

CONVENCIÓN SOBRE EL COMERCIO INTERNACIONAL DE ESPECIES
AMENAZADAS DE FAUNA Y FLORA SILVESTRES



Vigésimo séptima reunión del Comité de Fauna
Veracruz (México), 28 de abril – 3 de mayo de 2014

Interpretación y aplicación de la Convención

Comercio y conservación de especies

Nomenclatura normalizada

NOMENCLATURA REVISADA PARA *POICEPHALUS ROBUSTUS* Y *CORDYLUS*

1. Este documento ha sido preparado por la Autoridad Científica de Sudáfrica*.
2. El informe adjunto sobre la sistemática y filogeografía del lorito robusto (Coetzer *et al.*) se inscribe en el marco siguiente:
 - a) La nomenclatura actual adoptada por la CITES para *Poicephalus robustus* no está actualizada. Siguiendo esta taxonomía obsoleta, el lorito robusto, especie endémica y en peligro de Sudáfrica, está siendo actualmente objeto de comercio conjuntamente con *P. r. suahelicus*, lo que le dificulta la acción de conservación en Sudáfrica y el control del comercio de especímenes del lorito robusto.
 - b) Se pide al Comité de Fauna que examine la nomenclatura revisada actualmente utilizada por la Unión Internacional de Ornitólogos y BirdLife Sudáfrica y recomiende que sea adoptada para los Apéndices y las listas de referencia de la CITES.
3. La publicación adjunta de Stanley *et al.* (2011) se inscribe en el marco siguiente:
 - a) Una revisión taxonómica de la familia de lagartos subsahariana *Cordylidae* tuvo como resultado que las especies incluidas en el Apéndice II de la CITES dentro del género *Cordylus* ha sido transferida a los géneros *Smaug*, *Ninurta*, *Pseudocordylus*, *Ouroborus*, *Karusasaurus*, *Namazonorus* y *Hemicordylus*.
 - b) Se puede generar confusión cuando los operadores comerciales utilicen los viejos y nuevos nombres. Las especies exportadas a partir de Sudáfrica incluyen *Cordylus cataphractus* (ahora *Ouroborus cataphractus*), *Cordylus cordylus*, *Cordylus giganteus* (ahora *Smaug giganteus*) y *Cordylus niger*.
 - c) Se pide al Comité de Fauna que examine la nomenclatura revisada y recomiende que se actualicen de la manera correspondiente los Apéndices y listas de referencia de la CITES para garantizar que Autoridades Administrativas CITES puedan supervisar adecuadamente todos los especímenes que son objeto de comercio internacional.

* Las denominaciones geográficas empleadas en este documento no implican juicio alguno por parte de la Secretaría CITES o del Programa de las Naciones Unidas para el Medio Ambiente sobre la condición jurídica de ninguno de los países, zonas o territorios citados, ni respecto de la delimitación de sus fronteras o límites. La responsabilidad sobre el contenido del documento incumbe exclusivamente a su autor.

Informe intermedio de proyecto al Instituto Nacional de Sudáfrica para la Biodiversidad

Tesis doctoral: Sistemática y filogeografía del lorito robusto (*Poicephalus robustus*)

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Introducción

El lorito robusto (*Poicephalus robustus*) es endémico de Sudáfrica y su presencia se limita a los bosques Afromontane del Cabo Oriental y de las provincias de KwaZulu-Natal con vestigios de poblaciones en la provincia oriental de Mpumalanga y la provincia septentrional de Limpopo en Sudáfrica (Wirminghaus 1997). La distribución histórica de estos loritos se ha reducido drásticamente, especialmente en la parte meridional de KwaZulu-Natal y a lo largo de los escarpes de Mpumalanga (Downs 2005; Symes et al. 2004; Wirminghaus et al. 2000). Durante los años 1950 se observaron grandes bandadas de loritos robustos (Symes and Downs 2002), pero las poblaciones de este loro han estado disminuyendo a lo largo del último siglo (Downs et al. 2013). Los avistamientos ahora generalmente sólo tiene lugar cuando los loros se encuentran en situación de escasez de alimentos durante la cual se agrupan en huertos agrícolas de cultivo de pacanas (Downs et al. 2013). Se han atribuido varios factores a la disminución de la población, entre los que se incluyen la pérdida de hábitat y la enfermedad del pico y las plumas de los psitaciformes (Wirminghaus et al. 1999; Wirminghaus et al. 2000).

Aunque muchos autores anteriores (Clancey 1997; Perrin 2005; Wirminghaus et al. 2002), basándose en datos morfológicos, ecológicos y comportamentales, han sugerido que el lorito robusto debería ser considerado como una especie diferente, actualmente éste no ha sido reconocido por la Unión Internacional para la Conservación de la Naturaleza (UICN) como una especie diferente de *P.r. suahelicus* de África central y meridional. Ambos son considerados como subespecies de *Poicephalus robustus*. Estos dos taxa, conjuntamente con *P.r. fuscicollis* de África occidental pertenecen al complejo de especies *Poicephalus robustus* (Wirminghaus et al. 2002). *Poicephalus robustus* ha sido clasificada como "de menor preocupación" por la UICN. Sin embargo, el lorito robusto ha sido considerado como un taxón independiente por BirdLife Sudáfrica y reúne las condiciones para una clasificación como "en peligro". El lorito robusto ha sido incluido en el Apéndice II de la Convención sobre el Comercio Internacional de Especies Amenazadas de Fauna y Flora Silvestres (CITES) dentro del orden de los psitaciformes. Sin embargo, el control del comercio internacional del lorito robusto se ve dificultado por el hecho de que su comercio no se maneja y notifica separadamente del de *P.r. suahelicus* y *P.r. fuscicollis*. El hecho de que se reconozca como una especie independiente ayudaría al control del comercio tanto legal como ilegal y de las extracciones en el medio silvestre del lorito robusto. El objetivo de este estudio es investigar las relaciones filogenéticas entre el lorito robusto (*P.r. robustus*) y los otros dos miembros del complejo de especies *Poicephalus robustus*. Se utilizó un conjunto de ocho marcadores microsatélites, que habían sido caracterizados anteriormente para el lorito robusto (Pillay et al. 2010), con el objetivo de realizar una comparación genética entre *P.r. robustus*, *P.r. suahelicus* y *P.r. fuscicollis*.

Materiales y métodos

Muestreo y extracción del ADN

Para el análisis genético se recogieron un total de 77 muestras de las tres subespecies de *P. robustus* (48 de *P.r. robustus*, 19 de *P.r. suahelicus* y 10 de *P.r. fuscicollis*). Estas muestras incluían tanto aves criadas en cautividad como capturadas en el medio silvestre (Tabla 1). 40 de las muestras de lorito robusto fueron entregadas por la Universidad de Ciudad del Cabo y habían sido tomadas en dos lugares del Cabo Oriental (30 en Fort Hare y 10 en King William's Town). Otras ocho muestras de lorito robusto procedían de loros muertos en la región de Creighton en la zona de KwaZulu-Natal. Las muestras de *P.r. suahelicus* y *P.r. fuscicollis* eran todas muestras de sangre recogidas durante un estudio realizado en la Universidad de KwaZulu-Natal. También se utilizó una muestra de un ave híbrida de *P. robustus* x *P.f. suahelicus* criada en cautividad utilizando una tarjeta Whatman™ FTA™ Elute con protocolos normalizados. El espécimen híbrido fue añadido para ver si era posible identificar a un híbrido con la prueba de clasificación utilizada.

Se utilizó el kit NucleoSpin® Tissue (Macherey-Nagel) para la extracción del ADN a partir de las muestras de sangre y tejidos siguiendo los protocolos del fabricante. La extracción del ADN a partir de las tarjetas FTA se

realizó siguiendo el protocolo del fabricante y el ADN extraído fue eluido en 30 µl de agua destilada (dH₂O). Todos los ADN extraídos fueron almacenados a -20 °C.

Amplificación de microsatélites y análisis

Se seleccionaron ocho loci microsatélites a partir de una serie de marcadores caracterizadas anteriormente por Pillay et al. (2010). La amplificación se realizó en tres reacciones multiplex (Tabla 2). El kit KAPA2G™ Fast Multiplex PCR (KAPA Biosystems) fue utilizado en reacciones de 10 µl. Las reacciones PCR estuvieron compuestas por una mezcla de KAPA2G Fast Multiplex de 5 µl, 0.2 µM de cada iniciador, 0.8 µl de plantilla de ADN, y 3 µl de dH₂O para los Multiplex 1 y 3, y 3.4 µl de dH₂O para el Multiplex 2. Se utilizaron los siguientes parámetros del ciclo para la PCR: 94°C durante 4 min como paso inicial de desnaturalización, 30 ciclos a 94°C durante 15 segundos, 60°C durante 30 min, 72°C durante 30 min, con un paso final de elongación a 72°C durante 10 min y una retención a 10°C. Los productos amplificados fueron enviados al Laboratorio Central de Analítica de la Universidad de Stellenbosch (Sudáfrica) para el análisis de los fragmentos.

Se utilizó la aplicación informática Gene Marker® v2.4.0 (Soft Genetics) para la puntuación del genotipo. La frecuencia de alelos nulos fue determinada con la aplicación informática FreeNA (Chapuis y Estoup 2007). El análisis de la estructura de población se realizó con el programa informático Structure v2.3 (Pritchard et al. 2010). Este programa utiliza un marco bayesiano para asignar individuos a conjuntos/grupos con individuos genéticamente similares. Se seleccionó una duración de 1,000,000 réplicas de cadena Markov Monte Carlo tras una fase de prueba preliminar de 100,000 iteraciones y el número propuesto de conjuntos (K) con valores de 1 a 10. El modelo de frecuencia de alelos correlacionado fue seleccionado de manera que se pudiera detectar la ascendencia común entre las subespecies. Se seleccionó el modelo de ascendencia sin mezcla partiendo del supuesto de que cada individuo del que se tomó la muestra procedía o bien de una subespecie o de la otra. Pritchard et al. (2010) sugieren que el modelo sin mezcla es más conveniente para detectar estructuras genéticas sutiles. Se utilizó el recolector STRUCTURE (Earl 2009) para estimar el número óptimo de grupos genéticos utilizando la metodología establecida por Evanno et al. (2005). Las estimaciones de los valores FST y el número de alelos privados se calculó utilizando v3.5 (Excoffier et al. 2005) y GenAIEx v6.5 (Peakall and Smouse 2012). Estas medidas proporcionan una estimación del nivel de diversidad genética dentro de las tres subespecies y entre ellas.

Resultados

Se pudo establecer exitosamente el genotipo de las 77 muestras para al menos dos loci. Para seis de los ocho loci falta algún dato; la Prob 06 no dio amplificación para 4 de las 77 muestras; la Prob 15 dio 3 casos de no amplificación; la Prob 18 dio 7 casos de no amplificación; la Prob 25 dio 4 casos de no amplificación; la Prob 26 dio 2 casos de no amplificación; y la Prob 31 no logro amplificar en el caso de una muestra. Los diferentes programas utilizados durante los análisis compensan los casos de datos faltantes. La frecuencia de alelos nulos (r) se sitúa entre 0 y 0.21. La frecuencia de alelos nulos por debajo de 0.4 se consideran generalmente como aceptables en la mayoría de las series de datos de microsatélites (Dakin y Avise (2004) y la frecuencia de alelos nulos detectada en este estudio se sitúa muy por debajo de la norma ($r < 0.4$). El análisis FST por pares indica niveles significativamente elevados de variación genética entre las tres subespecies con valores inferiores a 0.05 (Tabla 3). Estos valores fueron representados en un gráfico mediante un análisis Principal Coordinate (Gráfico 1), y las tres subespecies se distinguen claramente desde un punto de vista genético.

La presencia de alelos privados es una buena indicación de diferenciación genética (Slatkin 1985). El análisis del número de alelos por locus muestra que cada una de las subespecies reconocidas tiene un número de alelos privados (Tabla 4). Los números de alelos calculados durante este estudio pueden ser relacionados con el tamaño del área de distribución de cada subespecie. De las tres subespecies *P. robustus*, *P.r. suahelicus* es la que tiene una área de distribución mayor (Perrin 2009; 2012), y también el mayor número de alelos privados ($n = 13$). El lorito robusto tiene una área de distribución más continua que *P.r. fuscicollis* de África occidental (Perrin 2009; 2012) y también tiene el mayor número de alelos privados, $n = 10$ y $n = 6$ respectivamente.

La prueba de asignación identificó dos grupos genéticos diferentes ($K=2$; Mean LnP(K) = -1968.21). Unos de los conjuntos incluía todos los especímenes de *P.r. robustus* (en verde en la Figura 2) y el otro estaba compuesto por todos los especímenes de *P.r. suahelicus* y *P.r. fuscicollis* (en rojo en la Figura 2). Hubo una mezcla limitada entre estos dos grupos genéticos lo que recalca el carácter único del lorito robusto. También se puede identificar claramente la muestra de híbrido conocida (extremo derecho de la Figura 2), pues se puede ver que comparte material genético de ambos conjuntos (rojo y verde). Según las pruebas de asignación dos de los especímenes de *P.r. suahelicus* también podrían ser especímenes únicos (señalados con el * en la Figura 2), pues también parecen compartir los alelos de ambos conjuntos. En ambos casos,

estos especímenes son aves criadas en cautividad, así pues es posible que se trate también de híbridos intencionales.

Debate

Los análisis taxonómicos realizados con 77 muestras de las tres subespecies de *P. robustus* indican una clara diferenciación entre *P.r. robustus* y el conjunto *P.r. suahelicus* - *P.r. fuscicollis*, como se puede ver en las pruebas de asignación que establecieron dos conjuntos genéticos diferentes (Figura 2). Estos resultados respaldan varias recomendaciones de que el lorito robusto debe ser considerado como una especie independiente, a saber, *P. robustus*, mientras que *P.r. suahelicus* y *P.r. fuscicollis* deben ser agrupados en el complejo de especies *P. fuscicollis* (Clancey 1997; Perrin 2005; Wirminghaus et al. 2002). Los resultados de las pruebas de asignación fueron corroborados por los análisis FST por pares y la presencia de numerosos alelos privados que definen cada subespecie. La diferenciación genética observada en nuestros datos entre *P.r. robustus* y el conjunto *P.r. suahelicus* - *P.r. fuscicollis* es comparable a los niveles que se observan entre otras especies de loros. Por ejemplo, un estudio realizado por Russello et al. (2010) utilizó nueve loci microsatélites para evaluar la situación taxonómica de *A. l. bahamensis*. Las pruebas de asignación bayesiana establecieron dos conjuntos genéticos diferentes que representan las poblaciones presentes en las islas de Abaco e Inagua. Estos datos, conjuntamente con los datos de la secuencia de ADN mitocondrial y las evidencias morfológicas (Reynolds y Hayes (2009), fueron utilizadas para clasificar estas poblaciones insulares como dos especies separadas.

La combinación de datos genéticos, morfológicos y comportamentales es importantes para diferencias las especies entre ellas (Chan et al. 2009). Los resultados del actual estudio, conjuntamente con los datos morfológicos, ecológicos y comportamentales publicados anteriormente con relación al lorito robusto (Clancey 1997; Perrin 2005; Wirminghaus et al. 2002), apoyan resueltamente la recomendación de que el lorito robusto sea considerado como una especie separada, a saber: *P. robustus*.

Trabajo futuro

Se realizarán muestreos adicionales de las poblaciones de KwaZulu-Natal y Limpopo para garantizar que se cubra toda el área de distribución del lorito robusto. Estas muestras adicionales formarán parte del análisis filogeográfico del lorito robusto poniendo de manifiesto la estructura genética correlacionada geográficamente. También se mejorará el tamaño de las muestras de *P.r. suahelicus* y *P.r. fuscicollis* con otras muestras de aves criadas en cautividad o extraídas del medio silvestre para así reforzar nuestros resultados actuales.

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Tabla 1. Lista de muestras de *Poicephalus* utilizadas para los análisis taxonómicos.

Subespecie	Origen	Número de muestras	Tipo de muestra
<i>P.r. robustus</i>	Cabo Oriental	40	DNA
	KwaZulu-Natal	8	Tejido
<i>P.r. suahelicus</i>	Cría en cautividad	1	Sangre
	Mpumalanga	4	Sangre
	Desconocido	14	Sangre
<i>P.r. fuscicollis</i>	Desconocido	10	Sangre
<i>P.r. robustus</i> X <i>P.r. suahelicus</i>	Cría en cautividad	1	FTA
Total:	77		

Tabla 2. Lista de paneles multiplex utilizados en este estudio.

Número del Multiplex	Locus	rango del tamaño del alelo (bp)
Multiplex 1	Prob6	236-272
	Prob15	132-176
	Prob26	342-386
Multiplex 2	Prob30	165-205
	Prob36	201-221
Multiplex 3	Prob18	205-241
	Prob25	184-228
	Prob31	129-165

Tabla 3. Valores F_{ST} por pares calculados utilizando Arlquin v3.5 (Excoffier et al. 2005).

<i>P.r. robustus</i>	<i>P.r. suahelicus</i>	<i>P.r. fuscicollis</i>
*		<i>P.r. robustus</i>
0.045 (0)	*	<i>P.r. suahelicus</i>
0.146 (0)	0.072 (0.00198±0.0004)	* <i>P.r. fuscicollis</i>

Nota: Los valores p asociados se presentan entre corchetes (nivel de significancia de 0.05)

Tabla 4. Alelos privados observados en cada subespecie de *Poicephalus*.

Población	Número de alelos privados
<i>P.r. robustus</i>	10 alelos en 7 loci (Prob 6, Prob 15, Prob18, Prob 25, Prob 26, Prob 30, Prob 31)
<i>P.r. suahelicus</i>	13 alelos en 7 loci (Prob 15, Prob18, Prob 25, Prob 26, Prob 30, Prob 31, Prob 36)
<i>P.r. fuscicollis</i>	alelos en 5 loci (Prob 15, Prob 25, Prob 26, Prob 30, Prob 36)

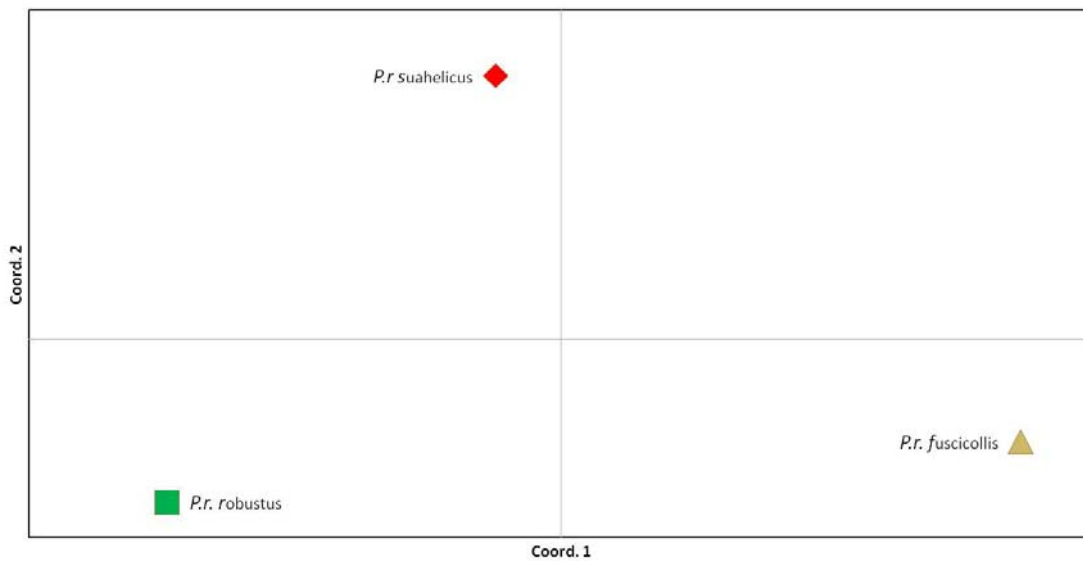


Figura 1. Representación gráfica de los valores FST por pares mediante un análisis Principal Coordinate realizado con el programa GenAlEx v6.5 (Peakall and Smouse 2012).

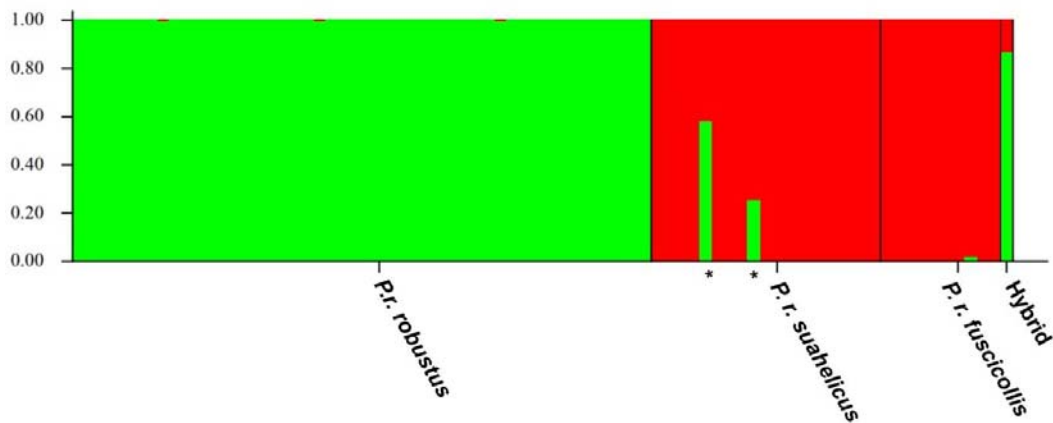


Figura 2. Representación en barras de la composición proporcional de cada individuo perteneciente a las tres subespecies. Cada individuo se representa mediante una barra vertical incluyendo una escala con un color diferente en el eje X. Cada conjunto genético se representa con un color diferente (verde: *P.r. robustus*; rojo: *P.r. suahelicus* y *P.r. fuscicollis*). El * indica los individuos híbridos potenciales



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Between a rock and a hard polytomy: Rapid radiation in the rupicolous girdled lizards (Squamata: Cordylidae)

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ABSTRACT

Girdled lizards (Cordylidae) are sub-Saharan Africa's only endemic squamate family and contain 80 nominal taxa, traditionally divided into four genera: *Cordylus*, *Pseudocordylus*, *Chamaesaura* and *Platysaurus*. Previous phylogenetic analysis revealed *Chamaesaura* and *Pseudocordylus* to be nested within *Cordylus*, and the former genera were sunk into the later. This taxonomic revision has received limited support due to the study's poor taxon sampling, weakly supported results and possible temporary nomenclatural instability. Our study analyzes three nuclear and three mitochondrial genes from 111 specimens, representing 51 ingroup taxa. Parsimony, likelihood and Bayesian analyses of concatenated and partitioned datasets consistently recovered a comb-like tree with 10, well-supported, monophyletic lineages. Our taxonomic reassessment divides the family into 10 genera, corresponding to these well-supported lineages. Short internodes and low support between the non-platysaur lineages are consistent with a rapid radiation event at the base of the viviparous cordylids.

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1. Introduction

The girdled lizards (Cordylidae) are a family of distinctively armored scinciform lizards endemic to Sub-Saharan Africa. There are 80 named taxa within the group, most of which are highly adapted for a rock-dwelling lifestyle, though the family encompasses a wide variety of morphologies, life histories and behaviors. The Cordylidae has traditionally been divided into four nominal genera (Loveridge, 1944; Lang, 1991): *Platysaurus* are highly flattened, lightly armored rock specialists occurring chiefly in southeast Africa, their extreme bauplan allowing them to use the narrowest of cracks as retreat sites; *Chamaesaura* are serpentine lizards with reduced limbs and greatly elongated tails that occupy grasslands of southern and eastern Africa; *Pseudocordylus* are crag-dwelling, moderately armored lizards that occur in the Cape Fold and Drakensberg mountain ranges of South Africa, Lesotho and Swaziland; and *Cordylus* are a morphologically and ecologically diverse group of heavily armored lizards that range from South Africa to Angola and Ethiopia. The family has a turbulent

taxonomic history, and evolutionary relationships between the members of the Cordylidae remain poorly understood, despite being the subject of several modern taxonomic treatments (e.g. Lang, 1991; Frost et al., 2001).

Gray (1845) placed all fully-limbed cordylids then known in the family Zonuridae, recognizing the genera *Cordylus* Gronovius 1763, *Zonurus* Merrem 1820, *Pseudocordylus* Smith 1838, *Hemicordylus* Smith 1838, and *Platysaurus* Smith 1844, along with what are now gerrhosaurids, lacertids of the genus *Takydromus*, and several anguids. Boulenger's (1884) reassessment of Zonuridae retained only *Zonurus* (incorporating *Cordylus*, *Pseudocordylus* and *Hemicordylus*) and *Platysaurus*, adding *Chamaesaura* (Fitzinger, 1843). The genus *Pseudocordylus* was resurrected one year later (Boulenger, 1885). This taxonomy remained relatively stable until Stejneger (1936) demonstrated that *Cordylus* Laurenti 1768 was a senior synonym of *Zonurus* Merrem 1820. Subsequent taxonomic works have consistently employed Cordylidae as the familial name of the group (Mertens, 1937; FitzSimons, 1943; Loveridge, 1944) although gerrhosaurids have been included in the same family by some authors (McDowell and Bogert, 1954; Romer, 1956; Townsend et al., 2004).

Lang (1991) presented the first phylogenetic analysis of the Cordyliiformes (Gerrhosauridae + Cordylidae) using morphological data. The resulting phylogeny recovered the serpentiform *Cham-*

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aesaura as the earliest diverging taxon, with *Cordylus* sister to a clade comprising *Platysaurus* and *Pseudocordylus*. This arrangement was consistent with previous works (Boulenger, 1884; Loveridge, 1944), which postulated that extensive armor is plesiomorphic in cordylids and that there was a reduction in osteoderms and spinose scales from *Cordylus*, through *Pseudocordylus*, to *Platysaurus* (Fig. 1a). However, this topology nests the oviparous *Platysaurus* deep within the otherwise viviparous members of the family, a phenomenon otherwise extremely rare among squamates (Lynch and Wagner, 2009). Furthermore, despite employing broad taxon sampling and using a large number of characters, Lang (1991) did not attempt to resolve species level relationships and assumed the monophyly of all of the cordylid genera, although he acknowledged that this assumption might prove to be incorrect.

Frost et al. (2001) analyzed sequence data from two mitochondrial genes, 12S and 16S, for 22 species in the first molecular phylogeny of cordylids. Their maximum parsimony analysis recovered a very different topology to that of Lang (1991). *Platysaurus* was shown to be the earliest diverging cordylid clade, which obviated the need to invoke a reversal in reproductive strategy, and was consistent with implications from cordylid life histories (Mouton and van Wyk, 1997). Additionally, Frost et al. (2001) identified *Cordylus* and *Pseudocordylus* as paraphyletic and polyphyletic, respectively, corroborating preliminary results from other studies (Herselman et al., 1992a; Mouton and van Wyk, 1997).

Frost et al.'s (2001) analysis retrieved a step-like phylogeny, with *Chamaesaura* and two separate lineages of *Pseudocordylus* nested among the 15 species of *Cordylus* sampled (Fig. 1b). Rather than implement a major taxonomic revision on the basis of an incompletely sampled phylogeny with limited resolution, the authors proposed that *Pseudocordylus* and *Chamaesaura* be synonymized with *Cordylus*. Some authors have adopted this arrangement (du Toit et al., 2002; McConnachie and Whiting, 2003; Cooper, 2005), but the traditional, four-genus taxonomy remains widely employed (Moon, 2001; Curtin et al., 2005; Costandius and Mouton, 2006; Menegon et al., 2006; Alexander and Marais, 2007; Eifler et al., 2007). Moreover, adoption of Frost et al.'s (2001) proposal would result in a number of nomenclatural conflicts with the necessity for replacement names e.g. *Pseudocordylus nebulosus* Mouton and Van Wyk (1995) would have become a junior homonym of *Cordylus nebulosus* A. Smith 1838 (= *Cordylus cataphractus* Boie 1828).

Some subsequent works have implemented a combination of the old and new taxonomies (Broadley, 2006; Vitt and Caldwell, 2008), maintaining *Pseudocordylus* in the synonymy of *Cordylus* but treating *Chamaesaura* as a valid genus. These arrangements have no phylogenetic basis but rather reflect the strong preference of many workers to reflect the morphological and ecological distinctiveness of these attenuate grass-swimmers.

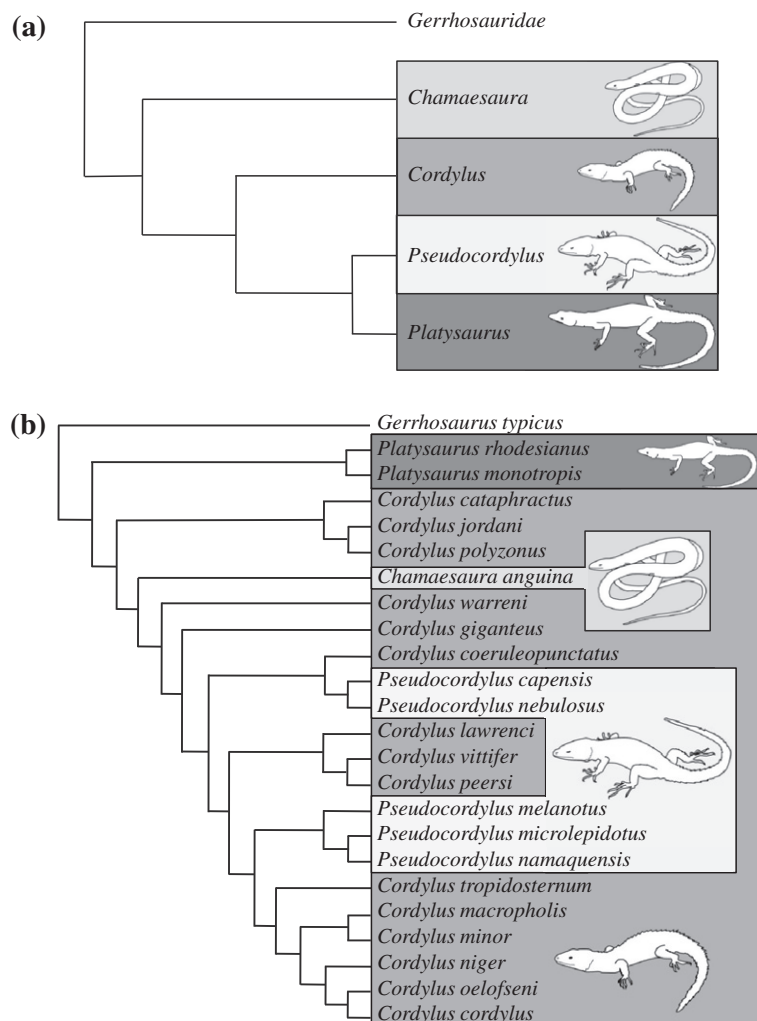


Fig. 1. Phylogenetic relationships of the Cordylidae as proposed by (a) Lang (1991) and (b) Frost et al. (2001).

Although Frost et al.'s (2001) taxon sampling was limited for *Chamaesaura* (1 of 6 taxa) and *Platysaurus* (2 of 26 taxa), the monophyly of these two genera has never been called into question, and in the case of *Platysaurus* it has subsequently been corroborated (Scott et al., 2004). However, the partial taxon sampling within *Cordylus* (15 of 38 taxa) and *Pseudocordylus* (3 of 10 taxa) limited the study's ability to accurately represent the species relationships of the family as a whole, and may have compounded weaknesses in the analytical methods (Heath et al., 2008). Furthermore, the genes utilized in this study may not, by themselves, be capable of resolving relationships at all depths of the tree, as mitochondrial DNA tends to evolve rapidly and becomes saturated at deeper nodes (Overton and Rhoads, 2004).

Four primary factors affect the ability of a molecular phylogenetic analysis to accurately estimate true historical relationships among species: (1) taxon sampling; (2) selection of genetic markers; (3) amount of sequence data analyzed, and (4) choice of analytical methods (Swofford et al., 1996). Our study aims to improve on previous analyses in all four of these areas to recover a robust and well-resolved phylogeny of the family Cordylidae. If a strong phylogenetic signal can be recovered by amending these compounding factors, a new classification may be proposed that is consistent with traditional groupings based on morphology and life history while still reflecting generic monophyly.

2. Materials and methods

2.1. Taxon sampling

Sequence data were obtained from 111 specimens, representing 51 cordylid taxa from all four genera. Taxon sampling was particularly dense in *Cordylus* and *Pseudocordylus* (Table 1), as previous studies have recovered these groups to be non-monophyletic.

Wherever possible, specimens from separate localities were included for each taxon. Increased sampling was employed for widely distributed species (*Cordylus polyzonus* and *C. cordylus*), or species with geographically discrete, well separated populations (*C. oelofseni* and *C. vittifer*) so as to include representatives from the species' entire geographic range (Table 2). Following previous phylogenetic assessments (McDowell and Bogert, 1954; Romer, 1956; Lang, 1991; Townsend et al., 2004) three species of gerrhosaurid, *Gerrhosaurus validus*, *G. nigrolineatus* and *Cordylosaurus subtessellatus*, were used as outgroups for the study.

2.2. Gene sampling

We analyzed sequence data from three nuclear and three mitochondrial genes. The mitochondrial genes 12S, 16S and ND2 were utilized in previous studies of cordylids (Frost et al., 2001; Odierna et al., 2002; Daniels et al., 2004) and were included in this study to facilitate comparisons with these prior analyses. Three rapidly evolving nuclear genes were selected: Prolactin receptor gene PRLR (Townsend et al., 2008), Myosin Heavy chain 2 MYH2 (Whiting et al., 2006) and Kinesin Family Member 24 KIF24 (Portik et al.,

in press). All three genes are protein coding and MYH2 also contains a rapidly evolving, non-coding intron.

2.3. Molecular data

Total genomic DNA was isolated from the liver or skeletal muscle of specimens preserved in 95% ethanol using the Qiagen DNeasy™ tissue kit (Valencia, CA, USA). DNA from fresh tissues of members of the *Cordylus warreni* complex and several other key species was isolated at the Leslie Hill Laboratories, South African National Biodiversity Institute (SANBI), Kirstenbosch, South Africa, using the protocols of Tolley et al. (2004).

Target genes were amplified using double-stranded Polymerase Chain Reaction (PCR). 2.5 µl of the extracted genomic DNA was combined with 2.5 µl forward primer (8.p.p.m), 2.5 µl reverse primer (8.p.p.m), 2.5 µl dinucleotide pairs, 2.5 µl 5× buffer, 2.5 µl MgCl 10× buffer, 0.18 µl Taq polymerase and 8.92 µl H₂O. PCR cycling was executed on an Eppendorf Mastercycler gradient thermocycler and each primer-set was initially amplified under the following conditions: initial denaturation for 2 min at 95 °C followed by 95 °C for 35 s, annealing at 50 °C for 35 s, and extension at 72 °C for 95 s (Greenbaum et al., 2007). Products were visualized with 1.5% agarose gel electrophoresis. If necessary, annealing temperatures were modified accordingly (Table 3).

Target products were treated with AMPure magnetic bead solution (Agencourt Bioscience, Beverly, MA, USA) to remove byproducts of the PCR process. The cleaned PCR product was then prepared for sequencing with the DYEnamic™ ET Dye Terminator Kit (GE Healthcare, Piscataway, NJ, USA). Sequencing reactions were purified with CleanSeq magnetic bead solution (Agencourt Bioscience, Beverly, MA, USA) and analyzed with an ABI 3700 automated sequencer. All genes were sequenced from both 3' and 5' ends separately and internal primers were used for genes over 800 bp long. The complimentary and contiguous sequences were aligned using the program Genious™ (Drummond et al., 2008). Ambiguous or conflicting bases were coded as heterozygotes. Multiple sequence alignment was performed with Muscle (Edgar, 2004) and visualized with Maclade (Maddison and Maddison, 2000) to confirm the amino acid reading frame and to check for stop codons.

2.4. Phylogenetic analysis

We employed a pluralistic approach for phylogenetic analysis, performing separate analyses with the three most commonly employed optimality criteria, Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI). Separate analyses were performed on each individual gene as well as concatenated sets of mitochondrial genes (ND2, 16S and 12S) nuclear genes (PRLR, MYH2 and KIF24), and all genes.

The maximum Parsimony analyses were run using PAUP* (Swofford, 2002) under the following conditions: 1000 random addition replicates, tree bisection-reconnection branch swapping, zero-length branches collapsed to yield polytomies, and gaps treated as missing data. Nodal support for this analysis was estimated using non-parametric bootstrapping (1000 iterations) and Goodman-Bremer support (Bremer, 1994).

ModelTest 2.2.3 (Posada and Crandall, 1998) was run to identify the most likely model of evolution for each of the individual genes. Both ML and BI analyses were partitioned by codon and gene, each partition employing the appropriate model estimated by ModelTest.

The Maximum Likelihood analyses were performed using RAX-ML HPC 7.2.3 (Stamatakis et al., 2008) on the CIPRES server. The analysis was performed using a GTR gamma model with gaps

Table 1

The total number of Cordylidae taxa, the number of taxa included by Frost et al. (2001) and the number of taxa present in this study.

Genus	Total named taxa	Taxa in Frost et al. (2001)	Taxa in this study
<i>Cordylus</i>	38	15	34
<i>Pseudocordylus</i>	10	5	8
<i>Chamaesaura</i>	6	1	3
<i>Platysaurus</i>	26	2	6

Table 2

Voucher numbers, localities and Genbank accession numbers for samples. (RSA = Republic of South Africa).

Taxon	Voucher	Locality	Coordinates	16s	12s	ND2	PRLR	KIF24	MYH2
<i>Chamaesaura aenea</i> 1	QP0041	Free State, RSA	28° 31' 58" S, 28° 39' 04" E	HQ167160	HQ167049	HQ166950	HQ167489	HQ167271	HQ167382
<i>Chamaesaura aenea</i> 2	QP0043	KwaZulu Natal, RSA	29° 22' 34" S, 29° 38' 06" E	HQ167162	HQ167051	HQ166952	HQ167491	HQ167273	HQ167384
<i>Chamaesaura aenea</i> 3	QP0042	Freestate, RSA	28° 31' 22" S, 28° 37' 28" E	HQ167161	HQ167050	HQ166951	HQ167490	HQ167272	HQ167383
<i>Chamaesaura anguina</i> 1	PEM195	Eastern Cape, RSA	33° 42' 24" S, 23° 52' 06" E	HQ167163	HQ167052	HQ166953	HQ167492	HQ167274	HQ167385
<i>Chamaesaura anguina</i> 2	SU2	Western Cape, RSA	34° 39' 04" S, 19° 27' 16" E	HQ167165	HQ167054	HQ166955	HQ167494	HQ167276	HQ167387
<i>Chamaesaura anguina</i> 3	SU1	Western Cape, RSA	34° 38' 48" S, 19° 27' 30" E	HQ167164	HQ167053	HQ166954	HQ167493	HQ167275	HQ167386
<i>Chamaesaura a. tenuior</i>	PEMR	Arusha, Kenya	02° 07' 30" S, 35° 19' 22" E	HQ167166	HQ167055	-	HQ167495	HQ167277	HQ167388
<i>Cordylus aridus</i> 1	PEMR16376	Western Cape, RSA	33° 08' 04" S, 22° 32' 20" E	HQ167170	HQ167059	HQ166959	HQ167499	HQ167281	HQ167390
<i>Cordylus aridus</i> 2	PEMR16371	Western Cape, RSA	33° 08' 04" S, 22° 32' 20" E	HQ167169	HQ167058	HQ166958	HQ167498	HQ167280	HQ167389
<i>Cordylus beraduccii</i>	WRB0037	Mtera, Tanzania	07° 07' 58" S, 35° 59' 43" E	HQ167172	HQ167061	-	HQ167501	HQ167283	HQ167392
<i>Cordylus breyeri</i>	MBUR00320	Limpopo, RSA	23° 17' 24" S, 28° 50' 25" E	HQ167173	HQ167062	HQ166961	HQ167502	HQ167284	HQ167393
<i>Cordylus campbelli</i> 1	MCZ27028	Namibia	25° 47' 32" S, 16° 25' 31" E	HQ167174	HQ167063	HQ166962	HQ167503	HQ167285	HQ167394
<i>Cordylus campbelli</i> 2	MCZ27028	Namibia	25° 47' 32" S, 16° 25' 31" E	HQ167175	HQ167064	HQ166963	HQ167504	HQ167286	HQ167395
<i>Cordylus cataphractus</i> 1	SU1	Western Cape, RSA	32° 26' 18" S, 18° 59' 52" E	HQ167176	HQ167065	HQ166964	HQ167505	HQ167287	HQ167396
<i>Cordylus cataphractus</i> 2	MBUR01792	Northern Cape, RSA	30° 24' 16" S, 18° 06' 06" E	HQ167177	HQ167066	HQ166965	HQ167506	HQ167288	HQ167397
<i>Cordylus coeruleopunctatus</i> 1	KTH329	Western Cape, RSA	34° 00' 03" S, 20° 26' 19" E	HQ167178	HQ167067	HQ166966	HQ167507	HQ167289	HQ167398
<i>Cordylus coeruleopunctatus</i> 2	QP0046	Western Cape, RSA	33° 56' 33" S, 20° 51' 51" E	HQ167181	HQ167070	HQ166969	HQ167510	HQ167292	HQ167401
<i>Cordylus coeruleopunctatus</i> 3	SU	Western Cape, RSA	33° 53' 32" S, 22° 24' 09" E	HQ167179	HQ167068	HQ166967	HQ167508	HQ167290	HQ167399
<i>Cordylus coeruleopunctatus</i> 4	QP0044	Western Cape, RSA	33° 48' 52" S, 22° 54' 39" E	HQ167180	HQ167069	HQ166968	HQ167509	HQ167291	HQ167400
<i>Cordylus cordylus</i> 1	AMB8168	Eastern Cape, RSA	32° 62' 40" S, 26° 15' 11" E	HQ167182	HQ167071	HQ166970	HQ167511	HQ167293	HQ167402
<i>Cordylus cordylus</i> 2	PEMR9714	Eastern Cape, RSA	31° 00' 41" S, 29° 19' 09" E	HQ167187	HQ167076	HQ166975	HQ167516	HQ167298	HQ167407
<i>Cordylus cordylus</i> 3	PEMR16382	Western Cape, RSA	33° 21' 60" S, 22° 21' 90" E	HQ167185	HQ167074	HQ166973	HQ167514	HQ167296	HQ167405
<i>Cordylus cordylus</i> 4	PEMR17466	Eastern Cape, RSA	34° 11' 43" S, 24° 50' 16" E	HQ167186	HQ167075	HQ166974	HQ167515	HQ167297	HQ167406
<i>Cordylus cordylus</i> 5	PEMR17464	Eastern Cape, RSA	33° 29' 46" S, 24° 31' 04" E	HQ167190	HQ167079	HQ166978	HQ167519	HQ167301	HQ167410
<i>Cordylus cordylus</i> 6	PEMR17467	Eastern Cape, RSA	33° 29' 44" S, 24° 31' 03" E	HQ167188	HQ167077	HQ166976	HQ167517	HQ167299	HQ167408
<i>Cordylus cordylus</i> 7	PEMR13511	Western Cape, RSA	33° 16' 56" S, 25° 43' 52" E	HQ167184	HQ167073	HQ166972	HQ167513	HQ167295	HQ167404
<i>Cordylus cordylus</i> 8	AMB8865	Western Cape, RSA	32° 50' 14" S, 17° 51' 27" E	HQ167183	HQ167072	HQ166971	HQ167512	HQ167294	HQ167403
<i>Cordylus giganteus</i> 1	MJC 5403	Free State, RSA	28° 16' 22" S, 29° 04' 39" E	HQ167193	HQ167082	HQ166981	HQ167522	HQ167304	HQ167413
<i>Cordylus giganteus</i> 2	MJC 6638	Free State, RSA	28° 09' 40" S, 29° 19' 02" E	HQ167194	HQ167083	HQ166982	HQ167523	HQ167305	HQ167414
<i>Cordylus giganteus</i> 3	MJC 6640	Free State, RSA	28° 09' 34" S, 29° 19' 01" E	HQ167195	HQ167084	HQ166983	HQ167524	HQ167306	HQ167415
<i>Cordylus giganteus</i> 4	MJC 6642	Free State, RSA	28° 16' 22" S, 29° 04' 39" E	HQ167196	HQ167085	HQ166984	HQ167525	HQ167307	HQ167416
<i>Cordylus imkeae</i> 1	MBUR01795	Northern Cape, RSA	30° 24' 16" S, 18° 06' 06" E	HQ167197	HQ167086	HQ166985	HQ167526	HQ167308	HQ167417
<i>Cordylus imkeae</i> 2	MBUR01796	Northern Cape, RSA	30° 24' 16" S, 18° 06' 06" E	HQ167198	HQ167087	HQ166986	HQ167527	HQ167309	HQ167418
<i>Cordylus jonesi</i> 1	AMB8396	Limpopo, RSA	24° 03' 19" S, 28° 24' 13" E	HQ167200	HQ167089	HQ166988	HQ167529	HQ167311	HQ167420
<i>Cordylus jonesi</i> 2	AMB8310	Limpopo, RSA	22° 41' 18" S, 29° 31' 16" E	HQ167199	HQ167088	HQ166987	HQ167528	HQ167310	HQ167419
<i>Cordylus jordani</i> 1	AMB5876	Namibia	29° 49' 52" S, 17° 22' 35" E	HQ167202	HQ167091	HQ166990	HQ167531	HQ167313	HQ167422
<i>Cordylus jordani</i> 2	MCZ27023	Namibia	25° 47' 45" S, 16° 25' 15" E	HQ167201	HQ167090	HQ166989	HQ167530	HQ167312	HQ167421

Table 2 (continued)

Taxon	Voucher	Locality	Coordinates	16s	12s	ND2	PRLR	KIF24	MYH2
<i>Cordylus lawrenci</i>	PEM285	Northern Cape, RSA	29° 15' 17" S, 17° 05' 38" E	HQ167203	HQ167092	-	HQ167532	HQ167314	HQ167423
<i>Cordylus machadoi</i> 1	KTH09059	Humpata, Angola	14° 57' 42" S, 13° 20' 59" E	HQ167204	HQ167093	HQ166991	HQ167533	HQ167315	HQ167424
<i>Cordylus machadoi</i> 2	KTH09080	Humpata, Angola	15° 10' 39" S, 13° 19' 17" E	HQ167205	HQ167094	HQ166992	HQ167534	HQ167316	HQ167425
<i>Cordylus macropholis</i> 1	AMB8874	Western Cape, RSA	32° 06' 37" S, 18° 18' 14" E	HQ167207	HQ167096	HQ166994	HQ167536	HQ167318	HQ167427
<i>Cordylus macropholis</i> 2	AMB8873	Western Cape, RSA	32° 06' 36" S, 18° 18' 13" E	HQ167206	HQ167095	HQ166993	HQ167535	HQ167317	HQ167426
<i>Cordylus mclachlani</i> 1	AMB8855	Western Cape, RSA	33° 16' 20" S, 19° 37' 42" E	HQ167208	HQ167097	HQ166995	HQ167537	HQ167319	HQ167428
<i>Cordylus mclachlani</i> 2	SU1	Western Cape, RSA	32° 12' 06" S, 19° 05' 52" E	HQ167209	HQ167098	HQ166996	HQ167538	HQ167320	HQ167429
<i>Cordylus meculae</i> 1	PEMR16203	Mecula, Mozambique	12° 02' 27" S, 37° 37' 21" E	HQ167234	HQ167123	-	HQ167563	HQ167345	HQ167454
<i>Cordylus meculae</i> 2	PEMR16202	Mecula, Mozambique	12° 02' 28" S, 37° 37' 21" E	HQ167233	HQ167122	-	HQ167562	HQ167344	HQ167453
<i>Cordylus meculae</i> 3	PEMR16165	Mecula, Mozambique	12° 02' 15" S, 37° 38' 19" E	HQ167211	HQ167100	-	HQ167540	HQ167322	HQ167431
<i>Cordylus meculae</i> 4	PEMR16164	Mecula, Mozambique	12° 02' 15" S, 37° 38' 19" E	HQ167210	HQ167099	-	HQ167539	HQ167321	HQ167430
<i>Cordylus minor</i>	SU	Northern Cape, RSA	32° 52' 04" S, 20° 33' 10" E	HQ167212	HQ167101	HQ166997	HQ167541	HQ167323	HQ167432
<i>Cordylus mossambicus</i>	PEMR5227	Mozambique	17° 24' 51" S, 33° 22' 51" E	HQ167213	HQ167102	HQ166998	HQ167542	HQ167324	HQ167433
<i>Cordylus namaquensis</i> 1	AMB6848	Namibia	27° 22' 06" S, 18° 51' 16" E	HQ167214	HQ167103	-	HQ167543	HQ167325	HQ167434
<i>Cordylus namaquensis</i> 2	AMB6849	Namibia	27° 22' 06" S, 18° 51' 16" E	HQ167215	HQ167104	-	HQ167544	HQ167326	HQ167435
<i>Cordylus niger</i> 1	AMB8875	Western Cape, RSA	32° 59' 14" S, 17° 52' 34" E	HQ167216	HQ167105	HQ166999	HQ167545	HQ167327	HQ167436
<i>Cordylus niger</i> 2	SU1	Western Cape, RSA	32° 59' 04" S, 17° 52' 37" E	HQ167217	HQ167106	HQ167000	HQ167546	HQ167328	HQ167437
<i>Cordylus oelofseni</i> 1	SU1	Western Cape, RSA	34° 02' 24" S, 18° 59' 54" E	HQ167219	HQ167108	HQ167002	HQ167548	HQ167330	HQ167439
<i>Cordylus oelofseni</i> 2	SU2	Western Cape, RSA	34° 02' 24" S, 18° 59' 54" E	HQ167220	HQ167109	HQ167003	HQ167549	HQ167331	HQ167440
<i>Cordylus oelofseni</i> 3	AMB8851	Western Cape, RSA	32° 54' 34" S, 19° 02' 06" E	HQ167218	HQ167107	HQ167001	HQ167547	HQ167329	HQ167438
<i>Cordylus oelofseni</i> 4	AMB8860	Western Cape, RSA	32° 46' 11" S, 18° 42' 10" E	HQ167221	HQ167110	HQ167004	HQ167550	HQ167332	HQ167441
<i>Cordylus oelofseni</i> 5	AMB8862	Western Cape, RSA	32° 46' 11" S, 18° 42' 10" E	HQ167222	HQ167111	HQ167005	HQ167551	HQ167333	HQ167442
<i>Cordylus polyzonus</i> 1	A38345	Namibia	27° 23' 53" S, 18° 25' 26" E	HQ167223	HQ167112	HQ167006	HQ167552	HQ167334	HQ167443
<i>Cordylus polyzonus</i> 2	JM1117	Northern Cape, RSA	30° 21' 47" S, 17° 53' 03" E	HQ167224	HQ167113	HQ167007	HQ167553	HQ167335	HQ167444
<i>Cordylus polyzonus</i> 3	PEMR17462	Eastern Cape, RSA	33° 29' 51" S, 24° 30' 45" E	HQ167225	HQ167114	HQ167008	HQ167554	HQ167336	HQ167445
<i>Cordylus polyzonus</i> 4	SU1	Western Cape, RSA	32° 16' 35" S, 19° 05' 09" E	HQ167226	HQ167115	HQ167009	HQ167555	HQ167337	HQ167446
<i>Cordylus peersi</i>	MB20710	Northern Cape, RSA	30° 42' 48" S, 19° 00' 01" E	HQ167227	HQ167116	HQ167010	HQ167556	HQ167338	HQ167447
<i>Cordylus pustulatus</i>	visser006492	Namibia	22° 46' 19" S, 16° 21' 57" E	HQ167228	HQ167117	HQ167011	HQ167557	HQ167339	HQ167448
<i>Cordylus regius</i>	AMB6171	Eastern Zimbabwe	19° 03' 25" S, 32° 36' 16" E	HQ167229	HQ167118	HQ167012	HQ167558	HQ167340	HQ167449
<i>Cordylus rhodesianus</i> 1	ELSPET4	captive	Unknown	HQ167230	HQ167119	HQ167013	HQ167559	HQ167341	HQ167450
<i>Cordylus rhodesianus</i> 2	ELSPET5	captive	Unknown	HQ167231	HQ167120	HQ167014	HQ167560	HQ167342	HQ167451
<i>Cordylus tasmani</i> 1	PEMR17394	Eastern Cape, RSA	33° 46' 18" S, 25° 39' 45" E	HQ167232	HQ167121	HQ167015	HQ167561	HQ167343	HQ167452
<i>Cordylus tasmani</i> 2	PEMR15012	Eastern Cape, RSA	33° 47' 57" S, 25° 46' 10" E	HQ167189	HQ167078	HQ166977	HQ167518	HQ167300	HQ167409
<i>Cordylus tropidosternum</i> 1	WRB0038	Tanzania	Unknown	HQ167236	HQ167125	-	HQ167565	HQ167347	HQ167456
<i>Cordylus tropidosternum</i> 2	WRB0042	Tanzania	Unknown	HQ167235	HQ167124	-	HQ167564	HQ167346	HQ167455
<i>Cordylus ukingensis</i>	WRB0039	Uzungwe Mts, Kenya	08° 17' 58" S, 35° 40' 43" E	HQ167237	HQ167126	-	HQ167566	HQ167348	HQ167457
<i>Cordylus vandami</i> 1	AMB8292	Mpumalanga, RSA	24° 56' 22" S, 30° 15' 09" E	HQ167240	HQ167129	HQ167018	HQ167569	HQ167351	HQ167460
<i>Cordylus vandami</i> 2	AMB8195	Limpopo, RSA	24° 03' 35" S, 30° 49' 33" E	HQ167239	HQ167128	HQ167017	HQ167568	HQ167350	HQ167459
<i>Cordylus vandami</i> 3	AMB8193	Limpopo, RSA	24° 03' 59" S, 30° 49' 56" E	HQ167238	HQ167127	HQ167016	HQ167567	HQ167349	HQ167458
<i>Cordylus vittifer</i> 1	AMB6073	Mpumalanga, RSA	26° 08' 00" S, 31° 08' 00" E	HQ167241	HQ167130	HQ167019	HQ167570	HQ167352	HQ167461

(continued on next page)

Table 2 (continued)

Taxon	Voucher	Locality	Coordinates	16s	12s	ND2	PRLR	KIF24	MYH2
<i>Cordylus vittifer</i> 2	AMB8274	Limpopo, RSA	24° 31' 49" S, 30° 38' 43" E	HQ167242	HQ167131	HQ167020	HQ167571	HQ167353	HQ167462
<i>Cordylus vittifer</i> 3	AMB8603	Swaziland	25° 18' 11" S, 30° 08' 51" E	HQ167243	HQ167132	HQ167021	HQ167572	HQ167354	HQ167463
<i>Cordylus warreni warreni</i>	ELS012	Mpumalanga, RSA	25° 54' 21" S, 31° 52' 21" E	HQ167244	HQ167133	HQ167022	HQ167573	HQ167355	HQ167464
<i>Cordylus w. barbertonensis</i>	RCBS2133	Molototja, Swaziland	26° 04' 57" S, 31° 15' 59" E	HQ167171	HQ167060	HQ166960	HQ167500	HQ167282	HQ167391
<i>Cordylus w. depressus</i> 1	MFB141	Limpopo, RSA	22° 58' 16" S, 29° 57' 23" E	HQ167191	HQ167080	HQ166979	HQ167520	HQ167302	HQ167411
<i>Cordylus w. depressus</i> 2	MCZF38871	Limpopo, RSA	23° 02' 10" S, 29° 25' 41" E	HQ167192	HQ167081	HQ166980	HQ167521	HQ167303	HQ167412
<i>Gerrhosaurus validus</i>	AMB 6090	Limpopo, RSA	24° 18' 13" S, 30° 50' 21" E	HQ167246	HQ167135	HQ167024	HQ167575	HQ167357	-
<i>Gerrhosaurus nigrolineatus</i>	AMB 8339	Limpopo, RSA	24° 03' 18" S, 28° 25' 19" E	HQ167245	HQ167134	HQ167023	HQ167574	HQ167356	-
<i>Cordylus subtesellatus</i> 1	AMB 4649	Northern Cape, RSA	28° 42' 26" S, 17° 07' 23" E	HQ167167	HQ167056	HQ166956	HQ167496	HQ167278	-
<i>Cordylus subtesellatus</i> 2	AMB 6928	Namibia	19° 05' 00" S, 13° 34' 07" E	HQ167168	HQ167057	HQ166957	HQ167497	HQ167279	-
<i>Platysaurus broadleyi</i>	AMB 4944	Northern Cape, RSA	28° 34' 45" S, 20° 17' 59" E	HQ167247	HQ167136	HQ167025	HQ167576	HQ167358	HQ167465
<i>Platysaurus capensis</i>	AMB 4524	Northern Cape, RSA	28° 07' 59" S, 16° 59' 20" E	HQ167248	HQ167137	HQ167026	HQ167577	HQ167359	HQ167466
<i>Platysaurus minor</i>	AMB8411	Limpopo, RSA	24° 14' 10" S, 28° 22' 31" E	HQ167250	HQ167139	HQ167028	HQ167579	HQ167361	HQ167468
<i>Platysaurus mitchelli</i>	MEEP XS173	Malawi	15° 52' 05" S, 35° 42' 15" E	HQ167251	HQ167140	HQ167029	HQ167580	HQ167362	HQ167469
<i>Platysaurus i. intermedius</i>	NMBR	Limpopo, RSA	23° 52' 00" S, 29° 56' 59" E	HQ167249	HQ167138	HQ167027	HQ167578	HQ167360	HQ167467
<i>Platysaurus i. nigrescens</i>	PEMR sample	Mashatu Botswana	Unknown	HQ167252	HQ167141	HQ167030	HQ167581	HQ167363	HQ167470
<i>Pseudocordylus capensis</i> 1	AMB8859	Western Cape, RSA	31° 42' 11" S, 18° 48' 05" E	HQ167255	HQ167144	HQ167033	HQ167584	HQ167366	HQ167473
<i>Pseudocordylus capensis</i> 2	AMB8857	Western Cape, RSA	34° 02' 48" S, 18° 59' 55" E	HQ167254	HQ167143	HQ167032	HQ167583	HQ167365	HQ167472
<i>Pseudocordylus capensis</i> 3	PEMR16378	Western Cape, RSA	33° 24' 59" S, 22° 42' 18" E	HQ167253	HQ167142	HQ167031	HQ167582	HQ167364	HQ167471
<i>Pseudocordylus langi</i> 1	NMBR8556	KwaZulu Natal, RSA	28° 44' 50" S, 28° 52' 53" E	HQ167257	HQ167146	HQ167035	HQ167586	HQ167368	HQ167475
<i>Pseudocordylus langi</i> 2	NMBR8555	KwaZulu Natal, RSA	28° 44' 50" S, 28° 52' 53" E	HQ167256	HQ167145	HQ167034	HQ167585	HQ167367	HQ167474
<i>Pseudocordylus melanotus</i>	AMB8210	Limpopo, RSA	24° 33' 00" S, 30° 51' 53" E	HQ167258	HQ167147	HQ167036	HQ167587	HQ167369	HQ167476
<i>Pseudocordylus microlepidotus</i> 1	SU4	Western Cape, RSA	32° 49' 00" S, 19° 23' 00" E	HQ167259	HQ167148	HQ167037	HQ167588	HQ167370	HQ167477
<i>Pseudocordylus microlepidotus</i> 2	SU3	Western Cape, RSA	32° 49' 00" S, 19° 23' 00" E	HQ167260	HQ167149	HQ167038	HQ167589	HQ167371	HQ167478
<i>Pseudocordylus nebulosus</i> 1	SU1	Western Cape, RSA	34° 02' 34" S, 18° 59' 54" E	HQ167262	HQ167151	HQ167040	HQ167591	HQ167373	HQ167480
<i>Pseudocordylus nebulosus</i> 2	SU2	Western Cape, RSA	34° 02' 33" S, 19° 00' 00" E	HQ167261	HQ167150	HQ167039	HQ167590	HQ167372	HQ167479
<i>Pseudocordylus sp. "Transkei"</i>	PEMR2701	Eastern Cape, RSA	32° 02' 28" S, 27° 49' 47" E	HQ167263	HQ167152	HQ167041	HQ167592	HQ167374	HQ167481
<i>Pseudocordylus spinosus</i> 1	NMBR8572	KwaZulu Natal, RSA	28° 41' 13" S, 28° 54' 38" E	HQ167264	HQ167153	HQ167042	HQ167593	HQ167375	HQ167482
<i>Pseudocordylus spinosus</i> 2	NMB R8572	KwaZulu Natal, RSA	28° 41' 13" S, 28° 54' 38" E	HQ167265	HQ167154	HQ167044	HQ167594	HQ167376	HQ167483
<i>Pseudocordylus spinosus</i> 3	NMB R8570	KwaZulu Natal, RSA	28° 41' 13" S, 28° 54' 25" E	HQ167266	HQ167155	HQ167043	HQ167595	HQ167377	HQ167484
<i>Pseudocordylus subviridis</i> 1	NMBR8558	KwaZulu Natal, RSA	28° 44' 49" S, 28° 52' 54" E	HQ167268	HQ167157	HQ167046	HQ167597	HQ167379	HQ167486
<i>Pseudocordylus subviridis</i> 2	NMBR8561	KwaZulu Natal, RSA	28° 43' 52" S, 28° 53' 33" E	HQ167267	HQ167156	HQ167045	HQ167596	HQ167378	HQ167485
<i>Pseudocordylus transvaalensis</i> 1	MFB	Limpopo, RSA	Unknown	HQ167269	HQ167158	HQ167047	HQ167598	HQ167380	HQ167487
<i>Pseudocordylus transvaalensis</i> 2	NMBR8548	Limpopo, RSA	23° 51' 13" S, 29° 54' 07" E	HQ167270	HQ167159	HQ167048	HQ167599	HQ167381	HQ167488

treated as missing data, 25 distinct rate categories, and run for 1000 rapid bootstrap iterations.

Likelihood decay index values were also calculated for each node of the tree, in addition to bootstrap support. This was

achieved by the following method. A maximum likelihood tree was created from the partitioned dataset using GARLI (Zwickl, 2006) under a GTR+gamma model, with the default genetic algorithm settings. This tree was used to create a command file from

Table 3

Primer information for the genes utilized in this study. The PCR column denotes the number of repeated cycles/annealing temp (°C) used in the PCR.

Primer	Gene	Reference	Sequence	PCR
16Sa	16S	Simon et al. (1994)	5' CGCCTGTTTATCAAAACAT 3'	34/52
16Sb	16S	Simon et al. (1994)	5' CCGGTCTGAACCTCAGATCACGT 3'	34/52
12sf700	12S	This study	5' AAAGTGGGATTAGATACCCCACTAT 3'	34/52
12sr600	12S	This study	5' GAGGGTGACGGCGGTGTGT 3'	34/52
L4437	ND2	Macey et al. (1997)	5' AAGCTTTCGGGCCCATACC 3'	34/52
H5540	ND2	Macey et al. (1997)	5' TTTAGGGCTTTGAAGGC 3'	34/52
R102	ND2	This study	5' CAGCCTAGGTGGCGCATG 3'	–/–
PRLRf1	PRLR	Townsend et al. (2008)	5' GACARYGARGACCAGCAACTRATGCC 3'	34/54
PRLRr1	PRLR	Townsend et al. (2008)	5' GACYTTGTGRACITCYACRTAATCCAT 3'	34/54
Kif24f	Kif24	Portik et al. (2010)	5' WGGCTGCTGRAAYTGTCTGGT 3'	34/50
Kif24r	Kif24	Portik et al. (2010)	5' SAAACGTRTCTCCMAAACGCATCC 3'	34/50
MYH2f	MYH2	This study	5' GAACACCAGCCTCATCAACC 3'	34/52
MYH2r	MYH2	This study	5' TGGTGCTCTCTCTCTTC 3'	34/52

the Partition Branch Support program, TreeRot v.3 (Sorenson and Franzosa, 2007). The output command file contains a series of constraint trees that represent every node on the original ML tree and each of the constraint trees was converted to serve as a negative constraint file. Each constraint file was incorporated into a GARLI analyses and run on the original dataset under the original conditions. The Likelihood decay index is the difference between the log likelihood score of each constrained tree and the log likelihood score of the unconstrained tree for each node.

The Bayesian analyses were conducted using MrBayes 3.1 (Ronquist and Huelsenbeck, 2003; Huelsenbeck and Ronquist, 2001) with default priors. Two runs were performed for 10,000,000 generations and the Markov chains were sampled every 1000 generations. If adequate convergence had not occurred after 5 million generations, additional generations were run until the average standard deviation of split frequencies was less than 0.01. The log likelihood was plotted against generation to identify the convergence point and the burn-in discarded. Topological convergence was tested for using the program Are We There Yet (Nylander et al., 2008). Nodes that returned clade posteriors above 0.95 were considered significantly supported.

To compare the similarity of phylogenetic signal between the different genes, partition homogeneity tests (with 100 replications) were conducted across the entire data set and between all individual partitions (Baker and DeSalle, 1997). The topologies of individual gene trees were compared to check for any obvious conflicts and a Partitioned Branch Support analysis was carried out using TreeRot V.3 (Sorenson and Franzosa, 2007).

Finally, the dataset was analyzed using Phycas, version 1.1.1. (Lewis et al., 2009), which allows unresolved tree topologies to be sampled during the course of a phylogenetic analysis in addition to fully-resolved tree topologies. A GTR+I+ Γ model was used on the concatenated dataset, as Phycas does not currently allow partitioning. The prior on the gamma shape parameter was set as an exponential distribution with a mean of 0.5. Polytomies were allowed, and an exponential distribution with mean 1.0 (e) was set

as the polytomy prior, as suggested by Lewis et al. (2005). Two MCMC chains were run for 500,000 cycles each, with trees sampled every 10 cycles (one cycle is equivalent to over 100 generations in MrBayes). The first 5000 trees were discarded as burn-in and the remaining trees summarized with TreeAnnotator V.1.5.4 (<http://beast.bio.ed.ac.uk>).

3. Results

3.1. Gene success

All six genes were successfully recovered with PCR amplification. However, for several species ND2 consistently failed to amplify (*Chamaesaura anguina tenuior*, *Cordylus lawrenci*, *C. namaquensis*, *C. beraducci*, *C. tropidosternum* *C. ukingensis* and *C. meculae*), so separate analyses were run on the concatenated dataset with these taxa excluded. These runs recovered the same topology as the full dataset, with comparable support for all clades. All the sequenced gerrhosaurid species contained a large insertion in MYH2 making it impossible to align with the ingroup sequences. *Platysaurus* represented the outgroup for remaining cordylids in analyses of MYH2. The concatenated dataset totaled 4503 base pairs, containing 532 autapomorphic characters and 1975 parsimony-informative characters with a total of 2983 unique patterns in the data matrix (Table 4).

3.2. Phylogenetic relationships of the Cordylidae

Dense taxon sampling and analysis of multiple nuclear and mitochondrial genetic markers recovers a phylogeny that contains 10 well-resolved lineages (clades A–J in Figs. 2 and 3). The parsimony analysis recovered 32 trees with a length of 11,348. The best ML tree had a log likelihood score of –60590.41. The same 10 monophyletic cordylid lineages were also consistently recovered from MP, ML, and BI analyses of the individual genes.

Table 4

Gene lengths in base pairs, number of informative sites, percentage of informative sites, percentage of nodes >0.95 posterior probability from Bayesian analysis, and appropriate model of evolution from ModelTest (Posada and Crandall, 1998).

Gene	Length (bp)	Informative sites	% Informative	% Sig. nodes	Model used
16S	570	208	36.5	41.9	GTR+I+ Γ
12S	975	492	50.5	61.6	GTR+I+ Γ
ND2	948	634	66.8	72.1	GTR+I+ Γ
PRLR	580	198	34.1	47.7	TVM+ Γ
Kif24	575	185	32.2	40.7	K81uf+ Γ
MYH2	855	258	30.2	50.0	GTR+I+ Γ
mtDNA	2493	1334	53.5	85.1	GTR+I+ Γ
nDNA	2010	641	31.9	77.0	K81uf+ Γ
All	4503	1975	43.9	87.9	GTR+I+ Γ

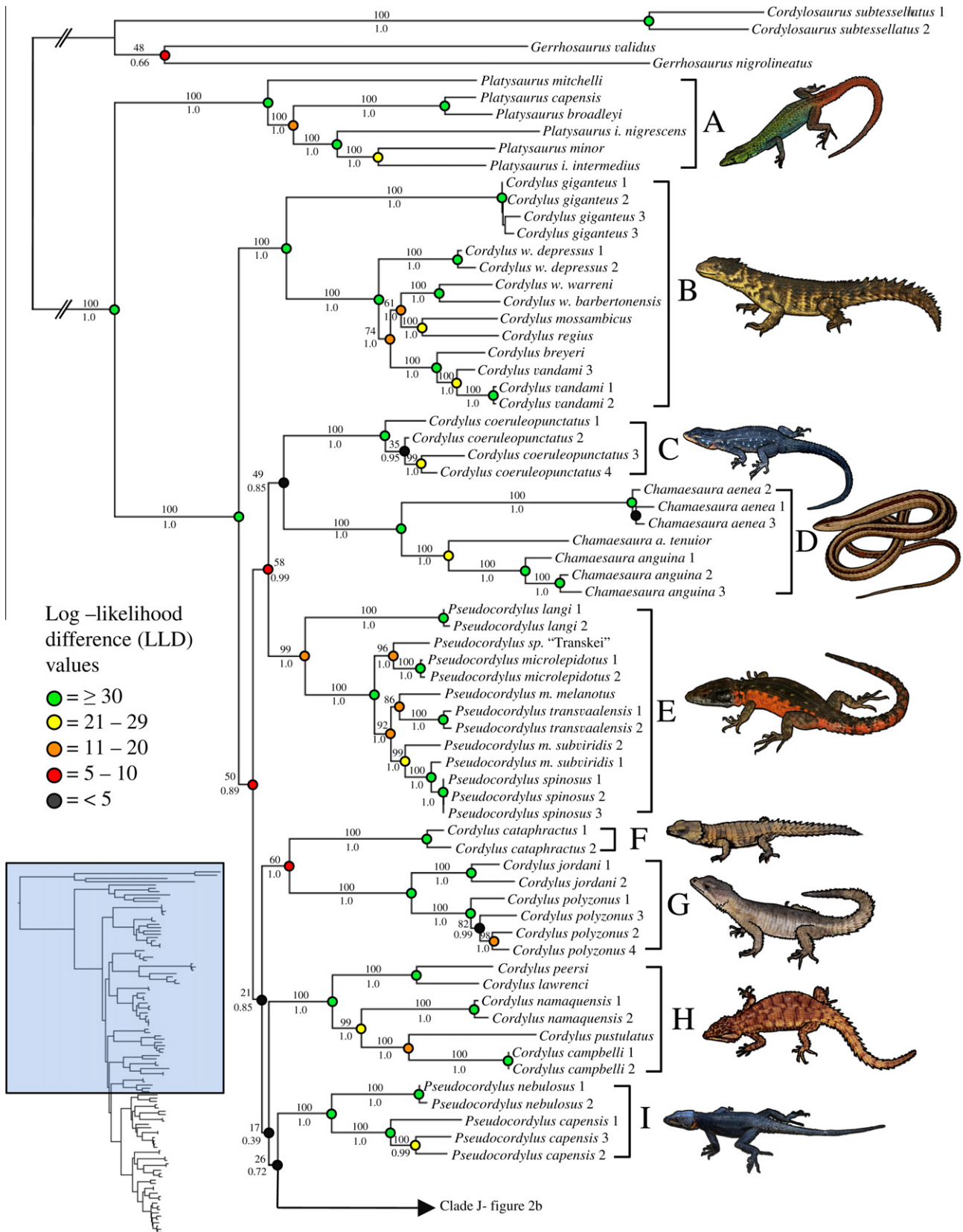


Fig. 2a. Maximum likelihood phylogram of the Cordylidae, based on a concatenated dataset of six genes. Likelihood bootstrap support shown above branches, Posterior probabilities below branches and colored circles on each node represent the likelihood decay index values. Well-supported lineages, A–I, shown with photos of representative species: A = *Platysaurus intermedius*, B = *Cordylus giganteus*, C = *Cordylus coeruleopunctatus*, D = *Chamaesaura anguina*, E = *Pseudocordylus m. melanotus*, F = *Cordylus cataphractus*, G = *Cordylus jordani*, H = *Cordylus namaquensis* and I = *Pseudocordylus capensis*.

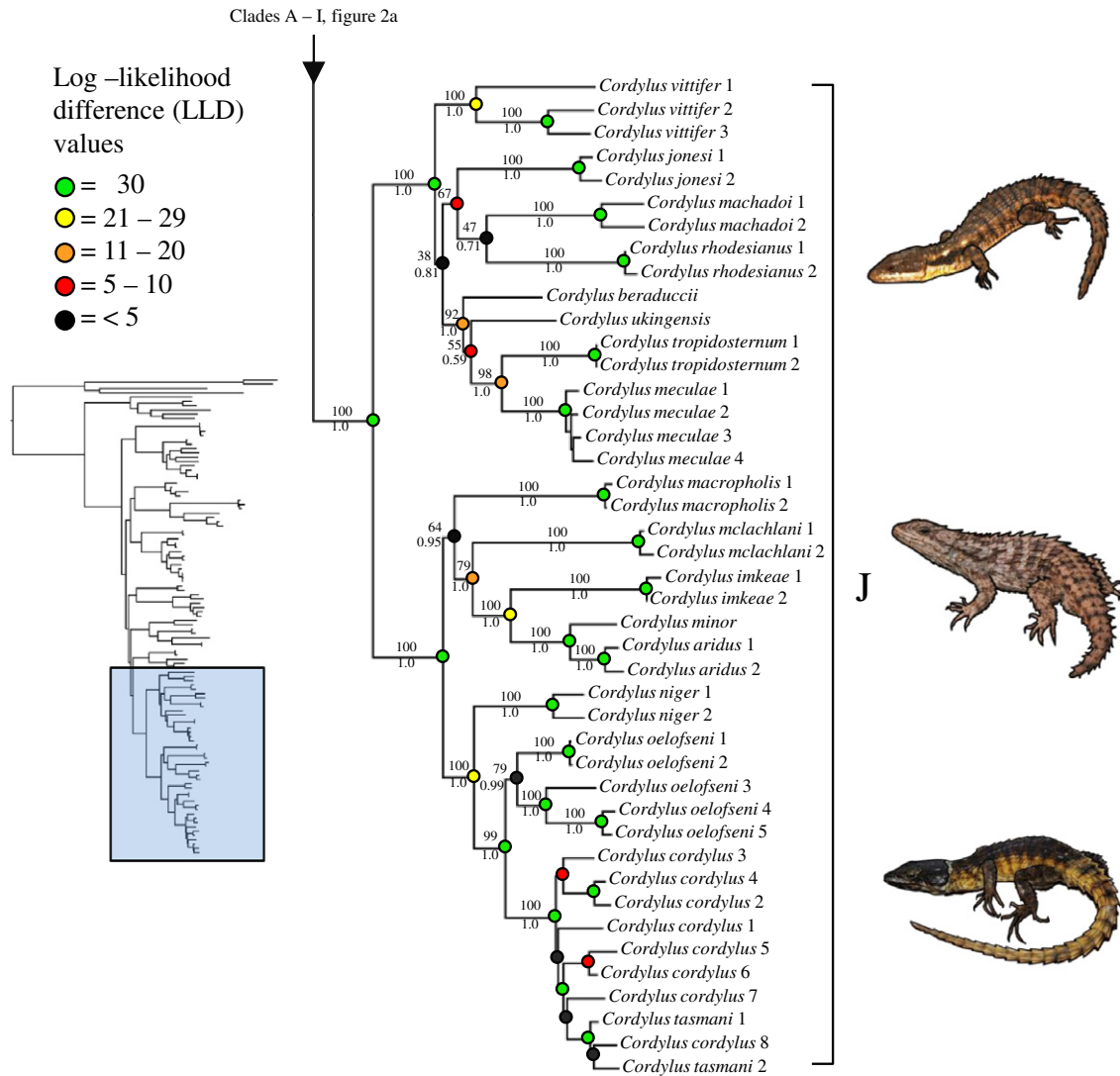


Fig. 2b. Maximum likelihood phylogram of the Cordylidae, based on a concatenated dataset of six genes. Likelihood bootstrap support shown above branches, Posterior probabilities below branches and colored circles on each node represent the likelihood decay index values. Well-supported clades shown with photos of representative species: *Cordylus tropidosternum*, *Cordylus macropholis* and *Cordylus cordylus*.

Parametric bootstrapping, log likelihood difference, Goodman-Bremer support and posterior probabilities of the nodes within these lineages and at the base of the tree are generally high, while support for the nodes between the lineages is consistently lower. Analysis of subsets of the genes returned the same pattern of support as the concatenated dataset and, although some variation is seen in gene topologies, the majority of conflict occurs around the weakly supported nodes at the base of the non-platysaur-cordylids.

The six *Platysaurus* species are consistently recovered as a monophyletic group (group A) that is sister to all other cordylids. The northern species *P. mitchelli* is recovered at the base of this clade with good support. A clade comprising the southwestern species, *P. broadleyi* and *P. capensis*, is sister to the remaining three species. *Platysaurus intermedius* is shown to be paraphyletic, with *P. i. nigrescens* sister to a clade of *P. minor* and *P. i. intermedius*.

The nine remaining major cordylid lineages are separated by short, often poorly supported internodes in all analyses. The lineage that contains *Cordylus giganteus* and members of the *C. warreni* complex is sister to all other non-platysaurs. The remaining cordylids

fall into two subclades, the first containing the species of robust *Pseudocordylus*, *Chamaesaura* and *Cordylus coeruleopunctatus*, the second containing the two species of gracile *Pseudocordylus* and the remaining *Cordylus* species.

Strong support is found for the monophyly of *Cordylus giganteus* and the members of the *Cordylus warreni* clade (group B). Four major lineages are recovered within the *Cordylus warreni* complex: (1) the Highveld and bushveld species *Cordylus vandami* and *C. breyeri*; (2) the Soutpansberg girdled lizard *C. warreni depressus*; (3) the chiefly lowveld forms *C. warreni warreni* and *C. w. barbertonensis* and (4) two species from Zimbabwe and Mozambique, *C. mossambicus* and *C. regius*.

The three *Chamaesaura* taxa form a monophyletic group (D), with *Chamaesaura anguina anguina* sister to *Chamaesaura a. tenuior*. Analysis of the nuclear genes MYH2 and Kif24 and the concatenated dataset recover *Chamaesaura* with *Cordylus coeruleopunctatus*, while analysis of the concatenated mtDNA genes places *C. coeruleopunctatus* sister to group J.

The large-bodied *Pseudocordylus* form a well-supported monophyletic group (E). Strong support for the basal position of *Pseudocordylus langi* is recovered for all analyses. The remaining robust

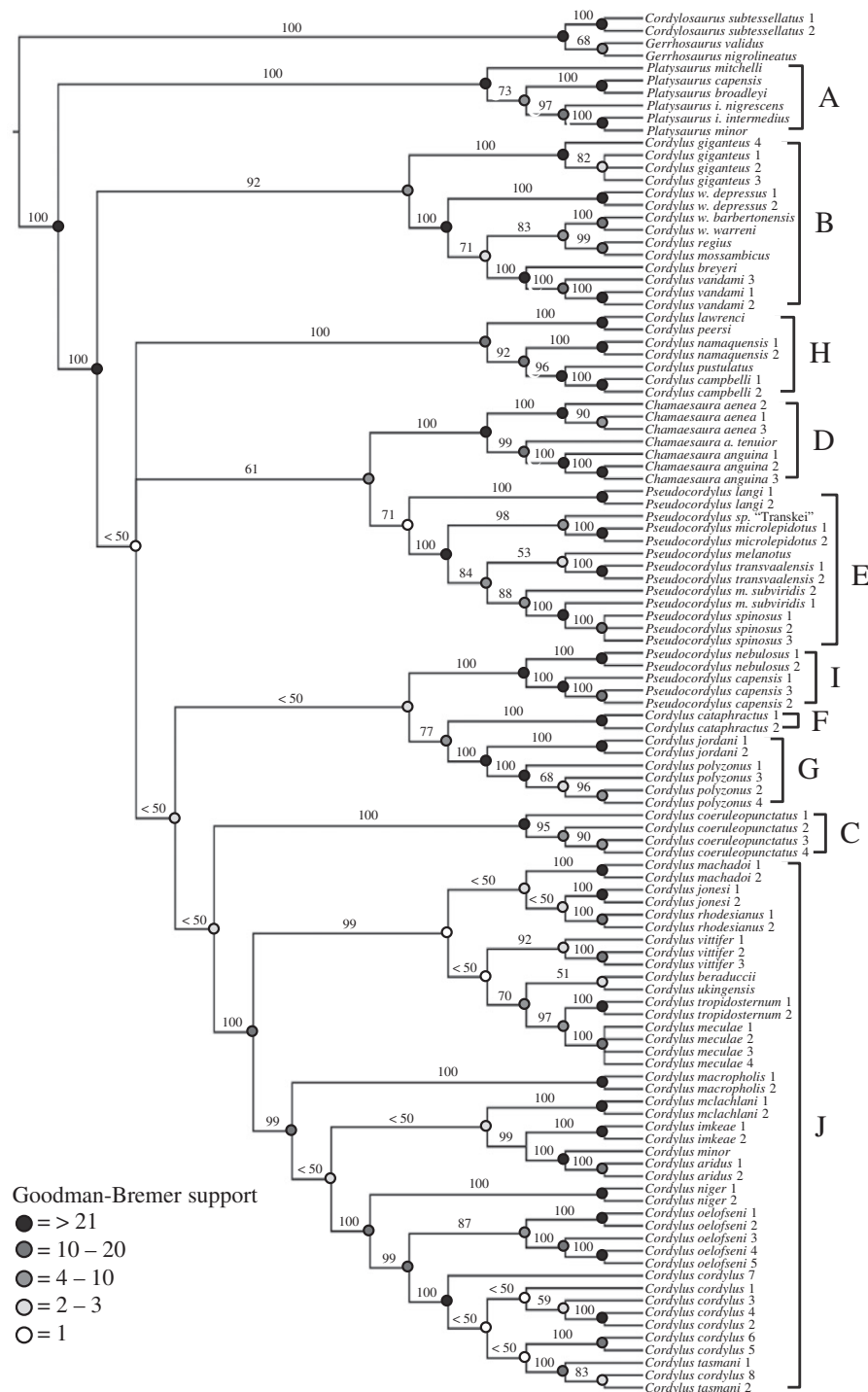


Fig. 3. Maximum Parsimony cladogram of the Cordylidae based on a concatenated dataset of six genes (50% majority rule from 32 trees). Non-parametric bootstrap support shown above branches and shaded circles on each node represent the Goodman-Bremner support values.

Pseudocordylus are divided into two lineages: *P. microlepidotus* and a putative species from the Transkei (Branch, 1998) represent a southern clade and the species of the Drakensberg and eastern escarpment form a second lineage. Within the later group, *P. melanotus subviridis* is polyphyletic; one individual clusters with *P. spinosus*, with the remaining specimen sister to this clade. *Pseudocordylus transvaalensis* and *P. melanotus* form a subclade that is sister to the *P. spinosus-subviridis* group.

Cordylus polyzonus and *C. jordanii* are unambiguously recovered as sister taxa (group G). Relationships within *C. polyzonus* are well

resolved, with the Namibian sample (*C. polyzonus* 1, Figs. 2a and 3) sister to the South African forms. Analysis of the fully concatenated dataset recovers *Cordylus cataphractus* (group F) as sister to the *polyzonus* clade. The support for this pairing in the concatenated tree results entirely from the strong signal of the mtDNA. No evidence of this relationship is seen in the individual or the concatenated analyses of the nuclear genes. Separate analyses of the genes Kif24 and MYH recover *Cordylus cataphractus* as sister to all non-platysaurs exclusive of *C. giganteus* and the members of the *C. warreni* complex.

A monophyletic group of cordylids from Namaqualand and central Namibia is returned by all analyses (group H). This group contains two well-supported, deeply divergent lineages: a Namibian clade, comprising *Cordylus pustulatus*, *C. campbelli* and *C. namaquensis* and a Northern Cape clade, of *C. peersi* and *C. lawrenci*.

There is high support for a clade containing the two reciprocally monophyletic species of gracile *Pseudocordylus* (group I). A deep divergence is observed between *P. capensis* from the Northern Langeberg and those from the western escarpment.

The final lineage (group J) is split into two geographically disjunct clades. One contains the small *Cordylus* that occur mainly from Mpumalanga, South Africa northwards. Within this, the southernmost species, *C. vittifer*, is recovered as the basal member and is represented in our sample by three well-separated lineages. *Cordylus ukingensis* is sister to *C. tropidosternum* and *C. meculae*, with *Cordylus beraduccii* recovered outside this clade. *Cordylus jonesi* is sister to *C. machadoi* plus *C. rhodesianus*. The second clade contains the small *Cordylus* species found in the Cape Fold Mountains and throughout the Western Cape. This group contains a well-supported subclade of dwarf taxa, *C. imkeae*, *C. aridus* and *C. minor*, with *C. mclachlani* sister to this group. *Cordylus cordylus* is sister to three distinct lineages of *C. oelofseni*, and these together form a monophyletic group with *Cordylus niger*. *Cordylus tasmani* is nested within *C. cordylus*. Likelihood and Bayesian analysis of the concatenated dataset recover *Cordylus macropholis* at the base of the clade of dwarf *Cordylus*, though maximum parsimony analysis places *C. macropholis* at the base of the entire southwestern lineage, and the Phycas analysis recovers a polytomy between the dwarf group, the *C. cordylus* group and *C. macropholis*.

3.3. Gene conflicts

Partition Homogeneity Tests reveal significant heterogeneity between all genes except ND2 and Kif24. Partitioned Branch Support analysis recovers gene conflict at several nodes but in the majority of cases the conflicting Goodman-Bremer support values were low. The only instance of conflict between mtDNA and nDNA with high Goodman-Bremer support was the pairing of *Cordylus polyzonus* with *Cordylus cataphractus*, recovered with strong support by mtDNA but not nDNA. This relationship had low support from parametric bootstraps and decay indices in the likelihood and parsimony analyses of the concatenated dataset. When a polytomy prior was added in the Phycas analysis there was a significant reduction in the posterior probabilities of the nodes at the base of the non-platysaur cordylids, with two nodes collapsing to polytomies.

4. Discussion

The ten cordylid clades recovered by this study correspond well to geographic distributions and morphology. There is great heterogeneity across the Cordylidae, but the phenotype of each sublineage is relatively conservative. For this reason, many of the relationships recovered by this phylogeny have been previously recognized on the basis of morphology. However, novel and unpredicted relationships were also revealed and permit a reassessment of generic clustering within the family.

Despite limited sampling, the study by Frost et al. (2001) included representative taxa from each of the 10 lineages recovered by our analysis. Some groupings remain consistent between both treatments, including the basal position of *Platysaurus*, the close relationship of *Cordylus cataphractus* to *C. polyzonus* + *C. jordani* (mtDNA support only) and the recovery of two separate lineages of *Pseudocordylus*. The relationships among the major lineages,

however, differ significantly between the phylogenies, although neither analysis resulted in strong support for these nodes.

The consistently weak support and short internodes at the base of the non-platysaur lineages for all analyses is consistent with a rapid radiation event. In this scenario, all nine lineages (B–J) diverged over a short period of time. The members of each lineage conform tightly to a morphological and ecological phenotype, and the large amount of variation seen within the family occurs between these clades, not within them. There are some notable exceptions, e.g. the obligate terricolous lizards *Cordylus macropholis* and *C. ukingensis* have convergent morphologies, but were found at different places within the generally rupicolous clade of small, typical *Cordylus*.

4.1. Taxonomic revision of the Cordylidae

If the rapid radiation constitutes a hard polytomy, several classification options are available. The classification proposed by Frost et al. (2001) is still fully compatible with our revised phylogeny. Their two-genus classification captures the clear evolutionary distinction between the oviparous *Platysaurus* and viviparous *Cordylus* lineages. However, the conservative nature of this arrangement has received limited support, primarily because it places the serpentine *Chamaesaura* in the synonymy of *Cordylus* and does not reflect the morphological and ecological variation seen within the Cordylidae. Given the strong support for each of the ten lineages, we adopt an alternative classification that recognizes less inclusive, but morphologically and ecologically distinctive groups as genera. Consequently, we continue to recognize the existing genera, *Cordylus* Laurenti 1768, *Platysaurus* Smith 1844, *Pseudocordylus*, Smith 1838, *Chamaesaura*, Schneider 1801, and *Hemicordylus* Smith 1838, and propose five new genera to accommodate the well-supported clades within this family. In the generic 'Content' (below), an asterisk indicates taxa unsampled in this study; however, based on morphological synapomorphies we consider generic allocation unambiguous.

Cordylidae Mertens, 1937.

Type Genus: *Cordylus* Laurenti 1768.

Content: Platysaurinae subfam. nov and Cordylinae Mertens, 1937.

Definition: Short, distally divided tongue covered in long papillae. Large square parietal plates present. Cranial osteoderms invariably present. Body scales large and in regular transverse rows or granular. Large rectangular ventral scales. Spiny or strongly keeled caudal scales arranged in whorls. Body often depressed. Femoral pores present.

Platysaurinae subfam. nov.

Type Genus: *Platysaurus* Smith 1844.

Content: *Platysaurus* Smith 1844.

Definition: As for sole constituent genus (see below).

Clade A:

Platysaurus Smith 1844.

Type species: *Platysaurus capensis* Smith 1844 by monotypy.

Content: *P. capensis* Smith 1844, *P. guttatus** Smith 1849, *P. torquatus** Peters 1879, *P. intermedius intermedius* Matschie 1891, *P. i. wilhelmi** Hewitt 1909, *P. i. rhodesianus** FitzSimons 1941, *P. i. natalensis** FitzSimons 1948, *P. i. nyasae** Loveridge 1953, *P. i. subniger** Broadley 1962, *P. i. parvus** Broadley 1976, *P. intermedius nigrescens* Broadley 1981, *P. i. inopinus** Jacobsen 1994, *P. minor* FitzSimons 1930, *P. orientalis orientalis** FitzSimons 1941, *P. o. fitzsimonsi** Loveridge 1944, *P. mitchelli* Loveridge 1953, *P. pungweensis* Broadley 1959, *P. p. blakei** Broadley 1964, *P. impera-*

*tor** Broadley 1962, *P. ocellatus** Broadley 1962, *P. maculatus maculatus** Broadley 1965, *P. m. lineicauda** Broadley 1965, *P. relictus** Broadley 1976, *P. monotropis** Jacobsen 1994, *P. lebomboensis** Jacobsen 1994, and *P. broadleyi* Branch and Whiting 1997.

Definition: Extremely dorso-ventrally flattened. Medium to very large-bodied (maximum snout-vent-length, SVL 73–146 mm), limbs long and digits unreduced. Granular dorsal scales, ventrals large, square or quadrangular, smooth, juxtaposed, in regular longitudinal and transverse series. Caudal scales not spinose and arranged in whorls. Osteoderms restricted to dorsum of head *fide* Lang 1991. Oviparous, laying 1–2 eggs. Sexually dichromatic, with brightly colored males and cryptic females.

Distribution: Zimbabwe, eastern and northwestern South Africa, extreme southern Namibia, Swaziland, Mozambique, Malawi, southern Tanzania.

Platysaurus is the most deeply divergent group in the Cordylidae, as was found by Mouton and van Wyk (1997) and Frost et al. (2001). Although the genus was comparatively under-sampled in our study, relationships retrieved are consistent with those of Scott et al. (2004), implying that species distributed north of the Zambezi River are sister to all the other members of the genus. On the basis of display behavior and scalation, Broadley (1978) had already indicated that the most primitive species was *P. mitchelli*, endemic to Mt Mulanje in southern Malawi. The placement of *P. intermedius nigrescens*, a taxon not sampled by Scott et al. (2004), again illustrates that the polytypic *P. intermedius* is paraphyletic. The grouping of the southwestern *P. capensis* and *P. broadleyi* is unsurprising, as the two species are isolated from all remaining congeners by over 800 km of Kalahari Desert. A comprehensively sampled phylogenetic analysis of the genus is currently being prepared by M. Whiting and J.S. Keogh (pers. comm.).

Cordylinae Mertens, 1937.

Type Genus. *Cordylus* Laurenti 1768.

Content: *Cordylus* Laurenti 1768, *Chamaesaura* Schneider 1801, *Hemicordylus* Smith 1838, *Pseudocordylus* Smith 1838, *Ouroborus* gen. nov., *Karusasaurus* gen. nov., *Namazonurus* gen. nov., *Smaug* gen. nov. and *Ninurta* gen. nov.

Definition: Moderately dorso-ventrally flattened or serpentine form, dorsal, lateral and ventral osteoderms on trunk variable. Limbs fully formed or reduced. Caudal osteoderms often present (absent in *Chamaesaura* *fide* Lang, 1991). Enlarged lateral spines at base of tail in limbed forms. Viviparous.

Clade B:

Smaug gen. nov.

Type species: *Cordylus giganteus* Smith 1844 here designated.

Content: *S. giganteus* (Smith 1844), *S. warreni warreni* (Boulenger 1908), *S. w. barbertonensis* (van Dam 1921), *S. vandami* (FitzSimons 1930), *S. w. depressus* (FitzSimons 1930), *S. breyeri* (van Dam 1921), *S. mossambicus* (FitzSimons 1958), and *S. regius* (Broadley 1962).

Etymology: *Smaug* is the name of the dragon encountered by Bilbo Baggins, the protagonist of J.R.R. Tolkien's book *The Hobbit*. According to Tolkien the name is derived from the Old German verb *smeugen* – to squeeze through a hole. Like the type species, *Smaug* lived underground and was heavily armored. Appropriately Tolkien was born in the Free State province, South Africa, the core area of distribution of the type species. The name is masculine.

Definition: Body subcylindrical in cross-section, large to very large (maximum SVL 112–205 mm), robust. Limbs of moderate length, digits unreduced. Dorsal and caudal scales enlarged and spinose; occipital spines greatly enlarged. Nasal scales not in contact with one another. Frontonasal scale in broad contact with the rostral scale. Tongue partly or fully pigmented. Osteoderms distributed across entire body. Viviparous, giving birth to 1–6 young.

Distribution: All the members of this clade occur in the north-eastern part of southern Africa and adjacent areas, with *S. giganteus* occurring chiefly on the steppes of the eastern Free State, and the members of the *S. warreni* complex distributed across the mountainous regions of Mpumalanga, KwaZulu Natal, and Limpopo provinces of South Africa, as well as in Swaziland, southern Mozambique, and eastern Zimbabwe.

Although Frost et al. (2001) did not recover *Smaug giganteus* and *S. warreni* as monophyletic, all taxa in this group are extremely large for cordylids, possess enlarged caudal and occipital spines and are found in the North-east of South Africa and the surrounding countries. The description of *Smaug breyeri* (van Dam, 1921) noted that the species was closely related to *S. giganteus*, from which it differs chiefly in size, and number and length of occipital spines. Indeed, the resemblance is so apparent that the Afrikaans name for *S. giganteus*, “Ouvolk”, is commonly applied to the members of the *S. warreni* complex as well. While *S. giganteus* is entirely terricolous, members of the *S. warreni* complex prefer deep, horizontal crevices in shaded rock outcrops.

Low genetic divergence is seen among the four specimens of *S. giganteus*. Although the grassland habitat of the Free State is now highly fragmented, there were, until recently, few natural barriers, and high levels of gene flow are likely to have prevailed. Jacobsen (1989) proposed that the members of the *S. warreni* species complex had been isolated from each other by the introgression of the Kalahari sands during the Pleistocene. However, the deep divergence recovered between the *warreni* taxa suggests that the species splits occurred prior to the spread of the Kalahari sands. A fuller discussion of genetic divergence and species boundaries within the *S. warreni* complex will be presented elsewhere (Stanley and Bates, in prep.).

Clade C:

Ninurta gen. nov.

Type species (monotypic): *Zonurus coeruleopunctatus* Hewitt and Methuen 1913 here designated.

Content: *N. coeruleopunctatus* (Hewitt and Methuen 1913).

Etymology: *Ninurta* (masculine) was, in Sumerian and Akkadian mythology, among his other attributes, the god of rain and of the south wind. The name references the sole species' occurrence along the cool, moist south coast of South Africa.

Distribution: The southern Cape region of South Africa.

Definition: Body gracile, limbs elongate, digits unreduced. Medium-sized (maximum SVL 82 mm). No occipital spines present, granular scales on nape. Keeled dorsal scales arranged in 40–46 transverse and 20–30 longitudinal rows. Spinose tail-whorls lacking. A band of granular lateral scales present between the dorsals and ventrals. Osteoderms widely distributed across body. Enamel blue spots on head and dorsum in eastern populations. Breeding males develop a yellow-to-orange gular patch. Viviparous, giving birth to 3–4 young.

The position of *Ninurta coeruleopunctatus* within the family remains unresolved. Analysis of the concatenated dataset returns *Ninurta* and *Chamaesaura* as sister clades, although the mtDNA-only analysis recovers *Ninurta* as sister to *Cordylus sensu stricto* (clade J). Previous studies (Methuen and Hewitt, 1914; Broadley, 1964; Branch, 1981; Herselman, 1991; Herselman et al., 1992b; Frost et al., 2001) have proposed a close relationship between *Ninurta coeruleopunctatus* and *Hemicordylus capensis*; both species possess similar patterns of granular lateral squamation, colorful gular patches (seen in juvenile *H. capensis*), and both occur in the Cape Fold Mountains. The placement of *Ninurta* in a clade with *Chamaesaura* is a novel proposal and somewhat more difficult to reconcile. However *N. coeruleopunctatus* is a rather gracile lizard,

and shares the reduction of osteoderms with both *Chamaesaura* and *Pseudocordylus*.

Clade D:

Chamaesaura Schneider, 1801.

Type species: *Lacerta anguina* Linnaeus 1758 designated by Fitzinger (1826).

Content: *C. anguina anguina* (Linnaeus 1758), *C. a. oligopholis** Laurent 1964, *C. aenea* (Fitzinger 1843), *C. macrolepis** (Cope 1862), *C. miopropus** (Boulenger 1894), and *C. tenuior* Günther 1895.

Definition: Body slender and attenuate with greatly reduced limbs and digits, maximum SVL 140–170 mm. Tail extremely elongate (3–4 times SVL). Dorsal scales strongly keeled and arranged in regular rows; no occipital spines present. Osteoderms limited to dorsum of head. Viviparous, giving birth to 6–12 young.

Distribution: Disjunct in grasslands of Southern and eastern Africa from South Africa to Angola, Democratic Republic of Congo, and Tanzania.

The monophyly of *Chamaesaura* is recovered unambiguously, and the clade is nested within *Cordylus sensu lato*, as Frost et al. (2001) had previously demonstrated. Highly specialized grass-swimmers like *Chamaesaura* are problematic for morphologically based phylogenies, as they are highly attenuate and like many reduced-limbed squamates, lack many characters that are informative among fully-limbed forms (e.g., Mott and Vieites, 2009). They also tend to be morphologically convergent with other grass-swimming specialists, like *Tetradactylus*. These factors probably resulted in Lang (1991) incorrectly identifying *Chamaesaura* as the basal cordylid lineage. In light of the new placement of the group, seemingly incidental observations from Lang gain new significance. For example, the flattened parietal table of *Chamaesaura* that suggests the group had evolved from a crevice dwelling form makes little sense under Lang's phylogeny, which places *Chamaesaura* outside the rupicolous specialist cordylines, but fits the new hypothesis that *Chamaesaura* had evolved from a more typically crevice-inhabiting “*Cordylus*” like ancestor.

Loveridge (1944) relegated *Chamaesaura tenuior* (Democratic Republic of Congo to Kenya and Tanzania) to a subspecies of *Chamaesaura anguina* (South Africa and Swaziland) because of the excessively variable diagnostic features used by Günther (1895). A sister relationship of the two taxa is reflected in the phylogeny and significant distance exists, both genetically and geographically, between the two taxa. Given that there are diagnostic features that define this race, we thus raise *C. tenuior* to full species status.

Clade E:

Pseudocordylus Smith 1838.

Type species: *Cordylus* (*Pseudocordylus*) *montanus* Smith 1838 = *P. microlepidotus* (Cuvier 1829) designated by Loveridge (1944).

Content: *P. microlepidotus microlepidotus* (Cuvier 1829), *P. m. faciatus** (Smith 1838), *P. m. namaquensis** (Hewitt 1927), *P. melanotus* (Smith 1838), *P. subviridis* (Smith 1838), *P. transvaalensis* Fitz-Simons 1943, *P. langi* Loveridge 1944, and *P. spinosus* FitzSimons 1947.

Definition: Body subcylindrical in cross-section, medium to very large-bodied (maximum SVL 76–145 mm), robust. Limbs long, digits unreduced. Dorsal scales granular or larger scales separated by granules, tail spiny; occipital spines not present. Tongue unpigmented. Osteoderms restricted to tail and dorsum of head. Sexually dichromatic in some populations. Viviparous, giving birth to 1–7 young.

Distribution: Drakensberg and Cape Fold Mountain regions of South Africa, Swaziland and Lesotho.

The basal position of *Pseudocordylus langi* within the genus agrees with the findings of Bates (2005, 2007), whereas Broadley (1964) identified it as a highly derived member of the genus. A clear divide is seen between the remaining eastern escarpment (*P. melanotus*, and *P. transvaalensis*) and Drakensberg forms (*P. subviridis* and *P. spinosus*) and *Pseudocordylus* from Transkei and the Cape Fold Mountains. The two *Pseudocordylus* taxa absent from this study (*P. microlepidotus fasciatus* and *P. m. namaquensis*) were included, with a form from the Transkei, in the *P. microlepidotus* complex by Bates (2005). While the undescribed putative species from Transkei (Branch, 1998) is clearly closely related to *P. microlepidotus*, greater sampling is needed to determine whether it constitutes a full species.

Pseudocordylus melanotus is clearly paraphyletic and we hereby assign full species status to *Pseudocordylus melanotus subviridis*. Bates (2005, 2007) investigated the phylogenetic relationships of the eastern escarpment and Drakensberg *Pseudocordylus* using morphology and the 16S gene. He reported that two clades of *P. melanotus sensu stricto* existed, with the remaining taxa sister to the southern (Drakensberg) population. This appears not to be the case with our data, as the northern forms, *P. melanotus* and *P. transvaalensis* form a well-supported clade, distinct from the *spinus/subviridis* complex. However, our study did not include any samples of *P. melanotus* from Bates' southern clade and if it had, perhaps the paraphyly would have been revealed. *Pseudocordylus spinosus* is recovered as nested within *P. subviridis* and displays little genetic divergence, suggesting that the diagnostic spinose scales of *P. spinosus* were recently evolved. *Pseudocordylus spinosus* occurs in piles of low-lying rocks scattered in montane grassland, often using crevices at or near ground level. Reduction of scales has been associated with use of vertical surfaces (Janse van Rensburg, 2009) and the opposite may be true here, with a rapid increase in spinose scales corresponding to an increase in terricolity. A greatly expanded phylogenetic analysis is warranted for the *Pseudocordylus* group, and a molecular study of the Drakensberg forms is currently in preparation (M. F. Bates, pers. comm.).

Clade F:

Ouroborus gen. nov.

Type species (monotypic): *Cordylus cataphractus* Boie 1828, here designated.

Content: *O. cataphractus* (Boie 1828).

Etymology: The *ouroborus* is the symbol of a dragon biting or swallowing its own tail to form a circle, and refers to the characteristic defensive behavior of the type species, in which the tail is grasped in the mouth and the plated dorsum and spiny tail presented to attackers (hence the common name armadillo lizard). Latinized version of the Greek Οὐροβόρος, oura – tail and boros – devouring. The word is masculine.

Definition: Body flattened to subcylindrical in cross-section, medium to large-bodied (maximum SVL 105 mm), robust. Limbs of moderate length, digits unreduced. Dorsal and scales greatly enlarged (in 15–17 transverse rows) and spinose, caudal scales forming large spines; six large keeled occipitals. Tongue darkly pigmented. Viviparous, giving birth to 1–2 young.

Distribution: Semi-arid regions of the western portions of the Western and Northern Cape provinces of South Africa.

The unusual defensive and social behavior displayed by these animals makes them highly distinctive members of the Cordylidae, leading Broadley (2006) to predict that *Cordylus cataphractus* would be placed in a monotypic genus. Analysis of the three nuclear genes recovers *O. cataphractus* near the base of the Cordylinae, along with the similarly robust, spinose genus *Smaug*. The associa-

tion of spinose forms is further supported by the presence of tongue pigmentation in both genera (Lang, 1991) and a large diploid chromosome number that is shared by *S. giganteus* and *O. cataphractus* (Olmo and Odierna, 1980; Odierna et al., 2002). However, analysis of both the mitochondrial genes and the fully concatenated dataset returns *Ouroborus* as closely related to *Karusasaurus*, a relationship that has been recovered by previous studies (Frost et al., 2001; Melville et al., unpublished data). The conflicting positions of *Ouroborus* and *Karusasaurus* from the nuclear and mitochondrial DNA are consistent with an ancient hybridization event with subsequent mitochondrial introgression.

Clade G:

Karusasaurus gen. nov.

Type species: *Cordylus polyzonus* Smith 1838, here designated.

Content: *K. polyzonus* (Smith 1838), *K. jordani* (Parker 1936).

Etymology: Derived from the Khoisan word *karusa*, meaning dry, barren, thirland, and the Latinized Greek *saurus* – lizard, and referencing the distribution of the type species which extends across the semi-arid Karoo. The word is masculine.

Definition: Body flattened in cross-section, large-sized (maximum SVL 113–127 mm), robust. Limbs of moderate length, digits unreduced. Dorsal scales small and smooth to keeled in 38–46 transverse rows; caudal scales enlarged and spinose; no occipital spines present. Lower eyelid with transparent disc. Tongue unpigmented. Osteoderms distributed across entire body. Viviparous, giving birth to 2–4 young.

Distribution: Widely distributed throughout semi-arid areas of South Africa and southern Namibia.

Previous studies have questioned validity of *Karusasaurus jordani* as a full species (Loveridge, 1944). This study recovers it as sister to *K. polyzonus* with sufficient genetic separation between the two taxa to suggest that it is a good species. Despite having one of the largest distributions of any cordylid species (Branch, 1998), little genetic divergence was seen between the widely distributed specimens of *K. polyzonus*, suggesting that it represents a single species. Increased taxon sampling and phylogeographic analysis may however recover structure within the species.

Clade H:

Namazonurus gen. nov.

Type species: *Zonurus pustulatus* Peters 1862, here designated.

Content: *N. pustulatus* (Peters 1862), *N. namaquensis* (Methuen and Hewitt 1914), *N. peersi* (Hewitt 1932), *N. campbelli* (FitzSimons 1938), and *N. lawrenci* (FitzSimons 1939).

Etymology: Masculine name derived from *Nama*, referring to Namaqualand as broadly construed, the area occupied by Nama speaking peoples, and *Zonurus*, girdle-tailed, the earlier name long used for *Cordylus sensu lato*.

Definition: Body flattened in cross-section, small-sized (maximum SVL 75–82 mm), robust. Limbs of moderate length, digits unreduced. Supernasals enlarged and tubular. Dorsal scales small and smooth to keeled in 22–32 transverse rows; caudal scales enlarged and spinose; head triangular; no occipital spines present. Lower eyelid with or without transparent disc. Tongue unpigmented. Osteoderms distributed across entire body. Viviparous, giving birth to 2–4 young.

Distribution: Namaqualand, South Africa and parts of southern and central Namibia.

Several studies have recognized the close relationship of the members of *Namazonurus*, but these studies also proposed that the species were closely related to *Karusasaurus polyzonus* (Peters, 1862), *Cordylus minor* (Loveridge, 1944; Visser, 1971), *C. cordylus* (FitzSimons, 1943; Broadley, 1965) or *C. vittifer* (Frost et al., 2001), findings that are not corroborated by our results. High levels

of genetic divergence reflect the large geographic disjunctions and gaps in suitable habitat between species in this group. The deep divide between the two subclades does not directly correspond to geographical distance, however, as the range of *N. namaquensis* is closer to the South African species than to the more closely related *N. campbelli*. The Orange River divides the lineages, and may be an ancient barrier to gene flow, as has been proposed for other squamates (Bauer, 1999; Scott et al., 2004), though many other factors, including the degree of fragmentary intermediary habitat, may have influenced the evolutionary history of the clade.

Clade I:

Hemicordylus Smith 1838.

Type species: *Cordylus* (*Hemicordylus*) *capensis* Smith 1838 by monotypy.

Content: *H. capensis* (Smith 1838), *H. nebulosus* (Mouton and van Wyk 1995).

Definition: Body gracile, somewhat flattened in cross-section, small-sized (maximum SVL 76 mm). Limbs long, digits long, slender, unreduced. Dorsal scales large and separated by granules; lateral body scales granular. Caudal scales keeled but not spinose; occipital spines not present. Tongue unpigmented, Osteoderms restricted to tail and dorsum of head. Melanistic and sexually dichromatic in some populations. Viviparous, giving birth to 1–3 young.

Distribution: Cape Fold Mountains of southwestern South Africa.

We here resurrect the genus *Hemicordylus* to contain the gracile forms that were previously contained within the genus *Pseudocordylus*. The two species within this group have a phenotype that appears to be intermediate between typical *Cordylus* and the large *Pseudocordylus*, and there have been repeated revisions to the placement of these taxa within the family. *H. capensis* was described as the sole representative of a separate subgenus of *Cordylus* but it was subsequently moved to *Pseudocordylus* by Loveridge (1944), and then to the expanded *Cordylus* of Frost et al. (2001) and finally, back to a subgenus by Broadley (2006). The recognition of *Hemicordylus* as a distinct genus removes the secondary homonymy that had existed between *C. nebulosus* (Mouton and van Wyk 1995) and *C. nebulosus* Smith 1838, a subjective synonym of *Ouroborus cataphractus* (Boie 1828). The results of this study clearly show *Hemicordylus capensis* and *H. nebulosus* as evolutionarily distinct from the robust pseudocordylids. The reduction in osteoderms seen in both groups appears to be convergent. *Hemicordylus* utilize vertical rock surfaces and this adaptation to a specialized environment is thought to have driven the evolution of lightly armored, agile forms (Eifler et al., 2007; Janse van Rensburg, 2009; Janse van Rensburg et al., 2009). Although originating as part of the rapid radiation, there is weak support for a close relationship to the clade of typical *Cordylus*.

Relatively deep levels of divergence are seen within *Hemicordylus capensis*, suggesting that there is little gene flow between the populations. Similar structure is seen in geckos of the genus *Goggia*, which have been shown to contain several species within the Cape Fold Mountains (Bauer et al., 1997). Herselman et al. (1992b) identified distinct phenotypes corresponding to four populations (including the synonymized *Hemicordylus robertsi*) but observed that variation between these groups was clinal in nature and therefore not diagnostic. Additional phylogenetic investigation into the structure of the group may therefore reveal cryptic species and necessitate further taxonomic revision.

Clade J:

Cordylus Laurenti, 1768.

Type species: *Cordylus verus* Laurenti, 1768 = *Cordylus cordylus* (Linnaeus, 1758) by Linnaean tautonymy (see Stejneger, 1936).

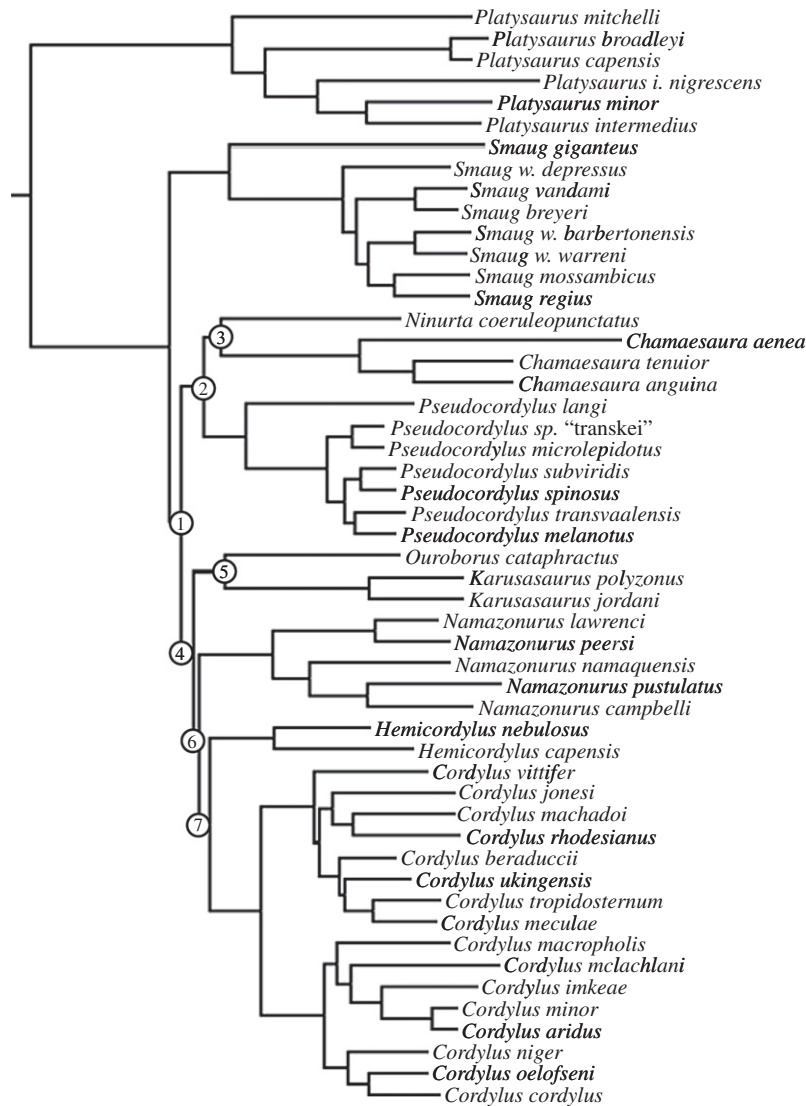


Fig. 4. Species level phylogram displaying the new taxonomic arrangement of the Cordylidae. Nodes 1 through 7 represent the putative rapid radiation of the nine major cordyline lineages; see Table 5 and the text for details of node support.

Content: *C. cordylus* (Linnaeus 1758), *C. niger* Cuvier 1829, *C. tropidosternum* (Cope 1869), *C. vittifer* (Reichenow 1887), *C. jonesi* (Boulenger 1891), *C. angolensis** (Bocage 1895), *C. rivae** (Boulenger 1896), *C. macropholis* (Boulenger 1910), *C. ukingensis*

(Loveridge 1932), *C. rhodesianus* (Hewitt 1933), *C. minor* FitzSimons 1943, *C. machadoi* Laurent 1964, *C. mclachlani* Mouton 1986, *C. oelofseni* Mouton and Van Wyk 1990, *C. aridus* Mouton and Van Wyk 1994, *C. cloetei** Mouton and Van Wyk 1994, *C. imkeae* Mouton and Van Wyk 1994, *C. nyikae** Broadley and Mouton 2000, *C. beraduccii* Broadley and Branch 2002, and *Cordylus meculae* Branch et al., 2005.

Table 5

Support values for the seven labeled nodes in Fig. 4, showing (a) Posterior probabilities from MrBayes, (b) Posterior probabilities from a Phycas analysis with polytomy priors added, (c) Maximum likelihood bootstrap support and (d) Maximum likelihood decay index values.

Node number	Posterior probability without polytomy prior	Posterior probability with polytomy prior	ML Bootstrap support	ML decay index
1	0.89	Node collapsed to polytomy	50	6.7597
2	0.99	1.0	58	5.0012
3	0.85	0.84	49	1.4511
4	0.85	0.63	21	0.9888
5	1.0	1.0	61	7.4891
6	0.39	Node collapsed to polytomy	17	0.115
7	0.72	0.38	26	0.1254

Definition: Body moderately flattened in cross-section, small to medium-sized (maximum SVL 66–95 mm), robust. Limbs of moderate length, digits unreduced. Dorsal scales small and smooth to keeled in 16–30 transverse rows; caudal scales enlarged and spinose; head triangular; no occipital spines present. Lower eyelid without transparent disc. Tongue unpigmented. Osteoderms distributed across entire body. Viviparous, giving birth to 1–3 young.

Distribution: Widely distributed in southern and eastern sub-Saharan Africa, as far north as Ethiopia.

Several East African taxa are missing from this study, but clear patterns are recovered from the samples included. The basal position of the Transvaal girdled lizard, *C. vittifer*, within the eastern clade suggests that the group expanded northward from South Africa, one clade (*jonesi-rhodesianus-machadoi*) occupying a disjunct range across subtropical Africa, and a second clade

(*C. beraduccii*, *C. ukingensis* and *C. meculae*) distributed throughout East Africa north of the Zambezi, possibly even to Ethiopia, if the very rare *C. rivae* (unsampled) forms part of this clade (Broadley and Branch, 2002). This migration northward is the converse of the movement hypothesized by Scott et al. (2004) for *Platysaurus*.

Our results disagree with Frost et al.'s (2001) placement of *C. vittifer* within *Namazonurus*, but are compatible with Broadley's (1971a) earlier assessment, which groups *C. vittifer* with *C. tropidosternum*, *C. jonesi*, *C. machadoi* and *C. rhodesianus*. De Waal (1978) and Jacobsen (1989) identified three morphs of *C. vittifer* that correlated well with geographic distributions and habitat types, and although these morphs do not match our sampling, deep genetic divergences and significant variation in phenotype suggests that *Cordylus vittifer* may consist of several valid species. An expanded phylogenetic analysis of the complex is currently in preparation (M. Cunningham and M.F. Bates, pers. comm.).

Cordylus machadoi was originally described as a subspecies of *C. vittifer*, based on the enlarged row of post-temporal scales seen in both taxa. Branch (1998) treated *C. machadoi* as a full species and our phylogeny supports this, recovering it as sister to the morphologically distinct and geographically remote *C. rhodesianus*. The area between the two groups is currently unsuitable for rupicolous lizards, mostly consisting of Miombo and Kalahari Acacia woodlands (Burgess et al., 2004). *Cordylus* specimens (currently referred to *C. tropidosternum*) have been collected on the northeastern border of Zambia (Broadley, 1971b; Haagner et al., 2000) but the corridor that must have existed between the eastern and western populations is presently unclear.

The four most-northerly species, *Cordylus beraduccii*, *C. tropidosternum*, *C. meculae* and *C. ukingensis*, form a well-supported clade. *Cordylus beraduccii* and *C. meculae* are genetically distinct from the widely distributed and morphologically similar *C. tropidosternum*, though a detailed phylogenetic analysis of *Cordylus tropidosternum* is necessary to fully understand evolutionary relationships of these northern species. The large range and conserved morphology of the species has resulted in a large list of synonyms, as new forms were described and subsequently reassigned to *Cordylus tropidosternum*. Loveridge (1944) was of the opinion that the Tanzanian forms may constitute a separate species from the southern forms, though this remains to be seen.

The clade of dwarf *Cordylus* (*C. imkeae*, *C. minor*, and *C. aridus*) likely contains a fourth species from the Fraserburg area, *C. cloetei* (Mouton and Van Wyk, 1994). The position of *C. mclachlani* and *C. macropholis* at the base of the dwarf and southern clades, respectively, matches their geographic position within the group; *Cordylus macropholis* is distributed along the western coast of South Africa, and *C. mclachlani* occurs on the inland edge of the Western Great Escarpment, both localities are close to the contact zone of the inland mountain chain that contains all four dwarf forms and the cape fold mountains, where the members of the Cape clade (*C. cordylus*, *C. oelofseni* and *C. niger*) occur. The Cape *Cordylus* species have been the subject of previous phylogenetic analysis and the relationships recovered by our phylogeny agree with the findings of Daniels et al. (2004). The populations of *Cordylus oelofseni* occurring at Landdroeskop (*C. oelofseni* 1 and 2), Dasklip Pass (*C. oelofseni* 3) and Piketburg (*C. oelofseni* 4 and 5) all display genetic distances comparable to those seen between good species elsewhere in the phylogeny and represent at least two valid species. Some phylogenetic structure is seen within the widely distributed *Cordylus cordylus*, with the inland and coastal forms separated into different clades, as was observed by Daniels et al. (2004). The two specimens initially referred to *Cordylus tasmani* Power 1930 are nested within coastal *Cordylus cordylus* and the former name is here placed in the synonymy of the latter, although further genetic and morphological analyses of topotypical "*C. tasmani*" would be desirable to confirm this.

4.2. Gene conflicts, hard polytomies and adaptive radiation

The increased sampling of genes and taxa has improved the resolution of relationships within and between the various cordylid lineages when compared to previous phylogenetic studies of the family. As shown in other studies (see Lee and Hugall, 2003; Lee, 2009; Thermudo et al., 2009) concatenation of the multiple datasets significantly increased the resolution from the individual gene trees and there is little evidence to suggest that the conflicts that are present in this dataset significantly pervert the overall topology.

Short internodes and poor support between the nine well-supported lineages of the Cordylinae was consistently recovered from the analyses of the individual genes and the concatenated dataset. The use of Phycas does not necessarily produce polytomies or reduce the support for short branches, as demonstrated by a recent study by Kodandaramaiah et al. (2010). Their use of Phycas in a five-gene study of butterflies showed more resolution using Phycas than MrBayes for nodes hypothesized to be part of a hard polytomy. However, our Phycas analysis returned significantly reduced posterior support for the nodes at the base of the Cordylinae, with two nodes collapsing to polytomies (Fig. 4 and Table 5). Little change was observed in the posterior probabilities for the other nodes in the tree. The increased instance of polytomies and reduction of support for the deep cordylid relationships suggests that much of the topological stability recovered in this part of the tree by the MrBayes analysis may be an artifact of our analytical methods. This, combined with the consistently short internodes and low of support at the base of the nine cordylid lineages suggests that the poor resolution seen in this part of the tree is not an artifact of sampling insufficiency but rather reflects a real evolutionary event, namely a period of rapid cladogenesis.

The conservative morphologies and ecologies of each of the ten cordylid genera suggest that the various phenotypes developed shortly after the radiation of the Cordylinae and the subfamily may have undergone an early adaptive radiation. Although the family contains several clades of lizards that are not primarily rock-dwelling (e.g. *Chamaesaura*, *Smaug giganteus*, and several species of *Cordylus*) these are all embedded in highly rupicolous clades and the family is unquestionably ancestrally rupicolous.

Our preliminary dating analyses place the diversification of the Cordylinae between 35 and 25 million years ago, during the Oligocene (Stanley, 2009), a period when southern Africa would have been cool and dry (Zachos et al., 2001; Bobe, 2006). The ability to give birth to live young has long been associated with adaptation to cold environments (Blackburn, 1982; Shine, 2002) and the reproductive strategies of the two cordylid subfamilies are consistent with this pattern, with the viviparous cordylines occurring in temperate areas, at higher altitudes and higher latitudes, and the oviparous platysaurines being restricted to the tropics and subtropics. Mouton and van Wyk (1997) proposed that the Cordylinae are a cool-adapted lineage and that viviparity developed in the family during cold conditions. The relatively cool, dry Oligocene would have been an ideal environment for the cold-adapted, rupicolous stem cordylines. A similar timeframe has been proposed for radiations of African birds (Fuchs et al., 2006), mammals (Kappelman et al., 2003) and other lizard families (Hipsley et al., 2009) and the Oligocene may have been an important period of cladogenesis in southern Africa in general.

We suggest that, following the basal radiation of cordylines, most of the constituent genera evolved within the constraints imposed both by the available geological (microhabitat/substrate) resources and by the thermal environment. As a result, each cordylid genus is relatively uniform in its morphology and localized in its distribution. The Cordylidae has received little attention relative to established model systems (Losos and Mahler, 2010), but the

apparent rapid diversification of cordylines and their subsequent phenotypic conservatism suggests that they would make an excellent study system to investigate processes and patterns of adaptive radiation.

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Taxonomic relationships of the subspecies of the Cape Parrot *Poicephalus robustus* (Gmelin)

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In Africa, four genera represent the family Psittacidae; of these, the genus *Poicephalus* Swainson is endemic and comprises nine species. Three subspecies of the Cape Parrot, *Poicephalus robustus* (Gmelin), are often recognized. The endangered nominate subspecies, *P. r. robustus*, inhabits afro-montane forest habitats and is endemic to South Africa. *Poicephalus r. suahelicus* (Reichenow) occurs in low-lying woodland in south-central Africa. The little-known third subspecies, *P. r. fuscicollis* (Kuhl), historically occurred from Angola through West Africa but is now common only in the Gambia where it occupies habitat similar to that of *P. r. suahelicus*. Validity of these subspecies has been examined using morphological and ecological characters. *Poicephalus r. suahelicus* and *P. r. fuscicollis* are most similar morphometrically and in plumage colour. The nominate subspecies and *P. r. suahelicus* showed several significant morphometric and colour differences, although local populations are parapatric in Mpumalanga Province, South Africa. Clancey's (1997) proposals are adopted with *P. robustus* considered a separate species from *P. fuscicollis* (with two subspecies *P. f. fuscicollis* and *P. f. suahelicus*).

KEYWORDS: *Poicephalus*, taxonomic status, afro-montane forest, conservation status.

Introduction

The species concept has been much debated and reviewed (Mayr, 1957; Lack, 1983; Brothers, 1985; Ridley, 1993), but criteria for recognizing taxa as subspecies include allopatric regional populations that differ in several traits. The presently recognized subspecies of *Poicephalus robustus* (Gmelin) share morphological similarities despite present disjunct distributions and different habitat preferences. Three subspecies of the Cape Parrot *P. robustus* are currently recognized (figure 1) (Forshaw, 1989). The nominate subspecies, *P. r. robustus* (Gmelin: no locality;

† Deceased

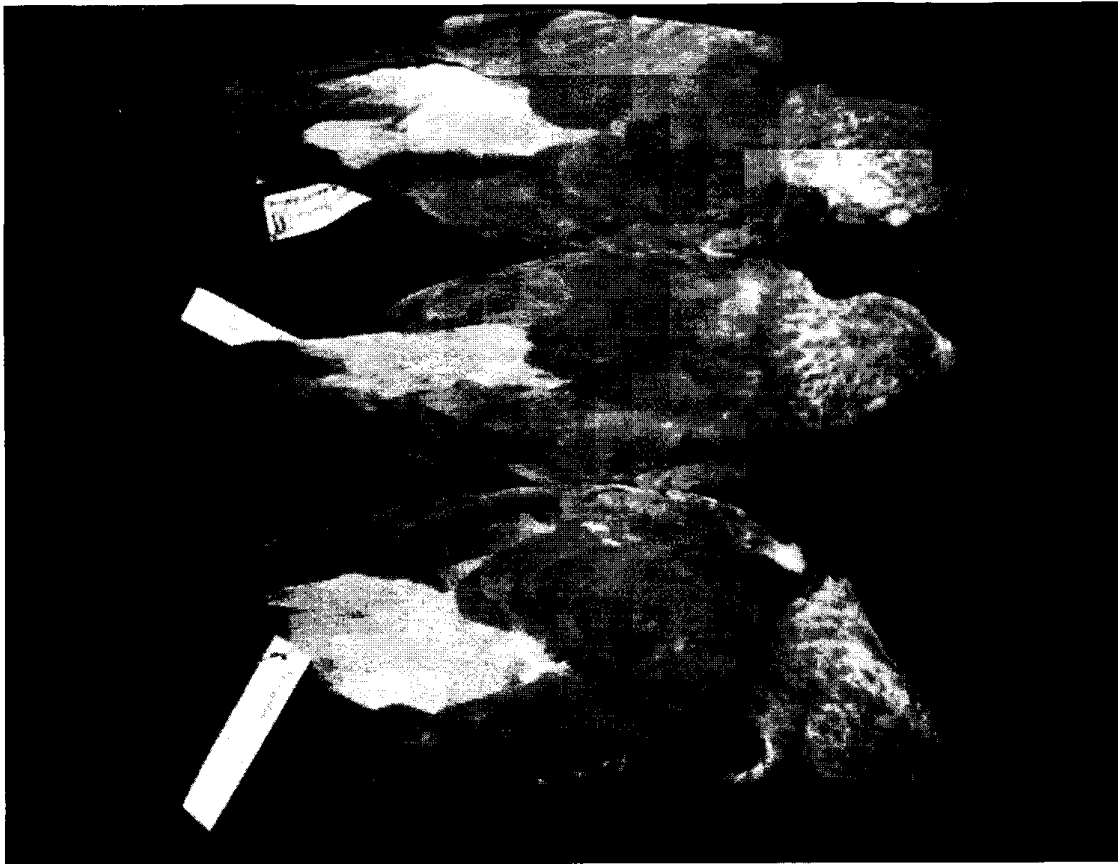


FIG. 1. The three previously recognized taxa of the Cape Parrot (top to bottom): *P. r. fuscicollis* (BM1929.2.8.111 from the Gambia); *P. r. suahelicus* (BM1890.10.10.48 from Zambezi River); and *P. r. robustus* (BM1890.10.10.39 from Natal).

though referred to as South Africa (Peters, 1937) or eastern Cape Province (Clancey, 1963)), is endangered (Downs 2000) (figure 2). *Poicephalus r. suahelicus* (Reichenow) occurs in south-central Africa (figure 2) where it is not regarded as threatened (Collar and Stuart, 1985), although trade in wild birds has increased, which could threaten remaining populations. A little-known, third subspecies, *P. r. fuscicollis* (Kuhl), historically occurred from Angola through West Africa, but is now only common in the Gambia (figure 2).

Disjunct distributions of flora and fauna have been extensively studied throughout Africa. Several species of trees of the afromontane forests have a very disjunct distribution (Donald and Theron, 1983) which is explained by the climatic change hypothesis (Coetzee and van Zinderen Bakker, 1970; Donald and Theron, 1983). The distribution patterns of extant forest-dwelling birds in southern Africa are thought to be a consequence of vicariance events affecting forest plants following climatic changes (Hamilton, 1989; Lawes, 1990).

The great majority of disjunctions shown by montane birds probably originated as a consequence of fragmentation of continuous ranges (Moreau, 1966). Cluster analysis of the distribution patterns of forest passerine birds in tropical Africa has shown three main categories: those with restricted distribution, those with disjunct distribution, and those with wide distribution (Diamond and Hamilton, 1980). Centres of species richness, endemism, and disjunction coincide spatially, and are identified as forest refugia; forest persisted in these areas throughout the climatic

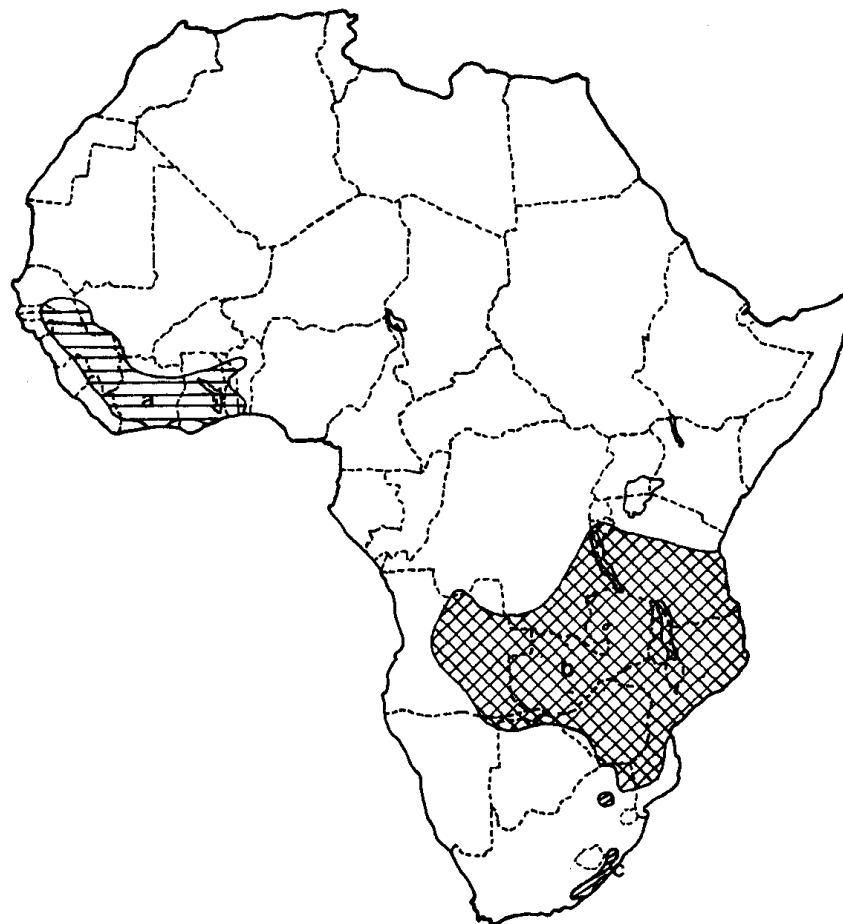


FIG. 2. Map of Africa with the distributions of the three previously recognized taxa: (a) *P. r. fuscicollis*; (b) *P. r. suahelicus*; and (c) *P. r. robustus* (after Forshaw 1989).

vicissitudes of the Quaternary (Diamond and Hamilton, 1980). The congruence of the disjunct avifaunal patterns with palaeoecological and geomorphological events support the forest refugia hypothesis (Crowe and Crowe, 1982).

Afromontane forest formerly extended over much greater areas of the sub-continent during interglacial periods but became fragmented and restricted during intervening drier periods (van Zinderen Bakker, 1969). The glacial maxima seriously affected the extent of evergreen forest in Africa, and many cases of disjunction shown by African forest organisms date back to the time of the last glacial maximum (Lawes, 1990). The present day range of *P. r. robustus* is confined to forests that were refugia during the last glacial maximum, i.e., afromontane forest patches in the Eastern Cape, KwaZulu-Natal and Mpumalanga (Lawes, 1990). Similarly, *P. r. fuscicollis* occurs in West African forest refugia created during the height of the glacial maximum. This suggests that separation and differentiation of these taxa occurred during the last glacial maximum. During the interglacial to preglacial period (100,000–18,000 BP) there was probably an extension of the *Poicephalus robustus* superspecies (including *P. r. fuscicollis*, *P. r. robustus*, *P. r. suahelicus* and *P. gulielmi* (Jardine)) across the entire range of miombo woodland and afromontane forest. At the glacial maximum (18,000 BP) separation appears to have occurred between sub-populations, with *P. r. robustus* confined to the southern afromontane areas and *P. r. suahelicus* to miombo woodland in the north. *Poicephalus r. suahelicus*

probably retained characters typical of the ancestral super-group including wide habitat tolerances, which enabled range extension during the post glacial. This radiation is supported by molecular analysis using RAPD data for the genus *Poicephalus* (Massa personal communication).

The Limpopo River Valley was an effective barrier during the Pleistocene interglacials and the ranges of several valid subspecies and species currently terminate at this arid river valley, including *P. r. robustus*, *P. cryptoxanthus* (Peters) and *P. meyeri* (Cretzschmar) (Clancey, 1994). Furthermore, the Limpopo River has marked altitudinal and ecological characteristics causing vicariance in the ranges of the birds breeding north and south of the river (Clancey, 1994). Clancey (1997) proposed that the Cape Parrot, *P. r. robustus*, be separated at the species level from the northern subspecies because of its restriction to the southern African afro-montane *Podocarpus* forest biome.

Because of the disjunct ecological distributions and variations in behavioural and plumage colour variations, the status of the *Poicephalus robustus* subspecies was examined using morphological and ecological parameters. Population numbers of *P. r. robustus* are low (Downs and Symes, 1998; Wirminghaus *et al.*, 1999), therefore recognition of its species status has major implications for its conservation.

Methods

One hundred and sixty-one specimens of *Poicephalus robustus* were examined: British Museum, Tring (54), Durban Natural History Museum (10), East London Museum (15), Transvaal Museum, Pretoria (34), Muséum National D'Histoire Naturelle, Paris (9), Field Museum of Natural History, Chicago, Illinois (4), National Museums of Kenya, Nairobi (2), Natural History Museum, Bulawayo (32) and one captive bird. A suite of 19 body measurements (table 1) and plumage colour codes, particularly for the head, body and tail (table 1), using a colour-formula guide (747 XR, Pantone Inc, USA), was recorded for each specimen. The plumage codes for the respective colours are presented in table 2. Morphological measurements taken were similar to those of Schodde *et al.* (1993) and included: wing (flattened chord), tail (base to apex of exposed rectrices), tarsus (notch on heel to knuckle of longest toe forward) and length, width and depth of maxilla and mandible (figure 3). Morphological data were analysed using Principal Components Analysis (Statistica, Statsoft Inc., USA) as a reduction method to determine reliable characters and eliminate redundant characters. Differences among taxa for the accepted morphometric characters were examined separately for adult males and adult females, using multiple analysis of variance (MANOVA, Statistica, Statsoft Inc., USA). Further analyses of variance (ANOVA, Statistica, Statsoft Inc., USA) for each morphological character, were performed between taxa and between sexes. Juveniles (<9 months) were excluded from all analyses to avoid variation caused by development or size. Criteria for separating juveniles from adult birds were absence of red coloration on the wing and tarsus, bill size and museum tag information.

Results

Sixteen female and 25 male *P. r. robustus*, 27 female and 40 male *P. r. suahelicus*, and six female and 15 male *P. r. fuscicollis* were examined and their geographic ranges are shown in figure 4. The distribution of collection localities is similar in

Table 1 Morphometric and colour characters of *Poicephalus* taxa.

Character	Measurement
MH1	Interorbit, distance between anterior orbit ridges measured across brow
MH2	Jaw-hinge, outer distance across jaw-hinge
ML	Length, cere-base to tail-tip along head contour
MW	Left wing length
MTL	Tail length using inner rectrices
MT	Tarsus length
MB1	Culmen, (from edge of cere along curve to bill tip)
MB2	Culmen and cere, from cere-base along curve to bill tip
MB3	Maxilla greatest depth, measured close to cere from cutting edge to bill-ridge
MB4	Smile length, maxilla tip to cutting-edge/cere join
MB5	Maxilla tip length, from nook anterior tooth to bill-tip but measured parallel to outer face
MB6	Maxilla actual length, shortest length from edge of cere on bill-ridge to bill-tip (sagittal plane)
MB7	Maxilla breadth, greatest distance across maxilla
MB8	Maxilla breadth at tooth (palatal ridge when viewed from underneath)
MB9	Ridge width, outside distance across ridge of maxilla at cere
MB10	Maxilla ridge distinctiveness; 0 = ridge rounded, 1 = sides of ridge vertical
MB11	Mandible depth, greatest distance from posterior cutting-edge to base
MB12	Mandible length, from tip to base in sagittal plane
MB13	Mandible width, taken closest to cere at cutting edge
ASex	Assigned sex on basis of forecrown colour, morphology and tag
AAge	Assigned age on basis leg & shoulder colour, morphology and tag; 1 = Ad., 2 = sub-ad., 3 = juv.
CH1	Bill colour
CH2	Forecrown colour
CH2a	Forecrown colour code; 1 = orange, 2 = some feathers with orange, 3 = no orange
CH3	Crown colour
CH4	Collar and nape colour
CH5	Upper chest colour (part of 'hood')
CH6	Chin and throat colour
CH7	Cheek colour
CH8	Ear coverts colour
CH9	Lore colour
CB1	Mantle colour (area between wings) on wings
CW1	Colour around edge of scapulars
CW2	Colour around edge of upper wing coverts
CW3	Colour of flight and tail feathers
CW4	Shoulder edge colour
CW4a	Shoulder edge colour code; 1 = orange, 2 = some orange, 3 = no orange
CB2	Back colour
CB3	Rump colour
CB4	Colour of upper-tail coverts
CB5	Belly and lower chest colour
CB6	Colour of under-tail coverts
CB7	Flank colour
CL1	Colour of plumage on tibiotarsal tibiotarsus feathers
CL1a	Tibiotarsus colour code; 1 = orange, 2 = some orange, 3 = no orange
CY	Presence (1) or absence (2) of yellow feathers in plumage

Table 2. Colour codes used for plumage colour assessment of museum specimens of *Poicephalus* taxa following the colour formula guide (747 XR, Pantone Inc., USA).

Colour codes		
Group	Code	Colour
blacks	10	matt black
	11	dark slate
	12	grey
browns	20	slaty-brown
	21	silvery grey-brown
	22	rusty grey-brown
	23	warm rust-brown
	24	dark earth brown
	25	dark yellow-brown
	26	tan
	30	orange-brown
reds	31	pale orange-grey
	32	pinkish-brown
	33	pinkish-orange
	34	orange-red
	35	orange-green
yellows	40	dark yellow
	41	old ivory
	43	dark yellow-green
greens	50	blue-green
	51	leaf green
	52	dark green
	53	dark oily green
	54	olive(brownish)-green
	55	yellow-green
	56	grey-green
	57	pale blue-grey
	58	pale green
	59	medium green
	60	white/bleached ivory

figure 2, which shows a representative sample of the range of the recognized subspecies.

Plumage colour

Twenty-five colour characters were measured for the three taxa (table 1). Juvenile birds (<12 months) were removed from the analyses as plumage colour changes during development (Wirminghaus *et al.*, 2001). All juveniles had red on the forecrown but had no red on the tibia or leading edge of the wing. Bill size and body size differences were also evident.

The plumage colour characteristics that were consistently different between the sexes of adults of the three taxa were: crown, collar and nape, upper chest (part of the 'hood'), chin and throat, cheek and under-tail coverts (table 3). Crowns of *P. r. robustus* were greener than those of the greyer *P. r. fuscicollis* or the brown-grey-green *P. r. suahelicus*. Constant colour differences suggest recognition (of species) of the former from the latter two. Sexual dichromatism was evident in all three taxa with females being characterized by a bright pinkish orange (red) forehead whereas

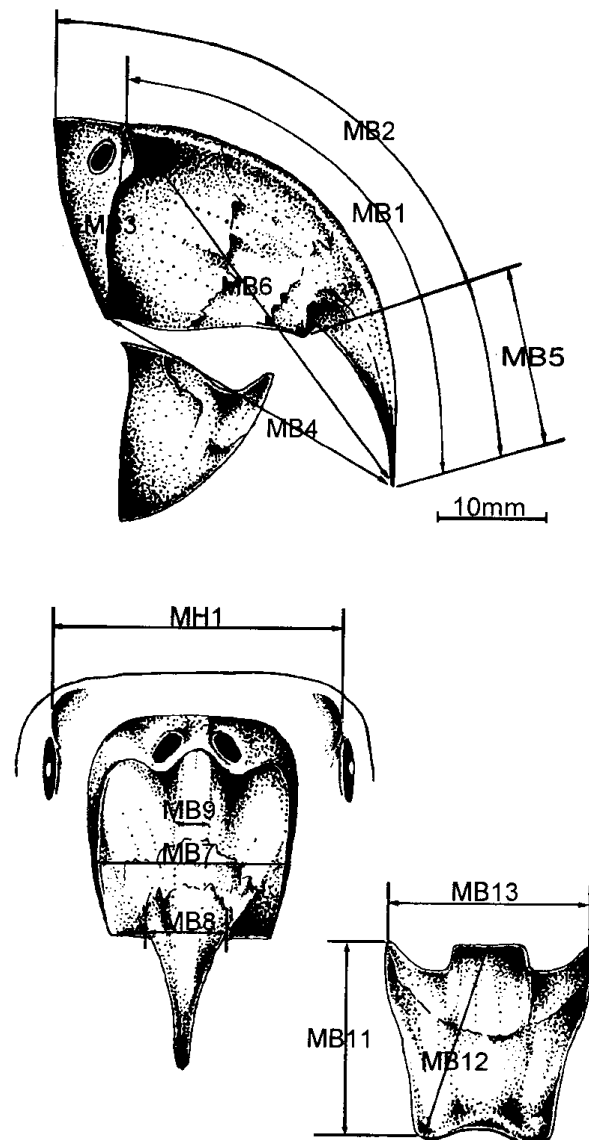


FIG. 3. Bill measurements obtained from the specimens measured.

males showed little or no red on the forehead (table 3). Presence of aberrant yellow plumage feathers is shown in table 4.

Juveniles of both sexes have an orange-red forehead in their first plumage, but only acquire red on the tibia and edge of the wing when they moult to adult plumage (Rowan, 1983; present study). In juveniles the colour is more salmon pink and extends further on to the crown than in adults. At 8–10 months this colour is replaced in males with an olive golden brown.

Morphometrics

Initially, the suite of morphometric characters measured for adult males was analysed using PCA with a minimum eigenvalue of 0.500, which resulted in five factor values (with percent of total variance in parentheses) as 11.51 (63.93%), 2.25 (12.53%), 1.31 (7.30%), 0.97 (5.36%), and 0.78 (4.36%) respectively. All bill measurements (12) were significantly correlated with factor 1. Left wing length (MW) and tail length using inner rectrices (MTL) were significantly correlated with factor 2.



FIG. 4. Localities of museum specimens measured to show their geographical distribution.

Factors 3–5 had only one significant variable each. The resulting distribution of morphological variables using factors 1 and 2 of adult males (all taxa pooled) is shown in figure 5. Similar PCA of adult females using a minimum eigenvalue of 0.500 resulted in six factor values with total variance (in parentheses) of 10.99 (60.88%), 2.12 (11.79%), 1.45 (8.08%), 0.93 (5.17%), 0.77 (4.29%) and 0.54 (2.98%) respectively. Most bill measurements (11) were significantly correlated with factor 1. Left wing length (MW) and tail length using inner rectrices (MTL) were significantly correlated with factor 2 and factor 3 respectively. Factors 2–5 had only one significant variable each. The resulting distribution of morphological variables of adult females (all taxa pooled) using factors 1 and 2 is shown (figure 5).

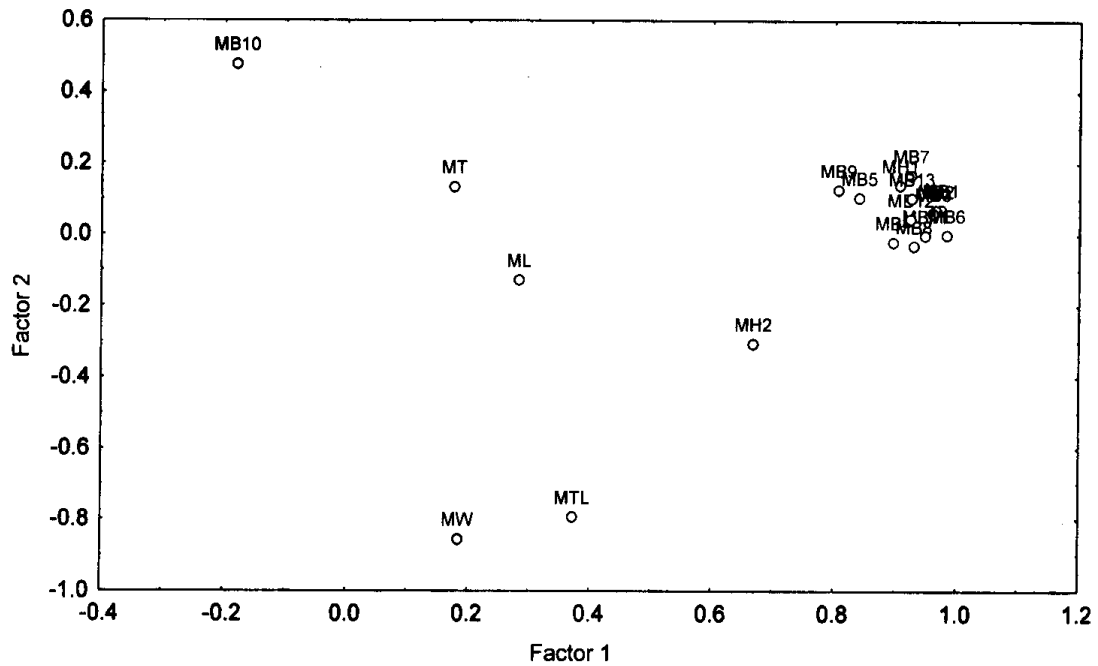
A general MANOVA of five morphological variables (MH2, ML, MW, MTL and MT) for adult males showed a significant difference between the three taxa of *P. robustus* (Wilks' lambda=0.4137*, Rao's $R=4.659^*$, $df=10, 84$, $p<0.05$). A significant difference between the three taxa was found using a general MANOVA of the 12 bill measurements for adult males (Wilks' lambda=0.1118*, Rao's $R=4.811^*$, $df=24, 58$, $p<0.05$). Scheffe tests showed that *P. r. robustus* and *P. r. suahelicus* were similar only in culmen breadth at tooth (MB8) and ridge width (MB9). However, *P. r. robustus* differed from *P. r. suahelicus* and *P. r. fuscicollis* in all other bill measurements, usually being smaller.

The three taxa differed significantly morphologically, (10 of 18 characters used

Table 3. Summary of median plumage colours of *Poicephalus* taxa.

Character	<i>P. r. robustus</i>		<i>P. f. suahelicus</i>		<i>P. f. fuscicollis</i>	
	male	female	male	female	male	female
CH1 Bill colour	41 old ivory	41 old ivory	41 old ivory	41 old ivory	41 old ivory	41 old ivory
CH2 Forecrown colour	24 dark earth brown	34 orange-red	22 rusty grey-brown	33 pinkish-orange	24 dark earth brown	33 pinkish-orange
CH3 Crown colour	54 olive-green	54 olive-green	22 rusty grey-brown	21 silvery grey-brown	22 rusty grey-brown	26 tan
CH4 Collar and nape colour	55 yellow green	55 yellow green	23 warm rust-brown	22 rusty grey-brown	56 grey-green	56 grey-green
CH5 Upper chest colour (part of 'hood')	55 yellow green	55 yellow green	22 rusty grey-brown	56 grey-green	22 rusty grey-brown	21.5 rusty grey-brown
CH6 Chin and throat colour	30 orange-brown	30 orange-brown	22 rusty grey-brown	23 warm rust-brown	22 rusty grey-brown	22 rusty grey-brown
CH7 Cheek colour	54 olive-green	55 yellow green	22 rusty grey-brown	23 warm rust-brown	22 rusty grey-brown	21.5 rusty grey-brown
CH8 Ear coverts colour	54 olive-green	55 yellow green	22 rusty grey-brown	22 rusty grey-brown	21 silvery grey-brown	21.5 rusty grey-brown
CH9 Lore colour	10 matt black	10 matt black	10 matt black	10 matt black	10 matt black	10 matt black
CB1 Mantle colour (area between wings)	53 dark oily-green	52 dark green	54 olive-green	54 olive-green	54 olive-green	54 olive green
CW1 Colour around edge of scapulars	53 dark oily-green	53 dark oily -green	52 dark green	52 orange-red	59 medium green	52 dark green
CW2 Colour around edge of upper wing coverts	53 dark oily-green	52 dark green	52 dark green	52 orange-red	59 medium green	56.5 pale blue-grey
CW3 Colour of flight and tail feathers	11 dark slate	11 dark slate	11 dark slate	11 dark slate	11 dark slate	11 dark slate
CW4 Shoulder edge colour	34 orange-red	34 orange-red	34 orange-red	34 orange-red	52 dark green	56 grey-green
CB2 Back colour	50 blue-green	50 blue-green	50 blue -green	50 blue-green	58 pale green	58 pale green
CB3 Rump colour	50 blue-green	50 blue-green	58 pale green	52 pale green	58 pale green	58 pale green
CB4 Colour of upper-tail coverts	50 blue-green	50 blue-green	58 pale green	50 blue-green	58 pale green	58 pale green
CB5 Belly and lower chest colour	50 blue-green	50 blue-green	51 leaf green	50 blue-green	54.5 yellow green	50 blue green
CB6 Colour of under-tail coverts	50 blue-green	50 blue-green	58 pale green	54 olive-green	54.5 yellow green	58 pale green
CB7 Flank colour	50 blue-green	50 blue-green	51 leaf green	50 blue-green	50.5 leaf green	58 pale green
CL1 Colour of plumage on tibiotarsal joint	34 orange-red	34 orange-red	34 orange-red	34 orange-red	34 orange-red	23 warm rust brown-orange red

a.



b.

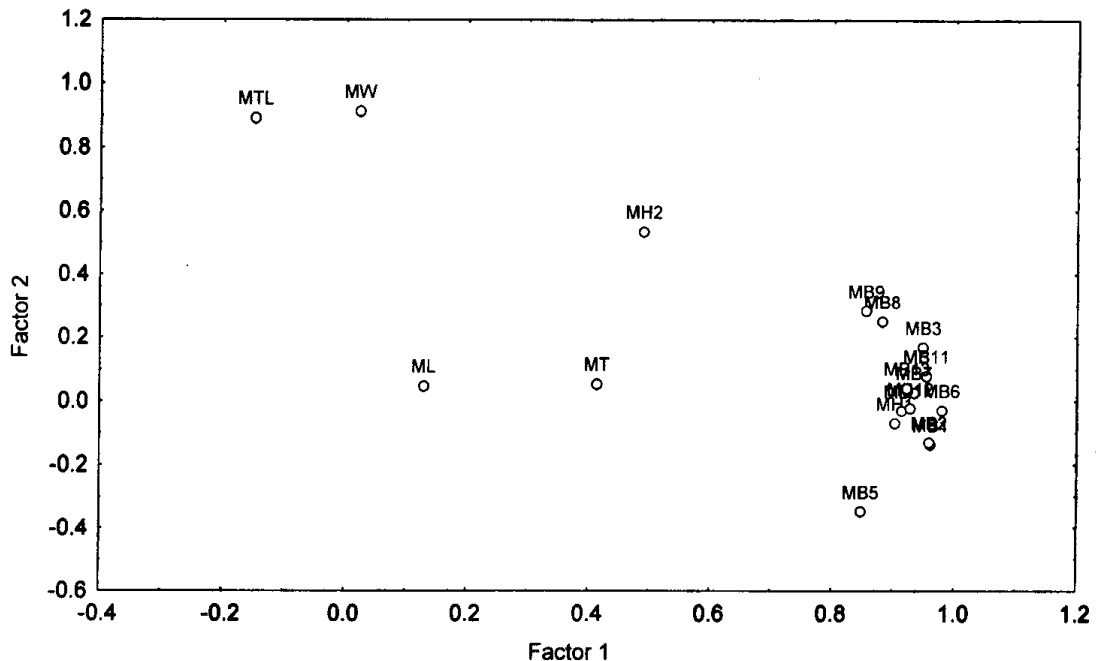


FIG. 5. Principal component analysis of the three previously recognized taxa where (a) includes adult males and females and (b) includes adult males only.

were significant, $p < 0.05$, ANOVA, table 5). Sexual dimorphism was very evident with males larger than females in stature and with a larger bill. *Poicephalus r. robustus* was the smallest of the three taxa (tables 5–6), particularly with its smaller bill dimensions. *Poicephalus r. suahelicus* and *P. r. fuscicollis* differed significantly morphologically (tables 5–6) although separation on plumage colours was more

Table 4 Presence of aberrant yellow plumage feathers in *Poicephalus* taxa

Subspecies	<i>n</i>	Yellow aberrant feathers present (%)	On scapula and wing coverts (%)	On body and head (%)
<i>P. r. robustus</i>	45	17.7	13.3	4.4
<i>P. r. suahelicus</i>	73	12.3	8.2	4.1
<i>P. r. fuscicollis</i>	21	19.0	14.3	4.8
Total	139	15.1	10.8	4.3

Table 5. Analysis of Variance results of morphological measurements of three *Poicephalus* taxa (marked effects are significant at $p < 0.05$).

Analysis of Variance Character	All taxa											
	All sexes				Females				Males			
	df Effect	df Error	<i>F</i>	<i>p</i>	df Effect	df Error	<i>F</i>	<i>p</i>	df Effect	df Error	<i>F</i>	<i>p</i>
MH1		92	18.64	0.00*	2	46	9.78	0.00*	2	77	21.16	0.00*
MH2		47	0.03	0.86	2	32	5.82	0.01	2	47	16.16	0.00*
ML		92	2.96	0.09	2	46	0.75	0.48	2	77	0.23	0.79
MW		91	0.14	0.71	2	43	0.53	0.59	2	76	2.72	0.07
MTL		92	1.93	0.17	2	46	1.32	0.28	2	77	0.58	0.56
MT		92	0.66	0.42	2	46	0.35	0.71	2	77	1.34	0.27
MB1		87	14.91	0.00*	2	43	35.87	0.00*	2	67	62.24	0.00*
MB2		87	10.07	0.00*	2	43	31.20	0.00*	2	67	57.31	0.00*
MB3		92	22.19	0.00*	2	46	27.62	0.00*	2	77	67.96	0.00*
MB4		87	8.33	0.00*	2	43	38.39	0.00*	2	67	40.07	0.00*
MB5		87	1.22	0.27	2	43	11.69	0.00*	2	67	14.03	0.00*
MB6		88	0.63	0.43	2	43	44.90	0.00*	2	68	55.38	0.00*
MB7		92	21.73	0.00*	2	46	27.75	0.00*	2	77	63.71	0.00*
MB8		92	24.76	0.00*	2	46	7.91	0.00*	2	77	13.02	0.00*
MB9		92	12.45	0.00*	2	46	2.22	0.12	2	77	2.60	0.08
MB11		92	9.20	0.00*	2	46	45.29	0.00*	2	77	104.22	0.00*
MB12		86	0.09	0.77	2	45	12.55	0.00*	2	73	24.74	0.00*
MB13		70	38.57	0.00*	2	30	14.35	0.00*	2	48	26.18	0.00*

difficult. Differences in body masses were not analysed as the data were incomplete. Body masses recorded for live Cape Parrots are summarized in table 7.

Discussion

Chapin (1939) described *P. r. robustus* as having a lower mandible <23 mm wide; the lighter, more greyish-headed *P. r. suahelicus* has a mandible 22.6–28.3 mm wide. Lower mandible width (<23 mm), together with other mandible and culmen measurements, was confirmed as a diagnostic feature for *P. r. robustus* in the present study. Davies (1907) described adult males of *P. r. robustus* from the Eastern Cape (Transkei) as being larger than females, with the hook at the end of the beak larger. The bill of *P. r. fuscicollis* has been described as larger and less yellowish (Chapin, 1939) than in *P. r. robustus*, which was supported by the present study. Bill differentiation is correlated with food preferences; however, it may also be used in phylogenetic studies (Darwin, 1899; Lack, 1983; Homberger, 1991, 1996). The Glossy Black-Cockatoo *Calyptorhynchus lathami* (Temminck) exhibits differentiation in bill size

Table 6. Morphological measurements of *Poicephalus* taxa.

(A) <i>P. r. robustus</i>												
Morphometric Characteristic	All			Males				Females				
	SE	<i>n</i>	$\bar{x}$	SE	<i>n</i>	Min	Max	$\bar{x}$	SE	<i>n</i>	Min	Max
MH1	30.13	0.15	45	30.6	0.2	25	29	33.3	0.2	16	28	30.9
MH2	35.58	0.28	43	36.3	0.3	23	32.7	39.1	0.5	16	31	37.6
ML	293.58	3.37	45	297.3	4.5	25	251	349	5.0	16	251	309
MW	215.07	0.93	42	218.3	1.1	24	210	231	1.0	14	205	219
MTL	92.50	0.63	45	94.8	0.5	25	90	98.9	1.1	16	79.6	97.2
MT	21.64	0.14	45	21.7	0.2	25	18.2	23.5	0.2	16	19.9	22.4
MB1	39.69	0.43	36	40.8	0.6	19	37	48	0.6	14	36	43
MB2	44.66	0.48	36	45.8	0.7	19	41	53	0.7	14	40	48
MB3	18.58	0.12	45	19.0	0.1	25	17.6	20.1	0.1	16	16.9	18.9
MB4	28.96	0.28	36	29.7	0.4	19	26.1	32.6	0.4	14	24.8	29.9
MB5	12.83	0.34	36	13.5	0.5	19	10.6	19.3	0.3	14	10.4	15.2
MB6	34.36	0.35	36	35.3	0.5	19	31.4	41.4	0.4	14	30.2	36.1
MB7	20.32	0.13	45	20.7	0.2	25	19	22.5	0.2	16	18.5	21
MB8	11.50	0.13	45	11.7	0.2	25	10.4	15	0.1	16	10.6	12.1
MB9	5.24	0.08	45	5.4	0.1	25	4.1	6.7	0.1	16	4.3	5.7
MB11	18.70	0.15	45	19.2	0.1	25	18.2	20.8	0.2	16	16.3	20.5
MB12	21.35	0.19	45	21.9	0.2	25	19.6	24.8	0.3	16	18.6	22.5
MB13	21.31	0.29	15	21.8	0.4	7	19.8	23	0.3	8	19.4	21.9

(A) *P. r. robustus*

Table 6. (Continued).

Morphometric Characteristic	All			Males				Females					
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	Min	Max	$\bar{x}$	SE	n	Min	Max
MH1	31.7	0.2	73	32.1	0.2	40	28.5	34.3	30.8	0.2	27	28	33.7
MH2	38.5	0.5	33	40.0	0.4	16	37	44	36.6	0.6	15	29.6	38.8
ML	290.7	2.7	73	294.0	3.8	40	217	340	286.6	4.6	27	247	343
MW	219.6	1.8	73	222.0	1.9	40	199	285	216.1	4.0	27	196	315
MTL	93.8	0.7	73	95.1	0.8	40	77	106	91.8	1.2	27	82.8	107
MT	22.1	0.1	73	22.2	0.2	40	19.2	25.5	21.7	0.2	27	18.5	24
MB1	45.7	0.3	70	46.9	0.4	38	42	52	44.2	0.5	26	38	49
MB2	51.7	0.4	70	53.0	0.4	38	47	58	49.9	0.6	26	44	55
MB3	20.4	0.1	73	20.9	0.1	40	18.9	23.6	19.6	0.2	27	16.4	22.3
MB4	32.8	0.2	70	33.7	0.3	38	30	37.6	31.7	0.3	26	27.6	34.5
MB5	15.9	0.3	70	16.5	0.4	38	11.3	20.5	15.5	0.5	26	10.3	19.9
MB6	40.6	0.9	70	40.7	0.3	38	37.7	44.8	38.5	0.4	26	33.6	43
MB7	22.2	0.1	73	22.6	0.1	40	20.8	24.4	21.4	0.2	27	19.6	23.6
MB8	12.1	0.1	73	12.3	0.2	40	9.8	15.2	11.8	0.2	27	10.1	13.9
MB9	4.9	0.1	73	5.1	0.1	40	3.4	6.6	4.7	0.1	27	3.6	6.2
MB11	21.8	0.2	73	22.4	0.2	40	18.6	23.8	21.0	0.2	27	16.8	23.8
MB12	24.0	0.3	69	25.1	0.3	37	21.9	28.6	22.5	0.3	27	20.1	26.9
MB13	23.2	0.2	52	23.5	0.2	29	21	25.6	22.9	0.3	19	21.1	26.1

(B) *P. r. suahelicus*

Table 6. (Continued).

Morphometric Characteristic	All			Males				Females				
	$\bar{x}$	SE		SE	n	Min	Max	$\bar{x}$	SE	n	Min	Max
MH1	32.4	0.3	21	32.8	15	29.4	34.8	31.5	0.4	6	30.6	32.9
MH2	38.1	0.7	15	38.4	11	33.2	42.9	37.5	0.6	4	35.8	38.3
ML	293.5	5.7	21	292.3	15	224	333	296.5	9.6	6	260	320
MW	215.0	2.7	20	214.9	15	187	232	215.2	5.7	5	201	227
MTL	93.3	1.1	21	93.6	15	82.8	101.1	92.5	1.5	6	88	97
MT	21.9	0.2	21	22.0	15	19.1	23	21.7	0.5	6	19.7	22.8
MB1	49.1	0.8	19	50.6	13	44	55	45.8	0.9	6	43	48
MB2	54.2	0.8	19	55.4	13	49	60	51.7	0.6	6	49	53
MB3	21.4	0.2	21	21.9	15	20.3	23.6	20.3	0.3	6	19.1	21.2
MB4	34.0	0.4	19	34.0	13	31.3	36	33.8	0.9	6	31	37.5
MB5	16.5	0.4	19	17.2	13	14	19.9	15.0	0.7	6	12.4	16.7
MB6	41.4	0.6	20	42.0	14	35.6	45.4	39.8	0.7	6	36.8	41.4
MB7	23.4	0.2	21	23.8	15	22	24.9	22.4	0.5	6	21.4	24.6
MB8	13.5	0.3	21	13.7	15	11.4	16.2	13.1	0.5	6	10.8	14
MB9	5.5	0.1	21	5.5	15	4.4	6.4	5.2	0.2	6	4.6	5.9
MB11	22.7	0.2	21	23.0	15	21.6	25.1	21.9	0.2	6	21	22.8
MB12	24.4	0.4	19	24.6	14	21.8	30.5	23.7	0.4	5	22.8	25
MB13	25.5	0.4	21	26.1	15	22.2	28	24.1	0.4	6	23.2	25.2

(C) *P. r. fuscicollis*.

Table 7. Body masses (g) of *P. r. robustus* and *P. r. suahelicus*.

	Male	Reference	Female	Reference
<i>P. r. robustus</i>	295	Rowan, 1983	295	Present study, wild, juvenile
	285	Present study, captive	327.5	Present study, captive
	315.1	Present study, captive	260	Present study, captive
	328.5	Present study, wild		Present study, wild
<i>P. r. suahelicus</i>	326	Rowan, 1983	320.7	Rowan, 1983

among geographical subspecies (Schodde *et al.*, 1993). Relationships of three core groups and two outlier groups of Glossy Black-Cockatoo *Calyptorhynchus lathamii* separated according to the first two principal components determined by canonical variate analysis of nine morphological variables recorded in males (Schodde *et al.*, 1993). Similar separation appears to have occurred in the *Poicephalus robustus* group.

Poicephalus r. robustus, the smallest of the three taxa examined (and an afro-montane forest-specific species), differed noticeably in appearance from the other two taxa. It has very specific nesting and habitat requirements (Wirminghaus *et al.*, 1999). *Poicephalus r. suahelicus* and *P. r. fuscicollis* differed significantly morphologically although they cannot be easily separated on plumage colours. Furthermore, they have similar habitat requirements (Rowan, 1983). Differences may have been caused by genetic drift of the smaller West African population, or by adaptation to a different habitat.

Clancey (1997) distinguished the two southern subspecies *P. r. suahelicus* and *P. r. robustus* by their head and neck coloration, body plumage colour and the size of the bill, which is supported by the present study. The bill of *P. r. suahelicus* is heavier basally than in *P. r. robustus* and the apex is longer and more tapered to a point, while culmen length measured from the cere is longer (Clancey, 1997; present study). Clancey (1997) proposed *P. robustus* be accepted as a separate species on morphological, biogeographical and ecological differences, but revised the arrangement of *P. fuscicollis*; with two subspecies *P. f. fuscicollis* and *P. f. suahelicus*, which is also supported morphometrically by the present study. The different taxa are therefore referred by these names from here on.

Plumage colouring of the adult male of *P. robustus* was described as olive-yellow by Rowan (1983). Head and neck plumage colouring of *P. f. suahelicus* was described as silvery grey (Rowan, 1983). Forshaw (1989) described the plumage colouration of *P. robustus* as less variable and seldom with a bluish tinge compared with the other two subspecies. These colourings are similar to those of the present analysis (table 3). The hood of *P. f. suahelicus* tends to extend further down the throat and on to the breast than in *P. f. fuscicollis*. Furthermore, the grey colour of the head is whiter in the former than the latter, where it is washed variable brown, tending to an earth brown colour from the top of the head (crown), down the nape and on to the mantle. The wing coverts are generally edged lighter green in *P. f. fuscicollis* than in *P. f. suahelicus*. Variation between sexes and within each sex makes separation of these two subspecies difficult using plumage characteristics.

There is unusual sexual plumage dichromatism in the three *Poicephalus* taxa, with females having orange-red foreheads. Adult female *Poicephalus robustus* have varied forecrown plumage patterns, with some having orange across the forehead and others having none; none of the males had this forehead coloration (Davies, 1907; Skead,

1971; present study). Similarly, adult females of the northern two subspecies have the forehead and fore-crown bright red, whereas in males these are silvery grey merely tinged with red (Chapin, 1939; present study). In the latter subspecies this characteristic appears consistent (Chapin, 1939). *Poicephalus flavifrons* (Rüppell), the Yellow-faced Parrot, *P. gularis*, Jardine's Parrot, and *P. senegalus* (Linné), the Senegal Parrot all show similar sexual dichromatism (Bricknell, 1987; Forshaw, 1989).

Juveniles of both sexes in all three taxa have orange-red colour on the forehead in their first plumage, but only have red on the tibia or on the edge of the wing when they moult to adult plumage (Rowan, 1983; present study). The colour is more salmon pink and extends further on the crown in juveniles than in adults. At 8–10 months this colour is replaced in males with colour corresponding to the hood plumage colour (pers. obs.). During this moult the forehead may gain a yellow tinge (pers. obs.). This sexual dichromatism may act to reduce male aggression and facilitate parental care in a species that has a closed nest, where both sexes participating in parental care, and where a male solicits a female (Wirminghaus *et al.*, 2001).

Aberrant yellow feathers were found in several of the museum specimens and have also been observed in wild birds (pers. obs.). Such aberrations are feathers which lack the black pigment melanin (Alderton, 1992). They are typically a single yellow feather in the wing coverts, flight (remiges) or tail (rectrices) feathers, and more rarely as yellow patches on the body or head. Davies (1907) found that some of the brightest-coloured females also had one or two bright yellow feathers amongst the median wing coverts, a yellow feather on one wing and none on the other, suggesting it was a further sexual dimorphic characteristic. However, in this study, both sexes were found to have these yellow feathers. Furthermore, distribution and frequency of these aberrant feathers showed that they were not a sexually dimorphic character. Aberrant feathers are more common in some local populations than others (pers. obs.) suggesting a genetic relationship. They are useful for identifying individuals in the wild, but may cause confusion and misidentification when identifying other *Poicephalus* parrots with overlapping distributions (Wirminghaus, 1995).

In conclusion, the behavioural evidence (Rowan, 1983), distribution data, specific habitat requirements (Skead, 1964; Wirminghaus *et al.*, 1999) and morphological differences presented here support that the southern taxon *P. r. robustus* is a separate species from the northern subspecies *P. r. suahelicus* and *P. r. fuscicollis*. Consequently Clancey's (1997) proposals are adopted with *P. robustus* as a separate species from *P. fuscicollis* (with two subspecies *P. f. fuscicollis* and *P. f. suahelicus*). As population numbers of *P. robustus* are low (Downs and Symes, 1998; Wirminghaus *et al.*, 1999), recognition of its species status has major implications for its conservation.

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(English only/ Unicamente en inglés/ Seulement en anglais)

A review of the taxonomic status and biology of the Cape Parrot *Poicephalus robustus*, with reference to the Brown-necked Parrot *P. fuscicollis fuscicollis* and the Grey-headed Parrot *P. f. suahelicus*

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A review of the taxonomic status of the critically endangered Cape Parrot *Poicephalus robustus* Gmelin 1788 has important implications concerning the conservation of this species and illegal trade. It is distinguishable from the Brown-necked Parrot *P. fuscicollis fuscicollis* Kuhl 1820 on the morphometrics of the body and bill, two mitochondrial DNA sequences and its ecology and behaviour. The Grey-headed Parrot *P. f. suahelicus* Reichenow 1898 is geographically and genetically isolated from the other taxa. Grey-headed Parrots and Brown-necked Parrots are more closely related to each other than either is to the Cape Parrot. Geographically, the Grey-headed Parrot is marginally parapatric with the Cape Parrot, and this account focusses on these taxa. The Cape Parrot is a dietary specialist, and its diet differs from that of the Grey-headed Parrot, which has a wider trophic niche, although both feed on the kernels of unripe fruit. Their feeding behaviour changes in response to seasonally available food and may involve long distance movements. Both species share similar breeding habits, but they breed at different seasons in different habitat types. The two taxa have distinct habitat requirements and distributions. Cape Parrots inhabit, nest and feed in Afromontane mixed *Podocarpus* forest above 1 000m asl in South Africa, whereas Grey-headed Parrots inhabit a wide range of lowland woodland habitats across south-central Africa. In parapatry, there is no record of hybridisation, probably because of spatial (geographical and altitudinal) and temporal segregation (different breeding seasons). On the basis of these criteria, the Cape Parrot is, and must be recognised, as an independent species.

Introduction

In a short note, Clancey (1997) recognised the Cape Parrot *Poicephalus robustus* (Gmelin 1788) as a valid species distinct from *P. fuscicollis* (Kuhl 1820), for which he recognised two subspecies, the Brown-necked Parrot *P. f. fuscicollis* and the Grey-headed Parrot *P. f. suahelicus* (Reichenow 1898). His argument for recognising two species was based on differences in habitat and distribution, head and body colouration, and bill measurements. Wirminghaus *et al.* (2002a) subsequently presented quantitative morphological data to confirm and substantiate Clancey's (1997) claims. Sibley and Monroe (1990, 1993) had proposed a division comprising two taxa, *P. robustus* and *P. suahelicus* (1898), overlooking the fact that the taxon *fuscicollis* (1820) pre-dates *suahelelicus* by 78 years. The taxon *P. suahelicus*, also used recently by Stevenson and Fanshawe (2002), is therefore incorrect. Here I review a wider range of additional and contemporary data to demonstrate that the species status of the Cape Parrot, *P. robustus*, is distinct from Brown-necked Parrot, *P. fuscicollis*.

Unjustified or unsubstantiated changes in taxonomy frequently lead to confusion. Nevertheless, failure to recognise a new species can result in the extirpation or extinction of the species before its taxonomic position is fully acknowledged and accepted. This situation faces the Cape Parrot because of its critically endangered status (Wirminhaus *et al.* 1999, Barnes 2000, Downs 2001) and low population density (Wirminhaus *et al.* 2001a, Downs in press).

Although subspecies rank is sufficient for a taxon to be conserved, with respect to some international conservation agencies such as IUCN, CITES and TRAFFIC, species status is necessary to better enforce conservation, particularly when documenting and controlling legal and illegal trade in commercially exploited parrots. Although CITES may recognise subspecies as a taxonomic unit worthy of conservation, it is only concerned with international trade, and illegal trade within the country of origin of a taxon requires national enforcement, often requiring species rather than subspecies status. This is particularly relevant for the Cape Parrot in South Africa.

Until it can be demonstrated that the *P. robustus* is threatened by illegal international trade, it cannot receive recognition and protection from categorisation as a CITES Appendix 1 species although it meets all, and exceeds several, of the demographic criteria. Trade in *P. robustus* cannot be monitored until taxonomists, aviculturists, conservators and law enforcement personnel accept its species rank. Previously, international trade in *P. robustus* was only reported collectively (combined) with data for the *P. f. suahelicus* and *P. f. fuscicollis*.

Reviewing evidence for the recognition and acceptance of the species status of the *P. robustus* was the primary purpose of this paper (Table 1). It elucidates differences between the southern African taxa, *P. robustus* and *P. f.*

fuscicollis. The second aim was to create awareness of the demographic fragility of *P. robustus* with respect to its ecology and environment.

Taxonomic status

Poicephalus robustus Gmelin 1788 Cape Parrot

Psittacus robustus Gmelin, 1788: Syst. Nat. 1(1): 344 (no locality)

Psittacus levaillanti Latham Syn. Suppl. p. xxiii (1802)

Pionus robustus Sclater, P.Z.S. 1866, p. 22 (Cathcart)

Pionias robustus Finsch, Papag. Li. p. 475 (1868)

Poeocephalus robustus Gurney, Ibis 1873, p. 255

Poicephalus robustus Clancey 1965

Poicephalus fuscicollis fuscicollis Kuhl 1820 Brown-necked Parrot

Psittacus fuscicollis Kuhl, Nova Acta Acad. Caes. Leop. Carol., 10, 1820. Comspectus Psitt. p. 93 (type locality unknown)

Poeocephalus rubricapillus Forbes and Robinson, Bull. Liverpool Museum, 1, 1898; p. 15. (West Africa) (Peters 1937)

Poeocephalus kintampoensis Alexander, Bill. Brit. Orn. Cl., 12, 1901, p. 10 (Kintampo, Gold Coast) (Peters 1937)

Poicephalus angolensis Reichenow, 1898. J.f.O. p. 314 (type locality: Angola)

Poicephalus robustus var. *angolensis*

Poicephalus robustus fuscicollis Bannerman, 1931. Birds Trop. W. Afr. II. p. 394, figs. 109, 110, Pl. xv.

Poicephalus fuscicollis fuscicollis (Clancey 1997)

Poicephalus fuscicollis suahelicus Reichenow 1898 Grey-headed Parrot

Poicephalus suahelicus Reichenow, 1898. Journ. f. Orn., 46, p. 314 (type locality: from Msua, near Bagamoyo, Tanganyika Territory, East Africa)

Poicephalus robustus suahelicus Reichenow, 1911. Wiss. D. Z.-Afr. Exp. III. p. 267. (Rugege forest; NW of Lake Tanganyika, 2 000 m)

In his paper 'The Cape Parrot: an additional valid species' Clancey (1997) recognised three taxa on the basis of head, colouration and bill dimensions, and preferred vegetation (habitat) types: *P. robustus* from

Podocarpus woodlands of south-east South Africa; *P. f. suahelicus* from *Brachystegia* savanna woodland regions of Africa to the south and east of the evergreen forest biome; and *P. f. fuscicollis* from mangrove woodlands of West Africa (however, see below for the habitat preference of *P. f. fuscicollis*). Clancey stated that there was no doubt that *P. robustus* and *P. fuscicollis* were separate species: and concluded that *fuscicollis* comprises two subspecies, *fuscicollis* and *suahelicus*. *P. robustus* stood on its own as a valid austral monotypic species.

Unfortunately, Clancey's (1997) account is discursive and general, with few sound taxonomic characters or criteria to substantiate his claims, and it contains at least one incorrect assertion, i.e. that *P. f. fuscicollis* is confined to mangrove forests.

Species concepts

There are many species concepts (Mayr 1970, Cracraft 1983, Paterson 1985, Mayden 1997, De Queiroz 1998, 1999) debated in the scientific literature, but what is critically and urgently needed for the recognition of species facing illegal trade and extinction, *inter alia*, are precise and definite guidelines for the assessment and recognition of species rank. Such guidelines have recently been defined and published (Helbig *et al.* 2002) by the Taxonomic Subcommittee of the British Ornithologists' Union, which proposes the following criteria: that species be defined in relation to other species; that taxa must be diagnosable; and that taxa must retain their genetic and phenotypic integrity.

Species are recognised and distinguished on characters or character states which may be morphological, behavioural, ecological and/or molecular. Since characters differ between taxa, genetic differences accumulate following a period of isolation. The extremes of taxa showing clinal variation do not represent separate species, and neither do hybridising taxa, because there will be intermediate individuals that do not meet the diagnostic criteria of either the geographical or the parental taxon.

Helbig *et al.* (2002) regard a species (taxon) as fully diagnosable if all individuals of one species can be distinguished from all members of another species by at least one qualitative difference, and/or by a complete discontinuity in

Table 1: Some contrasting characters of Cape Parrots (*P. robustus*) and Grey-headed Parrots (*P. f. suahelicus*)

	<i>P. robustus</i>	<i>P. f. suahelicus</i>
Habitat	Mixed Afromontane <i>Podocarpus</i> forest Specialist	Low-lying mopane and mixed broadleaf woodland, savanna and forest More generalist
Range	E Cape, Transkei and KwaZulu-Natal, South Africa	South-central Africa from Angola and South Africa to Uganda and Tanzania
Morphology	Smaller body dimensions Narrower and smaller bill	Larger body dimensions Bill heavier basally; apex tapered and longer
Colouration	Head colour olive-yellow	Silvery grey head
Vocalisations	Simple contact call No 'kraa' or click calls recorded	Complex contact call, clearer and more metallic 'Kraa' and click calls recorded
Diet	Specialist feeders on <i>Podocarpus</i> fruits, eaten when green and hard	Generalist feeders on a range of forest fruits and seeds
Reproduction	Usually nest in <i>Podocarpus</i> trees Usually nest September to December	Usually nest in <i>Adansonia</i> trees In south, breeds April to August

at least one continuously-varying character (e.g. wing-length), or by a combination of two or three fundamentally independent characters. Such character data sets can be interpreted with respect to the distributional relationships of species, i.e. whether sympatric, parapatric, allopatric or occupying a hybrid zone.

What are the data for assigning species rank to the Cape Parrot?

The species and subspecies status of the Cape Parrot taxonomic grouping are contentious. Collar (1997) in Del Hoyo *et al.* (1997) stated that the subspecies *suaahelicus* is sometimes considered a separate species from the nominate species, *P. robustus*, although morphological differences are small. Nevertheless, distinctive differences in habitat preference suggested that treatment as separate species was probably justified. Juniper and Parr (1998) recognised three subspecies of *P. robustus* (i.e. *robustus*, *fuscicollis* and *suaahelicus*) and stated that some authors treat the nominate (*robustus*) as a separate species. Rowan (1983) recognised two subspecies *robustus* and *suaahelicus* of *P. robustus* in the southern African subregion, and Forshaw (1989) recognised three in Africa — *robustus*, *suaahelicus* and *fuscicollis* — with different geographical distributions. Surprisingly, Harrison *et al.* (1997) did not discuss the species status of the Cape Parrot taxonomic grouping, although Clancey (1997) had already advocated separate species status for *P. robustus*, distinct from *P. fuscicollis fuscicollis* and *P. f. suaahelicus*. Wirminghaus *et al.* (2002a) supported Clancey's (1997) interpretation. More recent field guides and texts — for example, Sinclair and Ryan (2003) and Hockey, Dean, Ryan and Maree (in press) — recognise the Cape Parrot *P. robustus* as a separate species, whereas this level of distinction and taxonomic rank was not recognised previously.

Evolutionary implications

The Ethiopian region contains 10 parrot species belonging to the endemic genus *Poicephalus*; six taxa (*P. robustus*, *P. f. fuscicollis*, *P. f. suahelicus*, *P. gulielmi gulielmi*, *P. g. massaicus* and *P. g. fantiensis*) are large and closely related, with a recent common ancestor (Massa *et al.* 2000). *P. f. suahelicus* is a woodland subspecies whereas *P. robustus* is confined to Afromontane forests in South Africa (Wirminghaus *et al.* 2002a, Symes and Perrin 2004a). Their separation and subsequent speciation is thought to have occurred as a result of periods of aridity and fragmentation of forest and savanna habitats (Massa 1998). A major shift in vegetation occurred between 9 500–12 500 BP, resulting in an advance of forest vegetation (Hamilton 1974, Livingstone 1975). During the last dry period, when grasslands were more extensive, woodland habitat northwards was effectively reduced by an encroachment of desert, sub-desert and grassland from the south (Livingstone 1975, Diamond and Hamilton 1980, Crowe and Crowe 1982). This reduction in woodland and forest through Africa likely confined relict populations of the *P. robustus* superspecies (ancestral group) to relict forest in the south-east of South Africa (Cooke 1962). During this

period *P. robustus* may have become a habitat and dietary specialist and a separate species. During subsequent pluvial conditions, with a concomitant expansion of woodland habitat, *P. f. fuscicollis* may have extended its range into its present distribution.

Molecular characters

In a preliminary investigation of the phylogenetic relationships between the three taxa, 430 base pairs (bp) of the mitochondrial DNA (mtDNA) protein coding cytochrome b gene, as well as 400 bp of the more variable mtDNA control region, were compared (Solms 1999, Solms *et al.* 2000). The DNA sequence analysis of these loci found no variation within *P. robustus* and *P. f. fuscicollis* and very low levels of variability within *P. f. suahelicus* (<1% sequence divergence in the control region) (Solms 1999). All three taxa were genetically distinguishable, based on either of the two mtDNA regions. *P. f. suahelicus* and *P. f. fuscicollis* are more closely related to each other than either is to *P. robustus* (0.7–2% sequence divergence compared with 1.2–3% divergence), a finding in agreement with previous morphological and ecological studies (Clancey 1997, Wirminghaus *et al.* 2002a).

Distance matrices of cytochrome b and control region showed the following sequence divergence (in each comparison the cytochrome b divergence is given first, followed by the control region divergence): *P. robustus* vs *P. f. suahelicus* 0.012/0.03; *P. robustus* vs *P. f. fuscicollis* 0.015/0.02; *P. f. suahelicus* vs *P. f. fuscicollis* 0.007/0.02; *P. cryptoxanthus* (Brown-headed Parrot for outgroup comparison) vs *P. robustus* 0.08/0.10 (Solms 1999). The cytochrome b divergence of 1.2–1.5% between *P. robustus* and the other subspecies indicates recent divergence.

Future molecular studies should include more representative geographic sampling (especially in the area of parapatry, see below) of all three taxa and the inclusion of nuclear DNA genetic markers. Nevertheless, the *P. robustus* and the *P. f. suahelicus*, which have allopatric distributions, were identified as separate taxonomic units (Solms 1999).

Genetic distance considered alone is often not sufficient to determine species status, and that is certainly the case here, but genetic differentiation taken together with differences in morphology and ecology can be conclusive.

Morphology

There are significant differences between *P. robustus* and *P. f. suahelicus*, with respect to the dimensions of the skull — including inter-orbital distance, culmen length, maxilla depth, maxilla tip to cutting edge, maxilla breadth, mandible depth, mandible width — and some dependent variables (Wirminghaus *et al.* 2002a).

Analysis of five morphological variables (outer distance across jaw-hinge, body length, wing length, tail length and tarsus length) of adult males showed a significant difference between the three taxa (Wirminghaus *et al.* 2002a). A significant difference was also recorded between 12 bill measurements of adult males. Post hoc Scheffe tests showed that the *P. robustus* and *P. f. suahelicus* were similar only in culmen breadth at tooth and ridge width. However, *P. robustus*

differed from *P. f. suahelicus* and *P. f. fuscicollis* in all other bill measurements, usually being smaller (Wirminghaus *et al.* 2002a). Sexual dimorphism was very evident, with males being larger than females in terms of stature and bill size.

Chapin (1939) described *P. robustus* as having a lower mandible <23mm wide, whereas *P. f. suahelicus* has a mandible 23.0–28.3mm wide. Lower mandible width (<23mm), together with other mandible and culmen measurements, has been confirmed as a diagnostic feature of *P. robustus* (Wirminghaus *et al.* 2002a).

The bill of *P. f. fuscicollis* has been described as larger and less yellowish (Chapin 1939) than that of *P. robustus*. Although bill differentiation is correlated with food preferences, it may also be used in taxonomic studies (Lack 1983, Homberger 1991, 1996). Comparisons of bill morphology indicated the following differences: in *P. f. suahelicus* the bill was heavier basally, the apex longer and more tapering to a point, and the culmen (measured from the cere) longer, than similar features in *P. robustus* (Clancey 1997).

Colouration

Clancey (1997) distinguished between the two southern taxa, *P. f. suahelicus* and *P. robustus*, on the basis of their head and neck colouration, body plumage colour and the size of the bill (Figure 1). The crown of *P. robustus* is more golden than the greyish crown of *P. f. suahelicus* and the greyish-brown of *P. f. fuscicollis* (Wirminghaus *et al.* 2002a). Clancey (1997) also distinguished *P. robustus* from *P. f. fuscicollis* on head, neck and body plumage colouration. Head plumage colouring of adult *P. robustus* has been described as olive-yellow, whereas in *P. f. suahelicus* it is silvery grey (Rowan 1983, Wirminghaus *et al.* 2002a). Forshaw (1989) described the plumage colouration of *P. robustus* as less variable (and seldom with a bluish tinge) when compared with the other two taxa. The hood of *P. f. suahelicus* tends to extend further down the throat and breast than in *P. f. fuscicollis* (Wirminghaus *et al.* 2002a). Furthermore, the grey colour of the head is whiter in the former than the latter, where it is washed variable brown, tending to an earth-brown colour from the top of the head (crown), down the nape, and on to the mantle. The wing coverts are generally edged lighter green in *P. f. fuscicollis* than in *P. f. suahelicus*. Variation between the sexes and within each sex makes it difficult to separate these two taxa on the basis of plumage characteristics (Wirminghaus *et al.* 2002a).

Vocalisations

Cape Parrots have a distinctive vocal repertoire and the constituent calls have been identified, described (duration, frequency and composition) and named. The calls are used to maintain contact between foraging individuals, to denote alarm, and to threaten. They are particularly important in courtship and copulatory behaviour and are necessary for the maintenance of pair bonds.

P. f. suahelicus produces a 'tzu-wee' contact call similar to that of *P. robustus* (Symes 2001, Symes and Perrin 2004a) but additional short distance 'chirps and chatters' are added to produce a complex song type that varies in amplitude and may sound clearer and more metallic. It is given when perched, flying or moving to early morning feeding sites. In continuous flight, these syllables are given alternately and are

audible from a distance of c. 1 km. Sonograms have been recorded and published (Wirminghaus *et al.* 2000, Symes 2001, Symes and Perrin 2004a) although further research is required.

P. f. suahelicus shows controlled synchrony in duet calls, with complex and variable calls recorded between pairs, and is often associated with 'arch angel' wing displays. A resonating nasal 'kraa', reminiscent of a crow, not recorded in *P. robustus*, is noted frequently in *P. f. suahelicus*, and occurs while calling and socialising at activity centres (Symes and Perrin 2003a).

A defensive aggressive grating call is given by nestling *P. f. suahelicus* and by captive adult *P. f. suahelicus* and *P. robustus* when threatened or confined (Wirminghaus *et al.* 2000). A barely audible 'click' call, not known in *P. robustus*, is given mostly by male *P. f. suahelicus* to maintain contact with the female in the nest.

Feeding biology

P. robustus are food nomads, moving locally between forest patches in search of food, and occasionally making long foraging forays (Skead 1964). They are dietary specialists, feeding primarily (~70%) on the kernels (endocarps) of yellowwood *Podocarpus* spp., but also occasionally on other forest fruits (Wirminghaus *et al.* 2002b). The kernels of *Podocarpus* spp. are eaten when green and hard (Skead 1964). The benefits of exploiting these fruits, particularly *Podocarpus falcatus*, include the extended fruiting period and the fact that fruit is large, with a high fruit yield and a high energy and fat content (Wirminghaus *et al.* 2002b). The number of food species and plant families used is low. Monthly dietary diversity studies (percentage monthly dietary items of total dietary items) have shown a preference for *Podocarpus falcatus* and *Podocarpus latifolius*. Seasonal changes in species eaten reflect the changing availability of *Podocarpus* spp., since other fruiting species are eaten when *Podocarpus* spp. are unavailable (Wirminghaus *et al.* 2002b).

By contrast, *P. f. suahelicus* feeds on more than 25 tree species, through its range e.g. *Gmelina arborea*, exotic *Sclerocarya birrea*, *Erythrina coffra*, *Commiphora mollis* and exotic *Melia azaderach* (Symes and Perrin 2003b). In Limpopo Province, South Africa, it feeds regularly on the fruit of at least six tree species, during the non-breeding season (August–December), and eight species during the breeding season (April–August) (Symes and Perrin 2003b). It also feeds on the bark of three additional species during the breeding season. Feeding choice reflects seasonal fruit availability, and during any one month feeding occurs on a few tree species (Symes 2001, Symes and Perrin 2003b). Differences in foraging behaviour and foods eaten indicate the separation of trophic niches that characterise the two taxa. *P. f. suahelicus* is not known to eat *Podocarpus* fruits.

Breeding biology

Nest sites of *P. robustus* are limiting, as they have specific nesting requirements (Wirminghaus *et al.* 2001b). Nests are usually located in secondary cavities high up in dead *Podocarpus* spp. (snags). These are usually in forest canopy trees. Breeding occurs from August to February. Clutch size varies from 2–5, and incubation is by the female and lasts 28–30 days, with fledging taking a further 55–79

days (Wirminghaus *et al.* 2001b). *P. robustus* have been recorded nesting in six yellowwood trees (of which four were *Podocarpus falcatus*), a blackwood (*Acacia melanoxylon*) and another alien species (Wirminghaus *et al.* 2001b).

Historical nest site records for *P. f. suahelicus* include two in baobabs (*Adansonia digitata*), two in Tanzanian albizias (*Albizia tanganyicensis*), one in *Brachystegia randii*, one in *Acacia glaucescens*, one in *Hyphaena ventricosa* and two in unidentified trees (Vincent 1946, Jacobsen 1979, Rowan 1983, Beel 1994). Symes and Perrin (2004b) recorded 34 additional nest sites, including five that were occupied, all in baobabs. Nest sites of the two taxa have similar dimensions and occur at similar heights above ground (Wirminghaus *et al.* 2001b, Symes and Perrin 2004b); no nest sites of *P. robustus* have been located >1 km from Afromontane forest.

In the southern limit of its range in South Africa, *P. f. suahelicus* breeds from April to August (Symes and Perrin 2004b), although further north it breeds in other months of the year. Egg laying by the monogamous pairs is synchronous and 2–4 eggs are laid in natural cavities in baobabs (*A. digitata*). Post-breeding seasonal movements occur into regions where nest sites are scarce or possibly absent (Symes and Perrin 2004b).

Wirminghaus *et al.* (2001b) recorded *P. robustus* nesting in the Natal midlands of South Africa, once atypically in May, but characteristically in September (1), October (3), November (2) and December (2), with emergence and fledging from the nest sites in November, December and February — that is, during the summer rains. Breeding in the southern limit of *P. f. suahelicus* (in south-eastern Zimbabwe and north-eastern South Africa), however, occurs in the dry months. Egg laying occurs in the latter half of May, with chicks fledging in late July or early August (Symes 2001). Symes (2001) reported an interview with a trapper who always removed chicks from nests around 21 June each year, which indicates regular and synchronous breeding, following egg laying in April–May.

Habitat and distribution

P. robustus is a habitat specialist with a restricted range, confined almost entirely to the Amatole, Transkei and eastern mistbelt forests of South Africa (Von Maltitz *et al.* 2003). It also occurs as a small relict population within one of the three ecological subtypes within the Northern Mistbelt Forest, namely the mistbelt forest, which occurs at higher altitudes and with a closed canopy and moist interior. It does not occur in the other two subtypes where *P. f. suahelicus* has been reported (2003a, 2004a, Symes and Perrin in press, see below). These subtypes are semi-deciduous Scrub Forest, common at lower latitudes and with a low canopy and a dominance of the flame acacia *Acacia ataxacantha*, and semi-deciduous mixed forest, found at higher reaches of the main river systems and where the canopy is dominated by the rough-bark flat-crown acacia (*Albizia adianthifolia*).

Eastern Cape and Transkei mistbelt forests are small (>1 ha) to large (1 000–>1 500 ha) forests occurring on the east-west slopes at 850–1600m asl. The former occur in an extensive band along the mountains or escarpments (fire refugia) from the Eastern Cape to the midlands of KwaZulu-Natal. The habitat is characterised by heavy summer mist and the forests are dominated by lemonwood (*Xymalos*

monospora), Henkel's yellowwood (*Podocarpus henkelii*), *P. latifolius* and Outeniqua yellowwood (*P. falcatus*) (Von Maltitz *et al.* 2003). The Transkei mistbelt forests are dominated by *P. falcatus*, sometimes as an emergent, red pear (*Scolopia mundii*), *P. latifolius*, *X. monospora* and *Papanea melanophloeos*. They differ from the Eastern Cape mistbelt forests in the larger number of *P. falcatus* and *P. latifolius* and small number of *P. henkelii* (Von Maltitz *et al.* 2003).

Amatole mistbelt forests range from tall forest to scrub forest along a gradient, from cool mountain slopes with heavy summer mists to lowland areas in the Eastern Cape Province, and comprise two subtypes (Von Maltitz *et al.* 2003). The Amatole Escarpment Forests are relatively large, species-rich, middle-altitude forests found mainly in the Amatole Mountains, dominated by emergent trees of *P. falcatus*. The Albany Scarp Forests are a complex of scattered small forest patches along the lower east-west quartzite ridges found between the Zuurberg Mountains and King William's Town. The most prominent canopy trees are *P. falcatus*, red currant rhus (*Rhus chiridensis*) and white ironwood (*Vepris lanceolata*).

A survey of two Afromontane forests at Nxumeni and Hlabeni in the Natal midlands of South Africa, where *P. robustus* occurs, showed they were generally depauperate, with little variation in tree species composition (Wirminghaus *et al.* 1999). These are coarse-grained forests with shade-intolerant species dominating and with sporadic regeneration (Everard 1993). They generally lack middle-sized trees, probably as a result of past exploitation of timber by colonists and present exploitation of poles by rural populations (Everard 1993). This may negatively impact on the future of the *P. robustus* population (Downs and Symes 2004).

The little-known *P. f. fuscicollis* historically occurred from Angola throughout West Africa, but is now common only in the Gambia, where it occupies habitat similar to that of *P. f. suahelicus* (Symes and Perrin in press). It is widely separated in its geographical distribution from *P. robustus*. Little is known of the biology and abundance of *P. f. fuscicollis* (Juniper and Parr 1998).

P. f. suahelicus generally occurs in low-lying woodland or savanna throughout south-central Africa, from Angola and South Africa to Uganda and Tanzania (Wirminghaus *et al.* 1999, 2002a, Snow 1978, Fry, Keith and Urban 1988, Forshaw 1989). However, in the highlands of Eastern Zaire, it occurs in montane forest up to 3 750m asl. (Symes 2001, Symes and Perrin 2004b) and in the Nyika Plateau of Malawi it occurs in forest habitat but at a much higher latitude. *P. f. suahelicus* utilises a variety of habitat types throughout its range (Snow 1978, Forshaw 1989, Symes and Perrin in press), but unlike *P. robustus* is not confined to a specific habitat type (Symes and Perrin in press). The two parrots, therefore, never occur in the same habitat at the same latitude.

In South Africa, *P. f. suahelicus* inhabits mopane (*Colophospermum mopane*) woodland, mixed broadleaf woodland and disturbed secondary growth forest. During the non-breeding season, it is dependent on mabola plum (*Parinari curatellifolia*) (Symes and Perrin 2003b). Bird atlas records (Harrison *et al.* 1997) for South Africa indicated that the highest reporting rates were from mopane, miombo, valley bushveld and moist woodland (Wirminghaus 1997). In Zimbabwe, *P. f. suahelicus* occur in riverine woodland





Figure 1: A pictorial representation of the head and body colouration of (A) male *Poicephalus robustus*, (B) female *Poicephalus robustus*, (C) male *P. f. suahelicus*, (D) male *P. f. fuscicollis*, (E) female *P. f. suahelicus*, and (F) female *P. f. fuscicollis*
(All photographs © Cyril Laubscher)

(Benson and Irwin 1966, Irwin 1981), and in Zambia it is a bird of *Brachystegia* woodland (Benson and Irwin 1966). The range of *P. f. suahelicus* also includes Kalahari sand, *Acacia* and *Isobertinia* forest savanna mosaic, *Baikiaea* dry forest and moist woodland (Cooke 1962).

Seasonal movements of *P. f. suahelicus* are probably a response to the breeding cycle and availability of specific food sources (Symes 2001, Symes and Perrin 2003a, 2003b). In north-eastern South Africa, *P. f. suahelicus* occur outside the breeding season at sites where the mabola plum (*P. curatellifolia*) is fruiting. Similar movement patterns in Zambia and the Nyika Plateau (Malawi/Zambia border) and Zimbabwe (onto the central plateau) involve post-breeding movements (Symes and Perrin 2003a).

Clearly, *P. f. suahelicus* is a generalist with broad ecological pliability, which occasionally includes montane forest in its habitat. It is arguable that the niche of the Cape Parrot is contained within this range of specialisations, but the Cape Parrot has evolved morphological, behavioural and genetic distinctiveness, and is a habitat specialist.

Parapatry

Macro-distribution

P. robustus is parapatric, with *P. f. suahelicus* in part of its range, but allopatric with *P. f. fuscicollis*. Strictly speaking, parapatric taxa have abutting breeding ranges (i.e. they do not overlap) and do not interbreed (Helbig *et al.* 2002). Parapatric taxa tend to be separated altitudinally or by an ecotone (an abrupt break in habitat), but occasionally by a seemingly 'trivial' ecological barrier (e.g. toucans in Amazonia that are separated by a river: Haffer 1998). Parapatry reflects a situation where two taxa are ecologically identical or so similar that they cannot coexist in the same habitat. The fact that they do not hybridise, although occurring in proximity, indicates that some intrinsic reproductive isolation is very likely operating (Mayr 1970). This applies to *P. robustus* and *P. f. suahelicus*.

The present distribution of *P. robustus*, *P. f. fuscicollis* and *P. f. suahelicus*, shows highly fragmented ranges (Fry *et al.* 1988). If one assumes that the formerly continuous range became fragmented, it can be hypothesised that this process was caused by environmental changes during glacial periods (Massa *et al.* 2000). The three taxa and subpopulations (ranges) are now confined to differing habitat types. The present distribution of these three taxa, with disjunct populations in different forest patches, may reflect a past history of fragmentation and subsequent inability to recolonise new forest habitats after episodes of aridity. Even during pluvial periods, when tropical forests expanded, these taxa may have been unable to recolonise new patches (Massa *et al.* 2000).

Micro-distribution

A small, isolated and disjunct population of *P. robustus* occurs in the Woodbush-Wolkberg forests (c. 23°30'–24°30'S and 29°30'–30°30'E) in Limpopo Province, South Africa (Wirminghaus 1997, Barnes and Tarboton 1998, Downs 2000), close to the southern distribution limit of *P. f. suaheli-*

cus. This relict population, approximately 700km from the core population in the south, is thought to extend its range into the Soutpansberg, where less than 50 birds are thought to remain (Wirminghaus 1997, Barnes and Tarboton 1998, Downs and Warburton 2002). It is debatable whether this small single population, lying adjacent to the range of another taxon, can be considered parapatric with *P. f. suahelicus*.

Two study sites, at Levubu and Makuya in north-eastern South Africa — where *P. f. suahelicus* is relatively abundant, and where *P. robustus* has been inferred to occur with *P. f. suahelicus* — were investigated (Symes 2001, Symes and Perrin 2003b, in press). *P. robustus* was observed here and at Soutpansberg, but only at high altitude (Symes *pers. comm.*). Where the two taxa co-occur, *P. f. suahelicus* occupies mixed woodland habitats below 800m asl whereas *P. robustus* inhabits mixed *Podocarpus* Afromontane forest above 1 000m asl. They are, therefore, sympatric rather than syntopic.

Part of the reported distribution of *P. robustus* (Harrison *et al.* 1997) (Quarter Degree Squares 2330AA Ratombo, 2330AB Levubu, 2330CD Thohoyandou and 2330DC Gravelotte) should refer to *P. f. suahelicus* (Downs 2001). Recently, *P. f. suahelicus* was recorded in the first three of these grid squares, and may occur in the fourth (Symes and Perrin in press), whereas *P. robustus* was noted as absent from these squares (Symes, Venter and Perrin 2000). Therefore, in the northern part of its range, *P. robustus* is restricted to Duiwelskloof (2330CA), Tzaneen (2330CC), The Downs (2430AA) and Haenertsburg (2329DD) in Afromontane forests of the Drakensberg escarpment (Symes 2001, Symes and Perrin in press).

Apparent range overlap is unsubstantiated. *P. robustus* and *P. f. suahelicus* are separated on the basis of habitat and altitude. *P. robustus* depends on yellowwoods *Podocarpus* spp., which are very scarce in forests of the eastern Soutpansberg (Symes *et al.* 2000). Their presence there, if only 15–20 birds, is seriously questioned (Barnes and Tarboton 1998). The presence of *P. robustus* in the forests of the western Soutpansberg, where *Podocarpus* spp. are more common, is uncertain and requires investigation.

Limited range overlap does not damage the argument for niche and species separation. However, evidence is not available to demonstrate that the characters which define *P. robustus* and *P. f. suahelicus* are constant in these physically close populations.

Subspecies conservation?

Thomas *et al.* (1999) identified three reasons for defining races or subspecies as 'endangered' taxa. First, most of the genetic variation unique to a region is likely to be contained within endemic races. Second, endemic races are typically associated with ancient habitats that also contain other endemic or rare species. Locations of endemic races are likely to be highly aggregated, so the known distributions can indicate the existence of biodiversity hotspots, in terms of genetic variation at a taxonomic level below full species. This is consistent with Avise's (1992) conclusion that the distributions of relatively deep evolutionary divisions within species (clades) are often spatially concordant with those of

other species. Thus, effective conservation of the racial structure of some species is likely to go some way towards conserving the racial structures of other species occurring in the same habitats and regions. Finally, local characteristics and adaptations may be indicative of the existence of persistent biological systems and processes that can be conserved effectively.

For the purpose of devoting scarce or expensive resources to single-species conservation management, it is necessary to identify populations sufficiently distinct, from evolutionary and systematic perspectives, which merit special investment (Barrowclough and Flesness 1966). Isolation over time leads to the accumulation of genetic difference between populations. Accumulated genetic differences lead to observable differences among isolated populations and these observable differences are the essence of the phylogenetic species concept (Barrowclough and Flesness 1966).

Value judgements will have to be made about which taxa, within a relatively closely related species group, demand conservation status and action, given the limited resources available (Barrowclough and Flesness 1966).

The combination of morphological, molecular and ecological data provide evidence for the recognition of *P. robustus* and *P. fuscicollis* (comprising *P. f. suahelicus* and *P. f. fuscicollis*) as phylogenetic species. *P. robustus* is a primary candidate for urgent and comprehensive conservation attention while the two subspecies of *P. fuscicollis* also require consideration.

Conclusion

Data are reviewed which provide compelling evidence and argument for the recognition of species rank for the Cape Parrot *P. robustus*. This is essential in preventing its illegal trade and for its conservation.

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(English only/ Unicamente en inglés/Seulement en anglais)

The Cape Parrot: an additional valid species

P.A. Clancey

The Cape Parrot *Poicephalus robustus* is currently viewed as the southern representative of a polytypic species with a disjunct austral range from the Alexandria district of the eastern Cape to Transkei, Natal and western Zululand, north to the eastern highlands of the Transvaal. With the widespread interest in biodiversity it has been seen that this section of the range warranted possible separation at species level from the populations occurring further north in Africa on both environmental and biogeographical grounds. Foremost, it is required to be noted that this southern form is confined to the temperate mid-level *Podocarpus* forest biome and is part of the endemic bird fauna peculiar to Cape Province and adjacent regions of South Africa, its range being tightly encompassed in the "Tall grassland (Middleveld)" habitat of Maclean (fig. 7, 1985). At present, the core of the range is confined to the Transkei, East Griqualand and high western Natal particularly in the Ingeli/Weza district, the species extending narrowly northwards to about Tzaneen in the eastern Transvaal, where decidedly sparse. A further distributional parameter is that there is a major break in the distribution between elements of the north-eastern Transvaal, where the *Podocarpus* stands of forest terminate and the savanna woodland, miombo birds commence, and are there to be found in the interior of southern Mozambique. These latter birds differ from nominate *robustus* on the basis of their greyish and densely blackish mottled heads, rather heavier and basally more massive and sharply pointed bills.

The southern differentiates, endemic to the *Podocarpus* ecosystem to the south of the Limpopo R. differ at the species level from the savanna woodland elements, taking over from them in the Limpopo R. northwards on both ecological and numerical grounds, the range of the latter extending from Angola in the west (north to about 5° S. in the estuary of the Zaire R.), and throughout the south of Zaïre south of the rainforest to the northern limits of Namibia, Zambia, western Tanzania, Malawi and locally in East Africa, locally north in the Interior Lakes region to Uganda. While the savanna woodlands birds are in the main concentrated in *Brachystegia* woodland they also occur in the mid-Zambezi region in stands of high mopane (*Colophospermum* sp.). Interestingly, they tend to occur in larger aggregations (generally in parties from 12-20 birds) than in the case of *robustus* itself. In the north of Sul do Save, a party of some 40 birds flew over our camp twice a day moving to and from their feeding grounds (at Vila Franca do Save during June and July, 1971).

An interesting situation occurs in the case of the present parrot species complex in that it is effectively split into two major groups by a dissimilar forest dwelling species - *Poicephalus guthriei*, which effectively polarises the forms in the *robustus* complex into two allied paraspecies in south, eastern and far West Africa (*robustus* in the sense pursued herein and in the case of *P. f. swahelicus*), and a far west African form *fuscicollis* to the west of the Dahomey Gap.

A population of the *robustus*-type is again to be found in far West Africa to the immediate west of the Dahomey Gap and is restricted to a discrete vegetational zone, being confined to the mangrove biome in the present instance.

Lake Kariba (IR); White-rumped Swift - 17 August, Birkdale Estate (IH); Fiery-necked Nightjar - 18 August, Chizarira NP (IR); Carmine Bee-eater - 21 August, Chizarira NP (IR); White-throated Swallow - 18 August, Lake Chivero (F&TC), Nyanga (JW); Red-breasted Swallow - 10 July, Harare-Bindura road and 13 July, near Harare (CB); 11 August, Cynara (AC), 17 August, Birkdale Estate (IH). There appear to be a few early arrivals of this species each year but the main arrival is still in August. Lesser Striped Swallow - 30 June, Birkdale Estate (IH); Capped Wheatear - 27 June, Birkdale Estate (IH), 29 June, north Harare (CB); Barratt's Warbler - 20 August, Nyanga (JW).

Observers

SA - S Alexander; CB - C Baker; F&TC - F&T Couto; AC - AB Curtis; TE - T English; IH - I Howland; PK - PR Kennett; IR - I Riddell; JW - J Williams; AW - AJ Wood.

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BLACK EAGLE BREEDING REPORT MATOBO NATIONAL PARK - 1996

The team consisting of members of the Matabeleland branch of the OAZ monitored the breeding of the Black Eagle *Aquila verreauxii* in the Matobo National Park and the surrounding farmlands to the north, under changing conditions of entry. After over thirty years of free entry to the Park, the team, since March, were liable for an entry fee and were restricted from some areas of the Game Park where eagle nests were situated. This obstacle was overcome due to the good offices of Ngoni Cheweshe, Game Scout, who himself monitored the nests N62/72 and N32A. From 1 November the entry fee has been exorbitantly increased to \$20 per person and \$50 per car (\$100 for a four-wheel drive vehicle). This year fortunately our research is more or less completed, but next year increased sponsorship will be necessary to meet these extra costs.

A much improved rainfall was recorded for 1995/96 averaging 807 mm; the Maleme station recorded the maximum of 930 mm and Hazelside (Park) the minimum of 660 mm. This was the best rainfall season since 1988 when the average was much the same at 816 mm. Maleme Dam overflowed at the beginning of February after having been reduced to an area of some 80 x 60 m (see 1995 report). Toghwana and Mtsheli were restored to their normal size and Madingazulu, Chitamba and Nsvatuke which were completely empty, filled the latter for the first time in several years. As a result of this rainfall the roads deteriorated and little work has been done to restore them for the use of ordinary cars. Mtsheli Valley road, with at least three active nests is a case in point. It is only accessible to four-wheel drive vehicles.

Some forty territories were visited during the year, of which 35 were considered occupied. Territories T79, 97A and 101 were unoccupied, although a new nest in the Communal Lands, some 5 km south of N79 was occupied perhaps by the 79 pair. This needs confirmation. N61, last occupied between the years 1963 and 1967 was rebuilt, it is assumed by the 13A pair, who have abandoned this nest due to disturbance by tourists leaving their commercial vehicles to climb to the nest. Pair 28A having successfully used N28A in 1994 returned to their old nest N28 in 1996, where they reared a young eagle. It was last used in 1978. There were 23 attempts at breeding of which 7 were considered failures, two at the chick stage (N29 and N55). Thus 16 young eagles were successfully reared of which 11 were seen fledged giving a productivity figure of 0.46 young per pair.

Full figures for the year are:

Number of sites observed	40
Number of territories occupied	35
Number of breeding attempts	23 (66%)
Number of known failures	7
Number of pairs successful	16
Productivity, young per pair	0.46

On the basis of the vegetational types tenanted by these parrots, (a) represents *robustus* of the *Podocarpus* woodlands of the south-east of South Africa, (b) *suaehelicus* the *Brachystegia* savanna woodland regions of Africa to the south and east of the evergreen forest biome, and (c) *fuscicollis* of far West Africa, confined to stands of mangroves. Uniquely, the *robustus* complex itself is replaced by *P. guilelmi* of the equatorial/raforest belt, which does not appear to be closely allied to the *robustus* coterie as such, and their precise relationship is unclear in present circumstances. This situation is almost unique, with some four or five valid races in *P. guilelmi*: *P.g. fantiensis*, *P.g. aubryanus* (doubtful) = nominate *P. guilelmi*, *P.g. pernisus* and *P.g. massaicus*, effectively sundering the birds in the *robustus/fuscicollis* assemblage as a whole.

The two austral forms of *robustus*-type parrots are distinguishable on the basis of the head-top and neck coloration, body plumage-colour and the nature of the bill. In *suaehelicus*, the head and entire breast are clear grey, mottled with black, while the body parts are a paler green and markedly less saturated than in the southern *robustus*. In *suaehelicus*, the bill is substantially heavier basally, with the apex of the bill longer and more tapered to a point, the culmen-length from the cere measuring some 39 - 46, versus 31.5 - 34 mm. In the case of males, these often have the head marked with dull red and juveniles frequently have the fore-part of the vertex strongly marked with bright rose pink, but a sufficiency of material is not readily available to work out possible levels of individual age-related variability in the present species with any degree of confidence.

In the west African *fuscicollis*, Grönvold's portrait of the adult male in Bannerman's *Birds of Tropical West Africa*, vol. ii, 1931, pl.15, show this form to have an entirely red vertex, the hind neck mottled both light and dark brown, the belly-colour much as in *suaehelicus*. The bill-length reaches its maximum size in this race, namely 39 - 46, with the wings 204 - 223, and the tarsus 20 - 23 mm. The female averages slightly smaller.

While there is no doubt that both *P. robustus* and *P. fuscicollis* make good sense as separate species, the evergreen forest form *P. guilelmi* likewise constitutes an equally valid species on both biogeographical and ecological grounds on a like gamut of criteria. In the revised arrangement of *fuscicollis* comprises two minor races: nominate *fuscicollis* and *P.f. suaehelicus*, remain as the two basic subspecies of the 'Cape Parrot', with *P. robustus* now standing on its own as a valid austral monotypic species.

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