A new *Platysaurus* (Squamata: Cordylidae) from the Northern Cape Province, South Africa

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A new species of Platysaurus *is described from the Gordonia-Kenhardt district of Northern Cape Province, South Africa. Numerous features of scalation and colouration distinguish it from all other southern African* Platysaurus. *The new species is morphologically most similar to, and was previously confused with,* P. capensis *from northern Namaqualand, the Richtersveld and southern Namibia. There is no evidence for genetic exchange between the new species and* P. capensis, *which are separated by 100 km. Therefore, based on allopatry, the presence of two autapomorphies (dorsal forelimb scales subequal to those on hindlimb and unique male colouration), and significant differences in eight other scalation features, the Augrabies population meets the criteria for designation as a new species within an evolutionary species concept. These lizards occur in very high densities in the Augrabies Falls National Park where black flies (*Simulium *spp.) form a major food resource.*

Introduction

Flat lizards (*Platysaurus*) are a genus of colourful rupicolous cordylids that have undergone adaptive radiation on isolated granite, gneiss and sandstone outcrops, mainly in the northern and eastern regions of the African subcontinent (Broadley 1978; Branch 1988a). *Platysaurus capensis* Smith 1844 was the first species to be described. The genus was reviewed by FitzSimons (1943), Loveridge (1944) and Broadley (1978). Broadley described nine new taxa (species and subspecies) from south-eastern Africa (reviewed in Broadley 1978), and subsequently described a new taxon from eastern Botswana (Broadley 1982). Recently, Jacobsen & Newbery (1989) and Jacobsen (1994) reviewed the taxonomy of "Transvaal" forms, also describing several new taxa. As presently understood the genus contains 14 species of which 11 are endemic to southern Africa. Only a few species contain currently recognized subspecies: *P. intermedius* (9), *P. orientalis* (2) and *P. pungweensis* (2). Jacobsen (1994) noted significant geographical variation associated with several subspecies of *P. intermedius*, and a re-assessment of this species will almost certainly result in the recognition of further species.

Female and juvenile colouration within *Platysaurus* has remained conservative and varies marginally among species. *Platysaurus ocellatus* is the only exception, where females and juveniles never have the three pale longitudinal stripes found in all other species (Broadley 1978). Conversely, the scope of male colouration is broad and together with distribution, is the most important trait used in species level identification. Sexual dichromatism is evident in many lizard species, and may function in sex recognition, sexual behaviour (including mate choice and intraspecific agonistic behaviour) and the maintenance of reproductive isolation among closely related syntopic species (see review by Cooper & Greenberg 1992).

A dorsally-compressed body has enabled *Platysaurus* to exploit narrow rock fissures both as retreat sites and probably as havens from predators (escape success from predators within rock fissures has not been quantified). Due to their high degree of specialization on rocky outcrops *Platysaurus,* in general, appear to be poor dispersers (Jacobsen 1994). However, individuals of the new species described here were occasionally observed traversing small expanses of sand on their way to other rocky areas, generally to feed (MJW pers. obs.). Nonetheless, these movements were minor, and fragmentation of rocky habitats, thought to be a result of eastward movement of Kalahari sands, has created an "island effect" that appears to have promoted rapid speciation within the genus (Broadley 1978).

While reviewing *P. capensis*, Broadley (1978) initially considered the Augrabies Falls National Park

(hereafter Augrabies) population to warrant subspecific recognition, but delayed such recognition pending the availability of additional material. This caution was prompted by a series of specimens from Goodhouse, collected by FitzSimons (1938), that appeared intermediate in at least one scalation feature, i.e. number of subdigital lamellae of the 4th toe, considered by Broadley (1978) to be diagnostic of the putative taxa. Unfortunately Broadley (1978) examined no fresh Augrabies material and was therefore unaware that these differences were further supported by important differences in male colouration (Figure 1) between this population and those further west.

The subsequent availability of additional material resulting from surveys of the region, have permitted a re-evaluation of the complex. The purpose of this paper is to describe the eastern population (largely Augrabies) as a new species, based on a re-analysis of characters and using criteria delineated in the modified evolutionary species concept of Frost & Hillis (1990). No names applicable to the eastern population are available within the synonymy of *P. capensis* (Broadley 1978), permitting us to designate a new name.

Materials and Methods

Lizards were collected under permits issued by the Directorate of Nature Conservation of the Western Cape Province and the Director of National Parks of South Africa. Specimens were euthanised with pentobarbital, fixed in 4 % neutral-buffered formaldehyde, and stored in either 70 % ethanol or 55 % isopropanol. All new material was accessioned into the collections of the California Academy of Sciences, San Francisco (CAS), Port Elizabeth Museum, Humewood (PEM), Transvaal Museum, Pretoria (TM) and Museum of Natural Science, Louisiana State University, Baton Rouge (LSUMZ). Measurements were made to the nearest 0.01 mm using Sharpe & Brown Digi-Cal digital calipers.

Details of scalation and measurements follow Broadley (1978). Dorsal scale rows are recorded at midbody, and do not include intervening granules (i.e. minute scales less than 25 % the diameter of adjacent body scales). Counts of ventrals in transverse series at midbody start and end with the lateral ventral whose lateral midline margin is subequal to that of its midline neighbour. Scale counts on the upper right forelimb were taken along a line from the middle of the dorsal limb insertion, along the length of the humerus to the outer edge of the elbow. Two to three rows of very small granules at the limb insertion were not counted; neither were minute granules occasionally located between the scales on the limb. Head scale counts were recorded for both sides of an individual and the mean count used in subsequent analysis.

Prior to data analysis lizards were allocated to the following pre-defined groups (Figure 2): East (new species), Richtersveld, Namaqualand, Namibia, and West (encompassing the last three areas). Meristic and morphological variables were all log transformed prior to a two-way ANOVA by sex and location. For this analysis only lizards with SVLs of 68 mm or greater were used, thereby allowing accurate identification of sex. Differences in the frequency of specific scales or scale conditions were analyzed using the Kolmogorov-Smirnov and chi-square tests. The following variables, for which a complete data set was available, were subjected to a discriminant function analysis: Snout-vent length (SVL), supralabials anterior to subocular, number of scales in the collar (which may be split in the midline), longitudinal rows of ventrals, transverse rows of ventrals, transverse rows of dorsals, upper forelimb scale rows, and the number subdigital lamellae of the 4th toe. The observed patterns from the discriminant function analysis were subjected to MANOVA. All means are reported ± 1 standard error. Differences were considered significant at alpha < 0.05.

Results and Discussion

Allocation of Smith's name: Smith's (1844) type locality for *Platysaurus capensis*, i.e. "Great Namaqualand", is now usually used in reference to the area North of the Orange River, i.e. southern Namibia. However, in the early part of the 19th century that general region could have encompassed the whole of the lower Orange River area, including the Augrabies region. Kirby (1965) noted that Smith must have travelled North of the Orange River as he mapped the distribution of native tribes in the area. Smith is also known to have travelled extensively in the lower Orange River region from July to September 1828, crossing the river "within 20 miles of its confluence with the sea" (probably near Arris Drift) (Kirby 1965; p. 69), and also visiting Henkries (about 10 km west of Goodhouse) (Kirby 1965). There is, however, no indication that Smith visited Augrabies or any section of the Orange River east of Goodhouse.

The vagueness of Smith's (1844) type locality was queried by FitzSimons (1943: 471, "Probably from Little Namaqualand"), Broadley (1978: 157, "presumably in error for Little Namaqualand") and Haacke (1965: 29, "A. Smith's record from Great Namaqualand is doubtful, as he never visited this area."), and requires comment. There is evidence of intraspecific morphological variation within *P. capensis*, and although the presence of a small "internasal" between the rostral and frontonasal indicates that the specimen originates from the Little Namaqualand population, this condition does occur as a rare variant elsewhere in the species' range (see Variation). Haacke (1965) is wrong in stating that Smith never visited Great Namaqualand. Kirby's (1965) documentation shows that Smith visited sites throughout the range of *P. capensis*, from Komaggasberg in Little

Namaqualand to the Fish River in southern Namibia. We therefore do not feel justified in restricting the type locality of "Great Namaqualand" to a more specific region.

Andrew Smith's (1844) holotype of *P. capensis* is still in the Natural History Museum, London (BM 1946.8.29.26). The following features examined are relevant to the allocation of Smith's name to either eastern or western populations: number of lamellae under 4th toe, 18 right, 18 left; transverse dorsals, 79; transverse ventrals, 20; femoral pores, 18 right, 17 left; supranasals separated by small internasal. The colouration is faded, but three prominent pale dorsal stripes are present; the forearm and tail are of the same colour as the dorsum, and there is an indication of a vague dark "badge" on the lower belly. Scale counts and aspects of colouration indicate that the holotype is from one of the western populations (see below). As the break between the Augrabies and western populations appears to occur east of Goodhouse, we conclude that the name *Platysaurus capensis* Smith 1844 is applicable to western populations.

Although Smith (1844) did not identify the gender of the holotype, FitzSimons (1937) considered it to be a female. This was challenged by Broadley (1978) who also examined the specimen and identified it as a subadult male, albeit with typical female markings. Subsequent re-examination of the type (facilitated by a previous dissection along the posterior ventral midline and left tail base) revealed a clear right oviduct but no hemipenis (E.N. Arnold pers. comm., 21 February 1997). The specimen is therefore undoubtedly a female.

PLATYSAURUS BROADLEYI **sp. nov.**
English: AUGRABIES FLAT LIZARD
Afrikaans: AUGRABIES PLAT AKKEDIS

Platysaurus capensis (part). FitzSimons 1935: 535; 1943: 473; Loveridge 1944: 97; Rose 1950: 155; 1962: 156; Broadley 1978: 157; Branch 1988a: 165; van Wyk & Mouton 1996: 117; Cooper et al. 1997: 9; Whiting & Greeff 1997.

Type material: *Holotype*. TM 79828, adult male collected by M.J. Whiting, 12 November 1995. *Type locality*: Augrabies Falls National Park, Gordonia District, Northern Cape Province, South Africa (28° 35'S, 20° 20'E; quarter-degree unit 2820CB; approxim. 650 m a.s.l.). *Allotype*. PEM R12466, adult female collected by W.R. Branch, 22 June 1996. 400 m West of Augrabies Falls, Northern Cape Province (28°35'34"S, 20°20'13"E; 2820CB; approxim. 559 m a.s.l.). *Paratypes* (13 specimens): TM 79831-3, 79835, 79837, 79841, 79849, 80482-4, 80509, same locality as holotype, collected by M.J. Whiting between 1 September 1995 and 20 September 1996; PEM R12467, 12578, same locality and collector as allotype.

Additional material: (48 specimens, all from the Northern Cape Province): SAM 17377 (four specimens), Baks Putz, Bakriver (2720CC), S.H. Houghton; SAM 18368 (16 specimens), Augrabies Falls National Park (2820CB), R.F. Lawrence; CAS 126053-54, 125056, Augrabies Falls National Park, T. Papenfuss; TM 28034-37, 36750, 50224-25, 50935, 50948, 56227-29, 57593, 57618, 62879, 67133, 67796, 79830, 79834, 79843, 79848, 80501, Augrabies Falls National Park (28° 35'S, 20° 20'E; 2820CB), various collectors; TM 55344, Steyers Kraal (2819DA), C. Stuart; CAS 175091, Onseepkans (granite face on southern bank of Orange River; 2819CB), A.M. Bauer; PEM 12257, Klein Pella (2819CC), G. McLachlan.

Diagnosis: A medium-sized *Platysaurus* (adult SVL: 64-84 mm) distinguished from all other congenerics, except the Cape Flat Lizard *P. capensis*, in that the scales on the side of the neck are indistinguishable from those on the dorsum. From its nearest neighbour, *P. capensis*, it differs in many features of adult male colouration (condition in male *P. capensis* in brackets), most noticeably the possession of yellow, orange, or mixed yellow-orange upper surfaces to the forelimbs (blue); a tan dorsum on the tail (orange); a dark blue throat (light blue); and an extensive black belly (blue peripherally with a relatively smaller black central patch). It also differs from *P. capensis* in having significantly different numbers of gulars, longitudinal rows of ventrals, transverse rows of ventrals, dorsal forelimb scale rows, lamellae beneath the fourth toe, collar scales, and transverse dorsal scale rows (Tables 1-3). *Platysaurus broadleyi* is further distinguished from *P. capensis* by its smaller upper forelimb scales, these being subequal to those on the hindlimb (autapomorphic); and the nostril usually (58.4 %) piercing a large nasal, the latter in contact with its counterpart behind the rostral.

Description: *Holotype*. TM 79828, a male. Head strongly depressed, much longer than broad. Head length (tip of snout to anterior border of ear-opening, HL): 16.9 mm; Head width (HW): 13.1 mm; HL/HW: 1.29). Large supranasals in contact behind rostral; nostril directed slightly backwards and piercing the upper region of a very small nasal that contacts the rostral, first supralabial, a small postnasal and the large supranasal. Frontonasal hexagonal, as broad as long and in good contact on sides with loreal. Prefrontals in median contact, with a small azygous granule at this suture, slightly posterior to its junction with the frontal. Frontal longer (3.47 mm) than broad (max. width 2.71 mm), much wider in front than behind. A pair of frontoparietals, each in contact laterally with middle pair of supraoculars. Interparietal small, diamond-shaped, set in the middle of the two pairs of parietals, the anterior pair the smallest. Occipital absent, slightly enlarged granules in its position. Four supraoculars, the

Figure 1. Male breeding colouration in *Platysaurus broadleyi* (Paratype PEM R12578; Augrabies Falls National Park). Note the prominent yellow forelimbs and tan colour on the upper surfaces of the tail and hindlimbs.

first triangular and contacting the pentagonal preocular, the last the smallest. Four supraciliaries, anterior elongate, middle pair largest. Lower eyelid with a semi-transparent disc divided into a number of vertical septa. Three temporals bordering parietals on each side, middle one largest and longitudinally elongate, twice the length of posterior one. Two additional rows of enlarged scales present in dorsal temporal region, upper row vertically elongate and more than twice the size of lower row. Ventral temporal region covered with six rows of irregular granules, slightly larger than those along backbone. A small postnasal; a loreal and a preocular, the former much smaller than the latter. Four suboculars, only the second extensively bordering the lip below. Rostral pentagonal, broader than deep (rostral width: 2.82 mm; rostral depth: 1.35 mm). Six supralabials, four anterior to subocular. Mental subpentagonal. Infralabials five, with a row of five large sublabials, the fourth by far the largest, the fifth the smallest. A longitudinal median series of five enlarged quadrangular or polygonal gular scales, remainder smaller, elongate and rectangular; towards base of throat scales become smaller (particularly laterally), subgranular and rounded, increasing again in size towards collar, which consists of eight enlarged scales. Dorsal scales smooth, small, flat and rounded, with minute granules at junctions, and largest along backbone and on flanks, smallest dorso-laterally and minute on sides. Ventrals square or a little broader than long medially, arranged in 43 mainly regular transverse and 22 longitudinal series. Eight preanal plates, median pair largest, a little larger than ventrals. Limbs long and slender, length of tibia (17.3 right, 17.2 mm left) subequal to head length. Upper forelimb and thighs with subequal granules above. Forearm and tibia with enlarged keeled scales; a row of nine large transverse plates on underside of tibia, largest at midcalf. A series of 16 femoral pores on lower surface of right thigh, 17 on left, with 4 - 5 rows of modified granular scales anterior to these pores. Tail partially regenerated (distal 51 mm), depressed, tapering, with regular whorls of elongate, quadrangular scales, feebly keeled above, more strongly keeled and often shortly spinose on sides, smooth below.

Colouration of holotype: In preservative (70 % ethanol): Blue-black dorsally; top of head lighter with three pale stripes, the median one extending from frontonasal to backbone, lateral pair extending from anterior dorsal temporal region onto dorso-lateral region, all fading on forebody; hindbody and upper surface of tail grey-tan, darker along midline, with vague, paler spots laterally. Upper surface of hind limbs grey-tan with scattered paler and darker spots; upper surface of

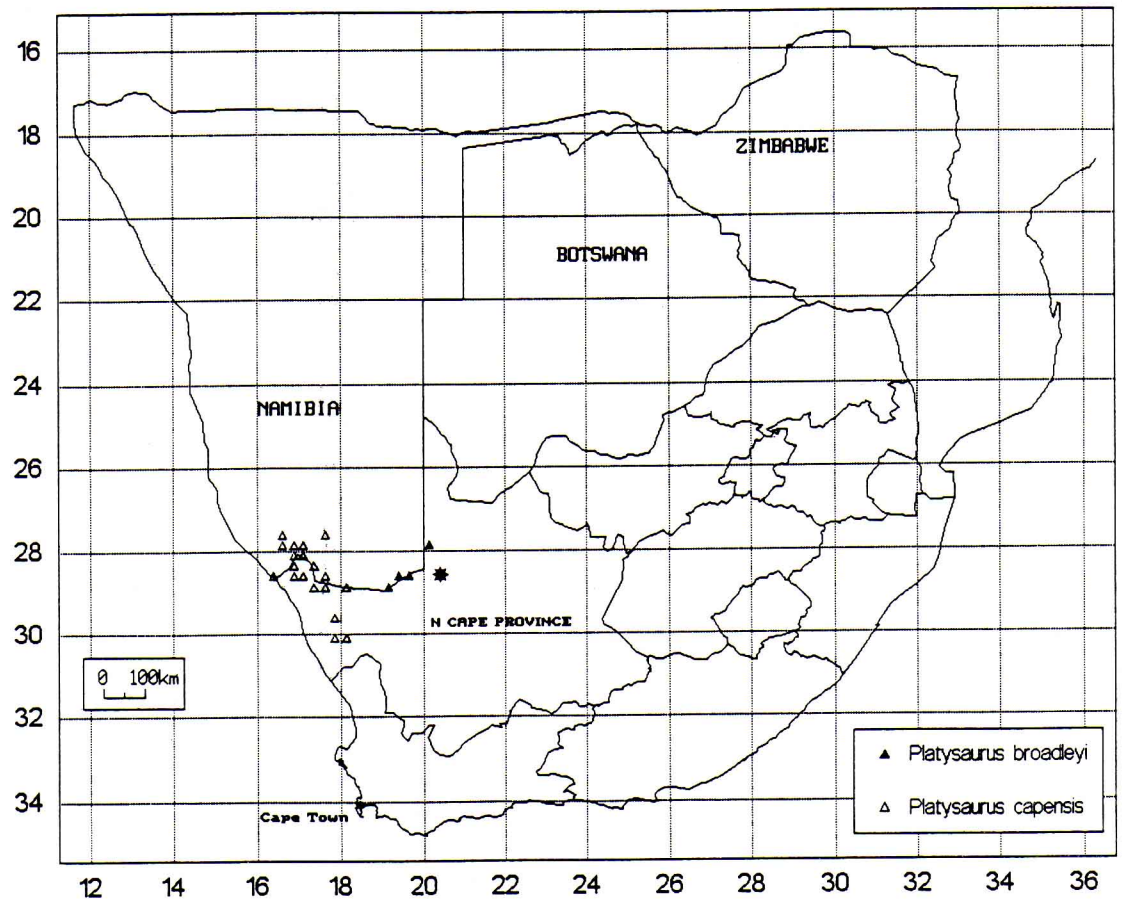

Figure 2. Distribution of *Platysaurus broadleyi* (solid triangles) and *P. capensis* (open triangles). Populations were analyzed as East (*P. broadleyi*), Richtersveld (south of Orange River excluding the three southernmost quarter degree units), Namaqualand (three southernmost quarter degree units), and Namibia (north of the Orange River); West consists of Richtersveld, Namaqualand, and Namibia combined (all *P. capensis*). Note that the southern border of Namibia is formed by the Orange River. The type locality for *P. broadleyi* (Augrabies Falls National Park; 2820CB) is indicated by the star.

forelimbs blue-green, merging to light blue on anterior and ventral surfaces. Throat, chest, belly and sides of head dark blue-black, merging to tan-pink on posterior third of belly; lower surfaces of hindlimbs, cloacal region, and tail base light pink (ivory cream on granular scales anterior to femoral pores); lower surface of tail becoming tan towards tip.

Allotype. PEM R12466, adult female with midventral incision between transverse ventral rows 15 - 28. SVL 74 mm; tail 34 mm (broken and distal portion lost); head length 17.08 mm; head width 11.12 mm; head depth 4.82 mm. Lepidosis similar to holotype with the following exceptions: supralabials in front of subocular, 5; gulars, 29; transverse rows of ventrals, 42; transverse dorsal scale rows at midbody, 116; scales on upper surface of forelimb, 28; subdigital lamellae beneath 4th toe, 22; femoral pores, 16 on both sides.

Colouration of allotype: In preservative (70 % ethanol): Grey-black dorsally; top of head lighter on snout with three pale stripes, the median one extending from frontonasal along midline and backbone, narrowing posteriorly and fading over the pelvic girdle; lateral pair extending from posterior supraciliaries onto dorso-temporal and dorso-lateral region, to fade on tail base. Throat pale grey, lightly blotched with diffuse blue-grey patches. Flanks greyish, heavily blotched with large scattered black spots and smaller pale spots. Upper surfaces of fore- and hindlimbs dark grey with large black spots that sometimes coalesce to form vague bands; lower surfaces of limbs pale cream-grey. Proximal portion of tail grey with dark vertebral streak, vaguely blotched on sides and pale grey beneath.

Variation in paratypes and other material: There were few significant differences in meristic characters and no significant differences in morphology (SVL, tail) between western populations (Richtersveld, Namaqualand and Namibia) (Tables 1 - 3). A four-group discriminant function analysis showed strong

overlap among the three western populations, which for clarity is not illustrated here. However, a discriminant function analysis of East versus West (Figure 3, Table 4) separates the two groups into morphological space with no overlap (MANOVA, group centroids unequal: $F = 18_{24, 371}$, $P < 0.001$). Figure 3 accounts for 99.28 % of variation. Transverse dorsal scale rows and dorsal forelimb scale rows load most heavily on axis 1 of the canonical variates, with transverse rows of ventral scales contributing most on axis 2 (Table 4). Similarly, ANOVA and post hoc pairwise tests revealed many significant differences among mean scale counts between East and West, and between East and individual western populations (Tables 2 & 3).

The holotype is unusual in having only four supralabials (five in all paratypes) anterior to the subocular. Lower (4) or higher (6) supralabial counts, either on both sides of the head or on one side, occur infrequently in all populations; i.e. East, 13. 3%, n = 45; Richtersveld, 8.6 %, n = 58; Namaqualand, 8.3 %, n = 12; Namibia, 9.7 %, n = 31; and West, 8.9 %, n = 101.

Table 1. Descriptive statistics (mean ± SE, range) of meristics and body size (SVL) for four populations of *Platysaurus*: East (*P. broadleyi*), Richtersveld, Namaqualand, and Namibia; West consists of Richtersveld, Namaqualand, and Namibia combined (all *P. capensis*). Sample sizes are in parentheses.

	East	Richtersveld	Namaqualand	Namibia	West
SVL (sexes combined; mm)	70.2 ± 1.1	72.2 ± 0.8	68.6 ± 3.3	70.9 ± 1.47	71.4 ± 0.7
	40 - 80 (45)	55 - 86 (58)	37 - 82 (12)	36 - 82 (31)	36 - 86 (101)
Males	73.0 ± 0.77	74.5 ± 0.95	74.3 ± 2.24	73.2 ± 0.86	74.0 ± 0.65
	67 - 80 (21)	66 - 86 (29)	71 - 82 (4)	65 - 82 (20)	65 - 86 (53)
Females	71.3 ± 0.71	72.4 ± 0.87	71.8 ± 1.18	72.0 ± 0.96	72.3 ± 0.62
	64 - 76 (18)	64 - 80 (23)	68 - 75 (6)	68 - 77 (8)	64 - 80 (37)
Supralabials anterior to subocular	4.9 ± 0.0	5.0 ± 0.0	5.0 ± 0.1	5.0 ± 0.0	5.0 ± 0.0
	4 - 5 (45)	4 - 5 (54)	4.5 - 5.5 (12)	4 - 5.5 (31)	4 - 5.5 (97)
Gulars	27.5 ± 0.4	25.8 ± 0.3	23.8 ± 1.4	25.1 ± 0.3	25.4 ± 0.2
	24 - 32 (24)	22 - 30 (49)	21 - 27 (4)	23 - 28 (30)	21 - 30 (83)
Scales in collar	9.2 ± 0.2	7.8 ± 0.2	7.7 ± 0.2	8.2 ± 0.2	7.9 ± 0.1
	7 - 11 (45)	5 - 10 (54)	6 - 8 (12)	6 - 10 (31)	5 - 10 (97)
Longitudinal rows of ventrals	20.7 ± 0.2	19.8 ± 0.2	19.7 ± 0.2	19.8 ± 0.2	19.8 ± 0.1
	19 - 23 (44)	18 - 22 (58)	18 - 20 (12)	18 - 22 (31)	18 - 22 (101)
Transverse rows of ventrals	43.3 ± 0.3	42.4 ± 0.3	40.4 ± 0.3	40.7 ± 0.4	41.2 ± 0.2
	40 - 48 (44)	36 - 48 (58)	38 - 42 (11)	37 - 46 (31)	36 - 48 (100)
Transverse rows of dorsals	105.0 ± 0.8	85.8 ± 0.6	83.1 ± 0.9	84.3 ± 0.6	85.1 ± 0.4
	92 - 117 (45)	77 - 97 (55)	77 - 86 (11)	78 - 91 (30)	77 - 97 (96)
Upper forelimb scale rows	25.8 ± 0.3	17.1 ± 0.3	14.7 ± 0.3	17.2 ± 0.3	16.8 ± 0.2
	21 - 30 (45)	13 - 23 (58)	13 - 16 (12)	14 - 22 (31)	13 - 23 (101)
Subdigital lamellae of 4th toe	20.6 ± 0.2	19.2 ± 0.1	17.9 ± 0.2	18.9 ± 0.2	18.9 ± 0.1
	18 - 22 (45)	17 - 22 (57)	17 - 19 (12)	17 - 21 (31)	17 - 22 (100)
Femoral pores	16.7 ± 0.1	17.0 ± 0.2	16.8 ± 0.4	15.8 ± 0.2	16.6 ± 0.1
	15 - 18 (38)	14 - 20 (56)	14 - 19 (12)	13 - 18 (30)	13 - 20 (98)

We found FitzSimons' (1943) and Broadley's (1978) observations that the nostril pierces a large nasal, and that the nasals are in contact behind the rostral, to be highly variable. FitzSimons' (1943) illustration (Figure 377), reprinted in Broadley (1978), shows a suture running from the nostril across the dorsal-posterior quadrant of the nasal to contact the frontonasal. We confirm this suture, but an additional suture running through the ventral-anterior quadrant of the nasal to contact the lower region of the rostral, just anterior to its contact with the first supralabial is also often present. In conjunction with this, a narrow strip of tissue runs between these sutures above the nostril. We interpret this as the nostril piercing the upper half of a small nasal scale, with large supranasal scales above and in contact with each other behind the rostral. This condition occurred significantly (Kolmogorov-Smirnov test, $P < 0.001$) more frequently in *P. capensis* (91.0 %, n = 111/122 individuals) than *P. broadleyi* (41.6 %, n = 32/77 individuals). The snout region of the holotype is in relatively poor condition, but vestiges of a small suture running across the ventral-anterior quadrant of the nasal, contacting the lower region of the rostral, occur (E.N. Arnold, pers. comm., 21 February 1997). An internasal was rarely present (10.0 %, n = 21/219 individuals; $x^2_1 = 139.8$, $P < 0.0001$), and its frequency did not differ between populations (*P. broadleyi*: 4.6 %,

Table 2. Results of two-way ANOVA of morphological and meristic variables for sex and location, for each population: East (*Platysaurus broadleyi*), Richtersveld, Namaqualand, and Namibia; West consists of Richtersveld, Namaqualand, and Namibia combined (all *P. capensis*). All data were log transformed prior to statistical analysis. Where locational differences were significant, post hoc pairwise comparisons were made using Scheffé tests (Table 3). A single asterisk indicates a larger mean value for males; a double asterisk a larger mean value for females.

Source	ss	ms	df	F	P
SVL (mm)					
sex	0.010	0.010	1	4.177	0.042*
location	0.020	0.005	4	2.093	0.083
sex x location	0.001	0.000	4	0.138	0.968
error	0.436	0.002	187		
Tail length (mm)					
sex	0.002	0.002	1	0.611	0.435
location	0.009	0.002	4	0.661	0.620
sex x location	0.004	0.001	4	0.335	0.854
error	0.618	0.003	187		
Supralabials anterior to subocular					
sex	0.001	0.001	1	0.410	0.523
location	0.005	0.001	4	0.414	0.799
sex x location	0.008	0.002	4	0.643	0.633
error	0.581	0.003	187		
Gulars					
sex	0.006	0.006	1	1.653	0.200
location	0.189	0.047	4	12.478	<0.001
sex x location	0.006	0.002	4	0.423	0.792
error	0.708	0.004	187		
Collar					
sex	0.004	0.004	1	0.299	0.585
location	0.774	0.194	4	14.630	<0.001
sex x location	0.087	0.022	4	1.650	0.164
error	2.473	0.013	187		
Longitudinal rows of ventrals					
sex	0.000	0.000	1	0.190	0.663
location	0.075	0.019	4	7.298	<0.001
sex x location	0.017	0.004	4	1.666	0.160
error	0.481	0.003	187		
Transverse rows of ventrals					
sex	0.003	0.003	1	1.140	0.287
location	0.095	0.024	4	8.162	<0.001
sex x location	0.004	0.001	4	0.329	0.859
error	0.541	0.003	187		
Transverse rows of dorsals					
sex	0.013	0.013	1	5.409	0.021**
location	1.417	0.354	4	147.981	<0.001
sex x location	0.010	0.002	4	1.043	0.386
error	0.448	0.002	187		
Upper forelimb scale rows					
sex	0.017	0.017	1	1.324	0.251
location	6.036	1.509	4	115.526	<0.001
sex x location	0.056	0.014	4	1.062	0.376
error	2.443	0.013	187		
Subdigital lamellae of 4th toe					
sex	0.003	0.003	1	0.930	0.336
location	0.229	0.057	4	18.136	<0.001
sex x location	0.001	0.000	4	0.104	0.981
error	0.591	0.003	187		
Femoral pores					
sex	0.001	0.001	1	1.226	0.270
location	0.013	0.003	4	5.379	<0.001
sex x location	0.001	0.000	4	0.499	0.737
error	0.114	0.001	185		

Table 3. Scheffé matrix of post hoc pairwise comparisons for significant values given in Table 2, by location: East (*Platysaurus broadleyi*), Richtersveld, Namaqualand, and Namibia; West consists of Richtersveld, Namaqualand, and Namibia combined (all *P. capensis*).

	East	Richtersveld	Namaqualand	Namibia	West
Gulars					
East	1.000				
Richtersveld	0.001	1.000			
Namaqualand	<0.001	0.162	1.000		
Namibia	<0.001	0.664	0.727	1.000	
West	<0.001	0.837	0.381	0.971	1.000
Longitudinal rows of ventrals					
East	1.000				
Richtersveld	<0.001	1.000			
Namaqualand	0.190	1.000	1.000		
Namibia	0.068	0.910	0.996	1.000	
West	<0.001	0.997	1.000	0.964	1.000
Transverse rows of ventrals					
East	1.000				
Richtersveld	0.696	1.000			
Namaqualand	0.015	0.111	1.000		
Namibia	<0.001	0.015	0.998	1.000	
West	0.010	0.313	0.553	0.346	1.000
Upper forelimb scale rows					
East	1.000				
Richtersveld	<0.001	1.000			
Namaqualand	<0.001	0.140	1.000		
Namibia	<0.001	0.909	0.051	1.000	
West	<0.001	1.000	0.115	0.886	1.000
Subdigital lamellae of the 4th toe					
East	1.000				
Richtersveld	<0.001	1.000			
Namaqualand	<0.001	0.015	1.000		
Namibia	<0.001	0.921	0.120	1.000	
West	<0.001	0.844	0.053	1.000	1.000
Femoral pores					
East	1.000				
Richtersveld	0.816	1.000			
Namaqualand	0.585	0.913	1.000		
Namibia	0.065	0.002	0.015	1.000	
West	1.000	0.792	0.588	0.019	1.000
Collar					
East	1.000				
Richtersveld	<0.001	1.000			
Namaqualand	<0.024	0.992	1.000		
Namibia	0.004	0.522	0.981	1.000	
West	<0.001	0.954	1.000	0.796	1.000
Transverse rows of dorsals					
East	1.000				
Richtersveld	<0.001	1.000			
Namaqualand	<0.001	0.479	1.000		
Namibia	<0.001	0.664	0.963	1.000	
West	<0.001	0.922	0.717	0.932	1.000

Table 4. Discriminant function loadings of the first two axes, from an analysis of meristic variables (including SVL) for *Platysaurus* listed in Methods. The per cent variance contribution of each variable is given in parentheses.

	Discriminant function axes	
Variable	axis 1	axis 2
SVL (mm)	-0.051 (86.334)	0.175 (2.976)
Supralabials anterior to subocular	-0.001 (98.319)	0.117 (0.831)
Collar	0.240 (90.211)	-0.518 (9.178)
Longitudinal rows of ventrals	0.170 (97.056)	-0.085 (2.924)
Transverse rows of ventrals	0.155 (95.198)	0.873 (4.504)
Transverse rows of dorsals	0.804 (99.058)	-0.058 (0.000)
Upper forelimb scale rows	0.775 (99.155)	-0.292 (0.001)
Subdigital lamellae of the 4th toe	0.083 (84.397)	-0.040 (1.871)
% trace:	axis 1: 97.46 %	axis 2: 1.82 %

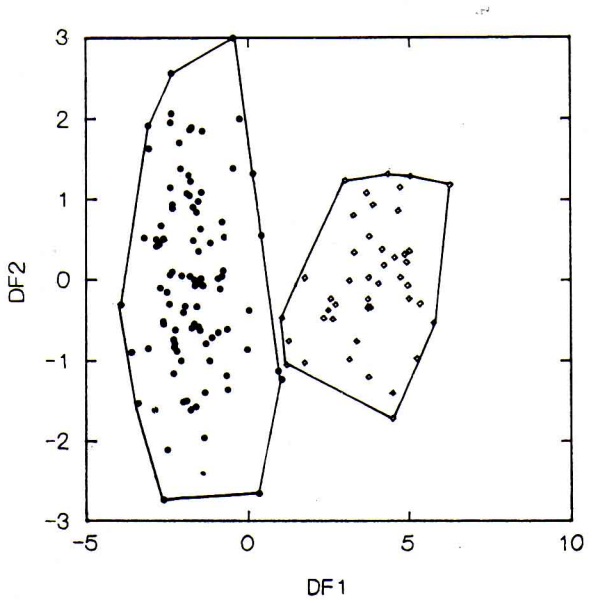

Figure 3. Discriminant function analysis of *Platysaurus broadleyi* (solid triangles) and *P. capensis* (open triangles). The first and second canonical variates accounted for 99.28% of variation.

P. capensis: 13.7 %; Kolmogorov-Smirnov test, $P > 0.05$). No difference (Kolmogorov-Smirnov test, $P > 0.05$) existed in frequency of supranasal contact between the two species (*P. broadleyi*: 85.3 %, n = 75/88 individuals; *P. capensis*: 83.2 %, n = 109/131 individuals); and supranasals were significantly (x^2_1 = 101.37, $P < 0.0001$) more often in contact (84.0 %, n = 184/219 individuals, both species combined) than not.

The Augrabies population (males) was highly polymorphic for colour in some features. Males had either yellow (Figure 1), orange, or mixed yellow-orange front legs, and the status signalling badge located on the lower abdomen was generally orange, but occasionally yellow or a yellow-orange combination. Other features of male colouration such as the orange ventral surface of the thigh, orange posterior third of the lateral side, and orange ventral surface of the tail were invariant. Head and dorsal colouration also showed some variation, but this may be ontogenetic and/or attributable to dominance. Despite this variability, Augrabies males were always distinguishable from those of western populations (see Diagnosis).

Size: The largest museum specimen (male) examined had a SVL of 80 mm (TM 79833); however, a living male from Augrabies measured 84 mm SVL (MJW, unpubl. data). Males grow significantly larger than females in *P. broadleyi* and *P. capensis* (Tables 1 & 2), however, there were no significant interspecific differences in adult SVL between *P. broadleyi* and all populations of *P. capensis* (Table 2).

The largest tail length/SVL ratio was 2.03 (male, SAM 18368; 67 mm SVL, 136 mm tail length). In adult *P. broadleyi* (SVL > 64 mm; van Wyk & Mouton 1996) the mean tail length/SVL ratio of original tails is 1.84 ± 0.027 (1.73 - 2.03; n = 13) for males, and 1.80 ± 0.022 (1.69 - 1.88; n = 9) for females. Sufficient intact original tails were present only in the Richtersveld population of *P. capensis*, where the mean tail length/SVL ratio was 1.78 ± 0.027 (1.70 - 1.94; n = 7) for males, and 1.75 ± 0.026 (1.69 - 1.86; n = 5) for females.

Etymology: The specific name is a patronym honouring Africa's pre-eminent herpetologist, Dr Donald George Broadley, on the occasion of his 65th birthday. It is particularly appropriate that a taxon of this exciting and

colourful genus be named after Don, who made the first detailed observations on their biology and whose taxonomic studies formed the bedrock from which this minor refinement flaked.

Habitat and Climate: Augrabies Falls National Park straddles the Orange River, approximately 120 km West of Upington, Northern Cape Province. It is the largest conserved area within the Orange River Nama-Karoo vegetation type (Hoffman 1996). The climate is characterized by predominantly erratic summer rainfall, ranging from <40 mm p.a. to 391 mm p.a. with a 50-year (1946 - 1996) average of 211 mm. The period 1986 - 1996 was dry, with below average rainfall that occurred mainly in December - February. Temperature was less erratic than rainfall, with cold winters (June - July, as low as -2.9°C) and hot summers (December - February, as high as 42.9°C) (Weather Bureau 1996). Bezuidenhout (1996) classified vegetation within the southern section of Augrabies, noting six major vegetation communities and nine subdivisions. Although *P. broadleyi* occurs in many of these communities where suitable rock surfaces are found, it is predominantly found in *Rhus populifolia-Schotia afra* Open Woodland and *Ceraria namaquensis* Open Shrubland. It utilizes rock cracks and flakes on the extensive outcrops of gneiss granite and other ultra-metamorphic rocks of the Namaqualand Metamorphic Complex where vegetation is extremely sparse. The predominant (usually the only) tree occurring syntopically with the lizard is the Namaqua fig (*Ficus cordata*). *Platysaurus broadleyi* may forage in or under this tree, and frequently uses it for shade.

Distribution: *Platysaurus broadleyi* is endemic to the Northern Cape Province. It is restricted to the vicinity of the Orange River, from Augrabies to Klein Pella, just west of Onseepkans (Figure 2). The most northerly record is Baks Putz, on the Bak River (quarter degree unit 2720CC), a northern tributary of the Orange River. It is the only locality some distance from the main course of the Orange River (albeit on a tributary). Klein Pella (2819CC) is the western-most (and most southern) record, which is approximately 100 km from the nearest *P. capensis* locality (Henkries, 2818CC). Figure 2 also shows the distribution of *P. capensis*, based on localities listed in Appendix 1.

Sclater's (1898) record for *P. capensis* from "Victoria West" (SAM 2106) is obviously in error, and was provisionally rejected by Broadley (1978). The specimen is an adult male with 79 transverse dorsal scales, 15 scales along the forearm, and supranasals separated by a small, partial "internasal". It is most likely derived from the Namaqualand population of *P. capensis*. Branch & Bauer (1994) have drawn attention to the numerous examples of incorrectly labeled "Namaqualand" specimens in the collection of the South African Museum. This resulted from poor curatorial practices at the museum around the turn of the century (Summers 1975). In addition, extensive field work in the Karoo (Branch & Braack 1989) and along the Nuweveldberg (Branch 1990) did not reveal populations of these colourful and conspicuous lizards.

Natural History: *Reproduction*: Broadley (1974) reported a clutch size of two based on a "few ovigerous *P. capensis* examined". Van Wyk & Mouton (1996) recently described the reproductive cycle of *P. capensis* (sensu lato). Samples of *P. broadleyi* from Augrabies were included in their analysis, but it is uncertain whether any differences in reproduction exist, or whether any such differences would be attributable to phylogeny or local climatic conditions. Briefly, both species exhibit sexual maturity at around 64 mm SVL (although no reference was made to sex) and eggs (two, based on three gravid females) are laid in November - December. Van Wyk & Mouton (1996) also suggested the possibility of a second clutch (late summer) in some females. Male and female cycles are well synchronized, characterized by autumn-winter reproductive activity peaking in spring, the time of mating.

Diet and feeding behaviour: At Augrabies, *P. broadleyi* feeds primarily on black flies (*Simulium* spp.), which occur in exceptional abundance, whilst other insects are taken opportunistically (MJW unpub. obs.). These lizards also feed readily on Namaqua figs (*Ficus cordata*) when available (Whiting & Greeff 1997). Facultative frugivory in *P. broadleyi* occurs in a competitive environment in which interference competition is strong. Lizards locating figs quickly move to areas free of conspecifics before feeding, and adults of both sexes frequently attempt to steal figs from feeding conspecifics (Whiting & Greeff 1997). Adult males and females exhibit similar fig-feeding behaviour, pressing a fig against a frictional surface to break it open; but males consume figs significantly faster than females (Whiting & Greeff 1997). Juveniles rely on figs already broken open, but also frequently sample individual fig seeds.

The first quantitative data on foraging mode in *P. broadleyi* was recently reported by Cooper et al. (1997), and compared to allied members of the Cordylidae in an attempt to assess the evolution of cordyliform foraging. *Platysaurus broadleyi* is an ambush forager performing several movements of short duration; measures of percent time moving, and number of movements per minute, are highly variable for the Augrabies population (Cooper et al. 1997).

Social behaviour: At Augrabies, *P. broadleyi* occur in large congregations on the granite banks of the Orange River, where they feed on emerging black flies (*Simulium* spp.). This aggregative behaviour has important implications for spatial patterns and social organization. Females often travel to sections of the

river where black fly prey is most concentrated (the faster flowing sections of the river). In turn, males able to establish territories in these areas appear to have the greatest access to females. However, not all males at Augrabies are territorial. Some appear to be sneakers (sneaker sensu Krebs & Davies 1993). Sneakers are generally found in the company of other males, possibly because they occur in areas in which territorial defence is too costly (MJW unpubl. data). Territorial defence involves the most spectacular aspect of male display behaviour - the flashing of a status-signalling badge (badge *sensu* Krebs & Davies 1993); but male-male displays may occur in other contexts as well. This appears to be a sexually selected trait that is currently under investigation (Whiting in prep.).

Conservation status: The species has a restricted distribution, currently known from only five quarter-degree units (Figure 2). However, much of its range, including that of the largest population, is situated within the well-conserved Augrabies Falls National Park. The species is therefore not currently threatened but could be included in the SA Red Data Book - Reptiles and Amphibians in the 'Restricted' category (Branch 1988b).

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Appendix 1. Material examined:

Platysaurus capensis. **NAMIBIA:** BM 1946.8.29.26, "Great Namaqualand" (holotype); CAS 201884-5, Farm Witputz Sud, Lüderitz District (27°40'18"S, 16°43'10"E; quarter-degree unit 2716DA; elevation 1165 m a.s.l.); TM 27983-84, 28270-75, 27985, 36829-32, Fish River Canyon, 72 km W Klein Karas, Lüderitz District (27°35'S, 17°37'E; 2717DA); TM 35330, Rosh Pinah, Lüderitz District (27°58'S, 16°46'E; 2716DD); TM 35335-45, 39974, 47646, SAM 43609, Farm Namuskluft, Lüderitz District (27°56'S, 16°50'E; 2716DD); TM 35380-82, Farm Spitzkop, Lüderitz District (27°52'S, 16°44'E; 2716DC); TM 35437-38, Kuamsib Mountain, Lüderitz District (27°59'S, 17°05'E; 2717CC); TM 35414, McMillan's Pass, 18 km E Rosh Pinah, Lüderitz District (27°56'S, 16°54'E; 2716DD); TM 35446-47, 35461, confluence of Fish and Orange rivers, Lüderitz District (28°06'S, 17°10'E; 2817AA). **SOUTH AFRICA, NORTHERN CAPE PROVINCE: Richtersveld and Lower Orange River.** TM 17867-79, Goodhouse, S bank Orange River (28°54'S, 18°14'E; 2818CC); TM 56157, 56450, Henkries pump station, Orange River (28°53'S, 18°08'E; 2818CC); SAM 18527, Vioolsdrift, Orange River (2817DC); SAM 45583, Hell's Kloof, Vioolsdrift (2817CD); SAM 18824, Richtersveld; SAM 45027-28, Granite Boss (Kuboos = Khubus), SW corner Richtersveld (2817CA); TM 24176-80, between Geligwerkberg and Doornkloof, Richtersveld; TM 15879-85, 15937, 27848-50, SAM 11348, 18681-82, 18684, Kuboos (= Khubus), Richtersveld (28°26'S,

16°59'E; 2816BD); TM 27857-60, Groenkloofrivier, Richtersveld (28°31'S, 16°58'E; 2816CB); TM 34212-13, 5 km from De Hoop to Numes, Richtersveld (28°10'S, 17°07'E; 2817AA); TM 35281-82, Numes Mine, Richtersveld (28°17'S, 16°58'E; 2816BD); TM 52584, Ploegberg, Richtersveld (2817CA); TM 52761, Tatasberg, Richtersveld (2817DA); TM 53846, 53855-64, Ploegberg, Richtersveld (28°37'S, 17°00'E; 2817CA); Aaron M. Bauer collection (AMB) 5056 (to be accessioned into Louisiana State University Museum, LSUM), 4.7 km towards Oenna, Richtersveld National Park (RNP) (28°05'11"S, 17°07'45"E; 2817AA; 400 m a.s.l.); AMB 5084 (to LSUM), 3.5 km S by road from the bottom of Hellskloof Pass, RNP (28°19'12"S, 16°58'30"E; 2816BD; 420 m a.s.l.); CAS 200057, Tierhoek, Ploesberg (28°37'59"S, 17°00'41"E; 2817CA; 425 m a.s.l.); PEM R7610, central grazed flats W of Nichodemus, RNP (28°20'39"S, 16°59'04"E; 2816BD; 700 m a.s.l.); PEM R7602, 1.3 km along path running SE from top of Hellskloof to Nicodaemus (28°20'39"S, 16°59'01"E; 2816BD; 677 m a.s.l.); PEM R7616-17, De Tuin ("Devil's Playground"), Tatasberg, RNP (28°18'49"S, 17°16'52"E; 2817AB; 681 m a.s.l.); PEM R7650, Nicodaemus camping area, RNP (28°21'07"S, 16°59'43"E; 2816BD; 749 m a.s.l.); CAS-SU 12089-90, Numes, RNP (2816BD); CAS 193359, main road at Potjiespram turn-off, RNP (2816BB); CAS 193385-90, 22.8 km E of Sendelingsdrift on main park road, RNP (2817AA); CAS 193446-68, 8.7 km E of Hellskloof Pass gate, RNP (2816BD); CAS193573-77, 16.2 km W of SE Gate, border of RNP (2817CA); CAS 193595, main road at Potjiespram junction (no. 1), RNP (2816BB); CAS 193628, 23.5 km E of Sendelingsdrift on main park road, RNP (2817AA); CAS 201932, Tierhoek, Plousberg, RNP (28°37'59"S, 17°00'41"E; 2817CA; 425 m a.s.l.); CAS 200066, 1.1 km N of Kook River Fountain road on track to Koubank River, Richtersveld (28°40'11"S, 17°10'14"E; 2817CA; 565 m a.s.l.). **Little Namaqualand:** TM 66318, Carolusberg, Springbok (29°38'S, 17°57'E; 2917DB); TM 13711-13, SAM 18068 (five specimens), 44320, Kamieskroon (30°11'S, 17°59'E; 3017BB); TM 34050, 34068, 5 km E of Kamieskroon (3017BB); TM 35209, 7 km NW of Liliefontein, Kamiesberg (30°15'S, 18°03'E; 3018AA); SAM 18024 (two specimens), Kamies. **Other:** SAM 2106, Victoria West (in error).