Zootaxa 1313: 1–38 (2006)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

1313

A new species of *Varanus* Merrem (Squamata: Varanidae) from the Pilbara region of Western Australia, with observations on sexual dimorphism in closely related species

KENNETH P. APLIN[1], ALISON J. FITCH[2,3] & DENNIS J. KING[4]

[1]*Australian National Wildlife Collection, CSIRO Sustainable Ecosystems, PO Box 284 Canberra, ACT, Australia; formerly Western Australian Museum, Francis Street, Perth, Western Australia 6000, Australia, E-mail: ken.aplin@csiro.au. To whom correspondence should be addressed*

[2]*School of Biological Sciences, Flinders University, GPO Box 2100, Adelaide, South Australia 5001, Australia; E-mail: alison.fitch@flinders.edu.au*

[3]*Evolutionary Biology Unit, South Australian Museum, North Terrace, Adelaide, South Australia 5000, Australia*

[4] *Deceased, formerly Research Associate of Western Australian Museum, Francis Street, Perth, Western Australia 6000, Australia*

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Accepted by S. Carranza: 16 Aug. 2006; published: 14 Sept. 2006

Abstract

We describe a new species of *Varanus* similar to *V. caudolineatus* and *V. gilleni* but distinguishable from each of these taxa on genetic and morphological criteria. The three species are closely related and together constitute a species group within subgenus *Odatria*. The new species is restricted to the Pilbara region of Western Australia and appears to be sympatric with *V. caudolineatus* at several localities. It is more widely separated from known populations of *V. gilleni*. The new species is associated with mulga woodland and is at least partially arboreal, but little else is known of its ecology. Combined morphometric and meristic analyses indicate complex patterns of sexual dimorphism in all three species, including relative body elongation in females that is reflected in higher modal presacral vertebral counts in females than males of each species. Body elongation of females needs to be taken into account in future analyses of sexual dimorphism in varanid lizards.

Key words: *Varanus*, goanna, Australia, taxonomy, mitochondrial DNA, sexual dimorphism

Introduction

Storr (1980: 250) remarked that specimens of *Varanus caudolineatus* Boulenger, 1885 from north of the Ashburton River in Western Australia "are larger (than the typical form), have more numerous midbody scale rows and show a tendency for dark spots on the tail to align transversely". He further noted that "in each of these characters the northernmost population of *V. caudolineatus* shows an approach towards its close relative and near neighbour *V. gilleni*".

Since the time of Storr's revision, additional examples of this distinctive monitor have been received at the Western Australian Museum, allowing for a more detailed assessment of its affinities using both morphological and molecular methods. As reported below, our analyses demonstrate that the north-western population constitutes a separate evolutionary lineage that is diagnosably distinct from each of *V. caudolineatus* and *V. gilleni* Lucas and Frost, 1895, and is found in regional sympatry with *V. caudolineatus*. It therefore warrants recognition as a distinct species. The three species form a discrete phyletic cluster within subgenus *Odatria* that we herein identify as an informal species group (the '*V. caudolineatus* group') pending more general revision of this complex subgenus (Sprackland 1991; Ziegler and Böhme 1997; Fuller *et al.* 1998; Ast 2000). The new species described herein is the taxon mentioned by Thompson (2004) as an undescribed relative of *V. caudolineatus*. Figure 1 shows the new species photographed in life; for other photographs, see Thompson (2004).

Materials and methods

DNA was extracted and sequenced from a total of 14 individuals (*V.* **sp. nov.**, n = 7; *V. caudolineatus*, n = 4; and *V. gilleni*, n = 3) from the tissue collections of the Australian

Museum, Sydney (AMS); Northern Territory Museum and Art Gallery, Darwin (NTM); South Australian Museum, Adelaide (SAM) and Western Australian Museum, Perth (WAM). *Varanus storri* Mertens (n = 2) was used as a near out-group, chosen on the basis of the phylogenetic analyses of Ast (2001). All tissue samples are associated with voucher specimens; locality details for these specimens are provided in Appendix I.

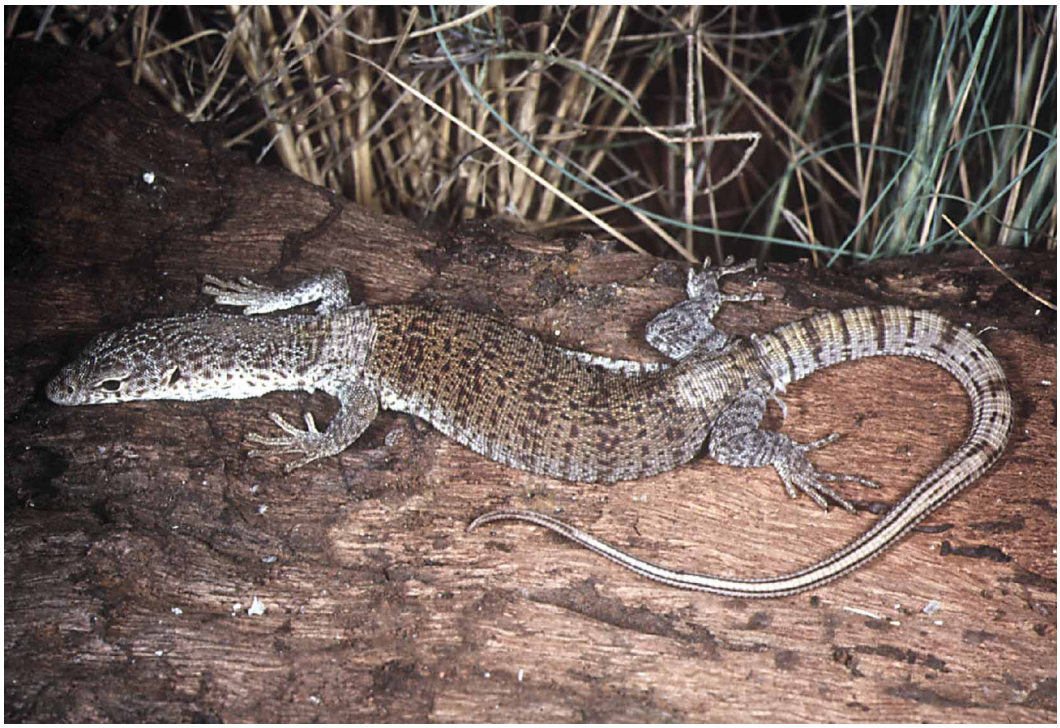

FIGURE 1. An adult *Varanus bushi* **sp. nov.** from near Roebourne, photographed in life by Robert Browne-Cooper.

Total cellular DNA was extracted from the tissue samples using DNAzol® homogenisation buffer (DNAzol) (Life Technologies), as per the manufacturer's instructions. Following extraction an approximately 886 base pair (bp) fragment of the mitochondrial DNA (mtDNA) genome, including the 3' end of the *NADH dehydrogenase 4* (*ND4*) gene (710 bp) and the tRNA genes $tRNA^{His}$, $tRNA^{Ser}$ and the 5' end of $tRNA^{Leu}$ (176 bp), was amplified by the polymerase chain reaction (PCR) using the forward primer: ND4: 5´ TGACTACCAAAAGCTCATGTAGAAGC 3´ (Forstner *et al.* 1995) and the reverse primer Leu1: 5´ CATTACTTTTTACTTGGATTTGCACCA 3´ modified from Leu (Arévalo *et al.* 1994). PCR amplifications were carried out in a final volume of 50 µL, using AmpliTaq Gold polymerase (Perkin Elmer), with the following reaction conditions: 9 min at 94°C, followed by 34 cycles of 45 s at 94°C, 45 s at 48°C, 1 min at 72°C; followed by a final extension of 6 min at 72°C. PCR products were purified using the UltraClean PCR clean-up DNA purification kit (Mo Bio Laboratories) following the manufacturer's

instructions. Both strands, using the same primers as those used for PCR amplification, were sequenced using the ABI PRISM BigDye v 3 Terminator Cycle Sequencing Ready Reaction kit (Applied Biosystems) and products resolved on an ABI PRISM 3700 DNA Analyser.

Sequences were aligned by eye using Se-Al v 1.0 α1 (Rambaut 1995). The tRNA genes were aligned using the secondary structure model of Macey and Verma (1997), optimizing the match between the sequences and conserved structural elements identified in the secondary structure model. GenBank accession numbers are DQ631868-DQ631883. Phylogenetic relationships were estimated using maximum parsimony (MP), maximum likelihood (ML) and LogDet minimum evolution (ME) methods as implemented in PAUP* v 4.0 β10 (Swofford 2002). Insertion-deletion events in the alignment were treated as in the simple gap coding method of Simmons and Ochoterena (2000).

MP analyses were conducted using the heuristic search mode with 1000 random stepwise addition replicates and tree-bisection-reconnection (TBR) branch swapping. ML analyses were carried out, under a model of sequence evolution determined by the Akaike Information Criteria (AIC) as implemented using Modeltest version 3.06 (Posada and Crandall 1998), using the heuristic search mode with "as-is" addition and TBR branch swapping. Parameters were estimated simultaneously from the data. LogDet distances (Lockhart *et al*. 1994) were used to construct trees under the ME criterion of optimality using the heuristic search mode and TBR branch swapping. Non-parametric bootstrap re-sampling was used to test the robustness of the optimal trees, with 1000 heuristic pseudoreplicates for MP and ME, and 100 pseudoreplicates for ML. The Bremer, or decay, index (Bremer 1988), implemented with Autodecay version 4.0 (Eriksson 1998), was also used to assess support for the MP trees.

All specimens in the collection of the Western Australian Museum (WAM) previously identified as either *V. caudolineatus* or *V. gilleni* were re-examined during the course of this study. Appendix II provides locality details for all voucher specimens examined.

The following measurements and counts were taken on preserved voucher specimens: Snout-Vent Length (SVL), measured from tip of snout to vent; Tail Length (TL), measured from vent to tip of complete tail; Head + Neck Length (HNL), measured from tip of snout to gular fold; Forelimb Length (FLL), measured along anterior margin from axilla to tip of longest digit but without claw; Hind limb Length (HLL), measured along anterior margin from groin to tip of longest digit but without claw; Midbody Scale Count (MSC), number of scales in a circumferential row positioned approximately mid-way between limbs; Ventral Scale Count (VSC), number of longitudinal scale series counted in ventral midline from gular fold to inguinal fold; and Pedal Subdigital Lamellar Count (PSLC), number of subdigital lamellar rows on fourth digit of pes (the longest digit), from first complete proximal row to apical pad. Body length (BL) was calculated by subtracting HNL from SVL.

The sex of most specimens was determined by dissection and examination of gonads.

Juveniles and poorly fixed or damaged specimens generally could not be sexed. Four males and four females of each taxon were x-rayed with the aim of obtaining vertebral and phalangeal counts. The sex of one putative female specimen of *V.* **sp. nov.** was subsequently reassessed after observation of sizable hemibaculi on the x-ray (Shea and Reddacliff 1986), giving a final sex-ratio for this taxon of three males to five females. Small numbers of other *Odatria* spp. were also x-rayed for comparative purposes.

Log-transformation of measurements is recommended for interspecific comparisons among varanids of strongly contrasting body size (Thompson and Withers 1997). We found no evidence of non-linear relationships between any pair of measurements. However, many measurements display a strong correlation between variance and size (i.e. animals in larger size classes are more variable) which can compromise statistical analyses including the comparison of regression slopes. To counter this effect, all regression analyses were performed on log-transformed data (natural log). Morphometric analyses were variously conducted in SPSS Version 6.0 and GenStat Release 6.1. Statistical results are regarded as 'significant' if test results indicated probabilities lower than 0.05.

Comparative investigation of growth patterns typically requires identification of a parameter (or a multivariate derivative) that can be regarded as an estimator of 'overall size'. In comparisons within a single species (or between species of similar size), this 'size' factor can also be regarded as a proxy for individual age. Although SVL is commonly used in this capacity in herpetological studies (e.g. Greer and Smith 1999), for interspecific comparison of varanids Thompson and Withers (1997: 128) recommended use of 'thorax-abdomen length' (= BL of this study) on the grounds that ratios based on BL gave "the best separation of species" as reflected in "the highest number of significant F-ratio values" in Analysis of Variance (ANOVA). In our view, BL is also theoretically preferable on the grounds that SVL is a composite of linear measurements of at least three anatomical components—the body, the neck, and the head—each of which may be subject to independent selection and evolutionary change. By the same logic, the length of either the head or neck might be even more appropriate as a 'size' estimator. Unfortunately, in varanids there is no clear external boundary between the neck and head; accordingly, we measured the more repeatable composite value HNL. Although our analysis stops short of a full treatment of this issue, we explore the relative utility of BL and HNL as alternative 'size/age estimators' in this group of *Varanus* species.

Results of molecular analysis

The aligned data comprised 763 sites, spanning from the 3´ end of the *ND4* gene to the 5' end of $tRNA^{Ser}$, 167 sites of which were parsimony informative. Three single site indels were present, none of which were parsimony informative. Two haplotypes were observed among the seven individuals of *V.* **sp. nov.**: haplotype 1 – R125105, R125520-1, R129912,

R131751, R135340 and haplotype 2 – R108999. All of the other individuals had unique haplotypes. A contingency χ^2 test of homogeneity of nucleotide frequencies among the sequences gave a non-significant result (χ^2 = 3.32, d.f. = 30, p = 1). Six equally parsimonious trees were found with a length of 330 steps. The LogDet ME analyses produced a single tree of length 0.465. The strict consensus of the six equally most parsimonious trees with MP and ME bootstrap proportions and decay indices is presented in Figure 2a.

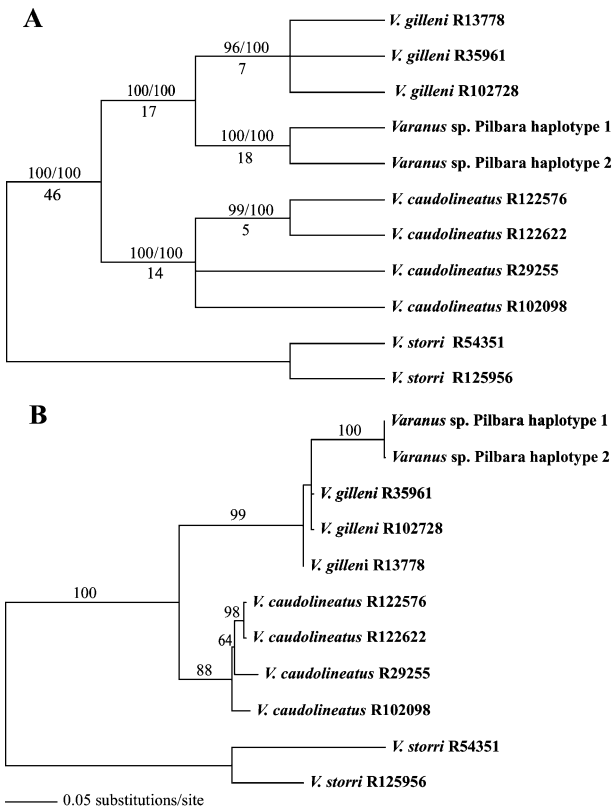

FIGURE 2. Relationships among unique mitochondrial haplotypes obtained through sequencing of various individuals of *V. caudolineatus*, *V. gilleni* and *V. bushi* **sp. nov.** Localities for each specimen are provided in Appendix I. (a). Strict Consensus tree of six equally most parsimonious trees (length of 330 steps). Numbers above branches represent Maximum Parsimony and Minimum Evolution bootstrap proportions (each based on 1000 pseudoreplicates); numbers below branches represent decay indices. (b). Maximum Likelihood tree (-InL = 2418.09) obtained using the GTR+I model of nucleotide substitution. Numbers above branches indicate bootstrap proportions (based on 100 pseudoreplicates).

The AIC indicated that the General Time Reversible model with proportion of invariable sites (GTR+I) (Rodriguez *et al*. 1990) was a suitable model of nucleotide substitution for the data. Model parameters estimated from the data were; nucleotide frequency: A = 0.304, C = 0.357, G = 0.098, T = 0.241; rates: A?C = 534.71, A?G = 2.089

x 10^4, A?T = 1233.2, C?G = 196.82, C?T = 8351.9, G?T = 1.0, and I = 0.602. The ML analyses found a single best tree with a negative log likelihood (-InL) of 2418.09. The ML tree, with bootstrap proportions, is presented in Figure 2b.

The MP and ME analyses produced trees of identical topology, featuring a major division between *V. caudolineatus* and a combined *V. gilleni* + *V.* **sp. nov.** lineage and reciprocal monophyly between *V. gilleni* and *V.* **sp. nov.** Both analyses show 100% bootstrap support for the primary division and >95% support for reciprocal monophyly of *V. gilleni* and *V.* **sp. nov.** The MP analysis also shows strong Bremer support for each taxon lineage. The ML analysis show the same primary division between *V. caudolineatus* and a combined *V. gilleni* + *V.* **sp. nov.** lineage, with bootstrap support >87%. However, within the latter lineage, *V. gilleni* and *V.* **sp. nov.** do not show reciprocal monophyly, rather *V.* **sp. nov.** is embedded within a paraphyletic *V. gilleni*.

The level of sequence divergence between each of the three taxa, corrected for saturation with the GTR+I model of nucleotide substitution, ranged from 6.8–8.0% between *V.* **sp. nov.** and *V. gilleni*, 16.0–19.4% between *V. gilleni* and *V. caudolineatus* and 18.2–21.0% between *V. caudolineatus* and *V.* **sp. nov.** Distances between these species are comparable to genetic divergences between species within the *subgenus Odatria* which range from 3.7–13.1% between *V. acanthurus* Boulenger and *V. baritji* King & Horner to 24.4–26.6% between *V. baritji* and *V. eremius* Lucas & Frost (A. Fitch, unpublished data).

Results of morphological analysis

Prior to the genetic analysis, Aplin and King examined all specimens identified as *V. caudolineatus* and *V. gilleni* in the collection of the Western Australian Museum and divided them into three morphotaxa based on details of lepidosis, pigmentation and body scale meristics. Confidence was gained from the observation that the resultant groups comprised specimens from three broad geographic regions: the southwest (most identified as *V. caudolineatus*; n = 204), the inland deserts (most identified as *V. gilleni*; n = 96) and the Pilbara (variously identified as *V. caudolineatus* or *V. gilleni*; n = 26). Subsequently, we were gratified to observe that specimens with related genotypes were correctly associated in the same morphological groups. The morphological characteristics are discussed below as background to the systematic treatment.

Osteology

Presacral vertebral counts in each taxon were determined from x-rays as follows (values are count, *n*; specimens identified in Appendix II) — *V.* **sp. nov.** males: 30 (2), 31 (1); *V.* **sp. nov.** females: 30 (2), 31 (3); *V. caudolineatus* males: 28 (3), 29 (1); *V. caudolineatus* females: 29 (2), 30 (2); *V. gilleni* males: 29 (4); *V. gilleni* females: 29 (2), 30 (2). In each taxon, females have modal counts that are one vertebra higher than in males. Although the

sample sizes are small for all taxa, the consistency of the pattern is sufficient to conclude that presacral vertebral counts in this group of varanids are sexually dimorphic. This finding is consistent with Greer's (1989:208) observations on a larger sample of *V. gilleni* for which he obtained mean presacral vertebral counts of 29.1 for males (n = 7) and 29.5 for females (n = 8) with a range of 29–30 in both sexes.

Given the relative lack of variation within individual *Varanus* spp., the presence of higher counts in *V.* **sp. nov.** (30–31) compared with each of *V. gilleni* (29–30) and *V. caudolineatus* (28–29) is regarded as a taxonomically significant difference. Specimens of other *Odatria* species had the following presacral vertebral counts: 29 in a female *V. glauerti* Mertens (WAM R103401); 29 in a male *V. pilbarensis* Storr (WAM R100766); 30 in a female *V. mitchelli* (WAM R83687); 27 in a male *V. acanthurus* (WAM R87751); 28 in two female *V. brevicauda* Boulenger (WAM R117242, R117243). The new counts for *V. brevicauda* are much lower than values of 31–35 (mean of 32.3, n = 7) for this taxon reported by Greer (1989:208) and we consider it likely that this widespread arid-zone taxon also conceals cryptic species.

The phalangeal formula was determined from x-rays as follows: for the manus either 1.2.3.4.2 (*V. caudolineatus*, n = 3; *V.* **sp. nov.**, n = 4; *V. gilleni*, n = 3) or 1.2.3.3.2 (*V. caudolineatus*, n = 1); and for the pes 1.2.3.4.3 (*V. caudolineatus*, n = 5; *V.* **sp. nov.**, n = 4; *V. gilleni*, n = 3). The limited variation within the group is consistent with previous observations on varanid osteology by Mertens (1950).

No osteoderms were visible on the x-rays of the three taxa of primary interest, nor in specimens of *V. mitchelli* and *V. glauerti*. Osteoderms were clearly visible in x-ray images of *V. brevicauda*, *V. acanthurus* and *V. pilbarensis*.

Lepidosis

Two kinds of body scales are present in *Varanus* species; these are referred to here as 'primary scales' and 'granules'. Granules typically encircle the larger primary scales on one or more sides; however, not all primary scales are surrounded by granules.

The basic pattern of lepidosis is very similar in each of the three taxa. The major point of distinction among them concerns the relative degree of elongation of the dorsal primary scales. These are almost round in *V. gilleni*, appreciably more elongate and hence ovate in *V. caudolineatus*, and even more elongate in *V.* **sp. nov.** (Fig. 3). The contrast between *V. gilleni* and *V.* **sp. nov.** is particularly striking. The dorsal primary scales on the neck and body of *V. caudolineatus* are slightly raised compared with a flatter morphology in the other taxa. This imparts a slightly rougher texture to the dorsal skin in *V. caudolineatus*. No sexual dimorphism was observed in scale shape in any taxon.

The tail in all three taxa is only moderately spinose compared with the condition in some other species of subgenus *Odatria* (e.g., *V. acanthurus, V. storri*). In *V. caudolineatus* the tail feels slightly rougher than in either *V. gilleni* or *V.* **sp. nov.**, especially over the

proximal 30–40 mm. This is due to a combination of larger individual dorsal and lateral primary scales, and more prominent development on each scale of the median keel. The interspecific distinction is less obvious over the distal two-thirds of the tail.

The post-cloacal scale cluster does not differ in morphology between the sexes but differs in various ways among the three taxa. In *V. caudolineatus* the scale cluster consists of two rows of nodular scales, with four of five spinose scales in the outer row and two weakly spinose scales in the inner row. In *V.* **sp. nov.** there are usually four weakly spinose scales in the outer row (occasionally two or three) with raised but non-spinose scales in the inner row. The scale cluster in *V. gilleni* is considerably more prominent and consists of 3–4 rows of nodular scales; six or seven scales in the outer row bear distinct spines, with three or more weakly spinose scales in the inner row.

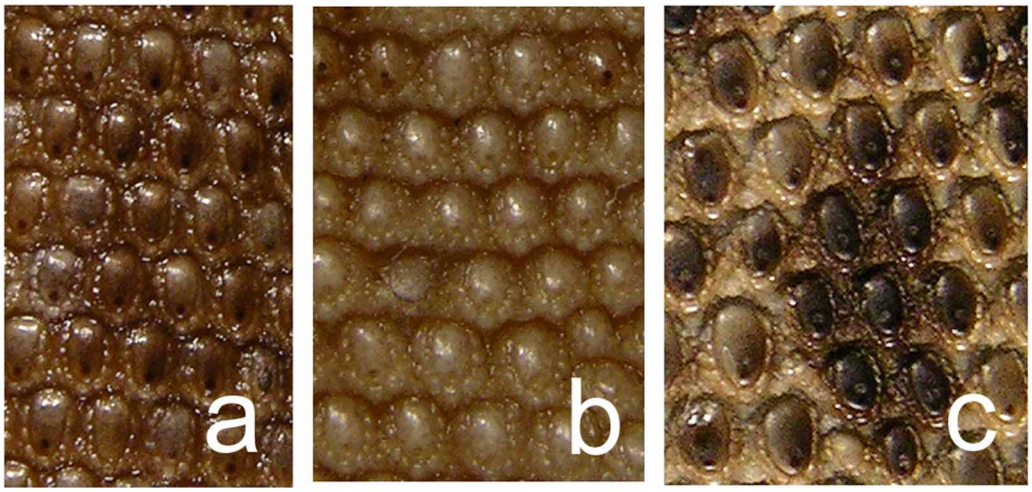

FIGURE 3. Details of scalation on dorsal midbody of representative specimens of three *Varanus* species. (a) WAM R135340 *V. bushi* **sp. nov.** Paratype ♀; (b) WAM R75792 *V. gilleni* ♀; c) WAM R135601 *V. caudolineatus* ♂.

A point of more general interest is the fact that in all three taxa the rows of ventral primary scales are non-overlapping, being narrowly separated by a single line of granules located along the posterior margin of each preceding scale. This condition contrasts with that found in most if not all other species of the subgenus *Odatria* and at least some of the larger varanids [e.g., *V. gouldi* (Gray), *V. salvator* (Laurenti), *V. varius* (White); specimens in Australian National Wildlife Collection, Canberra]. This previously unremarked feature may constitute a diagnostic feature and likely synapomorphy of a '*V. caudolineatus* species group'.

Meristic variation

Meristic data for each taxon are summarised in Table 1. Before any interspecific comparisons were made, the possibility of age-related variation in each taxon was

explored by plotting each meristic score against SVL, separately for each sex. Bivariate plots of SVL against MSC indicate a very weak linear association between VSC and SVL in males of *V. caudolineatus* ($F = 5.220$, d.f. = 1,32, $p = 0.029$; slope = 0.126±0.055, $R^2 = 0.140$), and no significant relationship in males of *V. gilleni* or females of either species. No size-related trends were observed for MSC or PSLC in males of either species, or for any variable in females. These results show convincingly that the meristic attributes are age-independent in these species of *Varanus*.

The extent of sexual dimorphism in meristic variables was explored using ANOVA. Significant sexual dimorphism is indicated only in VSC, with highly significant results in each of *V. caudolineatus* and *V. gilleni* (Table 1).

Interspecific comparisons, tested separately for each sex, show that mean values for MSC, PSLC and VSC are significantly lower for both sexes in *V. caudolineatus* than *V. gilleni* (Table 2). *Varanus* **sp. nov.** has significantly higher mean values for PSLC and VSC than *V. gilleni* in males, whereas only VSC is significantly higher in the smaller sample of females. Mean values for MSC do not differ for either sex between *V. gilleni* and *V.* **sp. nov.**

Pigmentation

In all three taxa smaller, immature individuals tend to be more brightly patterned than larger adults. However, only rarely is this ontogenetic fading so extreme as to obscure all traces of the primary pattern, which is distinctive in each of the three taxa (Figs 4–6). In *V.* **sp. nov.** (WAM R138949) the head and back are covered in irregular blotches, the majority covering clusters of 2–6 primary scales. A loreal streak is present and the neck bears irregular longitudinal streaks. Seven transverse bands are present on the lower back and basal portion of the tail; those on the tail are one scale wide and alternate with irregular rows of blotches. The distal part of the tail is longitudinally striped. The outer surfaces of the fore- and hind-limbs are spotted. The throat and venter are intensely spotted. Larger specimens typically show a diffuse spotting over the head, back and limbs, usually with faint transverse banding on the lower back. One large specimen (WAM R129632) has indistinct broad bands alternating with finer spotting on the lower back, mirroring the typical patterning of *V. gilleni* (see below).

In *V. caudolineatus* the head and dorsum are usually covered in larger and more intensely pigmented blotches. Those on the neck are often arranged in a reticulate pattern, while those on the back usually appear randomly placed. Occasional specimens show transverse alignment of the spots but this generally extends over the entire body rather than being limited to the lower back. More typically, the lower back and basal portion of the tail are usually heavily spotted but without the transverse banding seen in *V.* **sp. nov.** The dorsal pattern is usually well-developed in adults. In contrast, the limbs are generally weakly patterned in individuals of all ages. The throat and venter show a variable degree

TABLE 1. Mensural and meristic data for each *Varanus caudolineatus*, *V. gilleni* and *V. bushi* **sp. nov.** Data are presented separately for each sex, and for the total sample including unsexed individuals. Analysis of Variance (ANOVA) results indicate extent of sexual dimorphism for each variable; NS indicates non-significant contrasts with $p > 0.05$ (i.e. not significantly dimorphic). Abbreviations for variables are explained in Methods.

	♂♂	&&	All specimens	ANOVA (♂ vs ♀)
V. caudolineatus				
SVL	96.5 ± 1.18 62–120 107	94.76 ± 1.55 64–123 62	94.1 ± 0.98 48–123 194	F (1,167) = 0.801 NS
TL	123.7 ± 2.09 64–157 84	117.9 ± 2.10 77–142 52	119.1 ± 1.64 57–157 152	F (1,134) = 3.429 NS
HNL	35.2 ± 0.41 23–43 106	32.7 ± 0.44 23–41 61	33.6 ± 0.34 20–43 187	F (1,165) = 15.23 p < 0.01
BL	61.3 ± 0.82 37–81 106	62.0 ± 1.18 39–85 61	61.6 ± 0.67 37–85 169	F (1,165) = 0.214 NS
FLL	25.4 ± 0.29 16–31 105	23.7 ± 0.29 18–29 62	24.3 ± 0.23 14–31 188	F (1,165) = 13.99 p < 0.01
HLL	33.8 ± 0.43 24–42 99	31.0 ± 0.40 23–38 61	32.2 ± 0.34 17–42 178	F (1,158) = 19.75 p < 0.01
MSC	91.1 ± 0.68 80–107 66	91.0 ± 0.76 78–101 42	91.2 ± 0.48 78–107 117	F (1,106) = 0.008 NS
VSC	67.0 ± 0.71 60–78 32	72.9 ± 1.47 64–89 17	69.2 ± 0.76 60–89 52	F (1,47) = 16.722 p < 0.01
PSLC	20.9 ± 0,22 17–25 71	20.8 ± 2.09 16–26 45	20.8 ± 0.176 16–26 123	F (1,114) = 0.083 NS
V. gilleni				
SVL	124.7 ± 4.25 69–175 35	113.7 ± 4.45 80–153 24	116.6 ± 3.29 59–175 67	F (1,56) = 2.991 NS
TL	164.9 ± 7.41 90–230 28	151.2 ± 6.67 108–202 24	152.8 ± 5.26 75–230 59	F (1,49) = 1.809 NS

to be continued.

TABLE 1 (continued).

	♂♂	&&	All specimens	ANOVA (♂ vs ♀)
V. gilleni				
HNL	43.7 ± 1.31 27–60 34	39.4 ± 1.21 29–49 24	40.9 ± 1.01 24–60 65	F (1,55) = 5.250 p < 0.05
BL	81.7 ± 3.04 42–117 34	74.3 ± 3.28 51–104 23	78.7 ± 2.28 42–117 57	F (1,55) = 2.634 NS
FLL	31.4 ± 0.95 20–44 35	27.9 ± 1.06 20–37 24	29.1 ± 0.77 17–44 68	F (1,57) = 6.006 p < 0.05
HLL	40.0 ± 1.20 22–55 35	35.6 ± 1.27 26–47 24	36.9± 0.99 20–55 68	F (1,57) = 5.877 p < 0.05
MSC	110.7 ± 1.27 105–116 11	107.8 ± 2.50 96–118 8	109.4 ± 1.23 96–118 20	F (1,17) = 1.211 NS
VSC	82.4 ± 0.75 73–91 35	86.3 ± 0.77 81–98 24	83.9 ± 0.56 73–98 63	F (1,57) = 12.373 p < 0.01
PSLC	22.5 ± 0.34 19–27 35	22.2 ± 0.37 20–27 24	22.3 ± 0.19 19–27 65	F (1,57) = 0.467 NS
V. bushi **sp. nov.**				
SVL	114.0 ± 5.17 75–145 16	128.2 ± 4.54 108–140 6	114.5 ±4.92 66–145 24	F (1,20) = 2.493 NS
TL	158.2 ± 9.18 98–205 13	180.6 ± 16.13 162–205 5	159.3 ± 8.58 78–205 20	F (1,16) = 2.050 NS
HNL	40.5 ± 1.47 30–50 16	42.7 ± 1.31 37–46 6	40.0 ± 1.32 25–50 24	F (1,20) = 0.715 NS
BL	73.5 ± 3.78 45–95 16	85.5 ± 3.25 71–94 6	74.5 ± 3.66 38.95	F (1,20) = 3.363 NS
FLL	28.3 ± 1.09 20–36 16	30.8 ± 1.28 26–34 6	28.1 ± 1.09 17–36 24	F (1,20) = 1.745 NS

to be continued.

TABLE 1 (continued).

	♂♂	&&	All specimens	ANOVA (♂ vs ♀)
V. bushi **sp. nov.**				
HLL	36.3 ± 1.36 25–44 16	38.8 ± 1.89 32–45 6	35.8 ± 1.38 20–45 24	F (1,20) = 1.012 NS
MSC	106.0 ± 2.21 93–123 14	106.3 ± 1.52 103–112 6	107.4 ± 1.26 98–123 21	F (1.18) = 0.009 NS
VSC	87.5 ± 1.79 70–95 15	90.8 ± 2.21 81–96 6	90.1 ± 0.80 81–96 22	F (1,19) = 1.083 NS
PSLC	23.5 ± 0.45 21–26 15	23.7 ± 0.56 22–25 6	23.5 ± 0.330 21–26 24	F (1,19) = 0.029 NS

TABLE 2. Analysis of Variance (ANOVA) results for pairwise comparison of meristic variables between each of *V. caudolineatus*, *V. gilleni* and *V. bushi* **sp. nov.**, analysed separately for each sex. NS indicates non-significant contrasts with $p > 0.05$ (i.e. no difference between the two species). Abbreviations for variables are explained in Methods.

	MSC	VSC	PSLC
V. caudolineatus vs *V. gilleni* ♂♂	F (1,77) = 126.78 p <0.001	F (1,67) = 210.96 p <0.001	F (1,106) = 16.31 p <0.01
V. caudolineatus vs *V. gilleni* ♀♀	F (1,48) = 68.71 p <0.001	F (1,39) = 75.86 p <0.001	F (1,67) = 7.08 p <0.01
V. caudolineatus vs *V. bushi* **sp. nov.** ♂♂	F (1,78) = 85.88 p <0.001	F (1,84) = 28.32 p <0.001	F (1,45) = 301.80 p <0.001
V. caudolineatus vs *V. bushi* **sp. nov.** ♀♀	F (1,46) = 53.80 p <0.001	F (1,21) = 40.63 p <0.001	F (1,49) = 10.40 p <0.01
V. gilleni vs *V. bushi* **sp. nov.** ♂♂	F (1,21) = 1.26 NS	F (1,46) = 30.00 p <0.001	F (1,46) = 4.65 p <0.05
V. gilleni vs *V. bushi* **sp. nov.** ♀♀	F (1,12) = 0.23 NS	F (1,28) = 5.88 p <0.05	F (1,28) = 3.57 NS

of spotting; although no detailed analysis of geographic variation was performed, it was noted that specimens from the western part of the species' range are more often spotted on the venter than those from further east. Many specimens of *V. caudolineatus* have the spotting confined to the lateral margins of the venter.

The body pattern of *V. gilleni* is more distinct with fine longitudinal streaking on the head, spotting on the neck, and a bold pattern on the dorsum of the body made up of

alternating broad bands and zones of finer marbling. The base of the tail is banded as in *V.* **sp. nov.** Spotting is usually present on the throat in *V. gilleni* but is usually confined to the lateral margins of the venter.

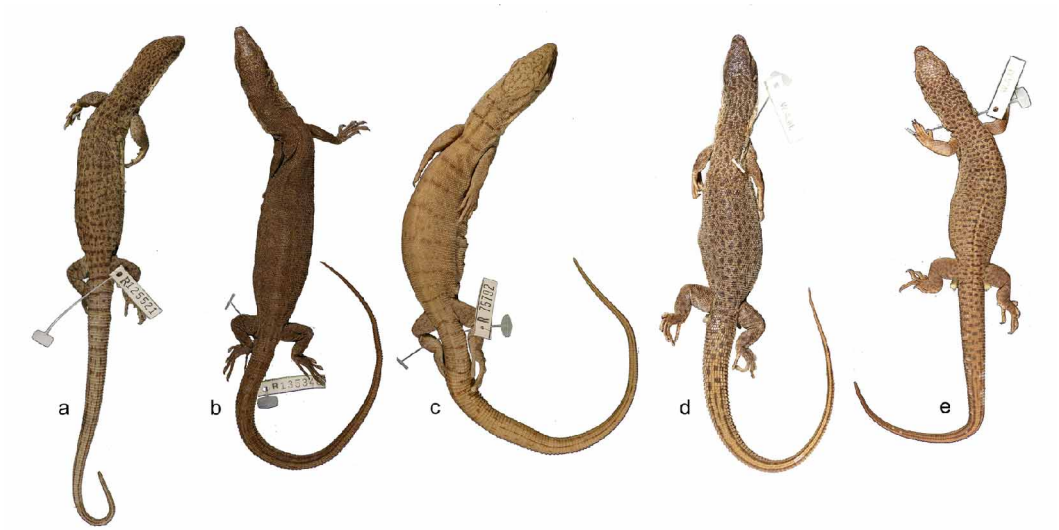

FIGURE 4. Dorsal views of representative specimens of three *Varanus* species. (a) WAM R125521 *V. bushi* **sp. nov.** Holotype ♂; (b) WAM R135340 *V. bushi* **sp. nov.** Paratype ♀; (c) WAM R75792 *V. gilleni* ♀; (d) WAM R135601 *V. caudolineatus* ♂; (e) WAM R138950 *V. caudolineatus* ♂.

FIGURE 5. Ventral views of representative specimens of three *Varanus* species. Same individuals as Figure 3.

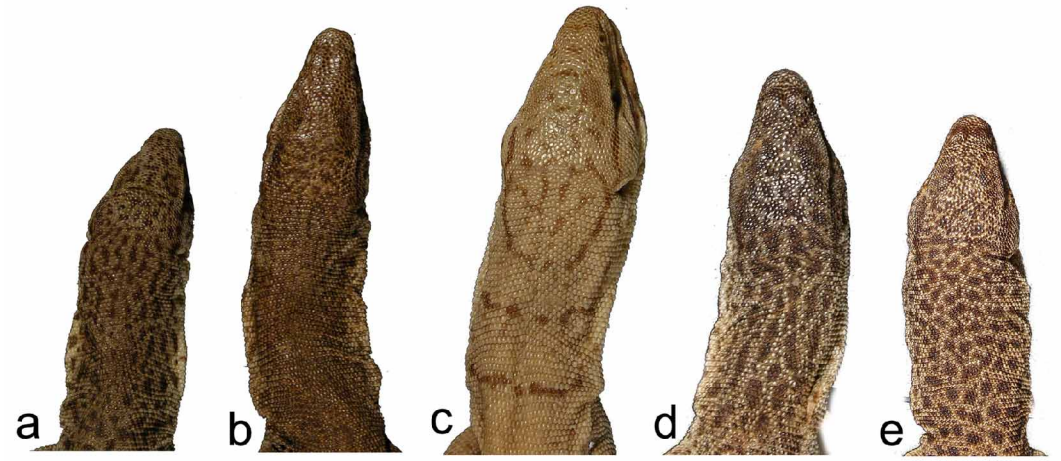

FIGURE 6. Dorsal views of head and neck of representative specimens of three *Varanus* species. Same individuals as Figure 3.

Hemipeneal anatomy

Everted hemipenes are available for several specimens each of *V. caudolineatus* and *V.* **sp. nov.** Detailed descriptions and good illustrations are also available in Branch (1982) and Ziegler and Böhme (1997) for the hemipenes of *V. caudolineatus* and *V. gilleni*. The hemipenis of *V.* **sp. nov.** (WAM R108899, R125521) is relatively short and broad, nude basally and finely papillose distally, and bears asymmetrical hemibacula. Left and right hemipenes are mirror-images. The spermatic sulcus is deep, shielded by non-papillose fleshy flaps, and opens onto a nude, flattened apical platform. The distal portion of the asulcal surface supports eight rows of finely papillose frill [paraphasmata sensu Ziegler and Böhme (1997)]; on R125521 all rows are continuous across the apical region, whereas on R108999 the distal 6 rows are interrupted by a nude fold that descends from the margin of the apical basin. The inner hemibaculum is elongate and protrudes through the tissue; the tip is curved towards the shorter outer hemibaculum. The tip of the outer hemibaculum protrudes but does not penetrate the overlying tissue. A flap of tissue descends from the outer hemibaculum to overlap but not join with the base of the inner hemibaculum; an erect papilla is situated near the end of this flap.

The hemipenis of *V. gilleni*, as described and illustrated by Branch (1982:29) and Ziegler and Böhme (1997: 70–72) closely resembles that of *V.* **sp. nov.** in general form and proportions. It differs primarily in having a smaller outer hemibaculum and a more complex inner hemibaculum that is variously interpreted as deeply bifid (Branch, 1982) or divided (Ziegler and Böhme 1997). The inner baculum as illustrated by Ziegler and Böhme (1997: Fig. 44) also appears to curve in the opposite direction to that of *V.* **sp. nov.**

The hemipenis of *V. caudolineatus* (e.g. R138950; also Branch 1982:27–28; Ziegler

and Böhme 1997: 68–69) has a longer truck and a shorter and narrower, less elaborate apex with fewer rows of frills [5 in R138950; previous accounts indicate 6–7 (Branch 1982) and 4–5 (Ziegler and Böhme 1997)]. The hemibacula resemble the condition in *V.* **sp. nov.**

Ziegler and Böhme (1997) considered hemipeneal similarities between *V. caudolineatus* and *V. gilleni* to indicate a close relationship between these species. Their view is vindicated by our molecular and extended morphological studies.

Morphometric variation

Basic body shape is remarkably conservative among varanids (Greer 1989; Pianka 1995; Thompson and Withers 1997), especially so in view of the huge range of body size involved. The three species we are concerned with here differ little in maximum size and show only slight differences in body proportions. Indeed, initial inspection of the series suggested that differences between males and females of each species could equal or exceed the differences among the species. For this reason, we investigated the nature of sexual dimorphism in some detail, prior to examining the interspecific contrasts. Summary statistics for the linear body and head measurements are given separately for males and females of each species in Table 1.

Analysis of sexual dimorphism

For each of *V. caudolineatus* and *V. gilleni*, the available specimens span almost the entire reported size range for each species and thus include all growth stages. For hatchling *V. caudolineatus*, Thompson (2004) reported mean SVL of 54.7 mm, mean tail length of 61 mm (thus, mean approximate total length c.116 mm). Our smallest individual of this species (R31382) measures total length = 116 mm and SVL = 62 mm. For *V. gilleni*, Horn (2004: Table 7.11) reported total lengths of 110–142 mm for several groups of hatchlings, while Eidenmüller and Wickler (1997) reported mean SVL of 63–65mm for three groups of hatchlings. Our smallest individual (R40887) of this species measures total length = 145 mm, SVL = 59.

Univariate ANOVA results indicate the presence of significant sexual dimorphism in each of *V. caudolineatus* and *V. gilleni* (Table 1). In *V. caudolineatus*, males are significantly larger than females in mean HNL, FLL and HLL but the sexes are not significantly different in mean SVL, BL and TL. In *V. gilleni*, males are significantly larger in mean SVL, BL, HNL, FLL and HLL but the sexes are not significantly different in mean TL. In *V.* **sp. nov.** females average larger than males for all measurements, with the strongest contrast being for BL. However, bivariate plots of each measurement against SVL (not shown) indicate that this is due to the absence of immature females in the sample. These plots further suggest that for individuals of the same SVL, males have relatively larger FLL, HLL and HNL, and relatively smaller BL.

For *V. caudolineatus*, the sample contains sufficient numbers of young individuals to explore whether sexual dimorphism is present throughout all stages of growth. For individuals with a SVL of 85 mm or less, the available sample comprises 16 males and ten females, with a similar spread of values for SVL in each sex. This sample of immature *V. caudolineatus* shows no indication of sexual dimorphism in any body measurement (Table 3). Accordingly, we adopted as a working hypothesis the notion that sexual dimorphism in this group of *Varanus* is acquired through life as a consequence of differential patterns of growth between the sexes.

TABLE 3. Mensural data for samples of *Varanus caudolineatus* of known sex with Snout Vent Length (SVL) of 85 mm or less. Analysis of Variance (ANOVA) results indicate extent of sexual dimorphism for each variable; NS indicates a non-significant contrast with $p > 0.05$ (i.e. no sexual dimorphism). Abbreviations for variables are explained in Methods.

V. caudolineatus	♂♂	♀♀	ANOVA (♂ vs ♀)
SVL	74.9 ± 1.87 62–85 16	74.4 ± 2.56 64–85 10	F (1,25) = 0.03 NS
TL	94.6 ± 2.84 64–109 16	96.3 ± 4.63 77–114 8	F (1,23) = 0.10 NS
HNL	27.9 ± 0.54 23–32 16	27.4 ± 0.83 23–32 10	F (1,25) = 0.32 NS
BL	47.0 ± 1.41 37–55 16	47.0 ± 1.83 39–53 10	F (1,24) = 0.00 NS
FLL	20.2 ± 0.44 16–23 15	20.5 ± 0.64 18–24 10	F (1,24) = 0.16 NS
HLL	26.3 ± 0.35 24–28 14	26.5 ± 0.83 23–31 10	F (1,23) = 0.07 NS

For reasons given in Methods, we employed BL and HNL as two potential estimators of 'size/age' for investigation of growth patterns. As illustrated in Figure 7 for male *V. caudolineatus*, bivariate plots of untransformed body measurements against each of BL and HNL show essentially linear patterns of growth of other body components. Plots against BL feature a strong contrast between the positive allometry of TL and the negative allometry of all other variables. In contrast, plots against HNL feature a three-way distinction between TL with high positive allometry, BL with moderate positive allometry,

and FLL and HLL, each with isometry or weak negative allometry. Broadly similar results were obtained for males of the other species and for females of all species but with slight differences in slope apparent between the sexes.

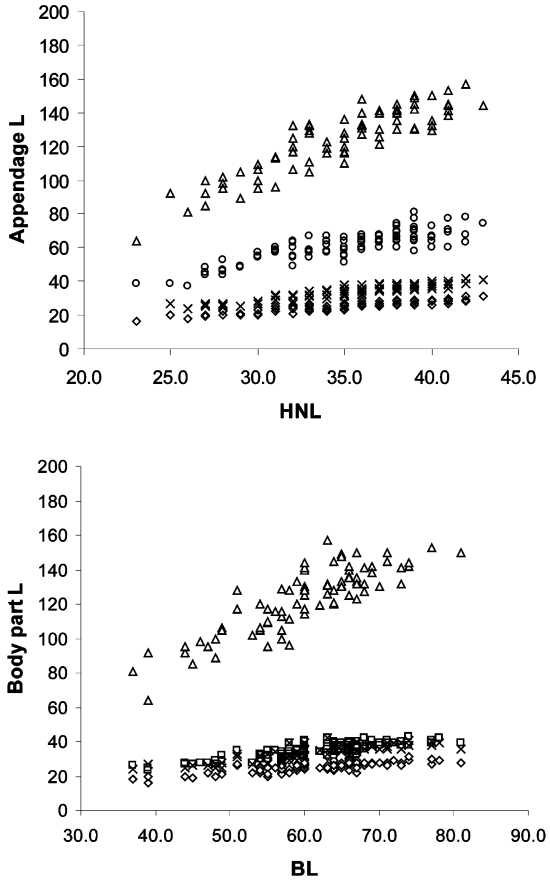

FIGURE 7. Bivariate plots of various external measurements against each of BL and HNL for male specimens of *V. caudolineatus*: Symbols used on each plot are: TL (triangle);BL (circle); HNL (square); HLL (cross); FLL (diamond).

The sex-related differences were explored further by regression analyses, using each of HNL and BL as alternative proxies of overall size/age (Table 4). The results obtained with each variable give very different impressions of sexual dimorphism in each species. In *V. caudolineatus*, analyses using BL as the 'size/age estimator' show significant heterogeneity of variance between the sexes for two variables (TL, HNL), despite log transformation (Table 5). Although this finding casts some doubt on the significance of contrasts for these variables, it is nonetheless noteworthy that regression coefficients are higher in males than in females for all variables, implying an overall more rapid growth in males of all body appendages relative to BL. In contrast, regressions based on HNL show no significant heterogeneity of variance between the sexes and significant sexual

dimorphism in two variables, with females having a steeper growth trajectory for BL and a lower trajectory than males for HLL (Table 5). In *V. gilleni* variances are generally homogenous and there are no significant contrasts in regression slope between the sexes, irrespective of whether these are based on BL or on HNL (Table 5). However, for regressions based on HNL, F-ratios approach significance for BL, with a steeper growth trajectory in females than males. In *V.* **sp. nov.** regression coefficients using BL are higher in females for all variables but sample sizes are too small to attain statistical significance in any analysis.

TABLE 4. Comparison of growth patterns in males and females of each species, using the method of simple linear regression of various body components against each of Body Length (BL) and Head+Neck Length (HNL), two variables selected as potential 'size/age estimators'. Values are regression coefficients (i.e. slope) ± s.e. All coefficients are statistically significant at $p<0.01$. Abbreviations for other variables are explained in Methods.

Linear regressions against BL	TL	HNL	FLL	HLL
V. caudolineatus ♂ ♂	1.84 ± 0.120	0.41 ± 0.027	0.28 ± 0.021	0.42 ± 0.028
V. caudolineatus ♀ ♀	1.38 ± 0.157	0.31 ± 0.032	0.17 ± 0.025	0.25 ± 0.033
V. gilleni ♂ ♂	2.01 ± 0.151	0.41 ± 0.020	0.29 ± 0.021	0.37 ± 0.027
V. gilleni ♀ ♀	1.94 ± 0.203	0.35 ± 0.027	0.31 ± 0.029	0.38 ± 0.037
V. bushi **sp. nov.** ♂ ♂	1.69 ± 0.285	0.34 ± 0.041	0.25 ± 0.036	0.33 ± 0.039
V. bushi **sp. nov.** ♀ ♀		0.39 ± 0.041	0.37 ± 0.065	0.44 ± 0.189
Linear regressions against HNL	TL	BL	FLL	HLL
V. caudolineatus ♂ ♂	3.86 ± 0.196	1.61 ± 0.115	0.63 ± 0.030	0.95 ± 0.041
V. caudolineatus ♀ ♀	4.12 ± 0.343	2.18 ± 0.188	0.56 ± 0.048	0.76 ± 0.063
V. gilleni ♂ ♂	4.84 ± 0.256	2.23 ± 0.112	0.70 ± 0.042	0.91 ± 0.039
V. gilleni ♀ ♀	5.52 ± 0.418	2.61 ± 0.182	0.83 ± 0.068	1.04 ± 0.063
V. bushi **sp. nov.** ♂ ♂	4.63 ± 0.802	2.48 ± 0.296	0.70 ± 0.078	0.93 ± 0.076
V. bushi **sp. nov.** ♀ ♀	-	2.44 ± 0.253	0.95 ± 0.115	1.24 + 0.368

For several reasons, we believe that HNL is more suitable than BL as a 'size/age estimator' in this group of varanids. Firstly, independent evidence for sexual dimorphism in BL comes from ventral scale counts that are higher on average in females than males of both species but without any obvious difference in scale shape or corresponding dimorphism in midbody scale counts (as might be expected if individual scales are smaller in females). In addition, as detailed above, the modal number of presacral vertebrae is probably also sexually dimorphic, with females typically having more vertebrae than males in all three species. Secondly, there is no obvious sexual dimorphism in head size or shape among varanids (King and Green 1993a, 1993b; Mertens 1950).

TABLE 5. Results of Analysis of Covariance (ANCOVA) of linear regression slopes between male and females for each of *V. caudolineatus* and *V. gilleni* and using each of Head+Neck Length HNL and Body Length (BL) as potential 'size/age estimators'; NS indicates a non-significant contrast with $p > 0.05$ (i.e. slopes not significantly different between the sexes). Abbreviations for other variables are explained in Methods.

	HNL		Homogeneity of Variance	ANCOVA
	♂ ♂	♀♀	F(d.f.), *p*	F(d.f.), *p*
Varanus caudolineatus				
TL	3.86 ± 0.196	4.12 ± 0.343	F(51,83) = 1.37 NS	F(1,133) = 0.42 NS
HNL	-	-	-	-
BL	1.61 ± 0.115	2.18 ± 0.188	F(60,105) = 1.22 NS	F(1,165) = 36.01 p < 0.001
FLL	0.64 ± 0.030	0.56 ± 0.048	F(60,104) = 1.15 NS	F(1,164) = 2.01 NS
HLL	0.95 ± 0.041	0.76 ± 0.063	F(60,98) = 1.05 NS	F(1,158) = 6.21 p < 0.05
Varanus gilleni				
TL	4.84 ± 0.256	5.52 ± 0.418	F(23,27) = 1.52 NS	F(1,45) = 1.94 NS
HNL	-	-	-	-
BL	2.23 ± 0.112	2.61 ± 0.182	F(23,33) = 1.26 NS	F(1,53) = 3.16 NS
FLL	0.70 ± 0.042	0.83 ± 0.067	F(23,33) = 1.89 NS	F(1,53) = 2.61 NS
HLL	0.91 ± 0.039	1.04 ± 0.063	F(23,33) = 1.00 NS	F(1,53) = 3.12 NS

continued.

	BL		Homogeneity of Variance	ANCOVA
	♂ ♂	♀ ♀	F(d.f.), *p*	F(d.f.), *p*
Varanus caudolineatus				
TL	1.84 ± 0.120	1.38 ± 0.157	F(51,83) = 1.76 p < 0.05	F(1,133) = 5.57 p < 0.05
HNL	0.42 ± 0.027	0.31 ± 0.032	F(60,105) = 1.50 p < 0.05	F(1,165) = 6.64 p < 0.05
BL	-	-	-	-
FLL	0.28 ± 0.021	0.17 ± 0.025	F(60,104) = 1.36 NS	F(1,163) = 10.11 p < 0.01

HLL	0.42 ± 0.028	0.25 ± 0.033	F(60,98) = 1.32 NS	F(1,156) = 11.61 p < 0.001
Varanus gilleni				
TL	2.01 ± 0.151	1.94 ± 0.203	F(22,27) = 1.34 NS	F(1,45) = 0.08 NS
HNL	0.41 ± 0.020	0.35 ± 0.027	F(22,33) = 1.72 NS	F(1,53) = 3.14 NS
BL	-	-	-	-
FLL	0.29 ± 0.021	0.31 ± 0.029	F(22,33) = 1.05 NS	F(1,53) = 0.23 NS
HLL	0.37 ± 0.027	0.38 ± 0.037	F(22,33) = 2.19 p < 0.05	F(1,53) = 0.06 NS

If we accept the argument that females have proportionally more elongate bodies than males in this group of varanids, the overall pattern of morphometric variation can be interpreted as follows. In *V. caudolineatus*, males average slightly larger than females in HNL, FLL and HLL. Although SVL, BL and TL are not significantly different between the sexes in this species, both mean and maximum values for SVL and TL are larger in males than females, whereas the reverse is true for BL. The lack of sexual dimorphism in the composite dimension SVL is thus explained by the proportionally longer BL of the otherwise slightly smaller females. Overall, *V. gilleni* appears to be more strongly sexually dimorphic than the smaller-bodied *V. caudolineatus*, with males averaging significantly larger than females in all measurements except TL (where comparisons are confounded by high variance). The weakest contrast is for BL which only just attains statistical significance, presumably reflecting a proportionally more elongate body in females. The small sample of *V.* **sp. nov.** also suggests that females of this species are smaller than males overall but possess a relatively more elongate body. However, larger samples are needed to determine the magnitude of sexual dimorphism in this species.

Analysis of interspecific differences

Overall, the three taxa are very similar in size and proportions, as remarked also by Thompson (2004) who found incomplete separation of the three taxa in a canonical variates analysis. Rather than pursue a multivariate classificatory approach, we decided to explore the contrasting patterns of relative growth in each of the three species through interspecific comparison of growth trajectories based on HNL as a 'size/age estimator', with separate analyses carried out for each sex. For *V.* **sp. nov.** these comparisons were possible for males only on account of the limited size variation within the sample of females.

Bivariate plots of untransformed body measurements against HNL reveal that, within

each sex, the smallest individuals of each taxon are very similar in size and proportions, with no clear segregation between the three species (Fig. 8). As postulated above for the ontogeny of sexual dimorphism in *V. caudolineatus*, we offer as a working hypothesis the suggestion that differences in adult body size and proportions between each of the taxa arise through a process of relatively slower or faster growth in different body components, combined with variable patterns of truncation or attenuation of growth. Statistical comparison of regression slopes for log-transformed variables confirms the presence of significantly different growth trajectories between *V. caudolineatus* and each of *V. gilleni* and *V.* **sp. nov.** (Table 6), although some comparisons (especially those involving TL) are confounded by heterogeneous variances. Among males, *V. caudolineatus* shows significantly slower growth (relative to HNL) for TL and BL. In contrast, among females, *V. caudolineatus* shows significantly slower growth for TL, FLL and HLL. No significant differences in relative growth rate are observed between *V. gilleni* and *V.* **sp. nov.**

TABLE 6. Results of Analysis of Covariance (ANCOVA) of linear regression slopes between *V. caudolineatus* (c) and *V. gilleni* (g), using Head+Neck Length (HNL) as an indicator of age/size. Separate results are given for each sex; NS indicates non-significant contrasts with $p > 0.05$ (i.e. slopes not significantly different between the species). Abbreviations for other variables are explained in Methods.

	Tail	BL	FLL	HLL
♂ ♂	c = 3.86 ± 0.196 g = 4.84 ± 0.256 F(1,110) = 13.48 p < 0.01	c = 1.61 ± 0.115 g = 2.23 ± 0.112 F(1,140) = 25.59 p < 0.01	c = 0.64 ± 0.030 g = 0.70 ± 0.042 F(1,138) = 2.44 NS	c = 0.95 ± 0.041 g = 0.91 ± 0.039 F(1,132) = 10.28 p < 0.01
♀ ♀	c = 4.12 ± 0.343 g = 5.52 ± 0.418 F(1,72) = 6.098 p < 0.05	c = 2.18 ± 0.188 g = 2.61 ± 0.182 F(1,82) = 9.520 p < 0.01	c = 0.56 ± 0.048 g = 0.83 ± 0.067 F(1,82) = 11.396 p < 0.01	c = 0.76 ± 0.063 g = 1.04 ± 0.063 F(1,81) = 15.714 p < 0.01

To summarise the morphometric findings, *V.* **sp. nov.** appears to be most similar to *V. gilleni* both in terms of the expression of sexual dimorphism and the ontogeny of body proportions in males. *Varanus caudolineatus* is more distinct in body form, being a smaller and less sexually dimorphic animal overall, but with proportionally more marked elongation of the body in females and of the hind limbs in males. The enhanced body length of female *V. caudolineatus* might be an adaptation for maximising clutch mass which is particularly high relative to body mass in this species (Thompson and Thompson 2002). Proportional elongation of the hind limb in male *V. caudolineatus* presumably reflects some locomotory or behavioural specialization but too little is known about the ecology and behaviour of these small monitors to speculate further.

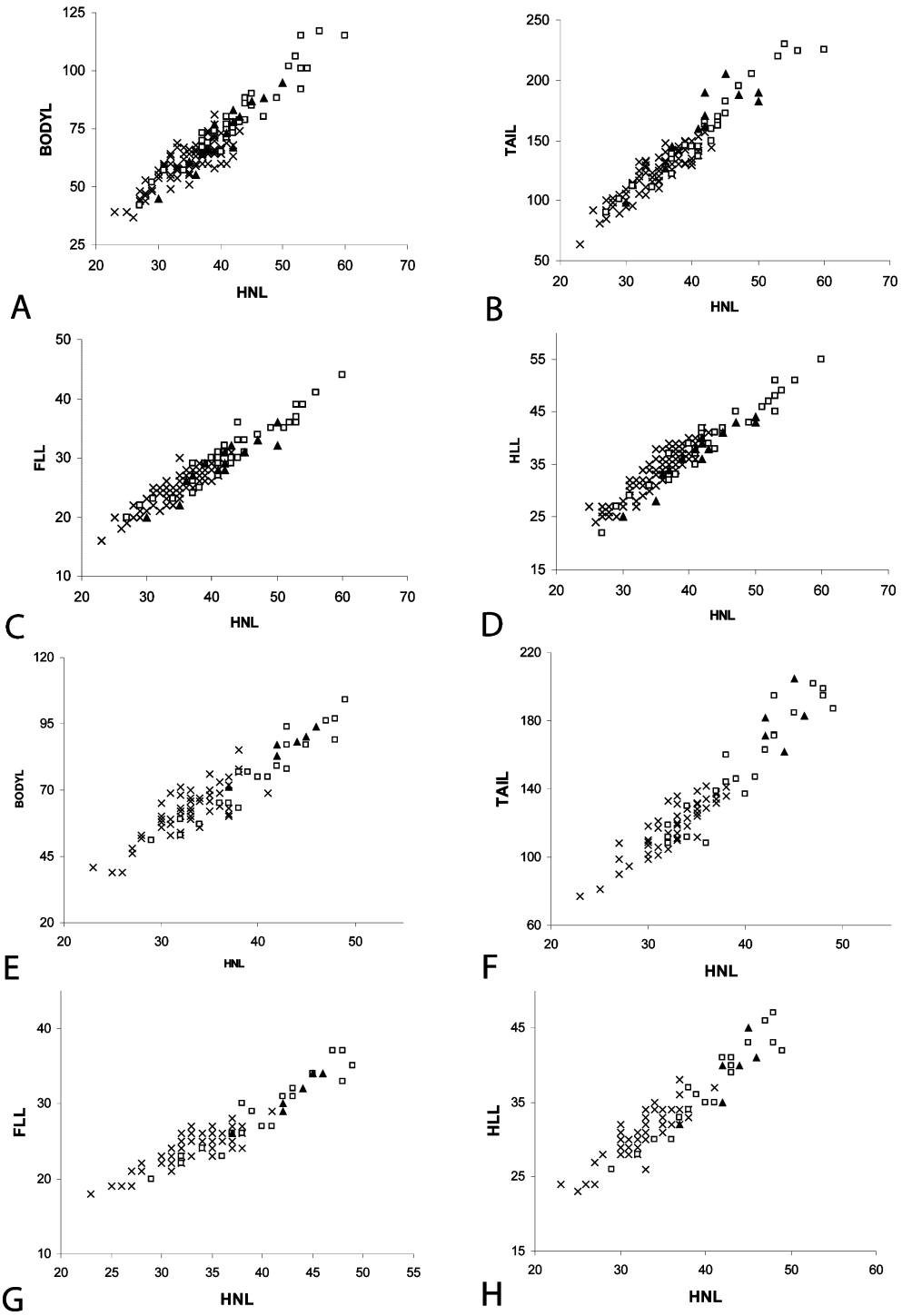

FIGURE 8. Bivariate plots of various external measurements of the three taxa, with separate plots for males (a–d) and females (e–h): (a,e) HNL vs BL; (b,f) HNL vs TL; (c,g) HNL vs FLL; (d,h) HNL vs HLL. Symbols used on each plot are *V. caudolineatus* (cross); *V. gilleni* (hollow square); *V. bushi* **sp. nov.** (solid triangle).

Systematics

Family Varanidae Gray

Genus *Varanus* Merrem

***Varanus bushi* sp. nov.**
Figures 1, 3–6

Holotype: Western Australian Museum R108999, adult male from Marandoo, Western Australia in 22^0 37' S 118^0 08' E. Collected on 20 June 1991 by Greg Harold. Specimen fixed in 10% formalin then stored in 70% ethanol. Liver sample stored in -80^0 C ultrafreeze at WAM.

Paratypes: Three additional specimens from Marandoo: WAM R54230, an adult male collected on 25 October 1976; WAM R56834, an adult female collected in April 1977; and WAM R62171 a juvenile of undetermined sex collected on 28 February 1979.

Diagnosis: A small-bodied member of the subgenus *Odatria* distinguished from most others by the combination of a longitudinally striped and only moderately spinose tail, unkeeled head and body scales, non-overlapping ventral primary scales, and an absence of longitudinal streaks on throat. Distinguished from *V. gilleni* by its slightly lesser average size, more elongate dorsal scales, more densely spotted venter and more irregularly spotted dorsum, less prominent linear patterning on the head and neck, and its more numerous presacral vertebrae, pedal subdigital lamellae and ventral scales. Males are further distinguished from *V. gilleni* by having hemipenes with an undivided inner hemibaculum. Distinguished from *V. caudolineatus* by its slightly greater average and maximum size, proportionally shorter fore- and hind-limbs, more elongate snout, higher average midbody and ventral scale counts, higher average sub-digital lamellar counts on pes, more finely scaled and less rugose proximal portion of the tail, more numerous presacral vertebrae, less conspicuously spotted head, more orderly alignment of dorsal pattern into transverse rows, and presence of transverse bands on the basal one-third of the tail. Males are further distinguished from *V. caudolineatus* by having a shorter hemipenis with more numerous papillose distal frills.

Etymology: We take pleasure in naming this species after naturalist and educator Brian Bush who has contributed enormously to our knowledge of the herpetofauna of Western Australia and of the Pilbara region in particular.

Distribution and sympatry: Endemic to the Pilbara region of Western Australia, northwest to the vicinity of Cooya Poonya and Tambrey, southwest to Mt Brockman and Mt Tom Price in the Hamersley Range, southeast to Mt Whaleback and northeast to Marillana and Hope Downs (Fig. 9). Two instances of regional sympatry with *V. caudolineatus* are recorded—at West Angelas and at Hope Downs, both on the southern margin of the Pilbara Uplands. Details of the relevant specimens are provided in the

Discussion.

Description of holotype: Adult male measuring SVL 145 mm, Tail 190 mm, Forelimb 32 mm, Hind limb 43 mm, Head and neck 50 mm. Both hemipenes are fully everted.

Vertebral column includes 30 presacral vertebrae. Phalangeal formula of manus 1.2.3.4.2; and of pes 3.4.3.2.1.

Head moderately depressed, depth at pineal organ 8.7 mm. Snout relatively elongate; lacking canthus rostralis. Nostril positioned 6.8 mm from tip of snout; 3.4 mm from anterior corner of eye. Ear aperture is vertically narrow and obliquely oriented.

Dorsal head scales unornamented; most are irregular polygons, sub-rounded in shape, and majority have a single scale organ. Supraocular scales are smaller than those on the rostrum, frontal and parietal regions. Granules are absent from head except in temporal region and on throat forward into genal groove. Dorsal primary scales on neck are raised but lack keels; all have scale organs. The dorsal primary scales on neck are rounded anteriorly but become more ovate posteriorly, merging smoothly with body scalation. Ventral primary scales on neck are small and almost round anteriorly, but become larger and progressively more elongate to rear; all ventral primary scales on neck are ringed laterally and posteriorly by small granules. Approximately one third of ventral neck scales bear scale organs, usually one per scale but not infrequently two or three. Gular fold is distinct, located 5 mm forward of anterior base of forelimb, and consisting of 4 rows of small scales, all lacking scale organs.

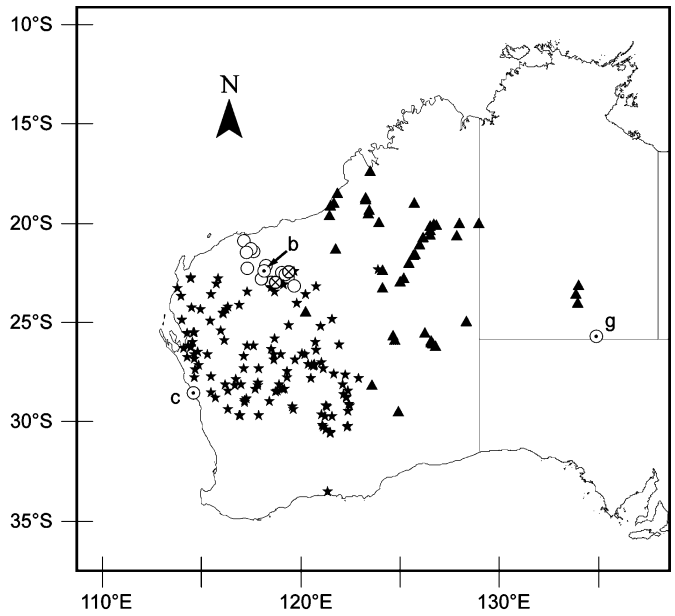

FIGURE 9. Distribution of the three *Varanus* species based on examined materials and type localities. The approximate wider distribution of *V. gilleni* is indicated by the dashed line. Symbols: Stars — *V. caudolineatus*; Triangles — *V. gilleni*; Circles — *V. bushi* **sp. nov.**; Circles with cross — s *V. caudolineatus* and *V. bushi* **sp. nov.** in local sympatry; Circles with dot – type localities.

Body scalation is relatively unspecialised. Dorsal primary scales are ovate, approximately twice as long as wide and lack keels; the majority have a single scale organ. Transverse scale rows are well-organised on the dorsum but tend to subdivide on flanks. Ventral primary scales are approximately 50% longer than and twice as wide as dorsal primary scales. All are ringed laterally and posteriorly by small granules. Single scale organs are present on the majority of scales towards the flanks but only about 15% of scales located along the mid-ventral area. Inguinal fold indistinct but located 1.5 mm forward of the anterior base of hind-limb. Position is marked by a change in scale size and shape, those behind the fold and back to vent being smaller, rounded and not arranged in transverse rows, and by occurrence of incomplete transverse series that terminate before reaching flank.

Scales on the inner surface of the fore- and hind-limbs are small and rounded while those on the outer surfaces are larger, more elongate and weakly keeled. Plantar surfaces of manus and pes with primary scales on small mounds of fine granules; all primary scales bear scale organs and some are pigmented. Subdigital surfaces with transverse lamellae made up of two or three rounded primary scales surrounded by granules. The apical lamella on each digit is single and more intensely pigmented. Longest digit (IV) of manus has 20 lamellae; longest digit (IV) of pes has 23. Claws on manus and pes are moderately large and darkly pigmented; all are laterally compressed and bear sharp, recurved tips.

Tail is slightly wider than deep at base, becoming more rounded in cross-section towards tip; it lacks a dorsal keel or other obvious specialisation. Dorsal primary scales near tail base are elongate but otherwise unspecialised. Moving distally, the primary scales first become more elongate, then develop a distinct midline keel, and finally develop smaller lateral keels. Ventral primary scales also change from elongate and lacking keels near the tail base, to even longer and with a strong midline keel distally. The overall effect is that the tail feels relatively smooth near the base but becomes more distinctly rasp-like distally. Circumferential scale counts decrease from 52 near tail base to 32 at one third of total length, then to 22 at two-thirds of total length. Longitudinal scale counts at the same positions are 8, 7 and 6 rows per cm.

The post-cloacal scale cluster is relatively poorly developed and consists of two rows of modified but unpigmented scales. The outer row consists of six nodular scales of which the lateral four scales are distinctly spinose. The inner row consists of four smaller, bluntly pointed scales.

The hemipenis measures 6.3 mm without the projecting hemibacula and 6.8 including these structures. The nude basal portion measures 3.3 mm. Further details were provided in an earlier section.

Ground colour of dorsum in preservative is a uniform pale-brown from rostrum to base of tail, becoming greyer on the flanks. Patterning on the head includes an irregular mottling of dark brown on the dorsum and sides, tending towards longitudinal streaking on the occiput, and a subdued temporal stripe on each side, running from the posterior corner

of the eye to above the ear. Irregular dark brown mottling is also present on the dorsum of the body, each 'spot' usually consisting of one or a few dark primary scales. The pattern is irregular on the anterior body but tends towards transverse alignment on the lower half of the back and above the hind limbs. The last three bars of this series are quite distinct and alternate with rows of small dark spots. The under surface of the throat, neck and body bears distinct pale grey spotting, each 'spot' usually comprised of two or three pigmented primary scales. These are most abundant on the throat and neck, and along the sides of the body, and less so in the mid-ventral region. The insides of the limbs are similarly patterned. The proximal 35 mm of the tail bears a series of eight more or less complete transverse bars. The next 38 mm bears a series of broken bars and irregular spots. The remainder of the tail supports a linear pattern consisting of five, more or less continuous dark stripes, each of which is one scale wide. The ventral surface of the tail is unpatterned throughout its length.

Variation among referred specimens: Mensural and meristic data for the complete sample of *V. bushi* **sp. nov.** is presented in Table 1; locality details for referred specimens are given in Appendix II. The holotype is the largest male specimen of *V. bushi* **sp. nov.**; SVL of the largest female (WAM R135340) is 140 mm.

Dorsal patterning in most individuals is similar to that of the holotype, with fine spotting on the anterior body, conspicuous banding only on the rear of the body and on the proximal segment of the tail, and longitudinal striping of the distal tail. In some individuals (e.g. WAM R125521 from the 'northern Pilbara') the entire head and body are more intensely marked with variable sized spots; these are randomly distributed on the head and neck but are aligned into more or less regular transverse rows posterior to the level of attachment of the forelimbs. All specimens of *V. bushi* **sp. nov.** have ventral spotting on the throat, neck and body. In comparison with the holotype, most individuals show more intense and evenly distributed spotting on the body. Some individuals also show a strong differentiation between abundant fine spotting on the throat and neck, with each spot consisting of a single pigmented primary scale, and less abundant but larger blotches on the body.

Dorsal ground colour in life is pale grey-brown, typically with a reddish tinge on the upper surface, from the crown of the head to between the hind limbs (Fig. 1). The ground colour of the tail is always paler than the body and generally has a cream wash on the distal one third of the upper surface.

Morphological comparisons: *Varanus bushi* **sp. nov.** is most similar overall to *V. gilleni*, a phenetic resemblance that is consistent with the phylogenetic conclusions of the molecular analyses. These species share a number of morphological attributes including a relatively elongate body with proportionally shorter limbs, high mid-body and ventral scale counts, high subdigital lamellar counts on the pes, a relatively non-spinose basal portion of the tail, and a tendency to include transverse bands in the dorsal patterning. As indicated in the diagnosis, *V. bushi* **sp. nov.** differs from *V. gilleni* in its lower average and

maximum body size, its more elongate dorsal scales, its more densely spotted venter, its less conspicuous linear patterning on the head and neck, its more numerous presacral vertebrae, its simpler heimbacular morphology, and some minor meristic differences.

Varanus bushi **sp. nov.** is more similar to *V. caudolineatus* in body patterning and this probably explains the former confusion between these species. Both species share a spotted rather than banded pattern on the dorsum, and both are typically spotted on the throat and to some degree on the venter. However, *Varanus bushi* **sp. nov.** is usually less heavily pigmented than typical *V. caudolineatus*, with smaller and less intense spots. The lower back and basal portion of the tail are distinctly banded in *V. bushi* **sp. nov.** but more irregularly patterned in *V. caudolineatus*. Body proportions also distinguish the two species, *V. bushi* **sp. nov.** having a more elongate body form with more numerous presacral vertebrae, higher ventral scale counts, more elongate dorsal primary scales, and relatively shorter fore- and hind-limbs. Although tail length is quite variable in both taxa, the majority of *V. caudolineatus* have proportionally shorter tails than *V. bushi* **sp. nov.** The head is also shorter and stockier in *V. caudolineatus*, produced mainly by a shortening of the rostrum. Midbody scale counts are typically higher in *V. bushi* **sp. nov.** and the hemipenes differ in several important details from those of *V. caudolineatus*.

The evolutionary polarity of most of the morphological characteristics that distinguish each of the three members of the *V. caudolineatus* species group is uncertain. Sprackland (1991) suggests that more heavily rugose tails and smaller body size are probably apomorphic within *Odatria*. On both counts, *V. caudolineatus* would rate as more derived than either of the other taxa. *Varanus caudolineatus* appears to be more primitive in hemipeneal morphology than either *V. bushi* **sp. nov.** or *V. gilleni*; of the latter two species, *V. gilleni* possesses a more derived hemibacular morphology.

Taxonomic remarks: Although the type specimens of *Varanus caudolineatus* Boulenger, 1885 and *Varanus gilleni* Lucas & Frost, 1895 were not examined as part of this study, the type localities of each of these taxa [Champion Bay, W.A. (= Geraldton) and Charlotte Waters, N.T.; see Fig. 9] is remote from the known geographic range of *V. bushi* **sp. nov.** and well within the ranges of these other taxa as currently understood. We are therefore confident that the various names are correctly associated with the biological entities as defined herein.

Ecological notes: Relatively little information is available on the ecology of Pilbara varanids and the new taxon is no exception. Most recent specimens of *V. bushi* **sp. nov.** have been taken from fallen or standing hollow trees in mulga or eucalypt woodland associations.

The sex ratio among the total sample of *V. bushi* **sp. nov.** is 34 males to 13 females. This situation is typical for opportunistically collected samples of varanids (King and Rhodes 1982; Greer 1989) and probably reflects different activity patterns between the sexes. The lack of immature specimens of *V. bushi* **sp. nov.** and the small numbers of very young individuals in the large samples of *V. caudolineatus* and *V. gilleni* is consistent with

previous comment that hatchling varanids are especially cryptic and poorly represented in wild caught samples (Horn and Visser 1991).

Identifiable stomach contents were observed in two of four *V. bushi* **sp. nov.** examined by D.J. King. WAM R73142 (male, SVL 96 mm) contained remains of a spider and a skink tail; WAM R54230 (male, SVL 135 mm) contained remains of a mole cricket (Gryllotalpidae).

Discussion

Taxonomy and distribution

Storr's assessment of the Pilbara goannas named herein as *V. bushi* **sp. nov.** was remarkably prescient. Our molecular analyses have confirmed his suggestion that the Pilbara taxon is closely related to each of *V. caudolineatus* and *V. gilleni*; and further, that it possesses a suite of morphological characters that are found in differing combinations with each of these taxa. However, whereas Storr elected to include the Pilbara populations in *V. caudolineatus*, we found that they are more closely affiliated with *V. gilleni*, both genetically and morphologically. Most critically, in each of the various molecular analyses, the various Pilbara individuals group consistently with *V. gilleni* to the exclusion of those referred to *V. caudolineatus*. Furthermore, while the phylogenetic significance of the various morphological features is less clearcut, the Pilbara goannas and *V. gilleni* are at least phenetically more alike in such features as basic meristics, body proportions and organisation of body patterning. In contrast, special resemblance with *V. caudolineatus* is limited to the overall 'spottier' appearance of these taxa in comparison with the more regularly banded *V. gilleni*.

Given the close resemblance of the Pilbara populations to *V. gilleni*, it is prudent to consider whether the Pilbara populations might not be included within an expanded *V. gilleni*. We have decided against this course of action for three reasons. The first is the observation of reciprocal monophyly between these groups in each of the MP and ME analyses of the molecular data. The second is the consistent morphological differences observed between the two groups, including the apparent differences in presacral vertebral number and hemipeneal morphology. The third is the lack of any observable geographic variation in either *V. bushi* **sp. nov.** or *V. gilleni* across their extensive geographic ranges. These observations justify the conclusion that *V. bushi* **sp. nov.** and *V. gilleni* represent evolutionarily divergent, integrated lineages and thus qualify as distinct species under a Phylogenetic Species Concept (Nixon and Wheeler, 1990).

The range of *V. caudolineatus* is essentially the mulga woodlands of the Yilgarn Plateau, with vouchered records stretching from the Carnarvon Basin coastline in the west to Mt Winderra, Cosmo Newbery, Yelma and The Well Spring in the east (Fig. 9; see also Thompson 2004). As noted earlier, *V. caudolineatus* is regionally sympatric with *V. bushi*

sp. nov. in several areas including the vicinities of West Angelas and Hope Downs (Fig. 9). Both localities have yielded one specimen of each taxon. Those from West Angelas are an adult *V. caudolineatus* of typical form (WAM R138950) and one immature *V. bushi* **sp. nov.** (WAM R138949), the latter showing a high ventral scale count (89) and a finely spotted dorsal pattern combined with a banded lower back and tail base. The specimens from Hope Downs (*V. caudolineatus*: WAM R140705; *V. bushi* **sp. nov.**: WAM R135340) are both adults and of typical form. The range of *V. caudolineatus* also approaches that of *V. bushi* **sp. nov.** along the southern margin of the Pilbara Uplands, with records of *V. caudolineatus* from the Ophthalmia Range (WAM R73624) and the vicinity of Turee Creek (WAM R25149). Two records of *V. caudolineatus* from Jiggalong Mission (WAM R13362, collected by E. Lindgren, June 1959; R26068-26070, collected by R. Kirkby, 20 November 1965) on the northeast margin of the Pilbara are here treated with scepticism as specimens obtained at the mission may have been gathered from quite far afield. More intensive field survey and genetic sampling in these areas is needed to clarify the extent of range overlap, the ecological basis of sympatry if it is observed, and the nature and extent of any genetic interaction between them.

The range of *V. gilleni* spans the inland sandy deserts of central and Western Australia, extending to the Ninety Mile Beach of the Great Sandy Desert [Fig. 9 and Horn (2004)]. The nearest records of *V. gilleni* to the Pilbara uplands are from 45 km NW of Mt Crofton, to the north (WAM R82606-82607), and from Beyondie in the Little Sandy Desert to the southeast (WAM R102728). The latter population also represents the nearest point of contact between the range of *V. gilleni* and *V. caudolineatus*. A very disjunct early specimen of *V. caudolineatus* from 'Well 29, Canning Stock Route' (WAM R3903, collector O. H. Lipfert, no date) falls well outside of an otherwise compact range and cannot be accepted without verification.

Varanus bushi **sp. nov.** is regionally sympatric across the Pilbara Uplands with five members of the subgenus *Odatria*: *V. acanthurus*, *V. brevicauda*, *V. eremius*, *V. pilbarensis* and *V. tristis* (Storr *et al*. 1983; Cogger 2000). Within this regional guild, *V. brevicauda* is significantly smaller (maximum SVL 126 mm; Thompson and Withers 1997) than the others, while *V. tristis* is significantly larger (maximum SVL 290 mm; Thompson and Withers 1997). Four of the species are essentially terrestrial or saxicolous—*V. acanthurus* and *V. pilbarensis* are associated with rocky habitats, the latter exclusively so, while *V. brevicauda* and *V. eremius* are found in spinifex hummock grasslands, usually on sandy substrate. *Varanus tristis* is perhaps closest to *V. bushi* **sp. nov.** in general ecology, combining arboreality with a willingness to utilise either hollow trees or rock piles as retreats (Pianka 1971; Greer 1989; Cogger 2000). Interestingly enough, the geographic range of *V. tristis* overlaps that of all three members of the *V. caudolineatus* species group. Morphologically, it differs from members of this group in attaining greater maximum body size and in having proportionally longer limbs (Thompson and Withers 1997). More detailed field studies of these and other small to medium-sized varanids are required

before we can begin to understand the ecological phenomena that regulate patterns of syntopic coexistence within these guilds of morphologically conservative lizards.

Analysis of size and body shape in varanids

Varanids are often characterised as being extremely uniform in body proportions, with size differences being the major factor separating the species (Greer 1989; Pianka 1995). Thompson and Withers (1997) presented the most detailed examination of this issue to date, based on morphometric analysis of 17 species. They also reported sexual dimorphism in several *Varanus* species including *V. caudolineatus* but were unable to decide whether "males had proportionally longer appendages, or alternatively, the TA (BL of this study) of females was proportionally longer than for males". In any case, their subsequent analysis of interspecific variation used pooled-sex samples.

Our analysis of morphometric and meristic variation in large samples of *V. caudolineatus* and *V. gilleni* has led us to conclude that females are smaller overall than males in both species, but have more elongate torsos, perhaps as an adaptation for carrying the relatively large egg clutch typical of small varanids (King and Green 1993a). Although interpretation of proportional differences of this kind is often highly ambiguous, we believe that the evidence in this case is quite strong. Our principal argument derives from the parallel meristic analysis that shows pronounced sexual dimorphism in ventral scale counts in both species. However, other support comes from the apparent sexual dimorphism in vertebral number and the observation that analyses based on HNL produced a more consistent and biologically intelligible result than analyses based on BL. Even better results might be obtained by using either head length or neck length alone, rather than the composite HNL.

Thompson and Wither's (1997) analysis of body size and shape among varanids revealed patterns of morphometric variation that appear to correlate with habitat association and foraging mode. However, we suspect that their results may be clouded somewhat by their use of pooled sex samples and their use of a sexually dimorphic parameter (TA; our BL) as a 'size/age estimator'. In view of the potential significance of this group of lizards as a 'model system for examining patterns of size evolution' (Pianka 1995), we believe that further analysis is warranted, perhaps with closer attention to the potential use of external meristic and osteological characters as independent makers of sexual dimorphism.

Acknowledgements

We thank all of the collectors who provided specimens, especially Greg Harold who has long championed the distinctiveness of the Pilbara monitors. In addition we thank Brad Maryan (W.A. Museum) who assisted with many aspects of this study, Angela Frost (Uni.

Queensland) who produced the photographic plates, and David Grice (CSIRO, Division of Sustainable Ecosystems) who assisted with statistical analyses. Robert Browne-Cooper generously supplied a photograph of a live individual of the new species. A grant from the Flinders University ARC small grants scheme supported the molecular studies of Fitch. The manuscript was completed with the support of CSIRO, Division of Sustainable Ecosystems, Canberra, and was improved on the basis of critical comments from Stephen Donnellan (South Australian Museum) and Tony Arthur (CSIRO, Division of Sustainable Ecosystems). Any remaining inadequacies are solely our responsibility.

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Appendix I — Specimens included in the molecular analyses

Institutional prefixes are explained in Methods. HS indicates a residential homestead; MS a mine site. Localities are in Western Australia unless otherwise indicated.

V. caudolineatus: SAM R29255, Leonora, 28°53'S 121°20'E; WAM R102098, Wongida Well, Barlee Range, 22°58'S 115°51'E; WAM R122576, R122622, 6 km W of Meedo HS 25°42'38"S 114°35'58"E.

V. bushi **sp. nov.**: WAM R108999, Marandoo 22°37'S 118°08'E; WAM R125105, Wandicoogina 22°43'08"S 119°03'07"E; WAM R125520-1, unspecified locality in northern Pilbara; R129912, West Angelas MS, 100km NE of Newman 23°11'09"S 118°45'16"E; WAM R131751, Four Corners Bore, Hamersley 22°26'43"S 117°52'47"E; WAM R135340, Hope Downs 22°40'S 119°24'E.

V. gilleni: NTM R13778, unknown locality in Northern Territory; SAM R35961, Alka Seltzer Bore, South Australia 26°18'S 136°01'E; WAM R102728, Little Sandy Desert 24°35'33"S 120°15'47"E.

V. storri: SAM R54351, Mt Isa, Queensland 22°44'S 139°28'E; AMS R125956, Kununurra 15°47'S 128°44'E.

Appendix II — Specimens included in the morphological analysis

All specimens are registered in the collection of the Western Australian Museum. HS indicates a residential homestead; MS a mine site. All localities are in Western Australia unless otherwise indicated.

Varanus caudolineatus

Males: R330 – 331, R10812 Quinns 27°04'S 118°38'E; R1191 Warriedar, via Yalgoo 29°08'S 117°11'E; R3415 – 3416 Laverton 28°38'S 122°24'E; R3818 Narloo, via Wurarga 28°19'S 116°11'E; R4732 Gullewa, via Yalgoo 28°39'S 116°19'E; R4933 Murchison Downs 26°48'S 118°39'E; R5048 Marilla 22°58'S 114°28'E; R7378 Belele, via Meekatharra 26°22'S 117°38'E; R8168 Warroora 23°29'S 113°48'E; R10611 Minilya 23°51'S 113°58'E; R13362, 26069 Jiggalong Mission 23°22'S 120°47'E; R14918 11 km S of Cue 27°32'S 117°54'E; R15785 Ejah Paddock, Mileura 26°22'S 117°20'E; R15789 Charlies Creek, Mileura 26°22'S 117°20'E; R19771 Kathleen Valley 27°24'S 120°39'E; R21100 32 km NE of Yelma HS 26°20'S 121°56'E; R21137 24 km SW of Wiluna 26°45'S 120°03'E; R21139 70 km SW of Wiluna 27°03'S 119°43'E; R21150 51 km SW of Sandstone 28°18'S 118°56'E; R22652 Fields Find 29°02'S 117°15'E; R22995 Ajana 27°57'S 114°38'E; R25149 2 Miles SE of Turee Creek 23°38'S 118°40'E; R26320 'Greenough' (probably Eastern Goldfields) 30°45'S 121°30'E; R28028 The Well Spring 25°01'S 121°35'E; R28290 Albion Downs 27°17'S 120°23'E; R28394, 28955 Coordewandy 25°36'S 115°58'E; R30967 – 30968 Albion Downs (within 13 km of HS) 27°17'S 120°23'E; R31381 – 31385 35 km NE of Mingenew 28°58'S 115°42'E; R34563, 39765 Callagiddy, 32 km SE Of Carnarvon 25°03'S 114°02'E; R34685 64 km N of Beacon. 29°53'S 117°52'E; R41793 Kalli, near Cue 26°54'S 117°07'E; R47347 Byro 26°05'S 116°09'E; R48151 5 km NW of Kirkalocka HS 28°32'S 117°43'E; R48152 16 km S of Mt Magnet 28°14'S 117°51'E; R49943 Woodleigh 26°11'S 114°33'E; R49992 Wilroy Reserve, 19 km S of Mullewa 28°44'S 115°30'E; R51092 60 km S of Leonora 29°25'S 121°20'E; R51189 1 km N of Orabanda 30°22'S 121°04'E; R52893, 52894, 52896 Mt Augustus 24°18'S 116°55'E; R54594 15 km E of Hamelin Pool 26°22'S 114°20'E; R54595 Wooramel HS 25°44'S 114°17'E; R57378 Woodleigh 26°11'S 114°33'E; R59607 20 km ENE of Meadow Station HS 26°39'S 114°48'E; R59620 34 km SSE of Nerren Nerren 27°19'S 114°51'E; R60130 Youanmi 28°37'S 118°50'E; R60429 2 km S of Overlander 26°26'S 114°28'E; R60642 13 km W of Mungawolagudi Claypan 26°48'S 115°19'E; R62865 22 km SE of Mt Keith 27°19'S 120°40'E; R64436 Cooloomia HS 26°57'S 114°18'E; R65820 12.0 km ENE of Comet Vale 29°54'25"S 121°14'05"E; R65883 8.3 km SSE of Mt Linden 29°23'20"S 122°28'05"E; R65886 8 km SSE of Mt Linden 29°23'00"S 122°27'30"E; R65961 2.5 km N of Mt Linden 29°18'20"S 122°25'00"E; R69118 18.5 km ENE of Yuinmery HS 28°31'55"S 119°11'35"E; R69315 12.5 km SSE of Banjawarn HS 27°47'55"S 121°40'55"E; R70831 24 km at 333°N from Mt Windarra 28°18'S 122°07'E; R70895 3.5 km at 5°N from Yowie Rockhole 30°26'30"S 122°21'00"E; R71062 Billabong Roadhouse 26°49'S 114°37'E; R72653 – 72654 Comet Vale 29°55'S 121°35'E; R72830 7.75 km SE of Mt Linden 29°22'55"S 122°27'05"E; R72892 7.75 km SSE of Mt Linden 29°22'55"S 122°28'05"E; R73223 2 km at 15°N from Yowie Rockhole 30°27'30"S 122°21'00"E; R73309 5.5 km at 137°N from Black Flag 30°35'30"S 121°16'30"E; R73433 9 km at 190°N from Mt Elvire HS 29°26'30"S 119°35'00"E; R73624 Ophthalmia Range 23°17'S 119°07'E; R74671 18.5 km ENE of Yuinmery 28°31'55"S 119°11'35"E; R78488 7 km NE of Yowie Rockhole 30°25'S 122°22'E; R78545 21 km SE of Mt Keith 27°19'S 120°40'E; R81917 Jibberding 29°51'30"S 116°58'00"E; R81922 White Well, 6 km W of Jibberding 29°53'S 116°55'E; R84443 14 km S of Dromedary Hill 29°11'S 118°24'E; R85239, 85241 Dead Horse Rocks 29°22'S 121°17'E;

R87661 13 km SSW of Mt. Phillip HS 24°31’S 116°14’E; R87770 12 km SW of Yinnietharra 24°45’S 116°06’E; R92900 14 km SW of Hamelin HS 26°30’49”S 114°05’44”E; R94715 Agnew 28°01’S 120°31’E; R95287 7 km N of Goolthan Goolthan Hill 28°03’S 116°44’E; R97786 Yoothapinna 26°32’S 118°30’E; R122622 6 km W of Meedo HS 25°42’38”S 114°35’58”E; R123783 14.5 km W of Pells Creek 25°07’09”S 115°25’36”E; R129980 Mt Joel 27°17’55”S 121°03’15”E; R129984 Mandilla Well 27°31’05”S 121°07’21”E; R131829 Lake Carey 29°10’S 122°21’E; R132181 Bandya Hill area 27°50’S 122°15’E; R132507 Jundee 26°35’59”S 120°47’57”E; R135601 Lake Carey 28°50’49”S 122°18’39”E; R138950 West Angelas 23°11’46”S 118°31’10”E; R140705 Hope Downs 22°40’25”S 119°24’58”E.

Females: R3423 Laverton 28°38’S 122°24’E; R3903 Well 29.Canning Stock Route 22°33’S 123°53’E; R4934 Murchison Downs 26°48’S 118°59’E; R7379 Belele via Meekatharra 26°22’S 117°38’E; R8167 Warroora 23°29’S 113°48’E; R12407 Kathleen Valley near Lenora 27°24’S 120°39’E; R13711 Overlander Roadhouse 26°24’S 114°28’E; R13857 Cosmo Newbery 28°00’S 122°54’E; R14240 Kalgoorlie 30°44’S 121°28’E; R14917 27 km E of Marillana 22°38’S 119°40’E; R15786 – 15788 Ejah Paddock, Mileura 26°22’S 117°20’E; R17681 Mt Margaret 28°48’S 122°11’E; R19600 Cosmo Newbery Mission 28°00’S 122°54’E; R21138 70 km SW of Wiluna 27°03’S 119°43’E; R21149 35 km N of Sandstone 27°40’S 119°18’E; R21178, 21179, 21181 11 km SW of Youanmi 28°41’S 118°44’E; R22870 Yalgoo 28°21’S 116°41’E; R25883 Ajana 27°57’S 114°38’E; R26068, 26070 Jiggalong, vicinity of Mission 23°22’S 120°47’E; R27231 Kathleen Valley, Wanjarri 27°19’S 120°33’E; R28956 Coordewandy 25°36’S 115°58’E; R29111 32 km S of Mt Magnet 28°21’S 117°51’E; R30969 Albion Downs, within 13 km of HS 27°17’S 120°23’E; R31681 14 km S of Menzies 29°49’S 121°02’E; R34564 Callagiddy, 32 km SE of Carnarvon 25°03’S 114°02’E; R39043 Youanmi 28°37’S 118°50’E; R44529 Woodleigh 26°11’S 114°33’E; R47374 Sandstone 27°59’S 119°18’E; R47793 30 km SE of Bulloo Downs 24°13’S 119°47’E; R49993 Wilroy Reserve, 19 km S of Mullewa 28°44’S 115°30’E; R52895 Mt Augustus 24°19’S 116°55’E; R57377 Woodleigh 26°11’S 114°33’E; R62866 – 62867 21 km SE of Mt Keith 27°18’S 120°40’E; R63655 25 km NW of Winning HS 22°56’S 114°27’E; R69293 9.5 km SSE of Banjawarn HS 27°46’55”S 121°39’45”E; R69295 12.5 km SSE of Banjawarn HS 27°47’55”S 121°40’55”E; R72749 12.25 km ENE of Comet Vale 29°55’25”S 121°14’35”E; R72893 7.75 km SSE of Mt Linden 29°22’55”S 122°28’05”E; R74689 8 km ENE of Yuinmery 28°31’15”S 119°05’30”E; R75858 Coomalbidgup, Lort River 33°43’S 121°22’E; R78546 21 km SE of Mt Keith 27°19’S 120°40’E; R78582 Mt Windarra area 28°29’S 122°14’E; R84028 37 km SE of Ashburton Downs HS 23°38’S 117°18’E; R85240 Dead Horse Rocks 29°22’S 121°17’E; R87637 12 km SW of Yinnetharra HS 24°45’S 116°06’E; R87754 4 km NNE of Mt. Phillip HS 24°23’S 116°19’E; R88098 11 km N of Nerren Nerren HS 27°02’S 114°38’E; R91684 15 km N of Karalunde 26°00’S 118°41’E; R95527 3 km S of Nannowtharra Hill 28°18’S 117°00’E; R101298 2 km N of Kathleen Valley shearing shed, Wanjarri Nature Reserve 27°20’S 120°39’E; R116670 Black Range, 15 km WSW of Marangaroon 23°47’18”S 115°28’02”E; R117117 Upper Gascoyne 24°43’S 116°04’E; R122854 5.6 km E of Mardathuna HS 24°26’35”S 114°30’42”E; R125540 Randall Well, 210 km NNE of Meekatharra” 25°21’S 119°24’E; R125889 31.2 km from Binthalya HS 24°31’23”S 114°57’56”E; R138077 10 km SE of Mt Augustus HS 24°29’S 116°54’E 140714 Hope Downs 22°40’25”S 119°24’58”E.

Unknown sex: R3881 Well 5, Canning Stock Route 25°22’S 121°00’E; R7279 Caron 29°35’S 116°19’E; R8257 Grants Patch 30°27’S 121°07’E; R12278 Mundiwindi 23°48’S 120°15’E; R19789 – 19790 Albion Downs 27°17’S 120°23’E; R21180 11 km SW of Youanmi 28°41’S 118°44’E; R23908 – 23910 Laverton 28°38’S 122°24’E; R37897 Callagiddy 25°03’S 114°02’E; R46618 Yarri Battery, NE of Kalgoorlie 29°47’S 122°22’E; R46621 Linden 29°18’S 122°25’E; R47630 Macquarie Mill, Mileura 26°22’S 117°20’E; R47794 23 km NW of Mt Bruce 22°30’S 117°58’E; R51157 5 km S of Warriedar HS 29°12’S 117°11’E; R66004

7.75 km SSE of Mt Linden 29°22’55”S 122°28’05”E 78594 22 km S of Mt Elvire HS 29°33’S 119°36’E; R96122 – 96125 Millrose area 26°10’S 120°43’E; R96679 17 km WNW of Wadina HS 27°56’S 115°28’E; R100314 Mt Lawrence Wells 26°48’S 120°12’E; R102016 5.4 km N of Joy Helen MS 23°14’15”S 115°46’23”E; R102098 Wongida Well, Barlee Range” 22°58’S 115°51’E; R115204 Eurardy 27°34’S 114°40’E; R122576 1.9 km W of Meedo HS 25°40’50”S 114°37’18”E; R125186 31.2 km from Binthalya HS 24°31’23”S 114°57’56”E; R127246 130 km NW of Mount Magnet 27°42’S 117°05’E.

Varanus gilleni

Males: R3970 Well 37, Canning Stock Route 22°09’S 125°27’E; R8715 Well 43, Canning Stock Route 21°12’S 125°59’E; R14653, 14654, 14656 Warburton Range 26°08’S 126°35’E; R14657 Newbore, 45 km NW of Warburton Mission 25°40’S 126°15’E; R15707 32 km SE of Warburton Range 26°20’S 126°48’E; R20608, 22007, 22021, 22022, 22211, 22212 Warburton Mission 26°08’S 126°35’E; R21000 – 21001 10 km SE of Warburton Range Mission 26°12’S 126°39’E; R28027 Injudinah Creek, La Grange 18°38’S 121°52’E; R28814 14 km NW of Mt Beadell 25°47’S 124°38’E; R28864 77 km SW of Mt Beadell. Sutherland Range 26°01’S 124°44’E; R40111 60 Miles E of No.24 Well, Canning Stock Route 23°22’S 124°08’E; R45768 – 45769 Between Emily Gap and Amoonguna, near Alice Springs 23°14’S 133°59’E; R46166 Anna Plains 19°15’S 121°29’E; R54073 Edgar Ranges Reserve 18°55’S 123°15’E; R57047 30 km NNE of Stretch Range 20°44’S 127°51’E; R57304 McLarty Hills 19°29’S 123°28’E; R63421 Twin Heads 20°15’S 126°32’E; R63960 Well No 30, Canning Stock Route 22°30’S 124°08’E; R75808 Nita Downs 19°05’S 121°41’E; R81443 Wildlife Well 22°53’S 125°10’E; R82606 approx. 45 km NW of Mt Crofton 21°25’S 121°45’E; R88546 55 km S of Anna Plains HS 19°44’S 121°28’E; R100593 15 km SSW of Giles 25°05’S 128°20’E; R101434 Plumridge Lakes Nature Reserve 29°36’S 124°54’E; R102728 Little Sandy Desert 24°35’33”S 120°15’47”E; R108565 7–8 km WSW of Point Salvation 28°15’S 123°36’E.

Females: R3995 Well 49, Canning Stock Route 20°10’S 126°41’E; R14655 Warburton Range 26°08’S 126°35’E; R15179 Elder Creek, 8 km NNW of Warburton 26°03’S 126°33’E; R15706, 15708 32 km SE of Warburton Range 26°20’S 126°48’E; R24437 16 km S of Ewaninga HS, Northern Territory 24°08’S 133°56’E; R26714 No locality but probably SW Kimberley 17°30’S 123°30’E; R46165, 46167 Anna Plains 19°15’S 121°29’E; R47674 Point Massie, Canning Stock Route 20°43’S 126°30’E; R53787 – 53789 near Alice Springs 23°42’S 133°52’E; R57302 – 57303 McLarty Hills 19°29’S 123°28’E; R60135 Injudinah Creek, La Grange 18°38’S 121°52’E; R63959 Well No. 30, Canning Stock Route 22°30’S 124°08’E; R64202 2 km at 90°N from Murguga Well No39, Canning Stock Route 21°45’S 125°40’E; R67579, 94371 Balgo Mission 20°09’S 128°57’E; R75791 24 km W of Joanna Spring 20°05’S 123°55’E; R75792 Dragon Tree Soak 19°39’S 123°23’E; R82607 approx. 45 km NW of Mt Crofton 21°25’S 121°45’E; R100859 10 km N of Charlies Knob 23°05’S 125°00’E.

Unknown sex: R3998 between Wells 49 and 50, Canning Stock Route 20°12’S 126°50’E; R4020 between Wells 39 and 51, Canning Stock Route 20°50’S 126°10’E; R19598 – 19599 Warburton Range 26°08’S 126°35’E; R40887 Mt Romilly, Canning Stock Route 20°28’S 126°30’E; R45262 Well 40, Canning Stock Route 21°40’S 125°47’E; R46123 32 km SW of Christmas Creek HS 19°05’S 125°43’E; R54125 Edgar Ranges 18°49’S 123°17’E; R67578 Balgo Mission 20°09’S 128°57’E; R102674 Little Sandy Desert 24°04’46”S 120°20’15”E; R112140 Warburton 26°08’S 126°35’E; R136033 Little Sandy Desert 24°55’50”S 120°31’18”E; R136034 Little Sandy Desert 24°35’33”S 120°15’47”E.

***Varanus bushi* sp. nov.**

Males: R4288 Tambrey 21°38’S 117°36’E; R54230 Marandoo 22°37’S 118°08’E; R73142 26.6 km at 225°N from Marillana HS 22°48’17”S 119°13’30”E; R76453 10 km SSW of Cooya Pooya HS 21°07’S 117°07’E; R108999 Marandoo 22°37’S 118°08’E; R125105 Yandicoogina 22°43’08”S 119°03’07”E; R125520 – 125521 northern Pilbara region 21°30’S 117°30’E; R129632 120 km NW of Newman 22°57’S 119°21’E; R129912, 138949 West Angelas MS, 100 km NE of Newman 23°11’09”S 118°45’16”E; R131494 Mt Whaleback 23°22’31”S 119°38’25”E; R135467 Mt Brockman area 22°28’S 117°18’E; R145260 5 km S of Mt Tom Price MS 22°49’02”S 117°45’50”E.

Females: R20241 near Kangiangi HS 21°41’S 117°17’E; R56834 Marandoo 22°37’S 118°08’E; R73143 26.6 km at 225°N from Marillana HS 22°48’17”S 119°13’30”E; R127789 5 km S of Mount Tom Price MS 22°47’49”S 117°47’20”E; R131037 Unknown locality; R135340 Hope Downs 22°40’S 119°24’E.

Unknown sex: R62171 Marandoo 22°37’S 118°08’E; R75834 Weano Gorge 22°22’S 118°15’E; R131751 Four Corners Bore, Hamersley 22°26’43”S 117°52’47”E; R138169 Hamersley Range National Park 22°35’S 118°12’E.