiation include both large-bodied species, which form a monophyletic subgroup (*Chondrodactylus*) (Lamb and Bauer 2002; Bauer and Lamb 2005), and members scattered among a monophyletic, small-bodied clade within *Pachydactylus* (Bauer and Lamb 2002). Based on phylogeny and ecomorphological predictions, one might expect the limb morphology of geckos employing the derived, terrestrial mode of locomotion to differ from the ancestral condition found among the climbing members of this group.

According to biomechanical predictions, ground-dwelling lizards should have long hind limbs with a high tibia:femur ratio (Zaaf and Van Damme 2001). This high-gear system of locomotion is believed to enhance the acceleration produced by the hind limbs during running (Zaaf and Van Damme 2001), as well as permit longer strides and decrease friction by raising the body from the ground (Van Damme et al. 1997). Among skeletal elements, the metapodials may be longer, allowing muscle to be located more proximally, resulting in a lightening of the distal segments (Bauer et al. 1996). Conversely, climbing lizards are at risk of falling backwards and thus are predicted to display shorter limbs, which provide increased stability by bringing the animal's centre of gravity closer to the surface being climbed (Pounds 1988; Zaaf and Van Damme 2001; Herrel et al. 2002).

Herein, we examine variation in locomotor morphology among species within the *Pachydactylus* radiation and investigate whether predetermined categorization of the ecology of the included taxa (climbing or terrestrial) can account for differences that may exist. The null hypothesis is that no significant differences exist between the limb proportions of climbing species of the *Pachydactylus* radiation, and that these species will be identical to those of the selected outgroup: two species of *Tarentola*, the sister taxon of *Pachydactylus* sensu lato + *Rhoptropus*. Similarly, it is predicted that the terrestrial members of the *Pachydactylus* radiation will not differ from each other, although they may differ in morphology from the outgroup species, which employ climbing locomotion. Our approach also provides a means to determine whether the analytical technique employed influences the results obtained, by comparing data compiled from external measurements with those obtained from skeletal dimensions.

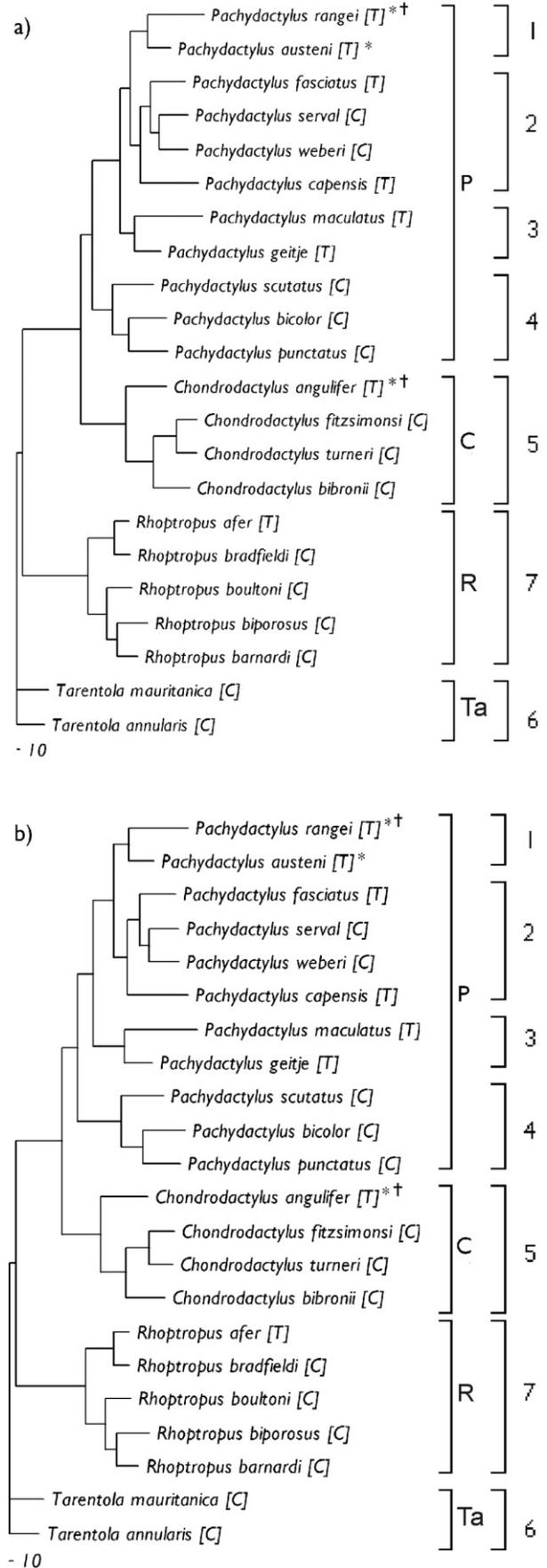


Table 1. Habitat details for the species investigated in this study.

| Species | Habitat | References |
|---|---|--|
| <i>Chondrodactylus angulifer</i> Peters, 1870 | Terrestrial: gravel plains, sandy flats and dunes; burrower | Haacke 1976 <i>b</i> ; Branch 1998 |
| <i>Chondrodactylus bibronii</i> (Smith, 1846) | Climbing: rock outcrops, under tree bark, on houses | Rieppel 1981; Jacobsen 1989; Branch 1998 |
| <i>Chondrodactylus fitsimensi</i> (Loveridge, 1947) | Climbing: rock outcrops | Branch 1998 |
| <i>Chondrodactylus turneri</i> (Gray, 1864) | Climbing: rock outcrops, under tree bark, on houses | Werner 1977; Branch 1998; Bauer and Branch 2003 |
| <i>Pachydactylus austeni</i> Hewitt, 1923 | Terrestrial: sand dunes; burrower | Haacke 1976 <i>a</i> ; Branch 1998 |
| <i>Pachydactylus bicolor</i> Hewitt, 1926 | Climbing: rock outcrops, in rock cracks | Branch 1998 |
| <i>Pachydactylus capensis</i> (Smith, 1846) | Terrestrial: grassland and savannah, under rocks and vegetation | Jacobsen 1989; Branch 1998 |
| <i>Pachydactylus fasciatus</i> Boulenger, 1888 | Terrestrial: savannah, under rocks and vegetation | Bauer and Branch 1991; Bauer et al. 1993; Branch 1998 |
| <i>Pachydactylus geitje</i> (Sparmann, 1778) | Terrestrial: under rocks and vegetation | Branch 1998 |
| <i>Pachydactylus maculatus</i> Gray, 1845 | Terrestrial: under debris and vegetation | Jacobsen 1989; Branch 1998 |
| <i>Pachydactylus punctatus</i> Peters, 1854 | Terrestrial: sandy soils, under rocks and vegetation | Werner 1977; Jacobsen 1989; Branch 1998 |
| <i>Pachydactylus rangei</i> (Andersson, 1908) | Terrestrial: sand dunes, river beds; burrower | Haacke 1976 <i>a</i> ; Werner 1977; Russell and Bauer 1990; Branch 1998 |
| <i>Pachydactylus scutatus</i> Hewitt, 1927 | Climbing: rock outcrops and boulders, in rock cracks | Bauer et al. 1993; Branch 1998 |
| <i>Pachydactylus serval</i> Werner, 1910 | Climbing: rock outcrops, under rock flakes | Branch 1998 |
| <i>Pachydactylus weberi</i> Roux, 1907 | Climbing: rock outcrops, in rock cracks | Branch 1998 |
| <i>Rhoptropus afer</i> Peters, 1869 | Terrestrial: gravel plains, sheet rock | Werner 1977; Odendaal 1979; Haacke and Odendaal 1981; Bauer et al. 1993; Branch 1998 |
| <i>Rhoptropus barnardi</i> Hewitt, 1926 | Climbing: rock piles or boulders | Odendaal 1979; Bauer et al. 1993; Branch 1998 |
| <i>Rhoptropus biporosus</i> Fitzsimons, 1957 | Climbing: rock piles or boulders | Branch 1998 |
| <i>Rhoptropus boultoni</i> , Schmisdt, 1933 | Climbing: large boulders, vertical surfaces | Odendaal 1979; Bauer et al. 1993; Bauer and Good 1996; Branch 1998 |
| <i>Rhoptropus bradfieldi</i> Hewitt, 1935 | Climbing: large boulders, vertical surfaces | Werner 1977; Odendaal 1979; Haacke and Odendaal 1981; Branch 1998 |
| <i>Tarentola annularis</i> (Geoffroy, 1823) | Climbing: trees and rock outcrops | Loveridge 1947 |
| <i>Tarentola mauritanica</i> (L., 1758) | Climbing: caves, trees, rock outcrops | Loveridge 1947; Martinez Rica 1974 |

Materials and methods

Specimens

Specimens (preserved in alcohol) from selected clades within the *Pachydactylus* radiation (Table S1)² were borrowed from museum collections and subjected to the measurement procedures outlined below. The array of species included taxa from the large-bodied *Pachydactylus* clade, now subsumed under the name *Chondrodactylus* (Lamb and Bauer 2002; Bauer and Lamb 2005); the small-bodied clade, now *Pachydactylus sensu stricto* (including the formerly separate taxon *Palmatogecko*) (Lamb and Bauer 2000; Bauer and Lamb 2002, 2005); *Rhoptropus*, the sister taxon of *Chondrodactylus* + *Pachydactylus*; and *Tarentola*, the sister

taxon of *Rhoptropus* + *Chondrodactylus* + *Pachydactylus* (see Fig. 1 for identification of these clusters). Specimens used were primarily adult males and females. Known habitat data for each species are provided in Table 1.

Morphological measurements

Specimens were measured using electronic calipers (Digimatic D20, Mitutoyo America Corp.; precision 0.01 mm); each measurement was repeated three times and the mean value was recorded. External measurements taken from the specimens are defined in Table 2 and depicted in Fig. 2. Measurements were combined to obtain external length measurements of total forelimb and total hind limb (Table 2, Fig. 2).

²Table S1 is available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0R6, Canada. DUD 4015. For more information on obtaining material, refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Table 2. Skeletal and external measurements taken from studied specimens.

| Measurement | Numbered point on Figs. 2a, 2b | Length |
|---------------------|--------------------------------|---------------------------------|
| External | | |
| Forelimb (Fig. 2a) | 1 | Brachium |
| | 2 | Antebrachium |
| | 3 | Metacarpus |
| | 4 | Digit IV of the manus |
| | 5 | Digit III of the manus |
| | 1–3 + 5 | Forelimb |
| Hind limb (Fig. 2b) | 1 | Thigh |
| | 2 | Crus |
| | 3 | Metatarsus |
| | 4 | Digit III of the pes |
| | 5 | Digit IV of the pes |
| | 1–4 | Hind limb |
| Skeletal | | |
| Forelimb (Fig. 2a) | 6 | Humerus* |
| | 7 | Ulna* |
| | 8 | Carpus |
| | 9 | Metacarpal III* |
| | 10 | Phalanx 1 of digit III* |
| | 11 | Phalanges 2 and 3 of digit III* |
| | 12 | Metacarpal IV* |
| | 13 | Phalanges 1 and 2 of digit IV* |
| | 14 | Phalanges 3 and 4 of digit IV* |
| | 10 + 11 | Digit III of the manus* |
| | 13 + 14 | Digit IV of the manus* |
| Hind limb (Fig. 2b) | 6–11 | Forelimb |
| | 6 | Femur* |
| | 7 | Tibia* |
| | 8 | Astragalocalcaneum |
| | 9 | Distal tarsal IV |
| | 10 | Metatarsal IV* |
| | 11 | Phalanges 1 and 2 of digit IV* |
| | 12 | Phalanges 3 and 4 of digit IV* |
| | 13 | Metatarsal III* |
| | 14 | Phalanx 1 of digit III* |
| | 15 | Phalanges 2 and 3 of digit III* |
| | 11 + 12 | Digit IV of the pes* |
| | 14 + 15 | Digit III of the pes* |
| 6–9 + 13–15 | Hind limb | |

*Measurements available for *Rhoptropus* species (see text for explanation).

Specimens were also radiographed using a Hewlett-Packard Faxitron radiology unit (model 43805N) and Polaroid® Type 55 black-and-white positive/negative film. A 1:1 ratio between the actual size of the specimen and the image size was obtained by placing specimens in direct contact with the radiograph film (Bergmann and Russell 2001). Radiograph negatives were enlarged by projection, and skeletal length measurements were taken from the projections with digital calipers (Table 2, Fig. 2). Measurements were adjusted by the appropriate magnification factor to obtain the actual lengths of the skeletal elements and were combined to obtain measurements of total forelimb and total hind limb lengths (Table 2, Fig. 2).

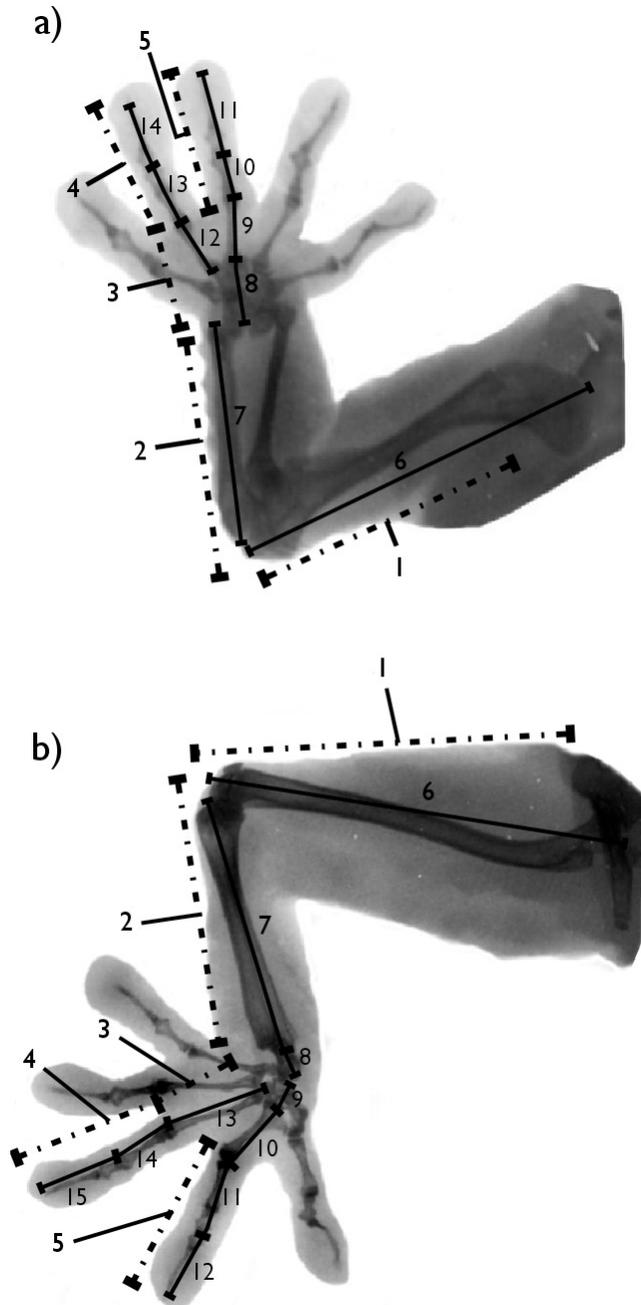
With the exception of snout–vent length (SVL), external measurement data were not available for the five species of *Rhoptropus*, and skeletal measurements were available only

for those limb components indicated by an asterisk in Table 2 (Bauer et al. 1996). All subsequent analyses including *Rhoptropus* employ only those measurements.

Statistical analysis

The mean values of all measurements were log-transformed prior to analysis to help normalize the data and reduce heteroscedasticity (Bauer et al. 1996). Potential differences between males and females were evaluated using analysis of variance (ANOVA) to compare the SVL and relative limb measurements (GMR residuals; see below) of the two sexes of each species, with the exception of the five *Rhoptropus* species, for which sex data were unavailable. Data for males and females were then pooled. All analyses were performed using PAST 1.25 (Hammer et al. 2001), SYSTAT 10.2 (Wilkinson 2002), Microsoft Excel 2000, and

Fig. 2. Dorsal radiographs of the left forelimb (a) and hind limb (b) of an adult female gecko (*Chondrodactylus bibronii*), indicating the external (dashed lines) and skeletal (solid lines) length measurements taken in this study (see Table 2 for explanation of measurements taken at each numbered point).



PDAP 5 (Garland et al. 1993). External and skeletal measurements were analyzed separately to determine the extent to which the source of data (external versus skeletal measurements) influenced the results obtained.

Principal components analysis (PCA) was performed following the methodology of Pimentel (1979) to reduce the large data set and identify biologically important relationships between species (Shea 1985). The factor scores of PCA provide information about the positions of individuals within

morphospace, allowing the variability and patterns of clustering of species to be evaluated (Pimentel 1979; Bergmann 2003). The covariance matrix model of PCA was used because all variables were single-dimensional, linear, continuous, and measured using the same scale (Pimentel 1979).

Six PCAs were conducted on the data. First, separate PCAs were used to evaluate three different sets of log-transformed measurements: external measurements, a complete set of skeletal measurements exclusive of *Rhoptropus* (hereafter referred to as skeletal measurement set A), and a more limited set of measurements (see above) with *Rhoptropus* included (hereafter referred to as skeletal measurement set B). These PCAs included size (SVL) and demonstrated its contribution to the overall variation among species (Pimentel 1979; Bergmann 2003). However, since size generally accounts for the majority of variation among species, it can swamp out other differences not related to size (Rohlf and Bookstein 1987).

Size effects were removed by regressing each limb component measurement against SVL for all of the species combined, using geometric mean regression (GMR). The GMR residuals for each species were then calculated using geometry to determine the distance between each point and the regression line (Ricker 1984). A second set of three PCAs was then performed on the GMR residual set, with external and skeletal measurements (sets A and B) once again being analyzed separately. PCAs using residual data have the effect of removing size, since all variables are scaled against size (SVL) for the regressions.

The number of principal components (PCs) from each PCA to be considered in subsequent analyses was determined using the Kaiser criterion. For a covariance matrix PCA, this criterion asserts that only components with eigenvalues greater than the average value of all of the eigenvalues are informative (Jolliffe 2002). Factor scores for the informative PCs of each PCA were calculated, and patterns of clustering between species were evaluated using 95% confidence intervals on these factor scores. The correlation between the eigenvectors and informative PCs of each of the size-free PCAs was calculated to determine the morphological characters and trends represented by each of the PCs.

Differences between species were evaluated by analyzing the factor scores from the size-free PCAs in a phylogenetic context using PDAP version 5 (Garland et al. 1993), employing phylogenetic analyses of variance by computer simulation (Garland et al. 1993; Vanhooydonck and Van Damme 1999; Zaaf and Van Damme 2001). The trees in Fig. 1 were entered into the PDTREE module of PDAP, and the informative factor scores of each of the size-free PCAs were entered as the tip data for each species. The analysis was repeated three times using constant branch lengths (Martins and Garland 1991; Price et al. 1997) and two sets of actual branch lengths representing the number of base pair differences between the species (Bauer and Lamb 2005; T. Lamb and A.M. Bauer, unpublished data).

The PDSIMUL module of PDAP was used to simulate the evolution of the characters being studied. One thousand simulations were conducted for the factor scores under the assumption of a speciation Brownian model of evolution with no boundaries. Finally, the PDANOVA module was

used to establish empirical F distributions from which a critical F value could be obtained by calculating the 95th percentile of the empirical F distribution.

Conventional ANOVAs comparing climbing and terrestrial species were performed on the factor scores of the informative PCs from the size-free PCAs of all three measurement sets. The F values from these analyses were then compared with the critical F values obtained from the appropriate empirical F distributions to determine whether the results were significant when phylogeny was taken into account. To evaluate potential differences between species related to phylogenetic clustering patterns rather than locomotor differences (climbing versus terrestrial), conventional ANOVAs were also conducted on the factor scores of the size-free PCAs comparing clades within the *Pachydactylus* radiation (Fig. 1). The F values from these ANOVAs were compared with critical F values obtained from an appropriate phylogenetic empirical F distribution as described above. If a significant difference was found, Tukey's test was used to evaluate which clades differed.

The above phylogenetic ANOVAs comparing clades did not allow for differences within clades to be determined. To identify potentially aberrant species within clades, conventional model I nested ANOVAs were performed on the factor scores from the size-free PCAs, with species nested within clades (Fig. 1). As before, external and skeletal measurements (sets A and B) were analyzed separately. If a significant difference was found, Tukey's test was used to evaluate which species or clades were responsible for the difference. If a species was found to be highly aberrant (e.g., *Chondrodactylus angulifer* Peters, 1870 and *Rhoptropus afer* Peters, 1869), then the phylogenetic analysis comparing clades was repeated with that species removed to determine whether the unusual species was solely responsible for the difference attributed to the clade.

Results

Sexual dimorphism

Members of the *Pachydactylus* radiation do not demonstrate visible sexual dimorphism; this observation was supported by statistical comparisons. Comparisons of SVL of males and females of each species revealed no significant differences in overall size between the two sexes (single factor ANOVAs; $df = 5-10$; $p > 0.05$). Similarly, in the majority of cases species showed no significant differences in relative limb proportions (GMR residuals) between males and females (single factor ANOVAs; $df = 5-10$; $p > 0.05$). Males and females did differ significantly for a few measurements in some species (*Pachydactylus bicolor* Hewitt, 1926, *C. angulifer*, *Chondrodactylus bibronii* (Smith, 1846), *Pachydactylus maculatus* Gray, 1845, and *Tarentola mauritanica* (L., 1758)); however, there was no consistent or strong pattern of differences in any of these species, and consequently the data for males and females were pooled for all subsequent analyses.

Principal components analysis

For all of the PCAs conducted on the log-transformed measurements with size included, the first component (PC1) explains the majority of the variation in the data (91.7% for the external measurements, 85.8% for skeletal measurement set A, and 78.4% for skeletal measurement set B). The eigenvectors for PC1 are positive for all measurements, indicating that PC1 is a size-related variable (Pimentel 1979). Plots of the factor scores for the size-inclusive PCAs show a clear pattern of clustering of species along PC1 according to their size (Fig. 3), with large species, such as *Tarentola* and *Chondrodactylus* species, clustered towards the right and the smaller *Rhoptropus* and *Pachydactylus* species clustered towards the left (Fig. 3). There is also some clustering of species along PC2 (Fig. 3); however, these differences are demonstrated more clearly by the size-free PCAs described below.

Based on the Kaiser criterion, the first two PCs are informative for the external measurements (eigenvalues greater than an average value of 0.001) and the first three are informative for skeletal measurement sets A and B (eigenvalues greater than average values of 0.004 and 0.005, respectively). The results of the size-free PCAs are summarized in Table 3. Plots of the factor scores of PC1 against those of PC2 for all measurement sets show a clear separation of *C. angulifer* along the axis of PC1 (Fig. 4). *Pachydactylus austeni* Hewitt, 1923 and *P. rangei* (Andersson, 1908) also differ from several other species along PC1. The eigenvectors of PC1 are both positive and negative, indicating that PC1 represents a shape variable (Pimentel 1979). PC1 is highly correlated with digit length for the external measurements and with the length of the distalmost phalanges (LP23D3ML, LP34D4ML, LP23D3PL, and LP34D4PL) for both sets of skeletal measurements (Table S2)².

The plots of the factor scores from the size-free PCAs also show clustering of species along PC2 (Fig. 4). *Pachydactylus austeni* differs from some of the other species along PC2 for the external measurements, and both *P. austeni* and *P. rangei* cluster separately from most other species along PC2 for skeletal measurement set A (Fig. 4). For skeletal measurement set B, all five *Rhoptropus* species segregate from most other species along the axis of PC2 (Fig. 4), and *R. afer* differs from the other species of *Rhoptropus* (Fig. 4).

Examination of the eigenvectors of PC2 for the analyses employing external measurements and skeletal measurement set A indicate that this component may be related to some species-specific aspect of size (Pimentel 1979), as the eigenvectors for PC2 are positive in these two analyses (Table S2).³ Conversely, PC2 represents a shape component when *Rhoptropus* is included (Table S2). The component correlations for PC2 are high and positive for overall limb length, proximal limb elements including the humerus, ulna, metacarpals, femur, tibia, and metatarsals (Table S2), and the proximal phalanges of the digits (Table S2), indicating that PC2 may represent a lengthening of these elements relative to the body size of the animal.

The factor scores for PC3 for the skeletal measurements show little or no clear pattern of clustering between the spe-

³Table S2 is available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0R6, Canada. DUD 4015. For more information on obtaining material, refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Fig. 3. Factor scores of principal component one (PC1) plotted against the factor scores of principal component two (PC2) from the principal components analyses of (a) snout-vent length (SVL) + external log-transformed length measurements (see Table 2 for complete list), (b) SVL + all skeletal log-transformed length measurements (see Table 2), and (c) SVL + skeletal log-transformed measurements marked with an asterisk in Table 2. Panel c alone includes five species of *Rhoptropus*.

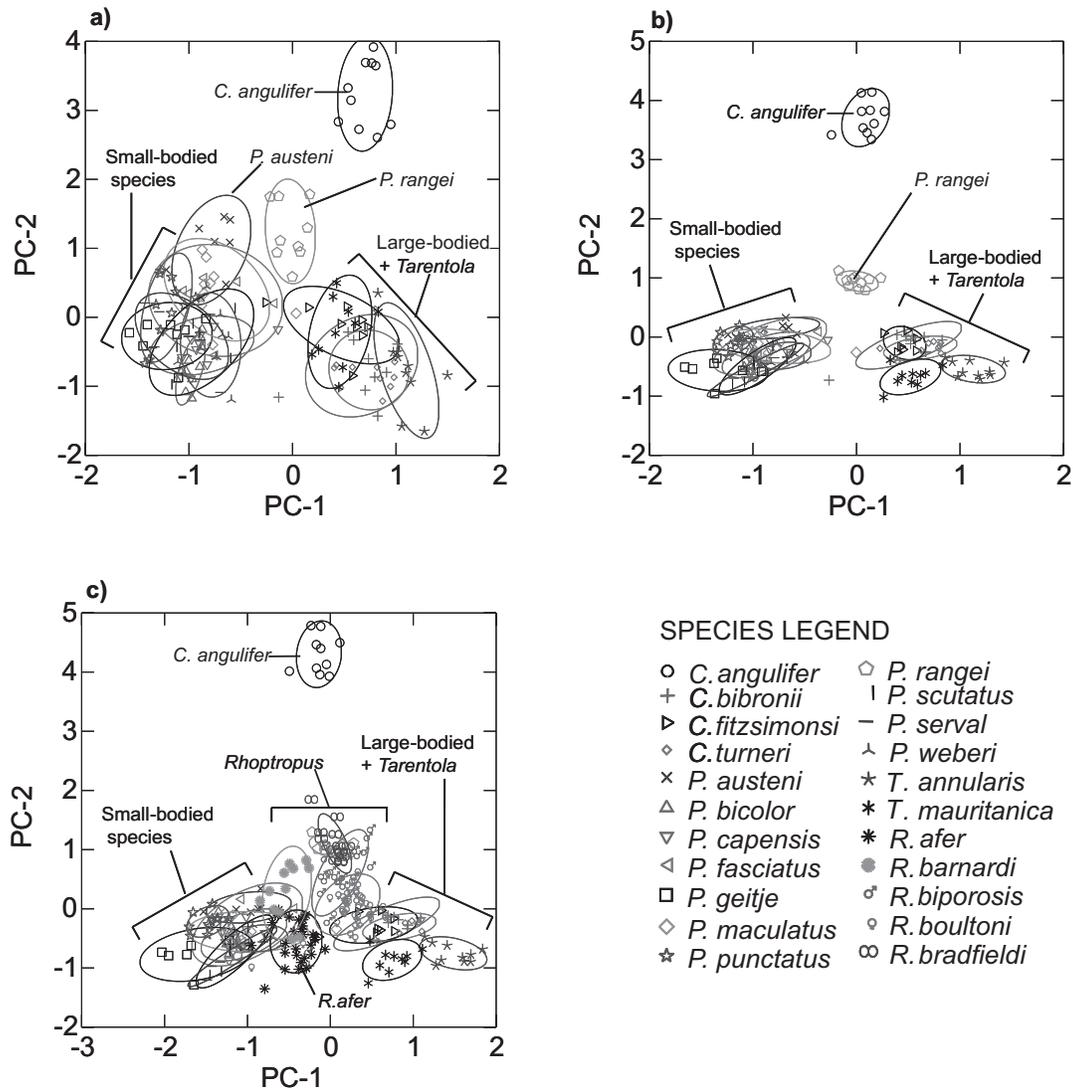


Table 3. Eigenvalues and the percentage of variation explained by informative principal components (PCs) obtained from size-free principal components analyses of the three sets of measurements.

| Measurement set | PC | Eigenvalue | % variation explained |
|-----------------|----|------------|-----------------------|
| External | 1 | 0.008 | 45.05 |
| | 2 | 0.004 | 25.48 |
| Skeletal A | 1 | 0.061 | 61.83 |
| | 2 | 0.014 | 14.30 |
| | 3 | 0.006 | 5.66 |
| Skeletal B | 1 | 0.043 | 46.55 |
| | 2 | 0.025 | 26.46 |
| | 3 | 0.009 | 9.86 |

cies except in the case of skeletal measurement set B, where *R. afer* differs significantly from all other species. However,

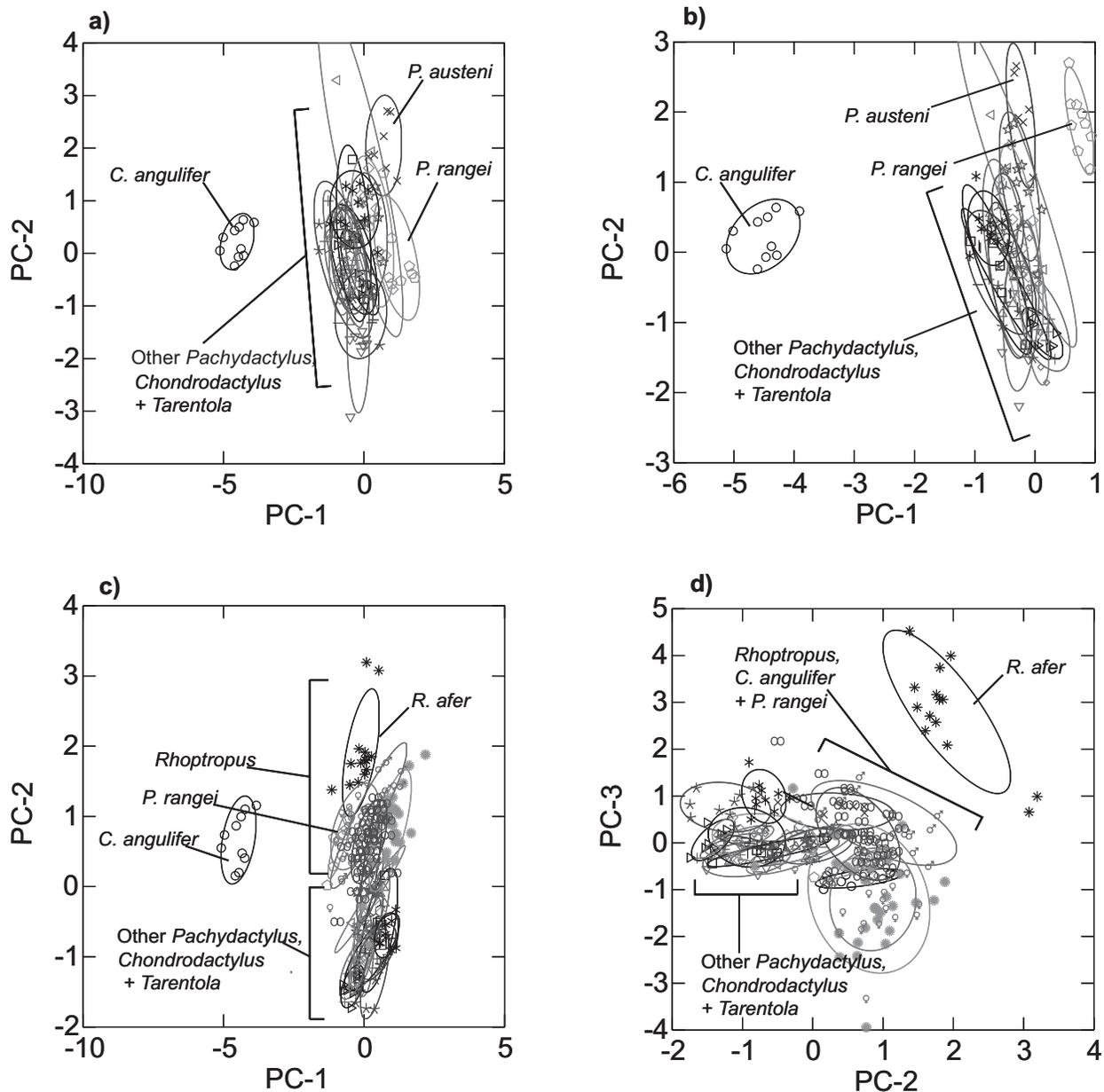
PC3 is not highly correlated with any particular limb component or set of components (Table S2).³

Phylogenetic analysis

The test statistics and critical *F* values for the phylogenetic analyses comparing climbing and terrestrial species are presented in Table 4, and those for the comparison of clades are presented in Table 5. Although the use of constant branch lengths resulted in a slight loss of power (Garland et al. 1993), the results obtained for the analyses using constant branch lengths did not differ from those obtained using either set of actual branch lengths (Tables 4 and 5). Thus, the results discussed below apply to all three sets of branch lengths.

The phylogenetic analyses comparing climbing and terrestrial species revealed differences between these locomotor groups for some cases, but not for others (Table 4). Significant differences were revealed only for the factor scores of

Fig. 4. Factor scores of principal component one (PC1) plotted against the factor scores of principal component two (PC2) from the principal components analyses of (a) residuals from the geometric mean regressions of the external length measurements (see Table 2 for complete list) against snout–vent length (SVL); (b) residuals from the geometric mean regressions of all skeletal length measurements (see Table 2) against SVL; and (c) residuals from the geometric mean regressions of the skeletal length measurements marked with an asterisk in Table 2 against SVL. (d) Factor scores of PC2 plotted against the factor scores of PC3 from the principal components analyses of residuals from the geometric mean regressions of the skeletal length measurements marked with an asterisk in Table 2 against SVL. Symbols for individual species are located in the legend of Fig. 3. Only panels c and d include *Rhoptropus*.



PC2 for skeletal measurement set A and for PC1 and PC3 of skeletal measurement set B (Table 4).

When clades were compared, the phylogenetic analysis of the factor scores of PC1 using external measurements revealed no significant differences between any of the clades (Table 5). In the analysis using skeletal measurement set A, a significant difference between clades was obtained for the factor scores of PC2, but not for those of PC1 or PC3 (Table 5). Further analysis of the factor scores of PC2 revealed that clade 1 (Fig. 1) differs significantly from other clades

(Tukey's test; $df = 125$; $p < 0.0001$) and that clade 5 (Fig. 1) differs from most of the others (Tukey's test; $df = 125$; $p < 0.0001$).

The phylogenetic analysis of the factor scores from the size-free PCAs using skeletal measurement set B revealed significant differences between clades for PC1 and PC2, but not for PC3 (Table 5). Clade 5 (Fig. 1) differed from the other clades along PC1 (Tukey's test; $df = 260$; $p < 0.0001$). However, the results of the conventional nested ANOVA on the factor scores of PC1 indicated that *C. angulifer* differs

Table 4. Results of the phylogenetic analysis of variance (ANOVA) comparing climbing and terrestrial species within the *Pachydactylus* radiation.

| Measurement set | PC | <i>F</i> value | df (group, error) | Critical <i>F</i> values | | | Significant ($F > F_{crit}$) |
|-----------------|----|----------------|-------------------|--------------------------|------------------|------------------|--------------------------------|
| | | | | Constant | Branch lengths 1 | Branch lengths 2 | |
| External | 1 | 0.06 | 1, 136 | 7.24 | 6.75 | 6.69 | No |
| | 2 | 4.57 | 1, 136 | 7.43 | 6.58 | 7.11 | No |
| Skeletal A | 1 | 5.71 | 1, 136 | 6.73 | 7.05 | 7.03 | No |
| | 2 | 38.17 | 1, 136 | 7.05 | 6.64 | 6.9 | Yes |
| | 3 | 3.42 | 1, 136 | 8.2 | 6.87 | 6.87 | No |
| Skeletal B | 1 | 35.49 | 1, 260 | 7.7 | 7.22 | 7.11 | Yes |
| | 2 | 2.57 | 1, 260 | 7.41 | 7.4 | 6.97 | No |
| | 3 | 12.48 | 1, 260 | 6.24 | 7.52 | 7.46 | Yes |

Note: The *F* values are from conventional ANOVAs and the critical *F* values are derived from an empirical *F* distribution constructed by computer simulations. The critical *F* values were found using constant branch lengths and two different sets of real branch lengths.

Table 5. Results of the phylogenetic analyses of variance (ANOVA) comparing clades within the *Pachydactylus* radiation.

| Measurement set | PC | <i>F</i> value | df (group, error) | Critical <i>F</i> values | | | Significant ($F > F_{crit}$) |
|-----------------|----|----------------|-------------------|--------------------------|------------------|------------------|--------------------------------|
| | | | | Constant | Branch lengths 1 | Branch lengths 2 | |
| External | 1 | 6.33 | 5, 136 | 17.84 | 16.61 | 19.57 | No |
| | 2 | 6.05 | 5, 136 | 18.87 | 17.56 | 15.65 | No |
| Skeletal A | 1 | 13.81 | 5, 136 | 19.47 | 18.92 | 17.20 | No |
| | 2 | 27.14 | 5, 136 | 19.03 | 17.44 | 18.71 | Yes |
| | 3 | 4.41 | 5, 136 | 18.93 | 17.39 | 18.57 | No |
| Skeletal B | 1 | 19.34 | 6, 260 | 17.95 | 18.03 | 17.35 | Yes |
| | 1a | 9.06 | 6, 250 | 19.63 | 18.02 | 17.08 | No |
| | 2 | 75.06 | 6, 260 | 17.84 | 17.88 | 16.91 | Yes |
| | 2a | 72.76 | 6, 247 | 20.09 | 18.93 | 18.42 | Yes |
| | 3 | 2.82 | 6, 260 | 19.84 | 17.66 | 17.34 | No |

Note: The *F* values are from conventional ANOVAs, and the critical *F* values are derived from an empirical *F* distribution constructed by computer simulation. The critical *F* values were found using constant branch lengths and two different sets of real branch lengths. Also shown are the results of the ANOVAs on PC1 with *Chondrodactylus angulifer* removed (1a) and on PC2 with *Rhoptropus afer* removed (2a).

substantially from the other species in clade 5 (Tukey's test; $df = 125$ or 245 ; $p < 0.001$), so the phylogenetic analysis was repeated with this species removed, resulting in the expunging of the significant difference between clades (Table 5). For PC2, clades 1 and 7 (Fig. 1) differed significantly from the other clades (Tukey's test; $df = 260$; $p < 0.0001$). The conventional nested ANOVA revealed that *R. afer* is highly divergent from the other species in clade 7 (Tukey's test; $df = 245$; $p < 0.001$). The phylogenetic analysis was repeated with this species removed, with unchanged results.

Discussion

Our results suggest that although there are some differences between climbing and terrestrial species in the *Pachydactylus* group, they are not consistent and are mostly attributable to unique morphological characteristics of certain species and clades (*P. rangei*, *P. austeni*, *C. angulifer*, and *Rhoptropus* species) within the radiation. Our results also highlight how different methodologies can influence the outcome obtained. Categorizing taxa broadly as either

climbing or terrestrial forms may obscure rather than clarify differences that can be related to more subtle aspects of the locomotor environment and phylogenetic history.

Significant differences between locomotor types and between clades were obtained only for the skeletal data, indicating that different methods of data collection can influence the results of ecomorphological studies. The differing results obtained are not surprising because although external and skeletal measurements correspond to similar parts of the limb, they do not measure exactly the same thing. External measurements represent those portions of the limbs that extend beyond the body wall and include components added to the length by soft tissues. They also combine certain sectors of the limb (such as the components of the tarsus and metatarsus or the individual sectors of digits) and thus have the potential to obscure subtle but important differences. On the other hand, skeletal measurements represent the total length of the bones, including parts located inside the body wall, and correspond to the actual lever arms used in locomotion (Russell and Bels 2001). Furthermore, there may be different selective pressures on external limb proportions

than on skeletal elements of the limb, potentially conflating differences between these two measures. The current results support those of previous studies in suggesting that differences between species can be more readily detected by employing skeletal measurements (Lundelius 1957; Bauer et al. 1996; Vanhooydonck and Van Damme 1999; Melville and Swain 2000; Zaaf and Van Damme 2001; Bickel and Losos 2002; Herrel et al. 2002), especially when the analysis is phylogenetically informed.

The results of the size-inclusive PCAs indicate that the species considered in this study are primarily distinguished from each other by their size (Fig. 3). Size differences between species are not unimportant and may be directly related to the type of microhabitat exploited. In situations where the ranges of these species overlap, interspecific competition may lead to selection for different body sizes and thus the exploitation of different microhabitats and prey among species (Pounds 1988). However, although size is the most important factor distinguishing the species, up to 20% of the variation between species results from morphological characteristics other than size.

The phylogenetic analyses comparing species assigned to climbing and terrestrial categories did reveal some significant differences between these two locomotor types, which initially suggests that terrestrial species possess shorter digits (PC1) and longer limbs (PC2) than climbing species (Table 4). However, a more in-depth analysis of clades within the radiation revealed that the categorization of species as climbing or terrestrial oversimplifies the patterns of morphological differences between the species and can be misleading. For instance, while some terrestrial species are highly divergent from the ancestral climbing body form, others are not. Thus, the inclusion of a few very different terrestrial species resulted in a significant difference of the entire terrestrial category in some cases. Also, some important morphological patterns were not revealed by simply comparing climbing and terrestrial species because some clades include species from both locomotor categories. For instance, no significant difference was found between climbing and terrestrial species along PC2 of skeletal measurement set B, but subsequent analyses revealed that the *Rhoptropus* clade differs from the rest of the radiation along this component. Since the *Rhoptropus* clade includes both climbing and terrestrial members, this pattern is obscured when climbing and terrestrial species are compared.

The phylogenetic analyses comparing clades provided a clearer picture of the patterns of morphological differences within the *Pachydactylus* radiation. The size-free PCA employing skeletal measurement set B (which included *Rhoptropus*) gave significant results for PC1, indicating that the large-bodied clade (clade 5), which includes the species *C. bibronii*, *Chondrodactylus turneri* (Gray, 1864), *Chondrodactylus fitzsimonsi* (Loveridge, 1947), and *C. angulifer*, differs from all other clades in the radiation. However, the results indicate that this difference is attributable to *C. angulifer*, which has diverged considerably from other species in the *Pachydactylus* radiation as well as from the other members of its own clade. This is supported by the plots of the factor scores of PC1, which show that *C. angulifer* is clearly separated from all of the other species, whereas the other species in clade 5 are not (Fig. 4).

PC1 for the size-free data set represents variation primarily in the length of the digits and, more specifically, the distal phalanges. *Chondrodactylus angulifer* has highly reduced distal phalanges (Haacke 1976b; Russell 1976). Its exploitation of terrestrial locomotion involves secondary loss of the adhesive system and thus deviates from the other examined members of the *Pachydactylus* radiation in this regard. It is possible that the unique morphology of *C. angulifer* is related to spending more time walking on open sand than on rocky surfaces (Table 1).

Differences between species were also obtained from the analysis of the factor scores for PC2 from the size-free data. Clades 1 and 5 (Fig. 1) differed from all other groups for skeletal measurement set A (which excluded *Rhoptropus*) (Table 5), suggesting that these groups of species have elongated limbs. In this case, *C. angulifer* does not differ significantly from the other species in its clade (Tukey's test; $df = 125$; $p > 0.05$), meaning that the entire *Chondrodactylus* clade has diverged from other species in the *Pachydactylus* radiation and that all *Chondrodactylus* species possess relatively longer limbs. This is intriguing, as *C. bibronii*, *C. turneri*, and *C. fitzsimonsi* are all climbers (Table 1), and long limbs are generally associated with increased stride length and thus faster locomotion on level surfaces and in open habitats (Garland and Losos 1994; Bauer et al. 1996; Melville and Swain 2000; Zaaf and Van Damme 2001). Such results may indicate that these species, although climbers, spend more time on the ground or on horizontal rock surfaces than other smaller, climbing species of *Pachydactylus*. It is also possible that the relatively longer limbs are related to the large size of the species in this clade or to some other unknown aspect of their ecology.

Clearly, the similar morphometrics exhibited by the large-bodied *Chondrodactylus* clade do not reflect identical limb function in all included taxa. The case of *C. angulifer* is particularly complex, as its long limbs may be interpreted both as a phylogenetic legacy of its affinities to the relatively long-legged *C. bibronii* and its relatives and as an exaptation associated with burrowing and (or) life on sandy substrates, characteristic also of *P. rangei* and *P. austeni* (clade 1) (Fig. 1).

Morphometric data indicate similarity in general limb form between *C. angulifer* on the one hand and *P. rangei* and *P. austeni* on the other hand, although limb morphology is visibly different (Haacke 1976a, 1976b). The elongation of limbs evident in these taxa may be associated with living on windblown sand and may be related, at least in part, to the adoption of elevated limb postures potentially associated with more effective sighting of prey (Werner and Broza 1969). Subtle differences in the mechanics of burrow construction in sands of different compactness may, however, be related to striking differences in the morphology of the digits and how these contribute to the overall measure of limb length in the otherwise convergent patterns of limb morphometrics (Bauer and Russell 1991).

In the case of the analysis of the factor scores of PC2 for skeletal measurement set B, the *Rhoptropus* clade differs from all other clades along PC2, even when the highly aberrant species *R. afer* is removed from the analysis (Table 5). These results suggest that the entire *Rhoptropus* clade has diverged from the other clades within the *Pachydactylus* radi-

tion and that within its clade, *R. afer* has diverged from the other *Rhoptropus* species. PC2 represents an increase in the length of the proximal elements of the limb, as well as the proximal elements of the manus and pes, corroborating observations that *Rhoptropus* species, and particularly *R. afer*, possess elongated limb elements (Bauer et al. 1996; Russell et al. 1997). In this instance, increased limb length and increased rapidity of locomotion are associated. Furthermore, *R. afer* continues this trend with the adoption of more terrestrial habits than is evident in other species of *Rhoptropus*.

In addition to the *Rhoptropus* clade, clade 1 (Fig. 1) also differs from all other clades for skeletal measurement set B (Table 5). This suggests that *P. austeni* and *P. rangei* also possess elongated limb elements relative to other species of geckos. However, although they possess similar limb proportions, *P. rangei* and *P. austeni* are very different from *Rhoptropus* species in ecology and behaviour. *Pachydactylus rangei* is a burrower in compacted dune faces of the Namib sand sea (Russell and Bauer 1990), and *P. austeni* has also been observed to dig burrows in sand, chiefly in consolidated coastal dunes. Thus, the limb proportions of these species and the loss of the adhesive apparatus in *P. rangei* and its reduction in *P. austeni* are likely related to fossoriality (Russell and Bauer 1990; Branch 1998). Conversely, *Rhoptropus* species are diurnal and run swiftly over rock surfaces when pursued. In this situation, increased limb length relative to that of other members of the *Pachydactylus* radiation may be related to celerity facilitating diurnal predator avoidance, and may have then been co-opted by *R. afer* for deployment in more terrestrial habitats (Bauer et al. 1996).

The phylogenetic analyses of the factor scores for PC3 did not reveal the significant difference for *R. afer* that was observed in the factor score plot (Table 5; Fig. 4). This difference was likely not revealed because it was swamped out by the other *Rhoptropus* species, which do not differ along PC3. Thus, although the analysis did not reveal this difference in *R. afer*, the factor score plots suggest that in addition to being different along PC2, *R. afer* also differs from all other members of the *Pachydactylus* radiation along PC3, providing further evidence that *R. afer* is highly divergent in its locomotor morphology.

Overall, our results indicate that there is no single trait or series of traits that distinguish species of the *Pachydactylus* radiation assigned to climbing and terrestrial categories. However, some species and groups of species are indeed highly divergent from other clusters of species within the radiation. In some cases, the divergent morphologies seem to be related to the adoption of a terrestrial lifestyle, but this is not consistent for all terrestrial species. Furthermore, some of the morphologically divergent species have retained the primitive, climbing lifestyle, suggesting that something other than mode of locomotion is responsible and that the classification of species as either climbing or terrestrial lacks the resolution to reflect their precise ecology.

Aside from *Chondrodactylus*, *Rhoptropus*, and *P. austeni* and *P. rangei*, no other groups of species were found to differ from the outgroup, *Tarentola*. This implies that most of the small-bodied *Pachydactylus* species, whether categorized as climbers or terrestrial forms, are not differentiable from one another by their proportions and have not diverged significantly from the ancestral body form. Thus, different pat-

terns of locomotion, as defined in this study, have been accommodated by relatively unchanged locomotor systems.

In general, the results of our study indicate that different methods of morphological measurement can yield different results, even for the same set of specimens, thus illustrating the importance of carefully considering the effects of methodology before drawing conclusions about the results. Furthermore, it is evident that the limb proportions of certain species of the *Pachydactylus* radiation have diverged from the basal pattern and that their morphology may, to some extent, reflect differences in microhabitat use, thereby supporting the principles of ecomorphology in a more subtle way. More extensive field studies focusing on habitat preferences are required before the ecomorphological significance of such findings can be fully assessed. Furthermore, to demonstrate that differences in limb proportions relate to adaptations to certain microhabitats, such traits must be linked to performance differentials, such as sprint speed or clinging and climbing ability, between species that vary in these traits (Aerts et al. 2000).

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