

The evolution of bipedal postures in varanoid lizards

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The bipedal posture (BP) and gait of humans are unique evolutionary hallmarks, but similar stances and forms of locomotion have had enormous influences on a range of phylogenetically diverse tetrapods, particularly dinosaurs and birds, and a range of mammalian lineages, including non-human apes. The complex movements involved in bipedalism appear to have modest evolutionary origins, and it is presumed that a stable and erect posture is a prerequisite for erect strides and other bipedal movements. Facultative bipedalism in several lineages of lizards is achieved by running, but some varanid lizards (genus *Varanus*) exhibit BPs without running. In these cases, BPs (BP_{standing}) are not used as a form of locomotion; rather, BP_{standing} is associated with defensive displays, and such postures also probably permit better inspection of the environment. Yet, in other varanids, BPs have been observed only during combat episodes (BP_{combat}), where both contestants rise together and embrace in the so-called clinch phase. Numerous other species, however, show neither type of BP. Past researchers have commented that only large-bodied varanids exhibit BP, a behaviour that appears to show phylogenetic trends. We termed this idea the King–Green–Pianka (KGP) bipedal hypothesis. In this article, we address two main questions derived from the KGP hypothesis. First, what is the phylogenetic distribution of BP in *Varanus* and close relatives (varanoids)? Second, is BP positively correlated with the phylogenetic distribution of large body size (e.g. snout–vent length, SVL)? In addition, we asked a related question: do the lengths of the femur and tail show body size-independent adaptive trends in association with BP? Because varanid species that show BP_{standing} also use these postures during combat (BP_{combat}), both types of BP were analysed collectively and simply termed BP. Using comparative phylogenetic analyses, the reconstruction of BP required three steps, involving a single gain and two losses. Specifically, BP was widespread in the monophyletic *Varanus*, and the single gain occurred at the most recent common ancestor of the African clade. The two losses of BP occurred in different clades (Indo-Asian B clade and Indo-Australian Odatria clade). BPs are absent in the sister group to *Varanus* (*Lanthanotus borneensis*) and the other outgroup species (*Heloderma* spp.). Our phylogenetic reconstruction supports the KGP prediction that BP is restricted to large-bodied taxa. Using the Hansen model of adaptive evolution on a limited, but highly relevant morphological dataset (i.e. SVL; femur length, FL; tail length, TL), we demonstrated that these characters were not equivalent in their contribution to the evolution of BP in *Varanus*. SVL was significantly correlated with BP when modelled in a phylogenetic context, but the model identified random processes as dominant over adaptive evolution, suggesting that a body size threshold might be involved in the evolution of BP. A Brownian motion (BM) model outperformed the selection model in our analysis of relative TL, suggesting that TL and BP evolved independently. The selection model for relative FL outperformed the BM model, indicating that FL and BP share an adaptive history. Our non-phylogenetic analyses involving regression residuals of FL and TL vs. SVL showed no significant correlation between these characters and BP. We suggest that BP in *Varanus* provides a convergent or analogue model from which to investigate various forms of bipedalism in tetrapod vertebrates, especially other reptiles, such as theropod dinosaurs. Because BP_{standing} in varanids is possibly an incipient stage to some form of upright locomotion, its inclusion as a general model in evolutionary analyses of bipedalism of vertebrates will probably provide novel and important insights. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 97, 652–663.

ADDITIONAL KEYWORDS: ancestral character reconstruction – body size – comparative evolutionary analysis – locomotion – selective regimes – tetrapod vertebrates – *Varanus*.

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INTRODUCTION

Varanus are morphologically conservative but vary in mass by nearly five orders of magnitude . . . no other terrestrial animal genus exhibits such a range of size variation. There is proportionately almost as much difference in mass among species within the genus Varanus as there is between an elephant and a mouse.

E. R. Pianka (1995)

Unlike the bipedal gait of humans, which is a rare form of locomotion among extant animals, assuming an upright posture, with or without movement – sometimes with the aid of a tail – has independently evolved in numerous lineages of terrestrial vertebrates, including marsupial and placental mammals, and both avian and non-avian reptiles. Bipedalism is entirely absent in modern amphibians (Snyder, 1962; Russell & Bels, 2001; Alexander 2006; Hutchinson 2006; Hutchinson & Gatesy 2006; Clemente *et al.* 2008). The postures and gaits associated with bipedality have had large impacts on the biology of the taxa that exhibit them, and there is a general consensus that many facets of human evolution, including social structure and intelligence, were profoundly influenced by bipedalism (Vallender & Lahn, 2004; Ackerman, 2006; Senut, 2006; Skoyles, 2006; Nicolas *et al.*, 2007; Sockol, Raichlen & Pontzer, 2007). Accordingly, understanding the origin, maintenance and phylogenetic distribution of bipedalism in varied tetrapods will provide important evolutionary perspectives that can contribute to the development of a general synthesis.

Beyond humans and birds, where bipedalism is the obligate terrestrial gait, various forms of obligate and facultative bipedalism occur in other animals, primarily mammals, such as pongid apes (chimpanzees, gorillas, orang-utans), kangaroos and related species, and some desert rodents. Bipedalism also occurs in several divergent lineages of lizards, primarily Agamidae, Crotaphytidae, Iguanidae and Phrynosomatidae (e.g. Hsieh, 2003; Bush & Hu, 2006; Clemente *et al.*, 2008). In all cases involving these species, bipedalism is achieved only by rapid locomotion (i.e. achieving speed and acceleration thresholds) on the ground, which may even extend to running short distances across the surface of water, for example the Neotropical *Basiliscus* spp. (Aerts *et al.*, 2003; Hsieh, 2003; Bush & Hu, 2006). In these circumstances, bipedalism is used as a mechanism to evade enemies and predators (Greene, 1988; Hsieh, 2003).

In several of the 58 or so species of extant varanid lizards, genus *Varanus* (Böhme, 2003), individuals can attain remarkably erect postures without running (Murphy & Lamoreaux, 1978; King & Green, 1999; Pianka & King, 2004). In these cases, the bipedal

posture (BP) is not used for locomotion (e.g. walking, running); rather, its function seems to be a defensive display and it permits an enhanced inspection of the environment (Pianka & King, 2004; C. Clemente, pers. comm.). This posture, moreover, resembles standing, but it also involves the use of a tail as an anchor to form a ‘tripod’ for balance, similar to stances by kangaroos (see plate 7 in King & Green, 1999). More commonly, BP is attained only during conspecific combat interactions, in which both contestants rise together and form a stable embrace in the so-called clinch phase (see plate 21 in King & Green, 1999; Earley, Attum & Eason, 2002). Yet, in other varanids, neither type of BP has been documented, even during conspecific combat (Thompson, Withers & Thompson, 1992; King & Green, 1999; Earley *et al.*, 2002; Pianka & King, 2004).

As discussed by King & Green (1999) and Pianka & King (2004): (1) only large varanids exhibit BP, and (2) BP appears to show phylogenetic trends (e.g. BP is absent in certain Australian species). In this article, we refer to this idea as the King–Green–Pianka (KGP) bipedal hypothesis. Because species that show BP_{standing} also use similar postures during combat (BP_{combat}), we analysed both types of BP collectively as BP. No other group of lizards varies in adult size to the degree shown in varanids (Pianka, 1995, 2004; Pianka & King, 2004), with the smallest species at 15–20 cm total length and 8–20 g (Australian pygmy monitors) to the largest of all lizards, the Komodo dragon (*V. komodoensis*), which can attain a total length of 3 m and a body mass of 150 kg (Auffenberg 1981). The extinct (Pleistocene) *Varanus (Megalania) prisca*, a close relative of *V. komodoensis* (Conrad, Rieppel & Grande, 2008), was as large as *V. komodoensis* and estimated to have been 3.45 m in total length and 118–158 kg (Pianka, 1995, 2004; Wroe, 2002; Head, FLS & Rayfield, 2009), and others (see authors in Pianka & King, 2004; also, see Gould & MacFadden, 2004) have discussed the ecological and evolutionary significance of body size variation in varanid lizards; hence, based on their findings and conclusions, any analysis of BPs in this group necessarily requires the incorporation of body size.

In this article, we performed comparative phylogenetic analyses to understand the distribution of BP among extant varanoid clades (Maddison & Maddison, 2000, 2006; Garland, Bennett & Rezende, 2005) and to test hypotheses of adaptive character evolution against a neutral model (Brownian motion, BM). Hansen (1997) introduced a phylogenetic comparative model, based on the Ornstein–Uhlenbeck process, which explicitly incorporates both drift (BM) and selection towards an optimum in modelling quantitative character evolution. The values of different adaptive optima are determined operationally using maximum

likelihood (ML) to parse the distribution of the quantitative character measured from taxa at the branch tips of hypothesized selective regimes. Adaptive optimum values are sensitive to evolutionary time (branch lengths), and selection can be modelled as two or more optima that characterize different regions of a phylogeny. The resulting hypothesis is a formal representation of adaptive zones with temporal and topological specificity, termed selective regimes. Selective hypotheses, which can be represented graphically as coloured (or shaded) regions of a phylogeny, can be statistically compared with a model based on non-directional evolution by BM (overviewed in Butler & King, 2004; see Bergmann, Meyers & Irschick, 2008). Accordingly, we sought to determine the adaptive importance of snout–vent length (SVL), femur length (FL) and tail length (TL) in the evolution of BP.

MATERIAL AND METHODS

MORPHOLOGICAL ANALYSIS

Data on the body size of 32 species of *Varanus* and three outgroup species were obtained from the literature (Thompson & Withers, 1997; Bennett, 1998; Blob, 2000) and, in several cases, live specimens held in zoos or private collections (Appendix). We used SVL, unbroken TL and FL in our various analyses. A single value represented an adult size for each species. Although conspecific combat by way of various BPs appears to be limited to males, both sexes are capable of bipedal stances (King & Green, 1999; Pianka & King, 2004). Moreover, sexual size dimorphism of the characters studied tends not to be a distinctive feature in *Varanus* and other varanoid taxa (Pianka & King, 2004; Beck, 2005; but see Thompson *et al.*, 2008). Accordingly, we did not use sex as a factor to adjust body size data. Regressions of the residuals of SVL on unadjusted FL and TL were inspected for significant relationships.

PHYLOGENETIC ANALYSES

Information on the presence or absence of BPs in varanoid taxa (ingroup + outgroups) was obtained from a recent review (Earley *et al.*, 2002), as well as from published accounts from scholarly books (and references therein) by Bennett (1998), King & Green (1999), Murphy *et al.* (2002), Pianka & King (2004) and Beck (2005). BP was treated as a discrete two-state character, present or absent (Appendix). The ingroup (*Varanus*) consisted of 32 species and contained representative members of all the major clades recovered by Ast (2001) and Jennings & Pianka (2004). The three outgroups consisted of the New World genus *Heloderma* (*H. horridum*, *H. suspectum*) and the Old World and monotypic *Lanthanotus bornensis* (sometimes presented as its own family, Lan-

thanotidae), the sister group to the monophyletic *Varanus* (Pregill, Gauthier & Greene, 1986; Townsend *et al.*, 2004; Lee, 2005; Kumazawa, 2007).

Bipedal states (1, present; 0, absent) for all outgroup and ingroup species were reconstructed onto a recent mitochondrial DNA (mtDNA)-based phylogeny of varanids (Ast, 2001: 219) using both Fitch parsimony (MacClade, version 4.0; Maddison & Maddison, 2000) and ML (Pagel, 1999) methods (Mesquite, version 1.12; Maddison & Maddison, 2006). In the MacClade analysis, character transformation type was unordered (i.e. all states were equally weighted) and equivocal cycling was used to recover all most-parsimonious reconstructions. The likelihood analyses employed a Markov *k*-state one-parameter model (Mk1; Lewis, 2001) and assumed a single rate between character state transitions. The best estimate of the character state at each node was determined using the likelihood ratio test. In this test, when the difference in the $-\log$ -likelihood values of two states was smaller than 2.0, an ancestral state reconstruction was considered to be ambiguous; when the difference was greater than 2.0, the state with the higher $-\log$ -likelihood value was rejected and the alternative state was chosen as the best estimate of the character state. Other DNA-based analyses of the phylogeny of varanoid lizards support the Ast (2001) topology of *Varanus* relationships (Jennings & Pianka, 2004; Fitch, Goodman & Donnellan, 2006). The Ast (2001) tree incorporated 40 ingroup taxa (*Varanus* species) comprising four major clades, i.e. African, Indo-Asian A (composed of two unnamed subclades), Indo-Asian B and Indo-Australian. The Indo-Australian clade is composed of a group of giants (*salvadorii* (*komodoensis* + *varius*)), which is sister to the clades *gouldii* + *Odatria*. Moreover, *Odatria* is composed of two unnamed subclades. Based on the KGP hypothesis, as well as accumulating information on the behaviour and morphology of varanoid lizards (e.g. Pianka & King, 2004; Beck, 2005), we predicted that BP in *Varanus* would be widespread in large-bodied taxa and losses would occur in small-bodied taxa, at least in one main region of the tree, i.e. the Indo-Australian *Odatria* clade (Ast, 2001; Pianka & King, 2004).

To assess whether BP is randomly distributed with respect to body size (i.e. SVL), we used the concentrated-changes test of MacClade (Maddison & Maddison, 2000; see Schuett, Gergus & Kraus, 2000) on the parsimony tree. The alternative hypothesis is that BP is more concentrated than expected by chance in species that have large SVL. We treated SVL as a two-state character (large or small) based on maximum sizes provided by Pianka (1995), with state 1 as SVL > 40 cm and state 0 as SVL ≤ 40 cm. A single most-parsimonious tree was produced with three steps (one gain and two losses). In the concentrated-changes

test analysis, SVL was the independent variable and we specified that the distinguished branches be state 1 (i.e. taxa with large SVL). Correlation probabilities were determined using simulation (5000 runs) and the ancestral node was set at 'either 0 or 1.' The alpha level of significance was $P \leq 0.05$.

EVOLUTIONARY ANALYSIS

We used the software OUCH (Ornstein–Uhlenbeck for Comparative Hypotheses; Butler & King, 2004; <http://www2.hawaii.edu/~mbutler/ButlerLab.data/OUwork.html>), in the open source software environment R, to apply the methods of Hansen (1997) to our morphological dataset (SVL, FL and TL) for 35 species of varanoid lizard (*Varanus* + outgroups). OUCH uses the Hansen model (HM) (Hansen, 1997; reviewed by Butler & King, 2004) to generate ML estimates of the strength of selection (α), strength of random drift (σ), values of any optima specified by the hypothesis (i.e. θ_k , where k denotes a specified selective regime) and the trait value at the root node (θ_0). Three model selection statistics were generated: a likelihood value ($-2\log L$), the Akaike Information Criterion (AIC) and the Schwarz (Bayes) Information Criterion (SIC). We used the likelihood ratio test as our primary tool for model evaluation and compared these results with AIC and SIC model evaluations. Where necessary, morphological data were square-root transformed to achieve normality. To remove the influence of body size (i.e. SVL) on FL and TL, we calculated residuals from regressions of FL and TL on SVL. To eliminate negative numbers in the OUCH analysis, the sets of residuals were shifted along the number scale until the minimum value in the set equalled unity.

HM is sensitive to time, and thus requires phylogenies with branch lengths (Hansen, 1997; Butler & King, 2004). We obtained branch lengths for varanoids (*Varanus* + outgroups) using the ultrametric (molecular clock) tree generated by Jennings & Pianka (2004: 81). Jennings & Pianka (2004) reanalysed Ast's (2001) dataset (with minor modifications) using ML procedures (GTR + γ + I substitution model) and generated ML branch lengths scaled to time. Based on the view that molecular sequences can evolve in a clocklike manner, branch lengths should thus reflect relative time (see Huelsenbeck, Bollback & Levine, 2002).

We tested our selection hypothesis (HM) with two optima against a neutral (BM) model. The two optima were empirically derived by the presence or absence of BP as reconstructed using MacClade and Mesquite; our selection model required three steps (a single gain and two subsequent losses). Transformation of SVL was not required to achieve normality; however, we transformed FL (square-root transformation

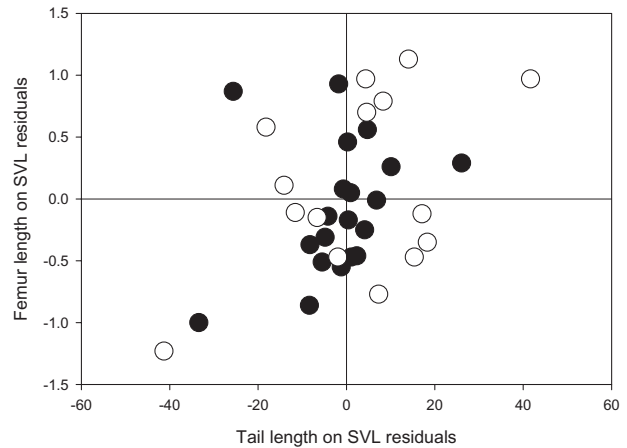


Figure 1. Plot of two sets of residuals from regressions of femur length [on snout–vent length (SVL) residuals] versus tail length (on SVL residuals). See Appendix for list of taxa (ingroup and outgroups) included in the analysis. Filled circles, bipedal posture (BP) present. Open circles, BP absent.

followed by residuals calculation) and TL (residuals calculation).

RESULTS

MORPHOLOGICAL ANALYSIS

Unadjusted morphological data are presented in the Appendix. The regression residuals of FL and TL on SVL (Fig. 1) revealed no significant trends in the varanoid taxa with respect to BP state. A simple chi-squared procedure used to test for differences in the distribution of positive and negative residuals produced non-significant P values (0.343–0.584, d.f. = 1) for the four combinations of TL and FL with BP and non-BP taxa. Our initial results, however, suggested that FL and TL roughly covaried with body length among taxa. Accordingly, we expected that the evolution of relative TL and relative FL was consistent with a BM model, and thus independent of BP. In addition, we hypothesized that SVL would perform well under the model for selection (HM), based partly on a nearly non-overlapping plot of maximum body lengths (derived from Pianka, 1995) for taxa arranged by BP state (Fig. 2). In taxa that were scored for BP, the mean (± 1 SE) SVL was 63.41 cm (± 2.19), mean TL was 87.68 cm (± 3.58) and mean FL was 8.63 cm (± 0.89). In taxa that do not show BP, the mean SVL was 24.01 cm (± 6.99), mean TL was 33.39 cm (± 3.59) and mean FL was 3.05 cm (± 0.38).

PHYLOGENETIC ANALYSES

BP was present in 15 of 32 ingroup taxa (*Varanus*) and absent in all ($N = 3$) outgroup taxa (Fig. 3 and

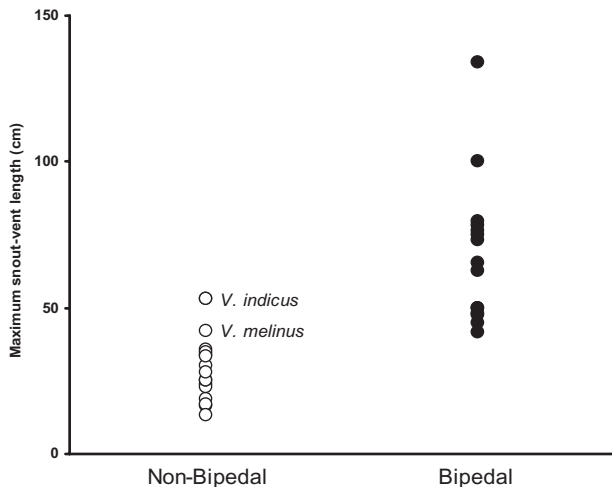


Figure 2. Maximum snout–vent lengths (SVLs) of extant species of *Varanus* (from Pianka, 1995: 405) where bipedal posture (BP) is either present or absent.

Appendix). MacClade and Mesquite produced identical topologies in the reconstruction of BP (1, present; 0, absent) in *Varanus* and required three steps (one gain, two losses) with no ambiguous character resolution; only the Mesquite analysis (tree) is presented (Fig. 3). The single gain was at the most recent common ancestor of the genus *Varanus* (African clade), and the two losses were in the Indo-Asian B clade (six of seven species) and the Indo-Australian Odatria clade (all 11 species). Using the BP and SVL trees produced in the MacClade analysis, the concentrated-changes test showed that BP was not randomly distributed in *Varanus* with respect to SVL ($P < 0.05$) and the null hypothesis was rejected; thus, the alternative hypothesis was supported, i.e. BP was statistically associated with taxa with large SVL.

EVOLUTIONARY ANALYSIS

The HM test results are summarized in Figure 4 and Tables 1 and 2. As predicted, the selection model (HM) outperformed the BM model ($P = 0.0001$) in the SVL analysis. Both AIC and SIC values corroborated this result. The calculated value of σ (strength of drift) was far greater than the α value (strength of selection), a result that is probably caused by the extreme range of SVLs among varanoids (Appendix; also see Pianka, 1995). Mean SVLs (BP present: 63.41 ± 2.19 cm; BP absent: 24.01 ± 6.99 cm) were consistent with OUCH-generated selective optima (θ) values, but θ_0 (root node value) was unrealistically low. Furthermore, θ_0 values were low in the FL analyses, but not in those for TL (see below). Butler & King (2004: 690) discussed similar results and concluded that low root node values were not problematic owing

Table 1. Performance of Brownian motion (BM, one parameter) and Hansen (HM, two parameters) models for bipedal postures (BPs) and three morphological characters using OUCH (Ornstein–Uhlenbeck for Comparative Hypotheses; see Butler & King, 2004)

	BM	HM
Snout–vent length (SVL)		
–2logL	324.1627	303.6911
AIC	328.1627	313.6911
SIC	331.2734	321.4679
LR		20.4700
<i>P</i>		0.0001
Tail length (TL)		
–2logL	291.9426	286.6758
AIC	295.9426	296.6758
SIC	299.0533	304.4525
LR		5.2700
<i>P</i>		0.1531
Femur length (FL)		
–2logL	5.715894	–4.86433
AIC	9.715894	5.13567
SIC	12.826590	12.91241
LR		10.58000
<i>P</i>		0.01420

AIC, Akaike Information Criterion; –2logL, likelihood value; LR, likelihood ratio test; SIC, Schwarz (Bayes) Information Criterion.

SVL, unadjusted; TL, residuals; FL, raw data square-root transformed before calculating residuals. FL and TL were regressed against SVL, and the residuals were adjusted to eliminate negative values. *P* values obtained from chi-squared distribution with three degrees of freedom.

to reduced dependence of the root node on the measured tip values. We calculated the contribution of tip values to the ancestral root values and found that they contributed little to θ_0 (i.e. 0.07% for SVL and 0.4% for adjusted FL residuals).

In contrast with the non-phylogenetic regression analysis, the HM analysis of FL produced a significant result ($P = 0.0142$). By using residuals in this analysis, we removed the effects of body size. The σ values were smaller than the α values, indicating that selection on FL was more important than drift or other random process. Mean FL (transformed and non-transformed) values agreed with values reconstructed by the model, supporting our confidence in the model's performance, although θ_0 was unrealistically low (see above).

For TL, the difference between BM and the selection model was not significant (Tables 1 and 2). Consistent with random processes, σ values were greater than α values for TL residuals. The mean TL of all

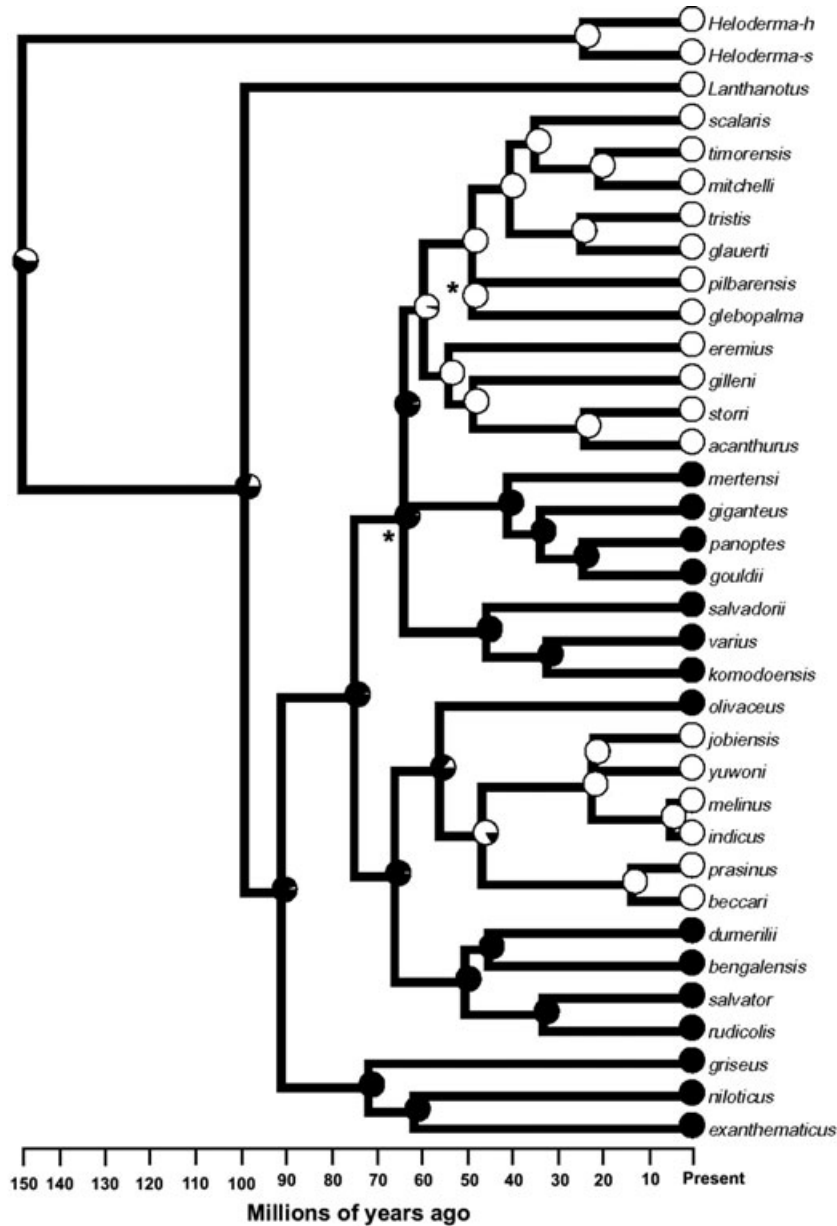


Figure 3. Maximum likelihood ancestral state reconstructions of bipedal postures (BPs) in *Varanus* and outgroups. The size of each wedge in the pie charts represents the relative likelihood of the two character states (i.e. BP present or absent) at each node (Maddison & Maddison, 2006). Character reconstructions were significant ($P < 0.05$) at all nodes based on likelihood ratio tests. The two polytomies (*) resulted from a lack of resolution of nodal dates and do not indicate uncertainty of relationships (see Ast, 2001: 219).

taxa in this study was 42.32 cm, which was consistent with θ values.

DISCUSSION

Our tests of the central tenets of the KGP hypothesis of bipedalism in varanoid lizards using comparative phylogenetic approaches provided support for its assertions that: (1) BPs are not randomly distributed

within the genus *Varanus*, and (2) large body size (i.e. SVL) is associated with the presence of BP. In addition, we evaluated two size-independent characters (relative FL and TL) related to BP. Although the analysis of residuals from regressions of SVL against FL and TL did not reveal significant patterns, examination of these characters using selection models (Hansen, 1997; Butler & King, 2004) revealed that FL, when considered independent of body size (SVL),

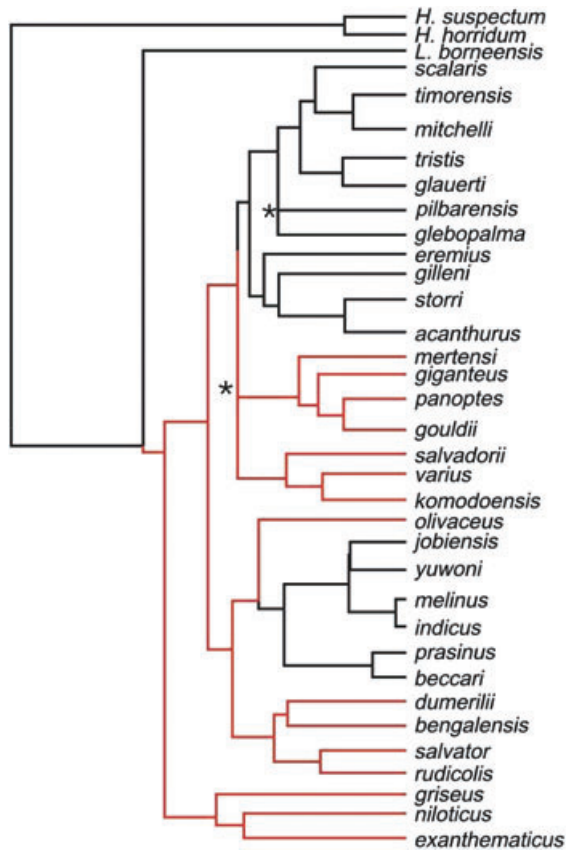


Figure 4. Tree produced from OUCH (Ornstein–Uhlenbeck for Comparative Hypotheses) analysis showing the distribution of bipedal postures (dashed branches) among varanoid taxa (see Butler & King, 2004). The tree topology was derived from Ast (2001) and Jennings & Pianka (2004); branch lengths were determined from the analysis of Jennings & Pianka (2004). As in Figure 3, the two polytomies (*) resulted from a lack of resolution of nodal dates and do not indicate uncertainty of relationships.

appears to have contributed significantly to the evolution and maintenance of BP in this group of lizards.

With the explicit integration of phylogeny to assess character reconstruction of BP in varanoids, we showed its presence in the early evolution of this group, with a single gain in the most recent common ancestor of *Varanus*. The two subsequent losses in the ingroup (i.e. reversals to the ancestral state) occurred in divergent clades (loss 1: Indo-Asian B clade; loss 2: Indo-Australian Odatria clade), but whose members, with one or two exceptions, are similar in that they tend to be small relative to other species of varanids (Appendix). The outgroup taxa used do not exhibit BP; however, male–male combat in *H. horridum* (beaded lizard), for example, often involves spectacular displays, which include body arching and rigid limb extension (Beck, 2005: 144). Similar types of

Table 2. Parameters estimated by OUCH (Ornstein–Uhlenbeck for Comparative Hypotheses) analysis

	BM	HM
Snout–vent length (SVL)		
α		7.18752200
σ	39.85455	71.11918000
θ_0	41.00008	0.06474774
$\theta_{BP \text{ absent}}$		21.75768592
$\theta_{BP \text{ present}}$		63.82725448
Tail length (TL)		
α		3.22257900
σ	25.15228	38.99391000
θ_0	32.11118	3.48376400
$\theta_{BP \text{ absent}}$		37.35110100
$\theta_{BP \text{ present}}$		46.58236800
Femur length (FL)		
α		5.58809100
σ	0.4214711	0.76914800
θ_0	1.6888140	0.01274180
$\theta_{BP \text{ absent}}$		1.62371320
$\theta_{BP \text{ present}}$		1.76847150

α , strength of selection; σ , strength of random drift; θ_k , values of optima specified by the hypothesis, where k denotes a given selective regime; θ_0 , trait value at the root node. See Table 1 and text for details of the analysis (Butler & King, 2004).

BM, Brownian motion; HM, Hansen model with presence or absence of bipedal postures (BPs) specifying two selective regimes.

posture are used by some varanids (e.g. *V. gilleni*) in which BP is not documented, such as in the Odatria clade (Carpenter *et al.*, 1976; Earley *et al.*, 2002).

The first loss of BP occurred in the Indo-Asian B clade, a group in which nearly all members are small- to medium-sized, slender and highly arboreal (Pianka, 1995: 405). Several species (e.g. *V. beccarii*, *V. prasinus*) possess long, prehensile tails capable of substantial gripping (Greene, 1986; Pianka & King, 2004). The main exception to this trend is seen in *V. olivaceus*, sister to all remaining species of the clade, which is large-bodied (maximum SVL = 730 mm; Pianka, 1995) and exhibits BP_{combat} (King & Green, 1999; Pianka & King, 2004). Although highly arboreal, adults of *V. olivaceus* spend considerable time on the ground foraging for specific fruits and small animals, such as crabs and snails (Auffenberg, 1988; Pianka & King, 2004).

The second loss of BP occurred in the Indo-Australian clade Odatria, which itself is composed of two subclades (Ast, 2001). Members of the Odatria group are commonly referred to as Australian pygmy monitors, which are the smallest members of *Varanus* (SVL range: 11.4–35.5 cm; Pianka, 1995). These taxa

occupy Australian deserts and most are terrestrial (e.g. saxicolous); several, however, show arboreal or aquatic tendencies (Pianka, 1995; Pianka & King, 2004).

Our analyses indicate that the loss of BP in these two groups is correlated with body size, but lifestyle habits probably play a role. In the Indo-Asian B clade, the various adaptations for arboreality appear to preclude a large body plan (except in *V. olivaceus*), and these adaptations might not favour (permit?) BPs. Similarly, members of the Indo-Australian clade Odatria are small and do not assume BPs. In this group, BPs would probably have little evolutionary utility as a defensive display. Rather, escape tactics (e.g. running to burrows, rock crevices, trees) and crypsis seem to have been selected in this group (Bennett, 1998; Pianka & King, 2004). Also, it is likely that BPs in these groups would not provide a significant height advantage to survey their environment. Perhaps, based on their small size, BPs would make them vulnerable to predation (e.g. birds of prey).

Our selection model (HM) revealed that SVL, FL and TL differed in their contribution to the evolution of BP in *Varanus*. Although SVL was robust in predicting the presence of BPs in non-phylogenetic analyses, FL and TL adjusted for SVL showed no correlation with BPs. Evolutionary analysis, however, recovered signal in TL data that was not evident in the analyses that excluded phylogenetic information. Our analysis of SVL suggests that random processes are as important as selection. Although the selection model for SVL performed significantly better than the BM model (indicating a shift towards either larger SVL in taxa with BP, or smaller SVL in taxa that lost BP), the strength of drift calculated by this model exceeded the strength of selection. This result does not imply that selection was not important in the evolution of body size in *Varanus*. Rather, it appears that additional factors, other than BP, had causal influence in the evolution of body size in these lizards (Pianka, 1995, 2004). We suggest that selection for BP favours an increase in body size up to a threshold of about 42 cm (based on maximum SVL values; Pianka, 1995), and beyond that size species vary in their SVL according to other selective or random factors (Fig. 2). For instance, it appears that two species (*V. indicus* and *V. melinus*) that exceed the aforementioned threshold value are not known at present to assume BP (Fig. 2). From our analyses, however, we predict that both of these species will show BP (BP_{standing} and/or BP_{combat}) when thoroughly tested.

In our evolutionary analysis of TL, we showed that BPs had no selective (directional) influence on TL in *Varanus*, perhaps because both long and short tails can be used to stabilize BP (e.g. a brace to form a tripod stance, or to steady a clinch embrace during conspecific combat). Alternatively, we favour the view that TL

might not contribute fully to our understanding of how the tail functions in BPs. Most large-bodied varanids, for example, have relatively long tails of large girth. Hence, other measurements, such as mass and circumference, should be included in future analyses.

The presence of BP in extant *Varanus* of the African clade, the sister group to the remainder of *Varanus*, suggests that it is an ancient trait. An African origin of *Varanus*, moreover, is possible based on fragmentary fossil evidence (reviewed by Molnar, 2004; Molnar & Pianka, 2004; see Smith, Bhullar & Holroyd, 2008). One of the oldest fossils assigned to the genus *Varanus* is from Rusinga Island (Kenya, Africa), and is from the early Miocene (c. 25 Mya) Hiwegi Formation (Molnar, 2004). This taxon (*V. rusingensis*) was large (~2 m in total length) and possessed a large, deep tail, suggestive of aquatic habits. Several species of large extant monitors that show BPs are highly aquatic, such as *V. mertensi*, *V. niloticus* and *V. salvator* (Pianka & King, 2004). *Varanus rusingensis* is a possible ancestor of the modern African species (Pianka & King, 2004: 91). A more recent fossil (a nearly complete posterior presacral vertebra) from Africa (simply termed YPM 57012) from an early Oligocene formation is the earliest African record of the *Varanus* stem-clade (Smith *et al.*, 2008). Although these fossils support an African origin, based on various lines of evidence, an Asian origin of *Varanus* is also supported (see Schulte, Melville & Larson, 2003), and '... the occurrence of stem *Varanus* in the early Oligocene of Africa complements the pattern of limited Paleogene Asian–African faunal exchange. . . .' (Smith *et al.*, 2008: 911; also see Amer & Kumazawa, 2008).

Many varanoid and varanoid-like fossils bear a strong resemblance to extant *Varanus* (Conrad, Rieppel & Grande, 2008), even as old as the Late Cretaceous (80 Mya) fossil *Saniwides mongoliensis* from Mongolia, which was medium-sized (≈ 1 m in total length) and had cranial features similar to modern varanids (see Jennings & Pianka, 2004; Molnar, 2004). Based on this fossil and others (e.g. *Saniwa ensidens*, the hypothesized sister to the crown-group *Varanus*; see Conrad *et al.*, 2008), it is possible that BP was present in this ancient assemblage of lizards owing to the presence of a large body size and long hind-limbs. Our analyses in the present study indicate that the prediction of BP should be possible in extinct varanids (and close ancestors) if sufficient morphological data are available.

Advanced bipedalism in Archosauria predated the origin of the dinosaurs, and some level of bipedal locomotion probably occurred in ancestral archosaurs (Hutchinson, 2006). To understand the early (incipient) stages of bipedalism, inspection of even earlier diapsids, especially those that resembled lepidosaurs,

would be fruitful. Numerous morphological and behavioural modifications contributed to erect gaits (Hutchinson & Gatesy, 2006; Hutchinson, 2006), but the earliest taxa that exhibited bipedalism probably had their origin when the sprawling gait was universal among tetrapods. Accordingly, we suspect that *Varanus* is a viable analogue of extinct forms whose descendants later became advanced bipeds.

In considering the origin of autonomous and stable erect postures in *Varanus*, we suggest that BP_{standing} evolved from BP_{combat}, which itself probably evolved by way of stereotypy of dominance contests. The few taxa known to show BP_{standing} (i.e. *V. giganteus*, *V. gouldii* and *V. panoptes*) form a small clade nested within taxa (*gouldii* group) that exhibit BP_{combat} (see Fig. 4; Ast, 2001). Although juveniles (1 m in total length) of *V. komodoensis* can rear up and show BP_{standing} to reach for a food item (J. Lemm, San Diego Zoological Society, CA, USA, pers. comm.), it has not been reported in wild-living individuals. In our analyses, the three *Varanus* species that exhibit BP_{standing} were not morphologically distinct from other species that show BP_{combat}, but future work might reveal differences in traits which influence the centre of gravity, such as hind-leg muscle mass and tail mass.

BPs of *Varanus* might also serve as a model in evolutionary studies of bipedalism and body size in terrestrial tetrapods. The bipedal gaits of humans, theropod dinosaurs, birds and running lizards are, to varying degrees, both convergent and derived conditions in these lineages (see Clemente *et al.*, 2008), and are assumed to have evolved from a simpler character state. As other researchers have demonstrated, transitional forms in evolutionary biology have repeatedly provided critical insights for interpreting character evolution, such as the origin of flight in birds (e.g. Chatterjee & Templin, 2007; Turner *et al.*, 2007). This approach has had utility in the study of bipedalism in mammals, including hominids. In extant mammals (Springer & Murphy, 2007), for example, the basal-most lineage (i.e. Monotremata) appears to be incapable of any sort of BP. However, members of the lineage Marsupialia (e.g. possums, shrews, wallabies), which is the sister group to the well-known and speciose Placentalia, exhibit various states of bipedalism for the first time, yet the bipedal gait referred to as stride (e.g. human walking) is absent. Only in placental mammals do we see the emergence of a full range of BPs and gaits, including those of humans and other apes (e.g. walking and running strides), and fossil evidence has added greatly to our understanding of the origin of bipedalism in these groups. Because BP in varanids might be an incipient stage to some form of bipedal locomotion, inclusion of this group in general theoretical analyses of the evolution of bipedalism will probably yield stimulating insights

concerning proximate determinants and ultimate causation (see Hutchinson & Gatesy, 2006; Thorpe, Holder & Crompton, 2007; Clemente *et al.*, 2008).

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APPENDIX

Morphological and behavioural data of varanoid taxa ($N = 32$), including outgroups ($N = 3$), used in the present analysis. Because species that show independent bipedal postures (BPs) also use these postures during combat, both types of BP were analysed collectively and simply termed BP. Sources of morphological information were Thompson & Withers (1997), Bennett (1998), Blob (2000) and, in several cases (*), from live specimens held in zoos or private collections. Presence or absence of BP was obtained from Earley *et al.* (2002), as well as accounts from scholarly books by Bennett (1998), King & Green (1999), Pianka & King (2004), Beck (2005), and references therein

Taxon	BP	SVL (cm)	TL (cm)	FL (cm)
Indo-Australian clade				
(Odatria group)				
<i>acanthurus</i>	0	17.86	22.61	1.98
<i>eremius</i>	0	13.94	22.90	1.58
<i>gilleni</i>	0	13.46	16.37	1.17
<i>glauerti</i>	0	19.96	36.91	2.56
<i>glebopalma</i>	0	29.79	42.81	4.38
<i>mittelli</i>	0	19.33	30.37	2.02
<i>pilbarensis</i>	0	13.74	21.51	1.80
<i>scalaris</i>	0	17.06	18.15	1.81
<i>storri</i>	0	11.45	15.12	1.27
<i>timorensis</i>	0	27.38	38.32	3.04
<i>tristis</i>	0	20.87	35.38	2.45
Indo-Australian clade				
(gouldii group)				
<i>giganteus</i>	1	44.22	46.74	6.01
<i>gouldii</i>	1	79.59	113.02	9.97
<i>mertensi</i>	1	32.06	43.50	3.76
<i>panoptes</i>	1	25.20	25.17	3.18
Indo-Australian clade				
<i>komodoensis</i>	1	136.23	136.23	17.27
<i>salvadori</i>	1	58.00	120.00	8.75
<i>varius</i>	1	75.00	117.00	9.99
Indo-Asian A clade				
<i>bengalensis</i>	1	59.22	93.92	9.59
<i>dumerilii</i>	1	56.51	80.81	8.55
<i>rudicolis</i>	1	63.25	93.29	9.29
<i>salvator</i>	1	86.85	130.27	11.26
Indo-Asian B clade				
<i>beccari</i>	0	31.00	54.20	4.35
<i>indicus</i>	0	41.10	61.65	6.03
<i>jobiensis</i>	0	18.41	30.48	1.90
<i>melinus*</i>	0	24.61	36.94	3.26
<i>olivaceus</i>	1	66.02	93.09	9.08
<i>prasinus</i>	0	29.05	67.69	4.11
<i>yuwoni*</i>	0	40.00	53.75	6.25
African clade				
<i>exanthematicus</i> † (<i>albigularis</i>)	1	50.00	50.00	7.27
<i>griseus</i>	1	38.25	46.66	4.93
<i>niloticus</i>	1	80.80	125.56	10.55
Outgroup taxa				
<i>Heloderma horridum*</i>	0	42.25	32.75	6.50
<i>Heloderma suspectum*</i>	0	34.00	14.50	3.50
<i>Lanthanotus borensis*</i>	0	14.90	15.30	1.02

FL, femur length; SVL, snout-vent length; TL, tail length.

†Owing to overall similarity in appearance, *V. albigularis* and *V. exanthematicus* have been frequently confused in the literature (Pianka & King, 2004). Accordingly, we tentatively accept that BP is present in both taxa, but report it through *V. exanthematicus*, as it, and not *V. albigularis*, appears in the Ast (2001) tree. Pianka (2004: 550) assigned *V. albigularis* and *V. exanthematicus* as sister taxa in his modification of Ast's (2001) topology.