

Body Form and Trackway Pattern in Australian Desert Monitors (Squamata: Varanidae): Comparing Zoological and Ichnological Diversity

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To what extent does ichnological diversity (the number of distinctive trace fossil morphologies) serve as a proxy for zoological diversity (species richness of trackmakers in the living fauna) in footprint assemblages made by terrestrial lower vertebrates? This question was investigated in a study of body form and trackway features of monitor lizards (varanids) from the Western Australian desert. Body-shape parameters deemed likely to affect trackway pattern of seven varanid species were measured. These lizards differ in average adult size, but there is considerable size overlap between adults of small-bodied species and juveniles of large-bodied species. Although subtle species differences in body form were detected, these were largely swamped by intra-specific variability. Furthermore, the most distinctive features in which trails of monitor species differ reflect inter-specific differences in foraging behavior rather than anatomical differences, and are features that would be difficult or impossible to recognize without actually capturing the trackmaker. These observations provide empirical support for the widely held belief that trace fossil diversity commonly under-represents zoological diversity. The degree to which this is so is likely to be influenced by trackmaker body size and metabolic physiology.

INTRODUCTION

A major component of renewed interest in vertebrate palichnology (e.g., Lockley, 1991, 1998; Lockley and Hunt, 1995; Lucas and Heckert, 1995) has been emphasis on the potential paleoecological utility of vertebrate trace fossils. One aspect of this work is the definition of vertebrate ichnofacies in which particular ichnotaxa are associated with specific sedimentary facies (Lockley et al., 1994A). A complementary approach assesses the accuracy with which vertebrate ichnotaxa can be correlated with zoological taxa (the latter of which, in the case of fossils, must be inferred from osteology; Farlow and Lockley, 1993; Farlow and Chapman, 1997).

The two approaches intersect in efforts to interpret species richness of ancient vertebrate communities in particular paleoenvironments from trace fossil data. To what extent does ichnological diversity (number of distinctive trace fossil types) reflect zoological diversity (number of

trackmaker species in the living fauna) in “lower” vertebrate faunas?

Zoological diversity, as defined here, should not be confused with osteological diversity, the number of zoological species thought to have been present in the living fauna on the basis of skeletal fossils. Although vertebrate paleontologists might hope that zoological species defined from skeletal fossils correspond to distinct species in the living fauna, this may not be so, due to systematic errors. Furthermore, taphonomic preservational biases will often cause osteological diversity to be less than zoological diversity.

Vertebrate paleoecologists gain understanding of the extent to which osteological diversity approximates zoological diversity through taphonomic studies of modern vertebrate faunas (Behrensmeyer et al., 1992). In like fashion, insight about the degree to which ichnological diversity can serve as a proxy for zoological diversity in early tetrapod paleocommunities might come from an actualistic approach, in which the variety of trace shapes of extant lower vertebrates is compared with the zoological diversity of their makers. Results of such an analysis for desert-living monitor (varanid) lizards from Western Australia are presented here. These lizards may provide the closest modern ecological analogs to Early Permian predatory pelycosaur and Early Triassic terrestrial carnivorous archosaurs; they are abundant and diverse, reach respectable body sizes, and live in environments where competition from mammalian carnivores is reduced.

Morphological features potentially relevant to footprint and trackway pattern, both within and across species, are examined. Next, features of trails made by these lizards, particularly those in which differences among species occur, are described. An evaluation is made of the extent to which species richness of the varanid fauna could be ascertained from their footprints alone. Finally, the extent to which these results can be generalized to extinct terrestrial lower vertebrates is considered.

MATERIALS AND METHODS

Varanids constitute a moderately diverse monophyletic clade of Old World tropical lizards (Greer, 1989; Cogger, 1992; Baverstock et al., 1993; King and Green, 1993; Pianka, 1995; Thompson and Withers, 1997). Australian species (colloquially known as “goannas”) range in total length from 20 cm to more than 2 m (Pianka, 1994). Some

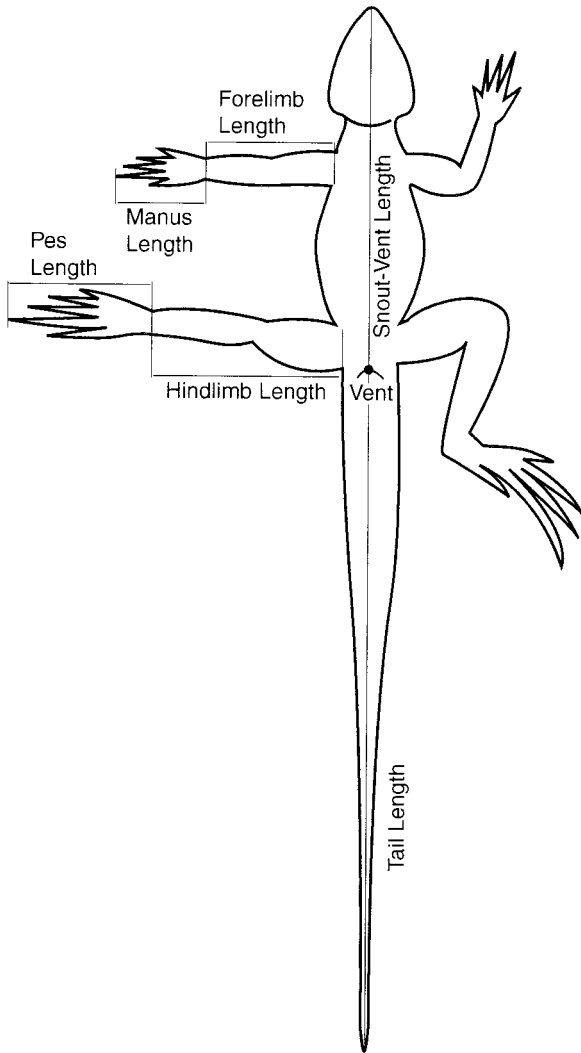


FIGURE 1—Body-size and limb-length parameters measured in this study.

species are semi-arboreal or saxicolous, and some mainly terrestrial; individuals of many species are wide-ranging, active, and seemingly intelligent animals (Pianka, 1986; King and Green, 1999).

The present study draws on data and observations made by Pianka over more than a quarter-century's worth of fieldwork in the deserts of Western Australia (Pianka, 1968, 1969, 1970a, b, 1971, 1986, 1994). Seven desert-living monitor species were studied: *Varanus brevicauda*, *V. caudolineatus*, *V. eremius*, *V. gilleni*, *V. tristis*, *V. gouldii*, and *V. giganteus*. In habits, *V. gilleni*, *V. caudolineatus*, and *V. tristis* are semi-arboreal, and *V. brevicauda*, *V. eremius*, *V. gouldii*, and *V. giganteus* are mainly terrestrial. As many as six of these species can be found at a single site.

Six body-size parameters that could be expected to affect trails made by lizards were measured (Fig.1). Snout-vent length (SVL, an overall size parameter commonly used by herpetologists) was measured from the tip of the snout to the cloacal vent. SVL is not an ideal proxy for lizard size in discussing trackways, simply because it includes the head and neck, which should not affect the way

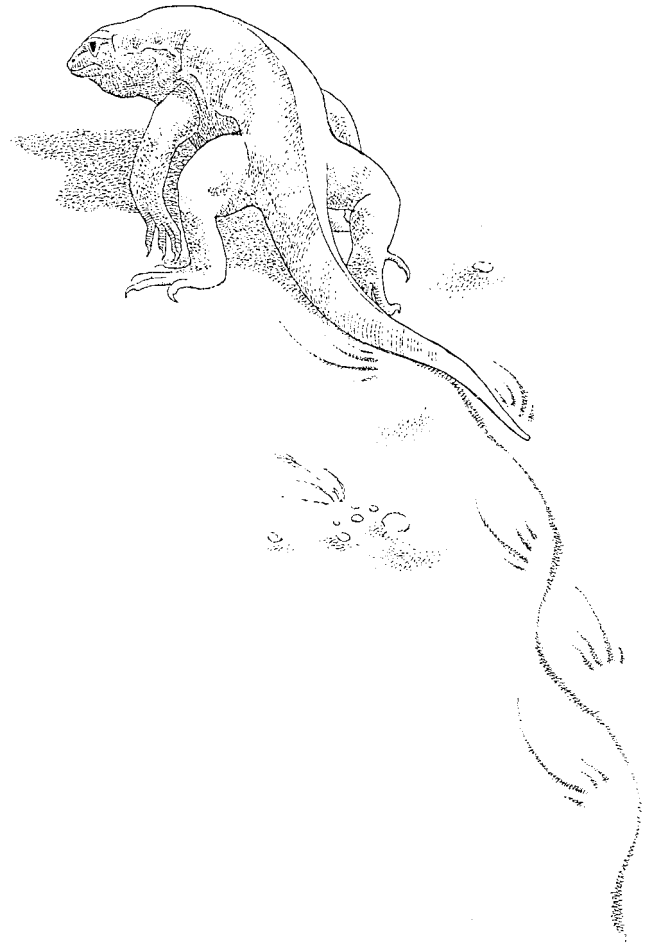


FIGURE 2—Limb carriage during locomotion in a varanid lizard (King and Green, 1999). Drawing by Frank Knight; used by permission of Dennis King and University of New South Wales Press.

the feet are placed on the ground. A better overall size parameter would be the shoulder-hip length, which was not measured. However, this parameter was measured, along with SVL, by Thompson and Withers (1997) for the same monitor species, and Thompson graciously provided us with their raw data. Using their data, shoulder-hip length

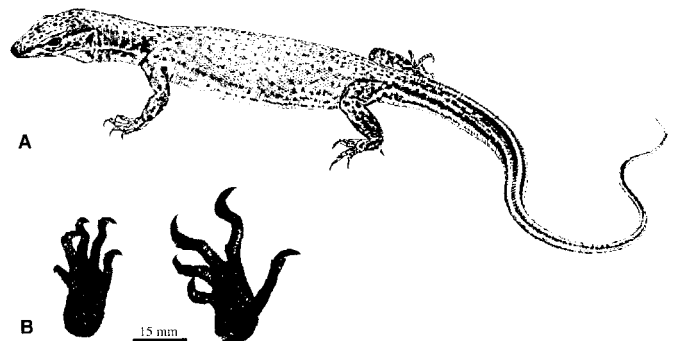


FIGURE 3—Varanid morphology. (A) *Varanus eremius*; based on a photograph by Harold Cogger. Snout-vent length of this species generally about 140–150 mm. (B) Undersides of the left manus (left) and left pes (right) of Western Australian Museum R 86451, *Varanus tristis*. Snout-vent length of this individual = 260 mm.

TABLE 1—Variability of body-size parameters among individuals of the various *Varanus* species in this study. All measurements in mm, and reported as: minimum–maximum (mean; number of specimens).

Species	Snout-Vent Length	Forelimb Length	Manus Length	Hindlimb Length	Pes Length	Tail Length
<i>V. brevicauda</i>	93–99 (95.5; 6)	7–10 (8.6; 5)	10–13 (11.5; 6)	12–15 (13.0; 5)	10–13 (11.7; 6)	75–84 (80.0; 4)
<i>V. caudolineatus</i>	72–114 (101.2; 13)	11–17 (14.0; 13)	8–14 (11.9; 13)	14–21 (18.5; 13)	12–19 (16.4; 13)	no data
<i>V. eremius</i>	59–155 (126.4; 108)	8–24.5 (17.3; 108)	8–20 (15.4; 108)	14–36 (28.0; 108)	11–29 (22.4; 108)	152–254 (211.4; 55)
<i>V. gilleni</i>	144–168 (152.3; 4)	16–18 (17.3; 3)	16–18 (16.7; 3)	22–25 (24.0; 3)	21–22 (21.3; 3)	224 (1)
<i>V. tristis</i>	173–276 (229.9; 79)	21–42 (32.5; 86)	24–33 (29.6; 86)	37–66 (51.9; 85)	32–48 (39.6; 86)	318–481 (411.0; 64)
<i>V. gouldii</i>	104–408 (265.2; 129)	14–95 (43.1; 114)	16–85 (37.4; 114)	21–161 (68.1; 114)	21–94 (46.1; 114)	115–560 (333.5; 49)
<i>V. giganteus</i>	508–890 (689.0; 10)	89–145 (107.5; 4)	60–85 (72.3; 4)	116–200 (145.5; 4)	94–130 (104.5; 4)	696–960 (832.0; 4)

was regressed against SVL for each species, and regression equations were used to estimate shoulder-hip length for each lizard in our data base. When estimated shoulder-hip length was substituted for SVL, results differed little in a principal components analysis (see below), justifying the use of SVL as a surrogate for overall lizard size.

Forelimb and hindlimb lengths (which might affect intermanus and interpedes distances, *sensu* Leonardi [1987]) were measured as straight-line distances from a lizard's body to the proximal end of its wrist or ankle, with the limb extended. Varanids do not walk with their epipodia extended straight from the body (Fig. 2), but data from

TABLE 2—Size range (snout-vent length unless otherwise indicated) in various varanid species. All measurements in mm. N = number of specimens.

Species	N	Minimum	Maximum	Size Range as % of Minimum Size	Source of Data
<i>V. brevicauda</i>	6	93	99	6	This study
	40	51	126	147	Thompson and Withers (1997)
<i>V. caudolineatus</i>	13	72	114	58	This study
	67	73	131	79	Thompson and Withers (1997)
<i>V. storri</i>	24	92	134	46	Thompson and Withers (1997)
<i>V. gilleni</i>	4	144	168	17	This study
	26	103	175	70	Thompson and Withers (1997)
<i>V. pilbarensis</i>	10	67	180	169	Thompson and Withers (1997)
<i>V. eremius</i>	108	59	155	163	This study
	54	68	185	172	Thompson and Withers (1997)
<i>V. scalaris</i>	56	72	268	272	Thompson and Withers (1997)
<i>V. acanthurus</i>	36	90	220	144	Thompson and Withers (1997)
<i>V. mitchelli</i>	23	118	253	114	Thompson and Withers (1997)
<i>V. glauerti</i>	28	90	239	166	Thompson and Withers (1997)
<i>V. tristis</i>	79	173	276	60	This study
	53	68	290	326	Thompson and Withers (1997)
<i>V. panoptes panoptes</i>	12	143	510	257	Thompson and Withers (1997)
<i>V. gouldii</i>	129	104	408	292	This study
	76	107	590	451	Thompson and Withers (1997)
<i>V. glebopalma</i>	31	152	397	161	Thompson and Withers (1997)
<i>V. rosenbergi</i>	38	150	422	181	Thompson and Withers (1997)
<i>V. mertensi</i>	26	150	460	207	Thompson and Withers (1997)
<i>V. panoptes rubidus</i>	17	141	535	279	Thompson and Withers (1997)
<i>V. bengalensis</i>		98 ^a	610 ^b	522	Auffenberg (1994)
<i>V. grayi</i>	102	160	730	356	Auffenberg (1988)
<i>V. giganteus</i>	10	508	890	75	This study
	25	159	660	315	Thompson and Withers (1997)
<i>V. komodoensis</i>		253 ^c	2520 ^d	896	Auffenberg (1981)

^a The smallest individual from a sample of 42 hatchlings.

^b The biggest individual from a large sample (N not explicitly stated).

^c Total length of the smallest of 37 hatchlings.

^d Total length of the largest of 50 individuals.

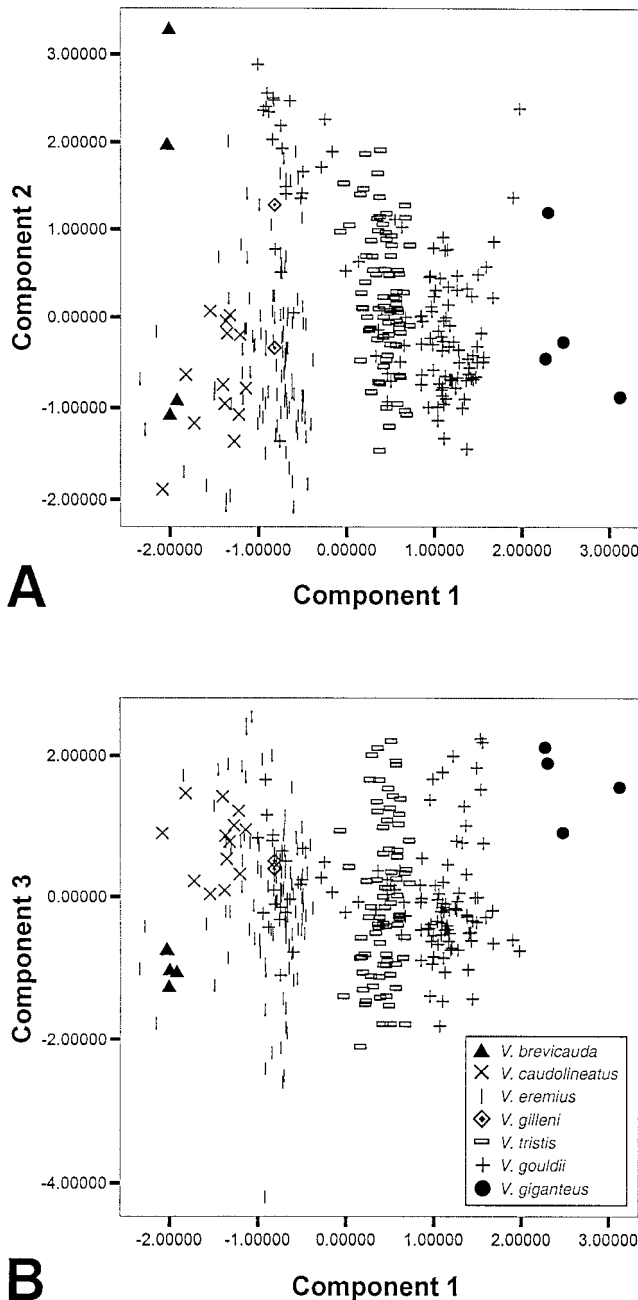


FIGURE 4—Principal components analysis of log-transformed values of snout-vent length and limb length parameters (Table 3) among seven species of Australian varanids. Component 1 is strongly related to overall body size. Component 2 contrasts lizards with relatively long autopodia (positive values) against those that have relatively long limbs excluding autopodia (negative values). Component 3 contrasts lizards that have a relatively long forelimb and foot (positive values) with those that have a relatively long hindlimb and manus (negative values). (A) Plotting component 2 against component 1 produces little separation of species apart from size. Separation along component 2 is more a matter of variation among individual lizards within species than differences among species. (B) Plotting component 3 against component 1 separates *V. brevicauda* (a species with a relatively short pes) from *V. giganteus* (a form with a relatively long pes) and *V. caudolineatus* (a long-forelimbed species). However, *V. eremius*, *V. tristis*, and *V. gouldii* overlap considerably with all other species along component 3.

TABLE 3—Principal components analysis (PCA) based on a covariance matrix of body proportion variables for the seven varanid species in this study. Data were log-transformed prior to the analysis.

Variable	Component 1 Loading	Component 2 Loading	Component 3 Loading
Snout-Vent Length	0.989	-0.008	-0.013
Forelimb Length	0.985	-0.129	0.106
Manus Length	0.983	0.156	-0.048
Hindlimb Length	0.987	-0.075	-0.131
Pes Length	0.981	0.126	0.113
Cumulative variance explained	97.040	98.293	99.229
Component Eigenvalues: Component 1 = 0.215; component 2 = 0.00277; component 3 = 0.00207			
Kaiser-Meyer-Olkin Measure of Sampling Adequacy = 0.872			
Bartlett's Test of Sphericity: chi-square = 3858.453, $p < 0.001$			

Thompson and Withers (1997) showed little difference across species in upper/lower arm and leg proportions, indicating that straight-line limb lengths are suitable for the present analysis. Manus (hand, forefoot) and pes (foot, hindfoot) lengths (which could affect manus-pes dimensional heteropody, *sensu* Leonardi [1987]) were measured from the proximal end of the wrist or ankle to the extended tip of the longest toe. Tail length was measured from the cloacal vent to the tip of the tail.

All monitors have a pentadactyl manus and pes (Houston, 1978; King and Green, 1993; Withers and O'Shea, 1993). In the manus, digit lengths increase from I through III and IV, which are often subequal in length (Fig. 3); V is shorter than IV, and the hypex between digits IV and V is proximally deep. The pes is similar, except that digit IV often extends well beyond the end of III.

Data were log-transformed before analysis. Limb-length parameters were analyzed together; tail length was treated separately due to a smaller sample size (Table 1).

Varanid species examined for this study vary greatly in adult body size (Table 1), but juveniles of large-bodied species overlap in size with adults of small-bodied species. Consequently, body proportions had to be considered when comparing morphological parameters among species, as well as absolute size.

Lizard body form was therefore analyzed in three ways. In the first analysis, log-transformed data for all lizards were subjected to principal components analysis (PCA) using a covariance matrix, and effects of lizard size on measurements removed as the first component.

In the second analysis, effects of size were factored out by comparing the body form of each lizard with that of an "average" varanid of the same SVL. For each of the seven species, log-transformed values of SVL, forelimb length, manus length, hindlimb length, and pes length were averaged for adult individuals (using SVL criteria of minimum adult size from Thompson and Withers [1997; table 3]). Thus, a set of mean log-transformed values of each parameter was generated for adults of each species. Each of the four log-transformed limb-length parameters was then regressed against log SVL, using mean values for each species as data, to create equations describing an average varanid. Reduced major axis equation slopes also were calculated for comparison with regression-line slopes. For each individual lizard (including juveniles), the

TABLE 4—Regression and reduced major axis equations for interspecific and intraspecific relationships (see Table 1 for the number of specimens of each species) between limb-length variables and snout-vent length in varanids; intraspecific equations for *V. brevicauda* and *V. giganteus* not included due to small sample sizes and/or too small a size range of individual lizards. SVL is the independent variable in all cases. Data were log-transformed prior to analysis. All equations are statistically significant (F test; $p < 0.05$), but the slope does not show statistically significant differences from 1 (positive or negative allometry) in all cases.

Group Treatment	Dependent Variable	Regression Slope (95% C.I.)	Regression Intercept	r ²	RMA Slope (95% C.I.) ¹
"Average" varanid	Forelimb Length	1.290* (1.054–1.527)	–1.538	0.975	1.306 (0.900–1.895)
	Manus Length	1.047 (0.929–1.166)	–1.025	0.990	1.052 (0.833–1.328)
	Hindlimb Length	1.279* (1.002–1.556)	–1.342	0.966	1.301 (0.839–2.018)
	Pes Length	1.125 (0.935–1.314)	–1.091	0.979	1.137 (0.810–1.596)
<i>V. caudolineatus</i>	Forelimb Length	0.886 (0.585–1.186)	–0.630	0.793	0.995 (0.491–2.016)
	Manus Length	1.085 (0.790–1.380)	–1.100	0.856	1.173 (0.671–2.050)
	Hindlimb Length	0.933 (0.648–1.217)	–0.604	0.826	1.026 (0.546–1.927)
	Pes Length	0.911 (0.692–1.130)	–0.613	0.884	0.969 (0.594–1.581)
<i>V. eremius</i>	Forelimb Length	0.866** (0.767–0.965)	–0.582	0.739	1.007 (0.799–1.269)
	Manus Length	0.863*** (0.784–0.942)	–0.626	0.814	0.956 (0.794–1.151)
	Hindlimb Length	1.025 (0.930–1.121)	–0.710	0.811	1.139 (0.945–1.373)
	Pes Length	0.828** (0.724–0.931)	–0.389	0.702	0.988 (0.767–1.272)
<i>V. tristis</i>	Forelimb Length	0.900 (0.602–1.197)	–0.619	0.321	1.589 (0.800–3.154)
	Manus Length	0.595*** (0.455–0.735)	0.0647	0.482	0.857 (0.531–1.384)
	Hindlimb Length	0.695* (0.440–0.950)	0.0722	0.279	1.316 (0.605–2.862)
	Pes Length	0.716** (0.526–0.906)	–0.101	0.422	1.101 (0.640–1.895)
<i>V. gouldii</i>	Forelimb Length	1.165*** (1.127–1.203)	–1.189	0.972	1.181 (1.107–1.260)
	Manus Length	0.821*** (0.782–0.859)	–0.413	0.942	0.845 (0.769–0.929)
	Hindlimb Length	1.143*** (1.105–1.182)	–0.939	0.969	1.161 (1.085–1.242)
	Pes Length	0.745*** (0.707–0.782)	–0.136	0.933	0.771 (0.696–0.854)

¹ Calculated as per Leduc (1987).

* Significantly different from 1 at $p < 0.05$.

** Significantly different from 1 at $p < 0.01$.

*** Significantly different from 1 at $p < 0.001$.

expected value of a limb-length parameter for an average varanid of the same size was calculated from the appropriate regression line, based on the lizard's SVL, and this expected value was subtracted from the actual value of that lizard's limb-length parameter. This deviation from predicted values was then expressed as a percentage of the predicted value. Positive values indicate that the lizard had a limb-length parameter larger than expected for an average monitor of the same size, and negative values a smaller than expected value. This procedure allowed consideration of whether legs, hands, and feet of particular varanid species were relatively long or short, as compared with a generalized varanid.

Finally, in the third analysis, variables were compared using simple bivariate plots of data for individual lizards, without trying to correct for size relative to an average varanid.

RESULTS

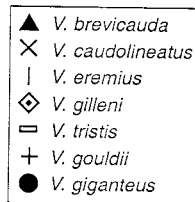
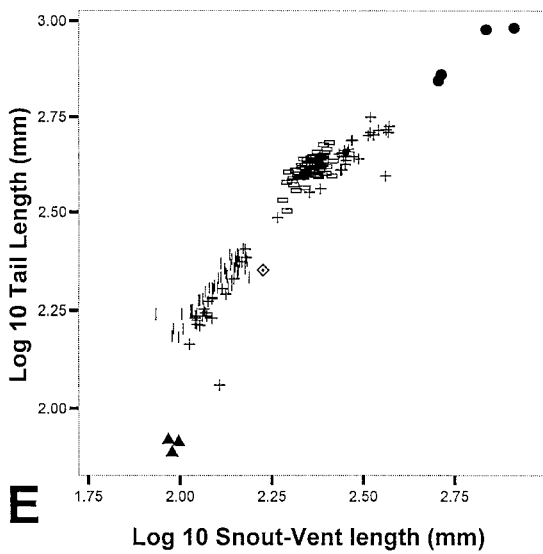
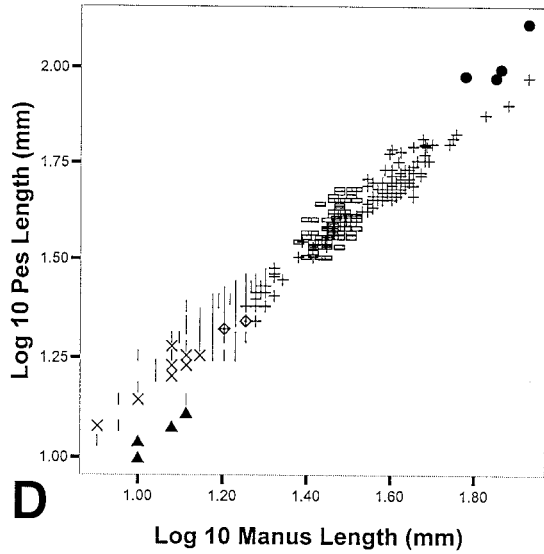
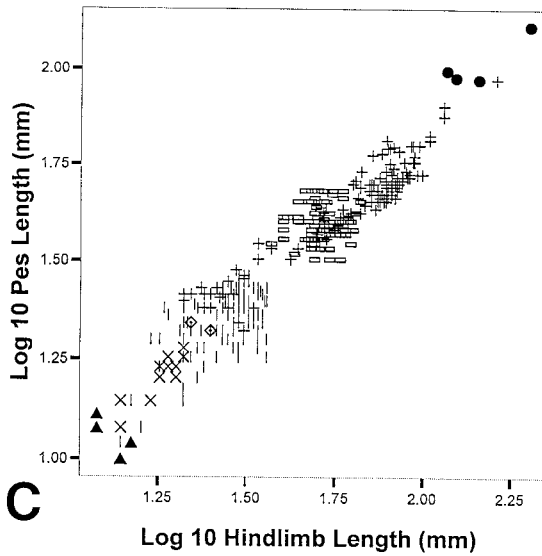
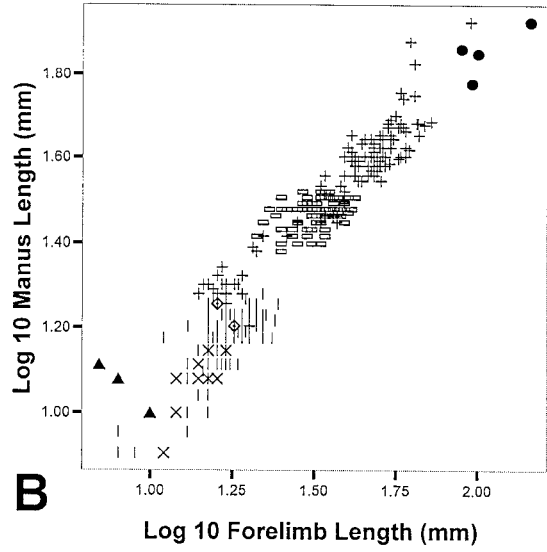
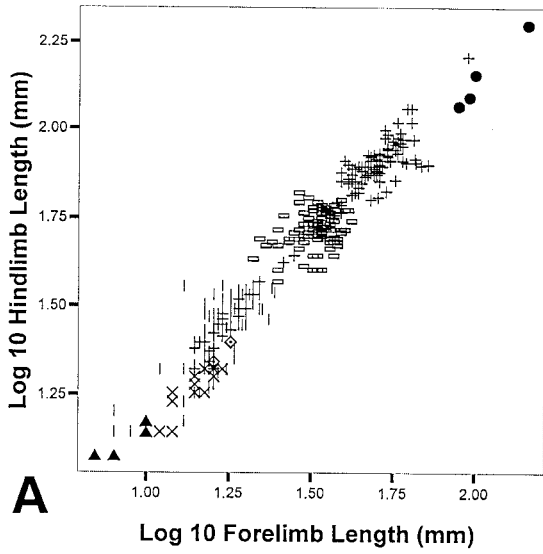
Size and Shape Within and Across Varanid Species

Even though varanid species in this study span a considerable size range (Table 1), nevertheless the species overlap in the various size parameters. Sample sizes are not very large for some species, and/or data for juveniles are lacking. If data from another study of varanid body form (Thompson and Withers, 1997), with more young lizards, are considered, size overlap across the seven species is even greater than in the present data set (Table 2).

Among monitors, species with large-bodied adults span a greater size range than do species with small-bodied adults (Table 2). Consequently, if those body proportions relevant to trackway pattern are similar enough across species, trails made by young individuals of large-bodied varanid species might be confused with trackways made by adults of small-bodied species, unless trail patterns differed among species in features unrelated to lizard morphology.

PCA of the four limb-length variables (Table 3) indicates that 97% of the variance is accounted for by body size alone (component 1). Component 2 contrasts lizards that have relatively long autopodia (positive values) with lizards whose forelimbs and hindlimbs (excluding autopodia) are relatively long compared with their hands and feet. Plotting component 2 against component 1 (Fig. 4A) shows considerable overlap among species in component 2; variation within varanid species in component 2 is as great as across species. Component 3 produces some separation of species (Fig. 4B), but this component accounts for an underwhelming less than 1% of variance in the data. To a first approximation, a goanna is a goanna is a goanna, consistent with the common belief that varanids are a morphologically conservative group (Shine, 1986; Greer, 1989; Pianka, 1995; Thompson and Withers, 1997).

As reported by previous workers (Christian and Garland, 1996; Thompson and Withers, 1997), limb-length parameters show positive allometry with SVL across species (Table 4: average varanid equations), although regression



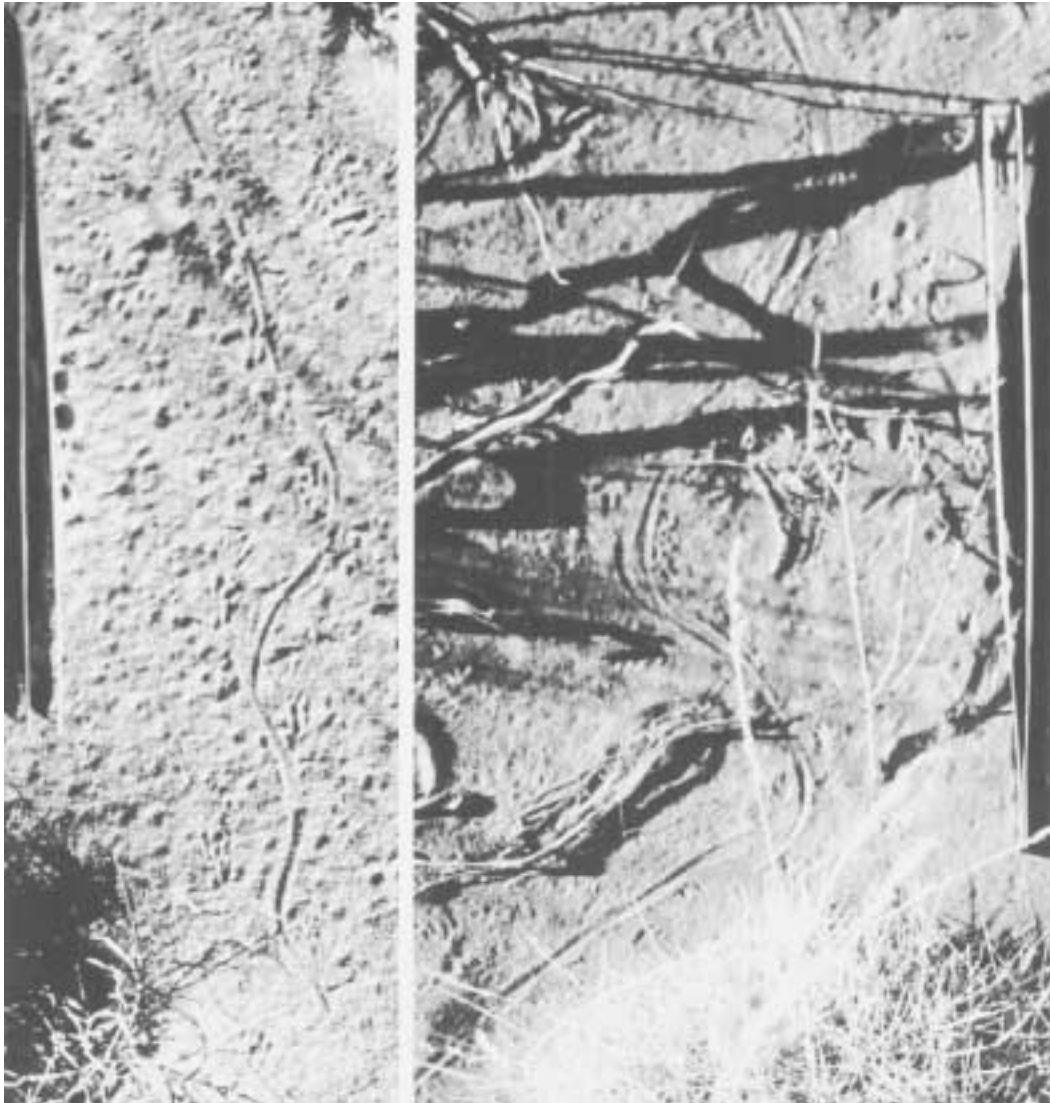


FIGURE 6—Trackways of *Varanus eremius*. Large forceps are c. 50 cm long. Photographs taken at the Red Sands study site on the Yamarna pastoral lease in the Great Victoria Desert at latitude 28° 12' S by longitude 123° 35' E, during January or February of 1996.

slopes in equations for the autopodia do not differ significantly from 1. This is probably due to the smaller number of species examined here. However, positive allometry does not necessarily apply intraspecifically. *Varanus gouldii*, for example, shows a clear tendency to reduce the relative size of autopodia with increasing SVL (Table 4). The same may be true for some other varanid species, but the trend is not as clear as for *V. gouldii*; regression and RMA slopes do not consistently show negative allometry, possibly due to small sample sizes and/or too small a size range of specimens of those species.

Compared with an average varanid, *V. brevicauda*, *V. gilleni*, and *V. giganteus* have relatively short forelimbs

and hindlimbs, while *V. caudolineatus*, *V. eremius* and *V. gouldii* are relatively long-limbed; *V. tristis* is intermediate in this regard (Table 5). Lizards with long forelimbs tend to have long hindlimbs, although some individuals of *V. tristis* and *V. eremius* have relatively short forelimbs compared with their hindlimbs, and *V. giganteus* and *V. caudolineatus* have relatively long forelimbs. The same pattern can be seen in a simple plot of hindlimb length against forelimb length (Fig. 5A). However, species overlap considerably in both comparisons.

Deviations of manus length and forelimb length from an average varanid do not vary together (Table 5); long-forelimbed forms are not necessarily long-handed. Again,

←

FIGURE 5—Bivariate plots of log-transformed morphometric parameters. (A) Hindlimb length (excluding pes) against forelimb length (excluding manus). (B) Manus length against forelimb length (excluding manus). (C) Pes length against hindlimb length (excluding pes). (D) Pes length against manus length. (E) Tail length against snout-vent length.

TABLE 5—Comparison of observed limb parameters with values predicted from “mean” varanid regression equations (Table 4) for lizards of a given snout-vent length. Deviations from predicted lengths (in mm) are expressed as percentages of the predicted length (in mm). Negative values indicate observed lengths less than predicted for a “mean” varanid, and positive values indicate greater lengths than predicted. See Table 1 for the number of specimens of each species.

Species	Parameter	Minimum	Maximum	Mean (Median)
<i>V. brevicauda</i>	Forelimb Length	-35.6	-1.7	-17.1 (-20.2)
	Manus Length	-11.9	12.1	1.9 (8.0)
	Hindlimb Length	-26.1	-5.2	-16.2 (-19.9)
	Pes Length	-25.7	-8.8	-15.4 (-11.8)
<i>V. caudolineatus</i>	Forelimb Length	15.1	52.6	25.7 (22.7)
	Manus Length	-10.7	8.1	0.3 (2.3)
	Hindlimb Length	-0.8	29.6	11.0 (9.5)
	Pes Length	1.7	20.4	12.4 (12.1)
<i>V. eremius</i>	Forelimb Length	-13.3	65.3	17.7 (16.4)
	Manus Length	-14.7	35.0	3.5 (2.2)
	Hindlimb Length	-9.4	67.2	26.7 (26.8)
	Pes Length	-10.8	54.3	20.6 (20.2)
<i>V. gilleni</i>	Forelimb Length	-25.6	-1.5	-9.8 (-2.3)
	Manus Length	-10.8	-9.5	-10.1 (-10.1)
	Hindlimb Length	-31.1	-7.9	-15.9 (-8.7)
	Pes Length	-14.9	-6.3	-9.4 (-7.0)
<i>V. tristis</i>	Forelimb Length	-30.6	20.5	0.2 (2.1)
	Manus Length	-14.0	25.1	5.5 (5.6)
	Hindlimb Length	-22.7	40.0	9.6 (9.7)
	Pes Length	-8.9	38.4	6.3 (5.7)
<i>V. gouldii</i>	Forelimb Length	-14.6	45.1	12.7 (12.4)
	Manus Length	-6.4	52.5	18.8 (14.8)
	Hindlimb Length	-9.9	50.9	20.5 (19.9)
	Pes Length	-13.0	62.4	13.2 (8.3)
<i>V. giganteus</i>	Forelimb Length	-12.8	4.7	-4.0 (-3.9)
	Manus Length	-19.9	13.6	-4.8 (-6.5)
	Hindlimb Length	-17.5	-8.5	-11.8 (-10.5)
	Pes Length	-15.5	10.3	-3.0 (-3.4)

overlap among species is considerable, although *V. brevicauda*, *V. tristis*, and some individuals of *V. gouldii* seem rather long-handed for their forelimb lengths, while *V. caudolineatus* and *V. eremius* look short-handed. A simple bivariate plot (Fig. 5B) shows the same tendencies.

Deviations of pes length and hindlimb length from an average varanid, unlike their counterparts in the forelimb, consistently vary in the same direction and magnitude (Table 5). *Varanus gilleni*, *V. brevicauda*, and *V. giganteus* tend to have relatively shorter hindlimbs and feet than the other monitors, but once again species broadly overlap. A simple bivariate plot shows little separation of species (Fig. 5C) on the basis of pes length relative to hindlimb length.

TABLE 6—Number of species of different lizard families found sympatrically at study sites in the desert of Western Australia. Data updated from Pianka (1986, 1994).

Family	Number of Species Found Together at Particular Sites	Total Number of Species in the Regional Fauna
Agamidae	2-8	11
Gekkonidae	5-11	14
Pygopodidae	1-4	4
Scincidae	6-19	30
Varanidae	1-6	7

Long-handed varanids also tend to have long feet (Table 5); *Varanus eremius*, *V. caudolineatus*, *V. tristis*, and *V. gouldii* tend to have long autopodia; *V. gilleni*, *V. brevicauda*, and *V. giganteus* have relatively short hands and feet. *Varanus brevicauda* has relatively long hands compared with its feet, while *V. giganteus* is long-footed (Fig. 5D). Yet again, however, overlap among species is considerable.

Because monitor lizards regularly lose distal portions of their tails due to the exigencies of life, tail length must be evaluated with caution. However, *V. brevicauda* lives up to its name (“short tail”), while *V. tristis* and *V. eremius* are relatively long-tailed species (Fig. 5E).

In summary, these data indicate that differences in body proportions exist that might affect trackway pattern across varanid species. However, differences are subtle and variable within species, making it doubtful that one could reliably discriminate among most trackmaker species in such features as trackway width (relative to footprint size), widths across forefoot impressions relative to widths across hindfoot impressions, manus-pes heteropody, and manus-pes distance. Trackway parameters should vary in absolute size across species, but with considerable overlap among species.

The preceding predictions are based on analysis of monitor body size and shape. The possibility remains that varanid trails might differ across species in features not readily extrapolated from lizard body proportions.

Varanid Trackway Patterns

Trails of some varanid species are regularly encountered in the field. Trackways of *V. eremius* are among the varanid spoor most commonly seen (Pianka, 1968). This little monitor (adult SVL about 140–150 mm) moves considerable distances while foraging; Pianka has followed individuals for up to half a mile. Lizards of this species appear to hunt visually—when foraging, they do not move their heads from side to side, and they drag their tail straight behind them. These lizards have little tendency to remain in a circumscribed area. They show particular interest in holes and diggings, but they seldom dig much themselves. They frequently change direction while on the move, often leaving looped tail patterns in the sand (Fig. 6), and even reversing direction of travel. The pes print is placed immediately behind the manus print in a manus-pes set.

Varanus tristis is larger (SVL about 250–260 mm) than *V. eremius*. Trails of *V. tristis* move fairly directly from one tree to another, and a lizard may travel as much as a mile in a day (Pianka, 1971). While on the ground the tail presses deeply into the substrate, creating a conspicuous, broad, sine-wave-shaped dragmark of low amplitude that is the most distinctive and visible feature of the trackway (Fig. 7). Tail dragging could be a means of leaving a scent trail (Thompson and Pianka, 1999; Thompson et al., 1999). Pes prints are sometimes superimposed on the rear margin of manus prints.

Varanus gilleni (like *V. tristis* a semi-arboreal species) is a rare species that makes a trackway very similar to that of *V. tristis*. However, *V. gilleni* is smaller (SVL about 150–160 mm) than *V. tristis*, comparable in size to *V. eremius*. It would be difficult or impossible to distinguish the trail of a small *V. tristis* from that of a large *V. gilleni*.

Varanus gouldii also ranges widely; Pianka (1970b) followed one individual for over a mile. When foraging, these large (SVL about 400 mm) monitors hold their bodies well up off the ground, and swing their heads widely from side to side while flicking their long, forked tongues over the substrate. Most prey are located using olfaction. *Varanus gouldii* bend their bodies and tails from side to side while walking. The tail is usually carried off the ground, but occasionally the tip of the tail makes a lashmark nearly at a right angle to the trackway. Individual footprints are usually very difficult to see. These lizards often abruptly change their direction of travel, and so trails of this species are seldom straight. During the course of their wide-ranging daily movements, *V. gouldii* often pass through several different habitats. These monitors often stop to dig for prey, making kidney-shaped holes with their stout forelegs.

The largest (SVL 500–900 mm) Australian varanid, *V. giganteus*, is another tail-dragger (Fig. 8), but the dragmark is relatively much narrower than that of *V. tristis*. Sinuosity of the tail mark is variable, but the amplitude is often greater than in *V. tristis*; furthermore, the dragmark is often discontinuous. The pes comes down right behind manus impressions of the same side, or even on top of their rear margins. Curved, concave-inward (toward the trail midline) drag marks may be created as the autopodium is lifted off the ground during protraction. Like *V. gouldii*, *V.*

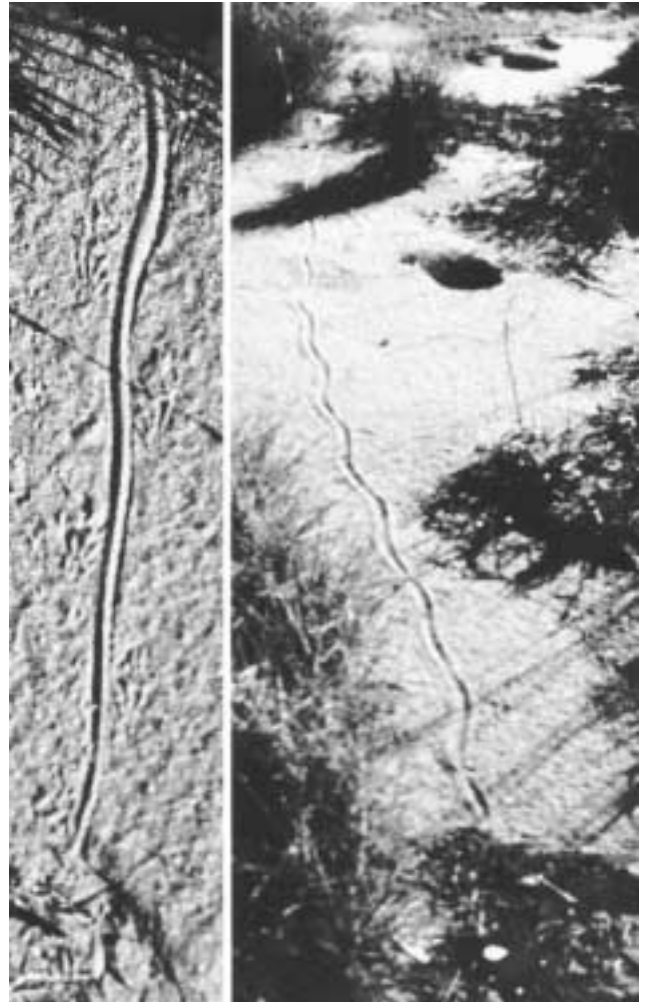


FIGURE 7—Trackways of *Varanus tristis*, Red Sands study site, Yamarna pastoral lease, Great Victoria Desert, January or February 1996.

giganteus locomote with their bodies well up off the ground.

Trackways of these varanid species can usually be distinguished by size and the distinctive features described above. However, on occasion all these species can walk in a similar fashion. Thus, *V. eremius*, *V. tristis*, and *V. gouldii* will all sometimes make short *V. giganteus*-like trails. Occasionally *V. giganteus* and even *V. tristis* will walk holding their tails up off the ground in a *V. gouldii*-like manner. Sometimes one must follow a goanna trail for some distance before the diagnostic trackway features of the species are seen.

Varanus caudolineatus and *V. brevicauda*, the two smallest varanids in this study, are found at only a few sites, and have not been observed to leave recognizable trackways during Pianka's fieldwork.

DISCUSSION

No matter how morphometric data were analyzed, results were the same. Differences among varanid species in relative limb, hand, and foot lengths are subtle, and often

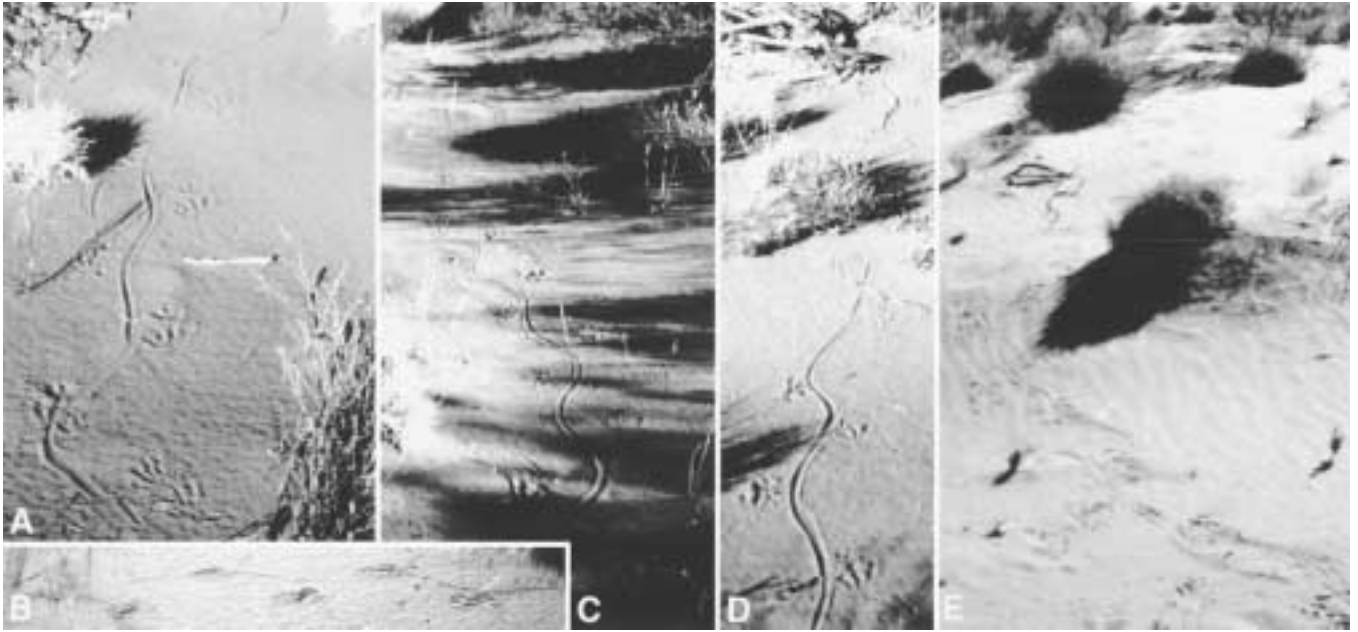


FIGURE 8—Trackways of *Varanus giganteus*. All photographs taken at the Red Sands study site, Yamarna pastoral lease, Great Victoria Desert; photographs (A), (B), and (D) were taken in January or February 1996, (C) in February 1979, and (E) in December 1990. (A) and (D) are different portions of a trail made by the same individual lizard.

swamped by intraspecific variability. Because these morphological parameters could be thought to affect trackway patterns, goanna trails are expected to be very similar in features related to body proportions.

As best can be ascertained from Pianka's photographs (which were not made with ichnological research in mind), these predictions are met. In those Western Australian species whose trackways have been observed, there are no obvious differences in manus-pes heteropody, position of the manus and pes prints in a manus-pes set, or trackway width across forefoot as opposed to hindfoot impressions. However, trackways of the Australian monitors do differ in one obvious feature from the trail of the much larger *V. komodoensis* illustrated by Padian and Olsen (1984). In the Komodo monitor, manus impressions are conspicuously closer to the trackway midline than pes impressions (Fig. 9), while in the Australian varanids the centers of forefoot and hindfoot prints seem to be about the same distance from the midline.

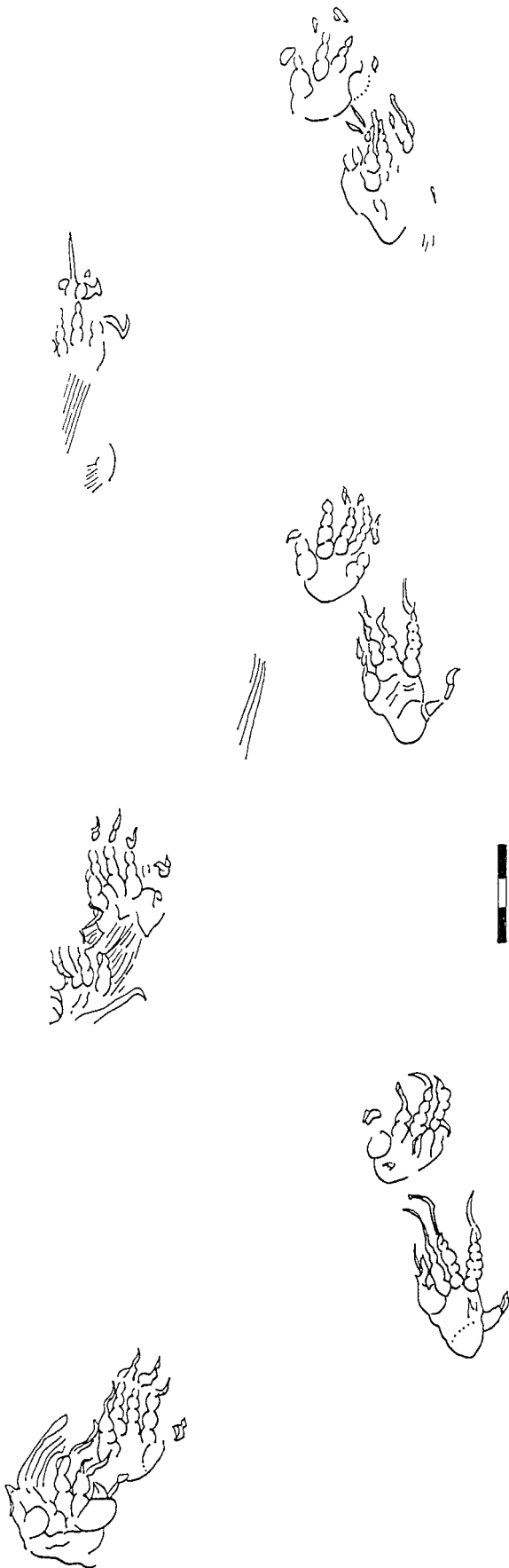
Observed differences in trackways among Australian varanids are in features that are not readily interpretable in terms of trackmaker morphology. Features in which observed varanid trackways differ across species seem to be related more to differences in foraging behavior than to lizard morphology.

Had the various trackway patterns described above been observed without knowledge of their makers (which Pianka gained only by tracking down and capturing lizards), the number of monitor species responsible for them probably could not have predicted *a priori*. A guess could have been made that the maker of the *V. tristis* trail pattern, with its conspicuous tail dragmark, was a different species than most of the others, but the maker of the *V. tristis* pattern might have been regarded as the adult of a species whose juveniles were responsible for *V. gilleni* trackways.

Similarly, some trackway segments of *V. eremius*, *V. gouldii*, and *V. giganteus* might have been interpreted as reflecting ontogenetic size differences, and intraspecific differences in behavior, instead of indicating different species of trackmaker.

Late Paleozoic and early Mesozoic tetrapods were not varanids, but results of the present study may nonetheless have implications for interpreting the extent to which trace fossil diversity can serve as a proxy for trackmaker species richness in reconstructing terrestrial paleocommunities. Tetrapod vertebrate ichnotaxa are often diagnosed on the basis of features related to body form of the trackmakers, such as trackway gauge, manus-pes heteropody, relative breadth of prints, number of digits in hand and foot impressions, relative digit lengths, angles between toemarks, print rotation with respect to the midline, and the way manus and pes prints are positioned in sets on the same side of the trackway (e.g., Peabody, 1948; Demathieu, 1970; Gand, 1987; Lockley et al., 1994b; Haubold et al., 1995). Varanids examined in the present study do not seem to vary much in these trackway features or their anatomical correlates, a result consistent with conclusions like those of Haubold et al. (1995, p. 136) about far older trackmakers: "Taxonomic diversity appears less in the ichnological record than in the osteological record because foot morphology is not diagnostic at a low taxonomic level among Permian tetrapods." Thus ichnological diversity may commonly underestimate diversity of zoological species responsible for trackways.

On the other hand, Australian desert varanids do differ considerably in adult size, which might justify using absolute footprint size as a criterion in defining ichnospecies (see studies cited above). Of course, this runs the risk that different names might be assigned to trace fossils made by juveniles and adults of the same species. Differences in size in otherwise similar footprints will often reflect spe-



cies differences, but this will not necessarily be so—as in varanids (Table 2), young individuals of large-bodied species can be expected to overlap the size of adults of smaller-bodied species. Given limits to how large a “workable” egg can be, the ontogenetic size range of oviparous vertebrates would be expected to increase with increasing adult size.

Ichnologists are clearly aware of this danger. “Other characters being equal, it is safe to assume that the local population of any one species consisted of individuals of different stages of growth. The alternative assumption that each trackway represents a different species is unnecessary and unwarranted” (Peabody, 1948, p. 355). Indeed, Haubold et al. (1995) considered just this kind of possibility when they speculated that the small pelycosaur trace fossil *Gilmoreichnus* might have been made by juveniles of the same species whose adults were responsible for *Dimetropus*.

Some ichnologists (e.g., Sarjeant and Kennedy, 1973; Sarjeant, 1975, 1990) have argued that trail features related to trackmaker behavior should be considered valid criteria (along with characters that reflect trackmaker morphology) upon which to base ichnotaxa, as is commonly done with invertebrate trace fossils. Species-level differences in trackways reflecting different foraging styles very likely existed in ancient terrestrial lower vertebrates. Unfortunately, there is no independent way of establishing that this was so. Consequently, using features like those that distinguish trails of *V. tristis*, *V. eremius*, *V. gouldii* and *V. giganteus* as the bases for recognizing different tetrapod ichnotaxa runs the risk of over-estimating trackmaker diversity, should species with non-stereotyped, plastic foraging behaviors actually have existed.

The most conservative approach to naming lower tetrapod ichnotaxa would be to use only features related to trackmaker foot and body form in defining ichnotaxa, and to disregard absolute size and features related to trackmaker behavior as diagnostic criteria (cf. Farlow and Chapman, 1997). If ichnologists took this cautious approach, the number of ichnospecies would likely be far fewer than the number of zoological species responsible for those trace fossils, as would be the case were this stringent stance applied to interpreting varanid trackways; the five species whose trails are known would be represented by two or three ichnotaxa, presumably ichnospecies.

On the other hand, results of the present study suggest that, if trackways of lower vertebrates that are identical in features related to trackmaker body form consistently differ in absolute size and also in features related to behavior, then it is likely—but not certain—that those trackways were made by different zoological species. With this more “relaxed” approach, the five varanid species whose trackways are known might each be represented by its own ichnotaxon—but remember that the various monitor species do sometimes make misleading trackway patterns similar to those of other goanna species.

However, even with this less stringent approach, lower vertebrate ichnological diversity probably will still com-

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FIGURE 9—Trackway of *Varanus komodoensis*. Scale bar divisions = 5 cm. Redrawn from Padian and Olsen (1984).

monly underestimate zoological diversity if more than a single guild of large-bodied species is considered. Most Permian and Triassic tetrapods were probably ectotherms (cf. Hillenius, 1994; Ruben et al., 1997), and ectothermy has profound consequences for vertebrate ecology (Pough, 1980). Small-bodied ectotherms have low resource requirements, and consequently can have small home ranges (Peters, 1983), and live in small microhabitats. They are often less vagile than larger animals and those with higher metabolic rates (cf. Schult and Farlow, 1992). On a landscape basis, small ectothermic tetrapods may be patchily distributed, their population densities can be quite variable (cf. Brown, 1995), and the number of species of small body size in any particular habitat can be fairly large.

Ectothermic tetrapods the size of small lizards may be diverse in many habitats, but unless sedimentary environments suitable for formation and preservation of trace fossils sample all microhabitats in a given region, many of these small vertebrates are likely never to be represented in the ichnological record. In this context, recall that Pianka found no trails of the two smallest varanid species (including *V. brevicauda*, one of the morphologically more distinctive species), known to occur at his study sites. Furthermore, small tetrapods often may not be heavy enough to leave recognizable footprints (Sarjeant, 1990).

For organisms in general, small to medium-body-sized taxa within a clade tend to be more diverse than large-bodied taxa (Dial and Marzluff, 1988). This can be seen clearly in Western Australian desert lizards (Table 6); varanids are represented by fewer species than most other families of lizards (which are smaller animals than monitors), both at particular sites and in the regional fauna.

Thus, trackways of small-bodied ectotherms that are preserved in the sedimentary record often may comprise morphologically indistinguishable traces made by a number of different species, some close relatives, but others only distantly related at best. As Sarjeant (1990, p. 306) plaintively asked, "How does one distinguish . . . between the tracks of the different groups of lepidosaurs, and can one separate these from the footprints of eosuchians or even (in some cases) small amphibians?" Even apart from considerations of footprint preservation, footprint assemblages may under-represent the diversity of small-bodied ectothermic vertebrates on a regional and probably even local basis for ecological and evolutionary reasons.

Large-bodied ectotherms will likely be represented by fewer morphologically similar species, and will likely range over a wider spectrum of habitats than smaller forms. But, even ectotherms as large as goannas show significant habitat specialization (Shine, 1986). As a rough generalization, though—or a hypothesis for testing—we would expect the degree to which ichnological diversity undersamples zoological diversity to diminish with increasing body size in ectothermic tetrapods.

Of course, the same issue of under-representation also arises with the osteological record. In many cases, zoological species (particularly small-bodied forms?) will not differ enough osteologically for species differences to be detectable in the skeletal record—recall how morphologically conservative the varanid species examined in this study are. Furthermore, whether bones of a given animal become fossilized will depend, in part, on whether it died in

or near sedimentary environments suitable for fossilization. Assessing which of the two kinds of fossil record, skeletal or ichnological, better samples ancient zoological diversity on a local and regional basis is complex. Although the skeletal record probably permits greater taxonomic resolution about faunal components, many taxa appear to be represented in the sedimentary record only by footprints (Lockley and Hunt, 1995).

In conclusion, the relationship between ichnological diversity and zoological diversity is not simply a matter of the question investigated here—the association (or lack thereof) between differences in morphology and differences in trackway features of potential trackmakers. Foraging behaviors must be considered, as well as the distribution of animal habitats and microhabitats and of track-forming sedimentary environments on a landscape; yet another consideration is the way habitat specialization is influenced by metabolic physiology and body size of potential trackmakers.

Vertebrate palichnology traditionally has been allied with sedimentary geology, and much has been gained from this association. Results of the present study suggest that the time has come to expand fruitful dialogue on another front, between ichnologists and vertebrate ecologists (cf. Frey and Pemberton, 1986; Cohen et al., 1993).

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