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Original article

The reptiles of southeast Katanga, an overlooked 'hot spot'

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Abstract.—A review of the reptiles recorded from southeast Katanga Province in the Democratic Republic of Congo, employing the evolutionary species concept, indicates that there are at least 119 species in the area (7 chelonians, 37 lizards, 4 amphisbaenians, 69 snakes and 2 crocodilians), 15 of which are endemic (12.6 %). Analysis of zoogeographical affinities shows that this reptile fauna is derived from all directions, with forest forms entering from the north accounting for 14.4 % and savanna forms entering from the east contributing 22 %.

Key words.—Reptiles, Katanga, Upemba, Kundelungu, taxonomy, zoogeography.

Schouteden and de Witte collected herpetological material in Katanga during 1924-26 and 1930-31 (Witte 1933) and de Witte reviewed the reptiles of Katanga in his 1953 study of the reptiles of the Upemba National Park (P.N.U.), while Laurent (1950, 1955) described several new taxa from the Kundelungu plateau, which is still poorly known. No major collections have been made in this area subsequently. Some specimens from the P.N.U. (including paratypes of new taxa) were transferred to the Umtali Museum collection (now in the Natural History Museum of Zimbabwe in Bulawayo) in exchanges of material during 1965-6 and additional material was borrowed from Brussels and Tervuren for revisionary studies.

All surveys of Katanga's biodiversity have been sporadic and patchy. By far the greatest effort has been devoted to Upemba National Park and its environs. Nevertheless, despite these gaps in knowledge, the overall patterns of species richness, faunal affiliations and endemism exhibited by the reptiles are sufficient for us to make an up to date assessment of zoogeographic patterns, and to determine the factors that account for the evolution of this rich fauna. These patterns are complemented by other vertebrates (Cotterill in press a,b; submitted). Together, this combined knowledge of Katanga emphasizes the interesting evolutionary history of the region. We re-emphasize the importance and further scope for research and conservation of the biodiversity in Katanga.

STUDY AREA

Extent, Physiography, and Habitats.—The approximate limits of the area under consideration are the Lualaba valley in the west, the Luvua River in the north, Lake Mweru and the Luapula River in the east and the Congo-Zambezi watershed in the south (Fig. 1). The geomorphology of the area has been described by Dapper (1981) and the geology mapped by Aderca (1966). The principal formations are Precambrian quartzites, metamorphosed sediments, and sedimentary Karoo formations. Extensive shallow alluviums represent recent episodes of deposition in shallow lakes, notably in the Lufira, Lower Luapula and Lualaba valleys (Fig. 2).

Three main areas of relief dominate the physiography of Katanga in the southeast Congo basin. The largest are the Bia, Kibara and Kundelungu plateaux, bordered by deep ravines and wide depressions eroded by a northerly flowing drainage system. The high, flat plateaux, notably Kibara, rise to altitudes over 1890 m above the Upemba swamps and floodplains. The latter lie at approximately 680m asl (Witte 1966; Dapper 1981). The hills, mountains and ravines and steep margins of the plateaux provide rocky habitats for rupicolous reptiles, especially along fault scarps.

This high physiographic diversity is expressed in a correspondingly rich flora. The Upemba-Kundelungu area lies in the Katanga-Bemba region, the northern subregion of the Zambezian Phytochorion as defined by Malaisse (1997). In addition to its many endemic plants, the flora is enriched by both Guineo-Congolian and Zambezian elements (White & Werger 1978). This diverse flora is represented in a corresponding variety of vegetation. It is principally mesic miombo savanna, but there are also important patches of forest, savanna woodlands, and alluvial and plateau grasslands. The diversity of forest patches varies from riparian and flooded to montane (Witte 1966; Lubini 1994a,b). Centred on these plateaux, this southeast corner of the Congo basin has an especially high endemism of savanna plant species (Colyn 1991; Linder 2001). Furthermore, species richness of plants is the highest in the miombo ecoregion; and Katanga lies within a centre of high species richness (> 3000 species) of the Afrotropical flora (Malaisse 1997; Burgess *et al*. 2004). The evergreen gallery forests (mushitu) confined along wetlands often grow within and are bordered by dambos. Mushitu are present across large gradients in altitude, from valley floors to tops of ravines abutting the highest plateaux (Witte 1966; Malaisse 1997).

The high flat plateaux are major landforms in Katanga. Their greater extents are covered with dilungu, shallow layers of fine loose sands. They have been reworked from Kalahari sands of Neogene and Plio-Pleistocene age. The finer structure of the landforms within dilungu comprises a varied and extensive micro-relief, which vary across a range of spatial and temporal scales. The largest are of fossil aeolian origin (probably Late Pleistocene), and more recent micro-topography of shallow dune ridges and pans. Dilungu support a vegetation of short grasses and fruit-bearing shrubs (including *Parinari capensis* spp. *latifolia*, and *Syzygium guineense* spp. *huillense* (Dapper 1988). These sandy habitats appear to be important for small vertebrates, including the herpetofauna and certain small mammals and birds. The most extensive dilingu cover the Kundelungu and Kibara plateaux, with much smaller patches on hilltops in the southwest, where they reach their southern limit at Kalene Hill in the Ikelenge Pedicle of northwest Zambia (Fig. 1).

The variety of wetlands in Katanga equals that of terrestrial habitats. This complexity includes upland ravines and streams, large rivers, both sedate and fast flowing, and huge swamps in

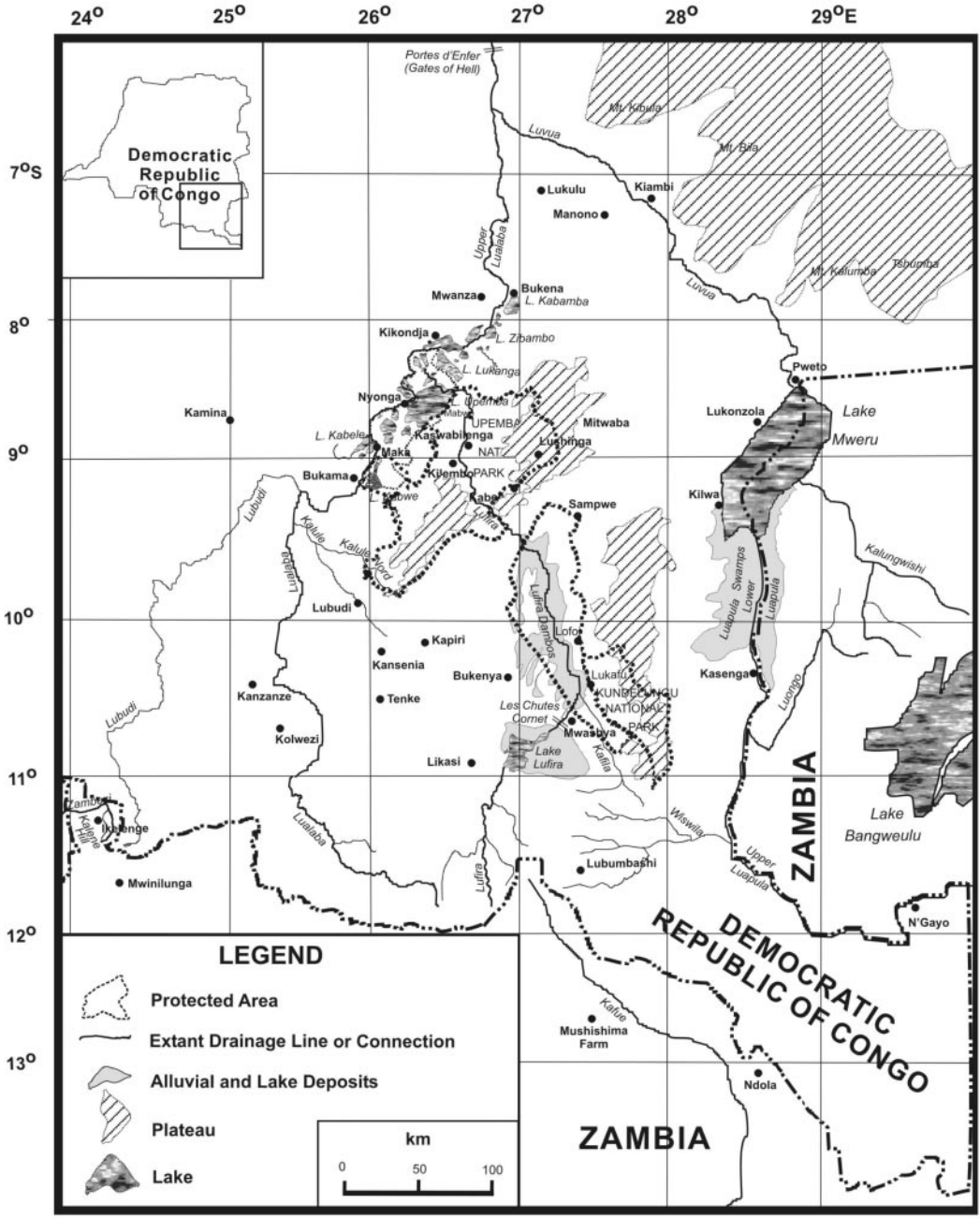

Figure 1. Protected areas and principal land forms in Katanga, Democratic Republic of Congo (DRC). Localities mentioned in the text are shown.

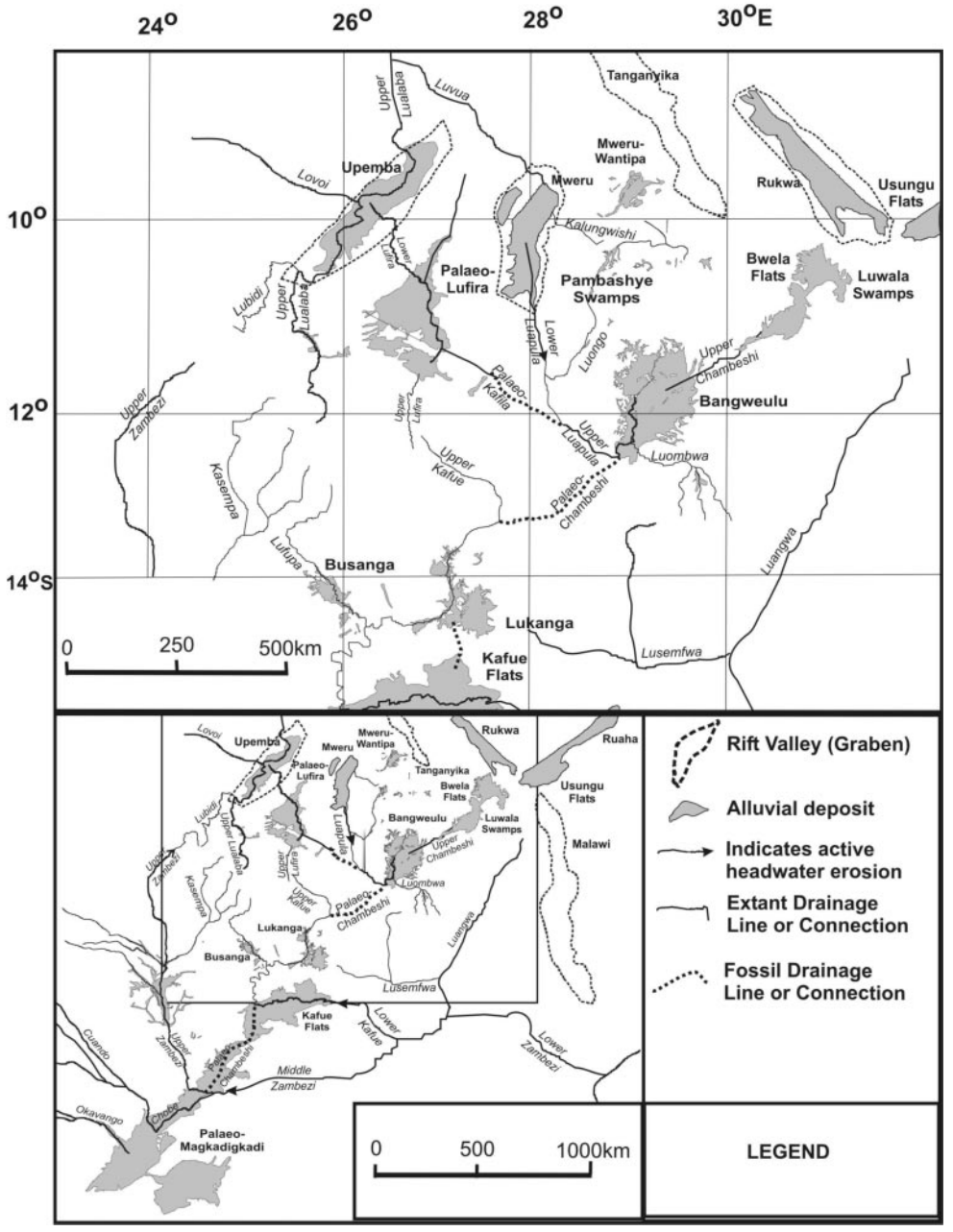

Figure 2. Map of south-central Africa depicting deposits of recent alluvium in the context of modern drainage systems. As explained in detail by Cotterill (2003), the original headwaters of the Palaeo-Chambeshi River were the modern Chambeshi River; when this drainage system terminated in Palaeo-Lake Makgadikgadi in the Kalahari basin. The proposed link between the Palaeo-Chambeshi and Upemba was across Palaeo-Lake Lufira through the channel of the Palaeo-Kafila River. The arrowheads depict predatory headwaters of the Luapula, and mid-Zambezi Rivers that broke up the Palaeo-Chambeshi in the vicinity of southeast Bangweulu, Kafue Flats and Victoria Falls. (Modified from Cotterill in press a)

and around large shallow lakes. Saline and thermal springs also occur. Dambos are important, which although individually of small area, collectively cover a vast area along tributaries and at their headwaters. Three of Africa's largest wetlands have formed in Katanga. These include Lake Mweru (and the associated Luapula Swamps to its south), Lake Lufira (and its associated mosaic of dambos downstream) along the upper Lufira River, and Upemba Swamps in the Kamalondo depression (Malaisse 1997). The latter is a large mosaic of exhoreic deflation lakes situated within extensive swamps of *Phragmites* and *Papyrus*, surrounded in turn by floodplains (Banister & Bailey 1979).

Both Mweru and Upemba lie in rift valleys - fed by the Luapula and Upper Lualaba rivers respectively (Dapper 1981, Fig. 1). Lake Mweru is shallow (average depth 10 m). Its levels appear to have fluctuated greatly in recent geological times; as indicated by extensive recent alluvium to its south that nearly equals the area of the modern lake. Mweru's major tributary, the Luapula River, drains the Bangweulu wetlands, which in turn are fed by the Chambeshi. In contrast to the valleys, cool, fast flowing streams drain the plateaux, fractured by many rapids and waterfalls (Witte 1966; Banister & Bailey 1979). The 342 m drop of the Loloi Falls, flowing into the Lufira depression off the western Kundulungu, is one of the highest in Africa (Demey & Louette 2001). The wetlands of Katanga form a distinct ichthyofaunal subprovince within the overall Congo basin, separated at the Portes d'Enfer (Gates of Hell) from the lower Congo River (Fig. 1). Its ichthyofaunal affinities are a mixture of Congolian and Zambezian species with a significant proportion of endemics (Teugels & Guégan 1994; Malaisse 1997).

Protected Areas and Conservation.—The conservation significance of Katanga's landscapes was noted early in the 20th century (Sharp 1956), decades before protected areas were proclaimed. The first to be declared a protected area was Upemba National Park (P.N.U.) in 1939 (Symoens 1963); and its boundaries were later extended to include the lakes and associated wetlands along the Lualaba. Kundelungu was only proclaimed in 1970, and is also complemented by a large annex to its north and west (Demey & Louette 2001, Fig. 1). The integrity and future of Katanga's protected areas (especially P.N.U.) has recently precipitated grave concern. Large mammal populations were decimated by commercial poaching in the 1980s (Wolanksi 1998; Hasson & Wolanski 1999). Fund raising and support by the conservation NGO Nouvelle Approaches has alleviated some problems in Kundelungu and Upemba, but much work remains (Wolanski 1998; Hasson & Wolanski 1999, http://www.nouvellesapproches.org).

ANNOTATED CHECKLIST OF THE REPTILES OF SOUTHEAST KATANGA

ORDER TESTUDINES
Family PELOMEDUSIDAE

Pelomedusa subrufa (Bonnaterre 1789).—The Helmeted Terrapin is found throughout the dry savannas of sub-Saharan Africa, but is absent from the Kibara plateau in the east of the P.N.U. (Witte 1953).

Pelusios gabonensis (Duméril 1856).—The Forest Hinged Terrapin has a wide distribution in the Congo basin and was recorded from Nyonga on the western shore of Lake Upemba in 1925 (Witte 1933).

Pelusios nanus Laurent 1956.—The Dwarf Hinged Terrapin occurs from central Angola along the Congo-Zambezi watershed into northern Zambia along the Chambeshi River (Broadley 1981). It has been recorded from Kanzenze and Lubumbashi (Witte 1953 [as *P.*

subniger]; Laurent 1956), but not yet from the P.N.U.

Pelusios subniger (Bonnaterre 1789).—The Pan Hinged Terrapin has a wide range in southeastern Africa and Madagascar, extending west to the Okavango delta and Katanga and north to Burundi (Bour 1983). It has been recorded from Kikondja on Lake Kisale and Kando, near Tenke (Witte 1933 [as *Sternothaerus derbianus*]).

Pelusios upembae Broadley 1981.—The Upemba Hinged Terrapin is endemic to the swamps in the Kamalondo basin, where it is sympatric with *P. subniger* and *P. rhodesianus*. It is the sister species of *P. bechuanicus* FitzSimons of the Okavango delta, upper Zambezi and central Angola (Broadley 1981).

Pelusios rhodesianus Hewitt 1927.—Described from southeast of Lake Bangweulu, the Zambian Hinged Terrapin has a wide range in central Africa, with relict populations in eastern South Africa (Broadley 1981; Bour 1983). Some specimens were collected on the Kundelungu Plateau. Many specimens from southeast Katanga in the Tervuren collection have been examined, but all the P.N.U. material listed by Witte (1953) as *P. subniger* needs to be sorted, as it includes all four species listed above.

Family TESTUDINIDAE

Kinixys spekii Gray 1863.—Speke's Hinged Tortoise has a wide range on the central plateau from Kenya to South Africa and west to Katanga (Broadley 1993). It appears to be replaced by *K. belliana* Gray further west in the D.R.C. and Angola. In the P.N.U. it occurs at lower altitudes, but was not found on the Kibara plateau (Witte 1953 [as *K. b. belliana*]).

ORDER SAURIA
Family AGAMIDAE

Acanthocercus atricollis (A. Smith 1849).—The Southern Tree Agama has a wide range in east and central Africa and is common in the P.N.U. and environs (Witte 1953).

Agama armata Peters 1854.—The Tropical Spiny Agama has a wide range in east and central Africa. It occurs throughout Katanga and in the P.N.U. it is mainly found on the Kibara plateau at 1300 to 1800 m (Witte 1953 [as *A. hispida aculeata*]).

Family CHAMAELEONIDAE

Chamaeleo gracilis Hallowell 1842.—This savanna species has an enormous range in west and central Africa and is found throughout the P.N.U. (Witte 1953).

Chamaeleo dilepis Leach 1819.—The Flap-necked Chameleon has a wide range in the savannas of east and central Africa and is common throughout the P.N.U. at lower altitudes (Witte 1953, who also listed *C. quilensis* Bocage, considering it a distinct species).

Chamaeleo anchietae Bocage 1872.—This terrestrial chameleon has a discontinuous distribution in montane grasslands from southwestern Angola to southwestern Tanzania. The synonym *C. a. vinckei* Laurent was described from the Kundelungu plateau and is common on the Kibara plateau in the P.N.U. (Witte 1953).

Family GEKKONIDAE

Pachydactylus (*Elasmodactylus*) *tuberculosus* (Boulenger 1894).—The Tuberculate Thick-toed Gecko ranges through savannas of central Africa from northeast Tanzania to the lower Congo region. In the P.N.U. and environs it is common below an altitude of 1000 m (Witte 1953). The synonym *Elasmodactylus triedus*

Boulenger was described from Kikondja in the Upemba rift.

Pachydactylus katanganus Witte 1953.—This small gecko is endemic to the P.N.U., where it occurs from Mabwe (585 m) to Lusinga at 1810 m on the eastern boundary of the park (Witte 1953). It was described as a subspecies of *P. capensis*, then placed as a northern race of *P. oshaughnessyi* (Broadley 1977b) and recently recognised as an evolutionary species (Broadley 2003).

Pachydactylus punctatus Peters 1854.—Although the Speckled Thick-toed Gecko ranges from Mozambique west to Namibia, there are few records north of the Zambezi. It is common in the P.N.U. below 1300 m (Witte 1953), but this population is well isolated from the nearest records in northern Malawi and southern Zambia (Broadley 2003).

Lygodactylus heeneni Witte 1933.—This rare arboreal dwarf gecko was described from Kapiri to the south of the P.N.U., and is almost endemic to southeast Katanga, but it has also been recorded from the northern Mwinilunga District in Zambia (Broadley 1991b). In the P.N.U. it only occurs on the Kibara plateau between 700 and 1750 m (Witte 1953). This form was described as a subspecies of *L. angularis* Günther, common on buildings on the Zambian copperbelt, but there is no indication of intergradation in throat pattern and they are best regarded as sister species.

Lygodactylus angolensis Bocage 1896.—The Angolan Dwarf Gecko has a wide range in south-central Africa from Angola to central Tanzania. It is common in the P.N.U. except on the Kibara plateau (Witte 1953).

Lygodactylus gutturalis (Bocage 1873).—This is the most widely distributed savanna species in the *L. picturatus* complex, ranging from Senegal east to the Sudan and south via the Albertine Rift to the P.N.U., which is its southern limit (Pasteur 1964). It does not occur on the Kibara plateau (Witte 1953).

Hemidactylus mabouia (Jonnès 1818).—The Tropical House Gecko seems to have originated in East Africa, but is rapidly expanding its distribution westwards and southwards due to accidental translocation by man. It is uncommon in the P.N.U. and was not found on the Kibara plateau (Witte 1953).

Family SCINCIDAE
Subfamily SCINCINAE

Sepsina hemptinnei Witte 1933.—This fossorial skink is widespread in Katanga and has been recorded from near Ujiji on the eastern side of Lake Tanganyika (Loveridge 1942). The species was described from the Kundelungu plateau and is found throughout the P.N.U. It was placed as a subspecies of *S. tetradactyla* Peters by Loveridge (1942), but it is a more gracile form with more rudimentary digits and a bronze rather than bluish tail.

Subfamily LYGOSOMINAE

The Afro-Malagasy skinks, formerly included in the New World genus *Mabuya* Fitzinger, are now correctly assigned to the revived genus *Trachylepis* Fitzinger (Bauer 2003).

Trachylepis maculilabris (Gray 1845).—The Speckle-lipped Skink has a wide range in forest and savanna through west, central and east Africa as far south as central Mozambique. It is common throughout the P.N.U. (Witte 1953).

Trachylepis upembae Witte 1953.—This skink is endemic to the P.N.U. It was described as a subspecies of *T. perroteti* (Duméril & Bibron) of the Sudanese savanna, distinguished by a higher number of midbody scale rows (32-36) and colour pattern. In fact *T. upembae* agrees with *T. perroteti* in the former character, but seems to be more closely related to *T. plani-*

frons (Peters) of East Africa, which occurs at Nyamkolo at the southern end of Lake Tanganyika (Loveridge 1933, 1957) and has 26-32 midbody scale rows. *Trachylepis perroteti* is a large robust skink with a relatively short tail (ca.160 to 180% of snout-vent length). *Trachylepis planifrons* is a more slender species with a long tail (ca 180 to 240% of SVL). *Trachylepis upembae* (two paratypes examined) is intermediate in build, but agrees with *T. perroteti* in tail length; its colour pattern differs from both.

Trachylepis pulcherrima Witte 1953.—This large rupicolous skink is endemic to the P.N.U. It was described as a subspecies of *T. quinquetaeniata* (Lichtenstein), but was recognised as a full species by Broadley & Bauer (1998).

Trachylepis megalura (Peters 1878).—The slender smooth-scaled Grass-top Skink ranges from Ethiopia south to central Mozambique and west to the Albertine rift. In the P.N.U., it occurs on the Kibara plateau above 1300 m (Witte 1953).

Trachylepis varia (Peters 1878).—The Variable Skink ranges from the Sudan to South Africa and west to Namibia. It is common throughout the P.N.U. and environs (Witte 1953).

Trachylepis striata (Peters 1844).—The Striped Skink ranges from Ethiopia to South Africa and west through northern Zambia to the P.N.U., where it is common throughout (Witte 1953).

Lygosoma afrum (Peters 1854).—The Mozambique Writhing Skink has a wide range from the Sudan to central Mozambique (Broadley 1966a), and extends west through northern Zambia to the P.N.U., where it occurs on the edge of the Kibara plateau (Witte 1953 [as *Riopa sundevalli*]).

Eumecia anchietae Bocage 1870.—Anchieta's Serpentiform Skink with reduced digits has an extensive range from southwest Angola through Zambia and the D.R.C. to western Kenya and Tanzania. It occurs throughout the P.N.U., but is more common on the Kibara plateau (Witte 1953).

Leptosiaphos dewittei (Loveridge 1934).—This slender skink ranges from western Angola to the P.N.U., where it occurs throughout, but is more common in the plateau areas. It is a sister species of *L. kilimensis* Stejneger of Kenya and Tanzania, Witte (1953) regarded it as a synonym (Broadley 1989).

Panaspis seydeli (Witte 1933).—Seydel's Snake-eyed Skink is only known from four specimens, which have the prefrontals in broad contact: the type of *P. seydeli* from Lubumbashi, the type of *Ablepharus moeruensis* (Witte) from Kilwa on Lake Mweru, the type of *A. anselli* FitzSimons from Kasempa, northwest Zambia, and BMNH 1940.1.19.34 from Mwenzo, northeast Zambia. Fuhn (1964, 1970) placed *A. anselli* in the synonymy of *Ablepharus tancredii* Boulenger of Ethiopia (known only from the type) and consequently all three southern taxa were provisionally assigned to *P. tancredii* by Jacobsen & Broadley (2000), but on zoogeographical grounds it seems better to separate them from *P. tancredii* under the earliest name. There is some variation; the type of *A. moeruensis* has three supraoculars instead of two and five labials anterior to the subocular instead of four. The Mwenzo specimen agrees with the type of *P. seydeli* in having 20 midbody scale rows, the others have 22.

Panaspis smithii (Witte 1936).—The Upemba Snake-eyed Skink is probably endemic to the P.N.U. and environs at low altitudes (Witte 1953). It is readily distinguished from *P. seydeli* by having the prefrontals separated or meeting at a point and having 24-26 midbody

scale rows. It also resembles *P. wahlbergii* in having white lateral stripes. In his list of material, Witte (1936) included MRAC 6774 from Lodja, in northern Kasai province 600 km northwest of the P.N.U., but in view of the wide gap, this specimen should be re-examined.

Panaspis wahlbergii (A. Smith 1849).—Wahlberg's Snake-eyed Skink is distinguished from the previous two by having the frontoparietals fused. It has a wide range in savannas from Ethiopia south to South Africa (Jacobsen & Broadley 2000) and reaches its western limits in the P.N.U., where it is common throughout (Witte 1953).

Subfamily FEYLININAE

Feylinia currori Gray 1845.—The Forest Limbless Skink ranges from Cameroon through the Congo basin to its southeastern limit in the P.N.U. (Brygoo & Roux-Estève 1983), where it occurs below 1300 m (Witte 1953).

Family CORDYLIDAE

Cordylus tropidosternum (Cope 1869).—The Tropical Girdled Lizard ranges from southeastern Kenya south to central Mozambique, west through northern Zambia to the P.N.U. (Broadley & Branch 2002). It is common on the Kibara plateau, but rare at lower altitudes, and is usually found in rocky places (Witte 1953).

Chamaesaura miopropus Boulenger 1894.—The Zambian Snake Lizard inhabits grasslands from Angola east to northern Malawi and southern Tanzania. The only records from the D.R.C. are from Pweto on Lake Mweru and the P.N.U., where it is only found on the Kibara plateau (Witte 1953). Although it has previously been treated as a subspecies of *C. macrolepis*, which lacks forelimbs (Broadley 1971d), the latter does not occur north of the Chimanimani Mountains in eastern Zimbabwe.

Family GERRHOSAURIDAE

Gerrhosaurus nigrolineatus Hallowell 1857.—The taxonomy of the Black-lined Plated Lizard is still in a state of flux, but it has a wide range in south-central Africa from coast to coast. It is found throughout the P.N.U., but is less common on the Kibara plateau than at lower altitudes (Witte 1953).

Gerrhosaurus bulsi Laurent 1954.—This large grey plated lizard ranges from northeast Angola through northwest Zambia (*G. nigrolineatus anselli* Broadley is a synonym) to southern Katanga. In the P.N.U. it is sympatric with *G. nigrolineatus* at lower altitudes (Witte 1953 [as *G. auritus*]). This species can be distinguished from both *G. nigrolineatus* and *G. auritus* by its strongly spinose proximal supracaudal scales. It has been erroneously treated as a synonym of the poorly known *G. multilineatus* Bocage of western Angola (Broadley 1971d). The status of the latter is still under investigation.

Tetradactylus ellenbergeri (Angel 1922).—The Zambian Whip Lizard ranges from eastern Angola through Zambia and southern Katanga to southeastern Tanzania. *Tetradactylus boulengeri* Witte (type locality: Kansenia) and *T. fitzsimonsi* simplex Laurent (type locality: Kundelungu) are considered synonyms (Broadley 1971d). The four specimens from the P.N.U. were all collected on the Kibara plateau at an altitude of 1750 m (Witte 1953 [as *T. fitzsimonsi boulengeri*]).

Family LACERTIDAE

Adolfus africanus (Boulenger 1906).—The Multi-scaled Forest Lizard ranges through central Africa from Cameroon to northwestern Zambia (Broadley 1991b) and Katanga. The specimens from the P.N.U. were collected at altitudes between 950 and 1750 m (Witte 1953).

Holaspis laevis Werner 1895.—The Eastern Serrate-toed Tree Lizard inhabits coastal forests and miombo woodland from northeast Tanzania south to central Mozambique (Broadley 2000). There are no records from Zambia, but it is recorded from Lubumbashi (Bourgeois 1964) and in the P.N.U. at altitudes between 890 and 1140 m (Witte 1953 [as *H. guentheri*]). The sister species *H. guentheri* ranges from Sierra Leone through the northern D.R.C. to Uganda and south to northeastern Angola (Laurent 1964).

Ichnotropis bivittata Bocage 1866.—The Angolan Rough-scaled Lizard ranges from Angola east through southern Katanga, northern Zambia and northern Malawi to southern Tanzania. In the P.N.U. it inhabits the Kibara plateau (Witte 1953).

Ichnotropis capensis (A. Smith 1838).—The Cape Rough-scaled Lizard has a wide range in south-central Africa. In the P.N.U. it occurs at low altitudes, 585 - 1050 m (Witte 1953 [as *I. longipes* Boulenger, a synonym]).

Family VARANIDAE

Varanus albigularis angolensis Schmidt 1933.—This subspecies inhabits Angola, northern Zambia and southern Katanga. In the P.N.U. it is common at low altitudes, but does not occur on the Kibara plateau (Witte 1953).

Varanus niloticus (Linnaeus 1766).—The Nile Monitor occurs throughout savannas of sub-Saharan Africa. In the P.N.U. it was not found above 1000 m (Witte 1953).

SUBORDER AMPHISBAENIA
Family AMPHISBAENIDAE

Zygaspis quadrifrons (Peters 1862).—The Kalahari Round-headed Worm Lizard has a huge range in southern Africa centred on the Kalahari, reaching the northern limits of its range along a line extending from the P.N.U. east to the Mweru Wantipa in northern Zambia (Broadley & Broadley 1997). In the P.N.U. this species is very common at low altitudes, but is not found on the Kibara plateau (Witte 1953 [as *Amphisbaenia quadrifrons capensis* Thominot, also including *A. q. katangae* Witte & Laurent, both are synonyms]).

Monopeltis remaclei Witte 1933.—This large spade-snouted amphisbaenian was described from Lukulu, just south of the Lualaba-Luvua confluence. It is otherwise only known from Kabalo, 80 km downstream from the confluence, and Nyunza 120 km east of Kabalo. It has not yet been found in the P.N.U.

Monopeltis adercae Witte 1953.—This large species was described from Bukena on the Luapula River just north of the P.N.U. and was subsequently recorded from Mamono, 80 km to the northeast (Broadley *et al*. 1976), so it is endemic to the area under consideration.

Monopeltis scalper (Günther 1876).—This moderate-sized species is endemic to Katanga, as the type localities for *M. scalper* (Kilembo) and its synonym *M. gerardi* Boulenger (Kikondja) are in the Upemba rift, and *M. scalper bulsi* Laurent (Kamina) on the western rim (Broadley *et al*. 1976). The specimens from the P.N.U. were taken between 585 and 890 m (Witte 1953).

SUBORDER SERPENTES
Family TYPHLOPIDAE

Rhinotyphlops angolensis (Bocage 1866).—The Angolan Blind Snake occurs in both forest and savanna from Cameroon south through the Congo basin to northern Angola, apparently reaching its southeastern limit at Kasenga on the Luapula River south of Lake Mweru (Roux-Estève 1974). The Zambian specimens that she recorded from Abercorn (= Mbala) are more likely to have been collected by H.J. Bredo in the Mweru Wantipa on the border of

Katanga. This species and the next two were transferred from *Typhlops* to *Rhinotyphlops* by Broadley & Wallach (2000).

Rhinotyphlops lineolatus (Jan 1864).—The Lineolate Blind Snake has a wide distribution through the savannas of sub-Saharan Africa from Senegal east to Kenya and Tanzania and south to northern Angola and Katanga (Roux-Estève 1974). The specimens from the P.N.U. were taken at altitudes between 1140 and 1700 m (Witte 1953 [as *T. punctatus* (Leach)]).

Rhinotyphlops schmidti (Laurent 1956).—This species has a wide range in Katanga, extending into northeast Angola (Laurent 1964) and northern Zambia (Broadley 1971d). Some of the specimens from the P.N.U. assigned to *Typhlops p. punctatus* by Witte (1953) are referable to *R. schmidti* (Laurent 1956). Roux-Estève (1974) placed *R. schmidti* (midbody scale rows 22-26) in the synonymy of *R. lineolatus* (m.s.r. 28 - 32, rarely 26); the two species may be sympatric (Laurent 1956).

Rhinotyphlops mucruso (Peters 1854).—The Zambezi Blind Snake is the largest in the world (maximum length 950 mm), ranging from coastal Kenya south to Zimbabwe and central Mozambique and west through the southern provinces of the D.R.C. to northeast Angola (Roux-Estève 1974 [as *R. schlegelii dinga*]). In the P.N.U. it does not seem to occur above an altitude of 1300 m (Witte 1953).

Rhinotyphlops (*Letheobia*) *gracilis* (Sternfeld 1910).—The Gracile Blind Snake has a restricted range extending from Kitungulu in southwest Tanzania (type locality) through northern Zambia to Katanga east of the Luapula River (Roux-Estève 1974). Witte (1953) assigned his material to *Typhlops leptosoma* Witte 1933, a synonym described from Lukafu at the foot of the Kundelungu plateau, while another synonym, *Typhlops katangensis* Witte, had been described from Lukonzolwa on Lake Mweru. The genus *Letheobia* Cope will be revived for the slender blind species included in the *Rhinotyphlops* Group VI of Roux-Estève (1974) (Broadley & Wallach, in prep.).

Rhinotyphlops (*Letheobia*) *kibarae* (Witte 1953).—This species is endemic to the P.N.U., but one of the paratypes from Kaswabilenga (type locality) at 700 m is actually a *R. gracilis*, establishing sympatry between these two species (Roux-Estève 1974). One paratype is from the Pelenge gorge (1250 m).

Family LEPTOTYPHLOPIDAE

Leptotyphlops kafubi (Boulenger 1919).—The Katanga Worm Snake was described from Lubumbashi and has a limited range in southern Katanga, extending into northwestern Zambia (Broadley & Broadley 1999). In the P.N.U. it is common below 1000 m, but does not occur on the Kibara plateau (Witte 1953 [as *L. emini emini* Boulenger of East Africa]).

Family PYTHONIDAE

Python natalensis A. Smith 1840.—The Southern African Python ranges across south-central Africa from Angola southeast to South Africa and north to the southeastern D.R.C., Burundi, Tanzania and the Kenya highlands (Broadley 1984). In the P.N.U. it was not encountered on the Kibara plateau (Witte 1953 [as *P. sebae*]), but Laurent (1956) recorded a specimen from the Kundelungu plateau at 1750 m [as *P. sebae*]. This taxon was originally revived as a subspecies of the Northern African Python *P. sebae* (Gmelin), but was reinstated as a full species when it became evident that the two forms overlapped in distribution by 900 km (Broadley 1999).

Family VIPERIDAE
Subfamily CAUSINAE

Causus lichtensteinii (Jan 1859).—Although the Forest Night Adder has not yet been record-

ed from the P.N.U., there are specimens from Lubumbashi and Kiambi on the Luvua River (Witte 1953). To the southwest it has been recorded from Ikelenge in northwest Zambia (Broadley 1991b).

Causus bilineatus Boulenger 1905.—The Lined Night Adder inhabits plateau areas of Angola and northwest Zambia, but occurs at lower altitudes in Katanga. Laurent (1956) described *C. Iineatus* from the Kundelungu plateau and also recorded it from Rwanda. Subsequently this was treated as a dwarfed subspecies of *Causus bilineatus* with lower ventral counts (Laurent 1964), but these differ little from those of the type series from "Benguela to Bihe", Angola.

Causus rhombeatus (Lichtenstein 1823).—The Rhombic Night Adder has an extensive range in moist savannas of south, central and east Africa, extending as far west as eastern Nigeria (Hughes 1978). It is common throughout the P.N.U.

Subfamily VIPERINAE

Bitis arietans arietans (Merrem 1820).—The Puff Adder occurs throughout the savannas of sub-Saharan Africa and is found in all parts of the P.N.U. (Witte 1953 [as *B. lachesis lachesis*]).

Bitis gabonica (Duméril & Bibron).—The Gaboon Viper is found in areas of forest-savanna mosaic throughout central and southeast. It is found throughout the P.N.U. up to an altitude of 1810 m at Lusinga (Witte 1953).

Atheris katangensis Witte 1953.—The Upemba Bush Viper is endemic to the P.N.U., where it was collected at altitudes between 1250 and 1480 m (Witte 1953). It appears to be related to *A. rungweensis*, which occurs 400 km to the east in northeastern Zambia (Broadley 1998).

Family ATRACTASPIDIDAE

Atractaspis leleupi Laurent 1950.—This stiletto snake seems to be endemic to the Kundelungu plateau at 1750 m and is only known from two specimens. These differ from the western *A. congica* Peters [Angola to Cameroon, east to western Katanga (below 1000 m) and northern Zambia (1300 m at Mbala) - Broadley 1971d, 1991b] by having 17 midbody scale rows instead of 19-21, so they do not fit into a cline.

Atractaspis bibronii A. Smith 1849.—Bibron's Stiletto Snake has a wide range in savannas of East Africa from Somalia to South Africa, west to eastern Katanga, Angola and Namibia (Broadley 1991a). In the P.N.U., which is on the northwestern periphery of the species range, this species was not found above 1300 m (Witte 1953).

Amblyodipsas polylepis (Bocage 1873).—The Common Purple-glossed Snake ranges from coastal Kenya to South Africa, west to Angola and northern Namibia (Broadley 1971b). The two specimens from the P.N.U. (the northwestern limit of the species range in the D.R.C.) came from below 1000 m (Witte 1953).

Amblyodipsas rodhaini Witte 1930.—This species is only known from four specimens, the only precise localities being Kikondja, 35 km north of Lake Upemba, and Kamina on the western edge of the Upemba rift valley. The latter is type locality of *Calamelaps ventrimaculatus katangensis* Witte 1951, which seems to be a juvenile of *A. rodhaini* (Broadley 1971b). This snake may be endemic to Katanga.

Amblyodipsas katangensis Witte & Laurent 1942.—This small species is only known from five specimens. The type series came from N'Gayu at the eastern end of the pedicle south of Lake Bangweulu. Witte collected two more at Mabwe on the eastern margin of Lake

Upemba (585 m) and there is one Zambian specimen from 14 km northwest of Ndola (Broadley 1971b), so the species is a near-endemic for Katanga. *Amblyodipsas katangensis ionidesi* Loveridge of southeast Tanzania should probably be regarded as a sister species.

Xenocalamus michelli L. Müller 1911.—This large quill-snout is only known from three specimens, one of which came from Bukena in the rift valley just north of the P.N.U. (Witte 1953). Laurent (1956) recorded another from Nyunzu, 240 km to the northeast.

Chilorhinophis gerardi (Boulenger 1913).—Gerard's Striped Burrowing Snake is found from Katanga south through Zambia to northern Zimbabwe. In the P.N.U. it was not found above 1300 m (Witte 1953).

Polemon christyi (Boulenger 1903).—Christy's Snake-eater is found from eastern D.R.C. and northern Zambia east to Uganda and western Tanzania. The P.N.U. specimens were taken between 1300 and 1810 m (Witte 1953 [as *Miodon christyi*]).

Hypoptophis wilsoni Boulenger 1908.—The rare Wedge-snouted Burrowing Snake occurs from Sankuru in the Congo basin south to Katanga and western Zambia (Broadley 1971b). In the P.N.U. it was only found below 900 m (Witte 1953).

Aparallactus moeruensis Witte & Laurent 1943.—This large centipede-eater is endemic to southeast Katanga. The type locality is Pweto on Lake Mweru and 11 specimens were collected in the P.N.U. below 900 m (Witte 1953).

Aparallactus capensis A. Smith 1849.—The Cape Centipede-eater ranges from Tanzania south to South Africa and west through Zambia and Katanga to Angola. It is found throughout the P.N.U. (Witte 1953 [as *A. c. punctatolineatus* Boulenger, a synonym]).

Family ELAPIDAE

Elapsoidea guentheri Bocage 1866.—Guenther's Garter Snake ranges from the lower Congo, south to Angola and east to Katanga, western Zambia and Zimbabwe (Broadley 1971a). In the P.N.U. it was not found above 1140 m (Witte 1953 [as *E. semiannulata semiannulata*]).

Boulengerina annulata stormsi Dollo 1886.—This water cobra was considered endemic to Lake Tanganyika, but there is a single record from Pweto on Lake Mweru (Witte 1953).

Naja anchietae Bocage 1879.—Anchieta's Cobra ranges from Angola and northern Namibia to northwestern Zimbabwe and western Zambia, reaching its eastern limit at Lake Bangweulu (Broadley & Wüster, in review). One specimen has been recorded from the Katanga pedicle south of the lake (Witte 1953 [as *N. haje anchietae*]).

Naja melanoleuca Hallowell 1857.—The Forest Cobra (or species complex) has a huge range in both forest and savanna through west, central and east Africa. In the P.N.U. it does not seem to occur above 900 m (Witte 1953).

Naja crawshayi Günther 1893.—This big spitting cobra is a sister species of *Naja nigricollis* Reinhardt. It occurs south of the Congo Basin, from Congo-Brazzaville, southern D.R.C., Angola, western and northern Zambia through northern Malawi to Tanzania (Broadley & Wüster, in prep.). It was described from Lake Mweru and is found throughout the P.N.U. (Witte 1953).

Naja mossambica Peters.—The Mozambique Spitting Cobra has a wide range from Tanzania south to South Africa and west to northern

Namibia. There is a relict population in the D.R.C. pedicle southwest of Lake Bangweulu, represented by a pair of specimens in Tervuren (Laurent 1956, pl. xxviii, fig. 1).

Dendroaspis polylepis (Günther 1864).—The Black Mamba has an enormous range throughout the savannas of sub-Saharan Africa. In the P.N.U. it was not found on the Kibara plateau, only below 1000 m (Witte 1953 [as *D. angusticeps*]). *Dendroaspis jamesoni* (Traill), a forest species, occurs at Kamina on the western periphery of the area under consideration, so may eventually be found in the P.N.U.

Family COLUBRIDAE
Subfamily LAMPROPHIINAE

Lycodonomorphus upembae Laurent 1954.—The Upemba Water Snake is endemic to Katanga, and was described from Nyonga on the western side of Lake Upemba. De Witte collected 20 specimens there in 1925 (Witte 1933 [as *Boodon lineatus* Duméril & Bibron]), but he did not get any from the eastern edge of the swamps during 1946-49. It was described as a subspecies of *L. subtaeniatus* Laurent, of the western D.R.C. and northeast Angola, but it is more robust and has lower ventral and subcaudal counts, while the hemipenis is bifurcate distally as in *L. rufulus* (Lichtenstein).

Lycodonomorphus leleupi Laurent 1950.—This endemic water snake was described from the Kundelungu plateau and also occurs on the Kibara plateau in the P.N.U. between 1250 and 1810 m (Witte 1953). It was described as a subspecies of *L. whytei* (Boulenger) of northern Malawi and adjacent Tanzania, but was later thought to be conspecific with *L. rufulus mlanjensis* Loveridge of southern Malawi and eastern Zimbabwe (Broadley 1967). These are now considered to be sister species, distinguished by ventral colouration: dark with yellow patches and a dark tail in *L. leleupi* and yellow with a few dark spots and a dark median stripe on the subcaudals in *L. mlanjensis*. The nearest populations are separated by a gap of 1000 km.

Lamprophis fuliginosus (Boie 1827).—The Sooty House Snake is found throughout west and central Africa, extending into the Horn of Africa and plateau areas of Kenya, being replaced on the coast by *L. capensis* (Duméril & Bibron) (Hughes 1997). Witte (1953) recorded it [as *Boaedon l. lineatus* (Duméril & Bibron)] throughout the P.N.U. and illustrated a specimen from Lubumbashi.

Mehelya poensis (A. Smith 1847).—This forest file snake occurs from Guinea east to Uganda, south to Angola and the D.R.C., apparently reaching the southern limit of its range in the P.N.U. at Munoi (Witte 1953).

Mehelya nyassae (Günther 1888).—The Nyasa File Snake inhabits savannas from Kenya to South Africa, west to Burundi, Katanga (P.N.U.), Zambia, Botswana and Namibia. In the P.N.U. it was not taken above 1140 m (Witte 1953).

Mehelya capensis capensis (A. Smith 1847).—The Southern File Snake has a wide range in savannas of eastern Africa from northeast Tanzania to South Africa and west to Katanga, Zambia, Angola and northern Namibia. Although not yet recorded from the P.N.U., Laurent (1956) noted that Witte (1953) had assigned a specimen from Lubumbashi to *M. poensis*.

INCERTAE SEDIS

Lycophidion multimaculatum (Boettger 1888).—The Blotched Wolf Snake ranges from Gabon south to Angola east to the southeastern D.R.C., Zambia and adjacent Tanzania (Broadley 1996). It is found throughout the P.N.U. (Witte 1953 [as *L. capense capense* (A. Smith)]).

Pseudaspis cana (Linnaeus 1758).—The Mole Snake is found throughout southern Africa, extending north to Angola, Zambia, Katanga, Rwanda and the Kenya highlands. In the P.N.U. it is found on the Kibara plateau between 1320 and 1810 m (Witte 1953), and it has been recorded from the Kundelungu plateau at 1750 m in *Tatera* burrows (Laurent 1956 [as *P. cana anchietae* (Bocage), a synonym]).

Grayia ornata (Bocage 1866).—The Ornate Water Snake inhabits rivers from Cameroon south to Angola and west to Katanga and northwestern Zambia (Broadley 1991b). In the P.N.U. it was taken at 700 to 800 m (Witte 1953).

Subfamily PSAMMOPHIINAE

Hemirhagerrhis nototaenia (Günther 1864).—The Southeastern Bark Snake has a wide range in southeast Africa from coastal Kenya to South Africa, east to Botswana, Zambia and Katanga (Broadley & Hughes 2000). It is common at low altitudes in the P.N.U., but is not found on the Kibara plateau (Witte 1953).

Psammophylax variabilis Günther 1893.—The Grey-bellied Grass Snake has a discontinuous distribution on the southern rift valley highlands, but also inhabits flood plains further west (Broadley 1977a). In the P.N.U. it occurs on the Kibara plateau at 1750-1830 m (Witte 1953 [as *Cerastes t. tritaeniatus*]). Laurent (1956) included these specimens in his new taxon *P. tritaeniatus festivus*, described from the Kundelungu plateau, and subsequently placed in the synonymy of *P. v. variabilis* (Broadley 1977a). The status of the subspecies of *P. variabilis* is being investigated by C.M.R. Kelly.

Psammophylax tritaeniatus (Günther 1868).—The Three-lined Grass Snake has a wide range in southeastern Africa, extending north to Tanzania and west to southern Angola (Broadley 1977a). Although widespread in Katanga, it has not yet been recorded from the P.N.U.

Rhamphiophis acutus (Günther 1888).—The Striped Beaked Snake ranges from Angola through Katanga and northern Zambia to southwestern Tanzania and Burundi (Broadley 1971c). In the P.N.U. it was only collected on the Kibara plateau (Witte 1953): Laurent (1956) included this material in his new taxon *R. a. wittei*, described from the Kundelungu plateau at 1750 m and synonymised by Broadley (1971c). It seems that *R. a. jappi* Broadley, described from the Barotse flood plains in western Zambia, is probably a good evolutionary species.

Dromophis lineatus (Duméril & Bibron 1854).—The Lined Olympic Snake has a wide range from Senegal east to Ethiopia, south to Angola, Zambia and northern Malawi. Although not yet recorded from the P.N.U., there are records from Bukena on the Luapula River just southwest of the park boundary, Pweto and Kilwa on Lake Mweru, and Lubumbashi to the south (Witte 1953). Two specimens recorded from the Kundelungu plateau by Laurent (1956) actually belong to *Psammophis zambiensis*.

Psammophis zambiensis Hughes & Wade 2002.—The Zambian Whip Snake was recently described from northern Zambia and ranges from northern Mwinilunga District (Broadley 1991b [as *P. sibilans leopardinus*]) to the Mweru Wantipa in Mporokoso District (Broadley & Pitman 1960 [as *P.* ? *sibilans*]). The "Abercorn" [= Mbala] specimens collected by H.J. Bredo probably came from the Mweru Wantipa while on Red Locust control operations. It was not collected at Mbala by D. Vesey-FizGerald, Bredo's successor. Two specimens from Kundelungu plateau at 1750 m were assigned by Laurent (1956) to the superfi-

cially similar *Dromophis lineatus* (Hughes & Wade 2002).

Psammophis mossambicus Peters 1882.—The taxonomy of the *P. sibilans* complex is still unresolved. This name was provisionally revived for eastern material previously assigned to *P. phillipsii* Hallowell of West Africa. The Olive Whip Snake ranges from the Sudan to South Africa, west through Katanga to Angola (Broadley 2002). It is common throughout the P.N.U. (Witte 1953 [as *P. sibilans sibilans*]).

Psammophis angolensis (Bocage 1872).—The Dwarf Whip Snake has a wide range in savannas of eastern Africa, from Ethiopia to South Africa and Mozambique, west through Zambia and Katanga, to Angola (Broadley 2002). In the P.N.U. it was not found on the Kibara plateau (Witte 1953).

Subfamily NATRICINAE

Natriciteres bipostocularis Broadley 1962.—This small marsh snake was described from northeastern Zambia and extends west through Katanga to the highlands of central Angola (Broadley 1966b). The specimens from the P.N.U. and environs were collected between 1320 and 1585 m (Witte 1953 [as *Neusterophis fuliginoides* (Günther)]), but were assigned to *N. olivacea uluguruensis* (Loveridge) by Loveridge (1958). This taxon was originally described as a subspecies of *N. olivacea*, and then placed as a subspecies of *N. variegata* (Peters) of West Africa (Broadley 1966b). It now seems better to recognise all the well isolated "races" as evolutionary species (Broadley & Kelly, in prep.).

Natriciteres fuliginoides (Günther 1858).—This forest marsh snake ranges from Guinea east to the D.R.C., reaching its southern limit at Lofoi at the base of the Kundelungu plateau, it is also recorded from Kapanga and Sandoa in western Katanga (Witte 1953 [as *Neusterophis fuliginoides*, part]).

Natriciteres olivacea (Peters 1854).—The Olive Marsh Snake has a wide range in savannas from Guinea, east to the Sudan and Ethiopia, south through southern Somalia to southern Mozambique and west to Gabon and Angola. In the P.N.U. it was only found below 1000 m, mainly at Mabwe on Lake Upemba (Witte 1953 [as *Neusterophis o. olivaceus*]).

Limnophis bangweolicus (Mertens 1936).—The Bangweulu Water Snake ranges from Zambia, west to Katanga and eastern Angola. It has not yet been found in the P.N.U., but it has been recorded from Pweto, Lubumbashi and near Kanzenze on a tributary of the upper Lualaba (Witte 1953 [as *L. bicolor* (Günther)]).

Subfamily BOIGINAE

Boiga blandingii (Hallowell 1844).—Blanding's Tree Snake inhabits forests and wooded savannas from Guinea, east to western Kenya, south to Angola, Katanga and northern Zambia (Mporokoso District). The P.N.U. specimen came from Pelenge gorge at 1250 m (Witte 1953); the other Katangan localities are Sandoa and Kanzenze, the latter being the southernmost record.

Dipsadoboa shrevei shrevei (Loveridge 1932).—This nocturnal tree snake ranges from the lower Congo and Angola, east through the D.R.C. and northern Zambia to southeast Tanzania (Rasmussen 1986). The only definite locality in Katanga is Lubumbashi (Bourgeois 1964), but there are numerous records from northern Zambia (Broadley 1971d, 1991b).

Dipsadoboa unicolor Günther 1858.—This slender arboreal snake occurs from Guinea to Cameroon, is apparently replaced by *D. weileri* (Lindholm) in the Congo basin, and then reappears along the Albertine rift (Rasmussen

1993). The southernmost specimens are from the P.N.U. and were taken between 1250 and 1300 m (Witte 1953).

Crotaphopeltis hotamboeia (Laurenti 1768).—The Herald Snake is common throughout moist savannas of sub-Saharan Africa, including the P.N.U. (Witte 1953).

Telescopus semiannulatus A. Smith 1849.—The Eastern Tiger Snake has a wide range in eastern Africa from Kenya to South Africa, west to the D.R.C., Angola and Namibia. It is found throughout the P.N.U. (Witte 1953).

Subfamily COLUBRINAE

Scaphiophis albopunctatus Peters 1870.—The Grey Beaked Snake ranges from Ghana east to Kenya, south to the D.R.C., northern Zambia and Tanzania (Broadley 1994). In the P.N.U. it was not found above 900 m (Witte 1953).

Prosymna ambigua Bocage 1873.—Bocage's Shovel-snout has an extensive range around the periphery of the Congo basin (Broadley 1980). In the P.N.U. it was not taken above 800 m (Witte 1953).

Philothamnus carinatus (Andersson 1901).—This forest species ranges from Guinea to eastern Kenya and Tanzania, south to Katanga (Hughes 1985). Specimens from the P.N.U. were taken at an altitude of 680 - 700 m (Witte 1953 [as *P. heterodermus carinatus*]). Hughes (1985) recorded sympatry between this species and *P. ruandae* Loveridge at M'bala about 90 km further west, but Laurent (1956) suggested that the locality data for the latter specimen is probably erroneous. Transposition of specimen labels at Tervuren is easy, as they are not tied to the specimens.

Philothamnus hoplogaster (Günther 1863).—The Southeastern Green Snake ranges through savannas from Kenya to South Africa and west to the southern D.R.C. and Angola. It is found throughout the P.N.U. (Witte 1953).

Philothamnus heterolepidotus (Günther 1863).—The Slender Green Snake ranges from Sierra Leone east to Ethiopia, south through the D.R.C. to Angola and northern Zambia (Hughes 1985). It is common throughout the P.N.U. and environs (Witte 1953).

Philothamnus angolensis Bocage 1882.—The Angolan Green Snake has a wide range in savannas from Cameroon east to the Sudan, south to South Africa (Hughes 1985). It is found throughout the P.N.U. (Witte 1953) [as *P. irregularis irregularis* (Leach) of West Africa].

Philothamnus semivariegatus (A. Smith 1847).—The Variegated Bush Snake has the widest range of any species in the genus, inhabiting savannas from Senegal east to Ethiopia, south to South Africa (Hughes 1985). It is found throughout the P.N.U. (Witte 1953).

Dispholidus typus (A. Smith 1829).—The Boomslang is found throughout the savannas of sub-Saharan Africa, including the whole of the P.N.U. (Witte 1953). Laurent (1955) assigned material from northern Angola and the southern D.R.C. to a new subspecies *D. t. punctatus*, which intergrades with his other new subspecies *D. t. kivuensis* in northeastern Zambia.

Thelotornis kirtlandii (Hallowell 1844).—The Forest Vine Snake ranges from Guinea-Bissau east through forested areas of West Africa and the Congo basin to Uganda and the southern Sudan, south to northern Angola, northwestern Zambia and south-central Tanzania (Broadley 2001). In the P.N.U. it was not found on the Kibara plateau, but was taken between 700 and 1320 m (Witte 1953).

Thelotornis capensis oatesii (Günther 1881).—This savanna vine snake has a wide range in

south central Africa (Broadley 2001). In the P.N.U. it was not found on the Kibara plateau (Witte 1953).

Dasypeltis scabra (Linnaeus 1754).—The Common Egg-eater is found throughout the savannas of sub-Saharan Africa, including the P.N.U. (Witte 1953).

ORDER CROCODYLIA
Family CROCODYLIDAE

Crocodylus cataphractus Cuvier 1824.—The Slender-snouted Crocodile ranges through forested areas from Senegal east to Lake Tanganyika and south to Angola and Katanga. It occurs in Lakes Upemba and Mweru and the Luapula River to the south (Witte 1953).

Crocodylus niloticus Laurenti 1768.—The Nile Crocodile occurs in rivers and lakes of sub-Saharan Africa south to eastern South Africa. In the P.N.U., it has always been less abundant than the previous species, but numbers of both crocodiles declined between 1925 and 1947-49 (Witte 1953).

ZOOGEOGRAPHY

Analysis of the distribution patterns of the reptiles of Katanga suggests that they can be roughly allocated to 13 range clusters, as follows:

Species endemic or near-endemic to Katanga (15).—Pelusios upembae; *Pachydactylus katangensis*; *Trachylepis upembae*; *T. pulcherrima*; *Panaspis smithii*; *Monopeltis adercae*; *M. scalper*; *Rhinotyphlops* (*Letheobia*) *kibarae*; *Atheris katangensis*; *Atractaspis leleupi*; *Amblyodipsas rodhaini*; *A. katangensis*; *Aparallactus moeruensis*; *Lycodonomorphus upembae*; *L. leleupi*.

Guinean-Congolian Forest species (17).—Pelusios gabonensis; *Feylinia currori*; *Adolfus africanus*; *Rhinotyphlops angolensis*; *Causus lichtensteinii*; *Bitis gabonica*; *Polemon christyi*; *Naja melanoleuca*; *Mehelya poensis*; *Grayia ornata*; *Natriciteres fuliginoides*; *Boiga blandingii*; *Dipsadoboa unicolor*; *Prosymna ambigua*; *Philothamnus carinatus*; *Thelotornis kirtlandii*; *Crocodylus cataphractus*. This list is probably incomplete, as some forest species recorded from the Ikelenge pedicle in northwest Zambia can be expected to occur in southeast Katanga, i.e., *Thrasops jacksonii* Günther and *Rhamnophis aethiopissa* Günther (Broadley 1991b; Broadley & Wallach 2002). *Dendroaspis jamesoni* (Traill) is also likely to occur.

Widespread sub-Saharan savanna species (10).—Pelomedusa s. subrufa; *Varanus niloticus*; *Bitis arietans*; *Dendroaspis polylepis*; *Natriciteres olivacea*; *Crotaphopeltis hotamboeia*; *Philothamnus semivariegatus*; *Dispholidus typus*; *Dasypeltis scabra*; *Crocodylus niloticus*.

Northern Guinean savanna species (8).—Chamaeleo gracilis; *Lygodactylus gutturalis*; *Trachylepis maculilabris*; *Rhinotyphlops lineolatus*; *Lamprophis fuliginosus*; *Dromophis lineatus*; *Scaphiophis albopunctatus*; *Philothamnus heterolepidotus*.

South-central African savanna species (20).—Pelusios rhodesianus; *Kinixys spekii*; *Lygodactylus angolensis*; *Sepsina hemptinnei*; *Gerrhosaurus nigrolineatus*; *G. bulsi*; *Ichnotropis capensis*; *Varanus albigularis angolensis*; *Monopeltis remaclei*; *Rhinotyphlops schmidti*; *Leptotyphlops kafubi*; *Xenocalamus michelli*; *Hypoptophis wilsoni*; *Chilorhinophis gerardi*; *Elapsoidea guentheri*; *Boulengerina annulata stormsi*; *Naja crawshayi*; *Lycophidion multimaculatum*; *Philothamnus angolensis*; *Thelotornis capensis oatesii*.

Southern rim of the Congo Basin species (15).—Pelusios nanus; *Chamaeleo anchietae*; *Lygodactylus heeneni*; *Eumecia anchietae*; *Leptosiaphos dewittei*; *Panaspis seydeli*; *Chamaesaura miopropus*; *Tetradactylus ellenbergeri*; *Ichnotropis bivittata*; *Rhinotyphlops* (*Letheobia*) *gracilis*; *Causus bilineatus*; *Rhamphiophis acutus*; *Psammophis zambiensis*; *Natriciteres bipostocularis*; *Dipsadoboa s. shrevei*.

Eastern savanna species (27).—Pelusios subniger; *Acanthocercus atricollis*; *Agama armata*; *Chamaeleo dilepis*; *Hemidactylus mabouia*; *Trachylepis megalura*; *T. varia*; *T. striata*; *Lygosoma afrum*; *Panaspis wahlbergii*; *Cordylus tropidosternum*; *Holaspis laevis* (+ coastal forest); *Rhinotyphlops mucruso*; *Python natalensis*; *Causus rhombeatus*; *Atractaspis bibronii*; *Amblyodipsas polylepis*; *Aparallactus capensis*; *Naja mossambica*; *Mehelya nyassae*; *M. c. capensis*; *Hemirhagerrhis nototaenia*; *Psammophylax tritaeniatus*; *Psammophis mossambicus*; *P. angolensis*; *Telescopus semiannulatus*; *Philothamnus hoplogaster*.

East African Savanna to Congo Basin (1).—Pachydactylus tuberculosus.

South-west savanna (2).—Pachydactylus punctatus; *Naja anchietae*.

Southeastern savanna (1).—Pseudaspis cana.

Kalahari sand fauna (1).—Zygaspis quadrifrons.

Southern rift valley highlands fauna (1).—Psammophylax variabilis.

Palaeo-Upper Zambezi - Okavango fauna (1).—Limnophis bangweolicus.

DISCUSSION

An encompassing explanation for the richness of this cosmopolitan herpetofauna needs to consider the ecological determinants of its composition. Faulting in the southwest branch of the African Rift created high, flat plateaux, whose steep sides surround wide valleys. This diverse geomorphology of Katanga is the template on which the many different habitats have evolved. This variety can be roughly classified into: wetland (lowland and highland), savannas and grasslands (in valleys, and on relief), aeolian sediments (dilungu on plateaux), lacustrine alluvium, and forest. The forests and savannas are especially variable in composition, context and extent.

Equally, elements of neighbouring biomes have significantly elevated the diversity of Katanga's herpetofauna. In its position under contemporary climatic conditions, Katanga straddles a broad transition zone of forest and savanna, juxtapositioned between the main Congo forest block and the Zambezian savannas. Climatic change has been as, if not more, important in changing the extent of habitats. This was especially so through the Plio-Pleistocene, with pluvials alternating with arid periods. These determinants have interacted in complex ways, which complicates attempts to tease out each of their influences on biogeographical patterns. Their relative importance has also varied across different scales of space and time. The contributions of these determinants are discussed below, with focus on the evolution of endemics in SE Katanga.

HABITAT DIVERSITY

Contemporary Ecological Conditions, and Elevated β and γ Diversity.—We can invoke contemporary patterns in the ecology of the landscape to explain the richness of reptile assemblages. The high hetereogeneity of habitats stands out as a major determinant. These

represent a great range in ecological conditions: from mesic forest to comparatively arid dilungu. High heterogeneity is exhibited both within and among the various habitats. An example is how altitude augments variety in the miombo and forests, from lowlands to plateaux, across a large altitudinal range (400 m in the Lualaba valley to over 1800 m on Kibara and Kundelungu plateaux), and these gradients are often steep (exemplified across the Upemba horst). This high richness of terrestrial habitats is matched by (and integrated with) a complementary richness of wetlands (Dapper 1981). For example, ecological diversity is enhanced by thermal and saline springs where the thermophilic crustacean, *Thermobathynella adami* occurs. This was the fourth parabathynellid ever described - isolated from a hot spring in Upemba (Schminke 1987). Another interesting vertebrate endemic, the cichlid fish, *Oreochromis salinicola* (Poll 1948), is known only from Mwashya geothermal saline springs north of Lake Lufira (Trewavas 1983; Malaisse 1997). Overall, this great variety in both physiography and vegetation (resplendent in the high β and γ diversity of the flora) is the proximate determinant of the high species richness of reptiles, and indeed the rich biodiversity of Katanga.

The Example of Guineo-Congolian Elements.—The 17 species of forest reptiles in the contemporary fauna exemplify the biogeographical consequences where mushitu has persisted deep within the miombo savannas. This forest-savanna mosaic is a more apparent aspect of elevated habitat hetereogeneity, and thus landscape structure, in the Katanga region. Mushitu not only elevates β and γ diversity, but is a critical habitat for those species of Guineo-Congolian affinity up to 250 kms south of the main belt of moist forest. This augments species richness of reptiles significantly. Edaphic conditions appear to be the singular geomorphological control that structures this forest-savanna mosaic in the landscape. Higher, and perennial, availability of soil moisture along drainage lines supports gallery forests both on more gentle slopes (in drainage basins between interfluves), and also in steep valleys and ravines. Thus, ecological conditions in these forested drainage channels feeding the Lualaba differ markedly from that on the interfluves under the more extensive miombo woodlands (White & Werger 1978). Plants hold a keystone role in structuring these patches of habitat in which other forest biota persist. The overall result has been an enrichment of the region's biodiversity by forest organisms, as indicated by certain invertebrates and small vertebrates (Cotterill 2002a,b).

CLIMATIC CHANGE

Shifting Habitats.—Both the composition and extent of habitats across Africa changed radically through the Tertiary, during which climates varied across a range of scales in space and time. An important influence on the contemporary biodiversity of Katanga has been alternations between pluvial and xeric regimes. These altered ranges and composition of principal habitats, notably wetland, grassland, forest and savanna (Colyn 1991). In addition to mushitu, signatures of these changes through recent geological time are represented by the remarkable sandy habitats - the dilungu - on Katanga's plateaux. These record comparatively recent arid episodes in variable climates, where regimes of precipitation and temperature fluctuated in complex ways through the Plio-Pleistocene and Holocene (Dapper 1981, 1988; Colyn 1991).

There are at least two likely reasons why the biodiversity in Katanga has been especially influenced by these climatic changes. One is its strategic position abutting the great equatorial divide — between the Zambezian and Guineo-Congolian regions (Fig. 2); in this situation the region has been influenced by both biotic (notably phytogeographic associations) as well

as physiographic events (especially exchanges between drainage systems, see below). Second, patches of both xeric and mesic habitats have persisted successfully, with elements of their biodiversity intact, sheltered in the region's physiographically diverse landscapes. Contemporary examples are the dilungu on Katanga's plateaux, and mushitu forests in valleys, respectively (Malaisse 1997).

Evolutionary Significance of the Persistence of Forests.—A subtle connectivity of Katanga's gallery forests with moist forests in the Congo lowlands is the most plausible explanation for not only why Guineo-Congolian species occur deep within mesic miombo savanna, but also recent speciation. The congruent pattern is of species isolated from sister species in the main forest block, with their ranges restricted within the southern Congo basin against the Congo-Zambezi watershed. This is exemplified in the biodiversity of the Ikelenge pedicle on the southwest border of Katanga. Examples include three small mammals currently collected only from the Ikelenge Pedicle, namely: Ansell's long-footed rat, *Malacomys australis* Ansell; Ansell's musk shrew, *Crocidura anselorum* Hutterer & Dippenaar, and Sakeji horseshoe bat, *Rhinolophus sakejiensis* Cotterill (Cotterill 2002a,b). It appears that a congruent evolutionary history is exhibited by particular reptile endemics in Katanga, notably *Atheris katangensis*.

Interestingly, a parallel example of this landscape pattern (namely a forest-savanna mosaic) occurs in the Amazon Basin. Likewise, gallery forests account for forest species occurring deep into Neotropical savanna; where their persistence has sometimes resulted in evolution. Gallery forests are not only refugia for forest organisms, but have also fostered speciation of these relict populations (Meave *et al*. 1991).

Evolution of Endemics.—Katanga's endemic reptiles are represented in forest and wetlands, as well as alluvial and aeolian sediments. In total, they account for at least 12% of overall diversity. One of these species exhibits forest affinities and likely speciated according to the forest-savanna model described above. Fossorial endemics point to vicariant speciation in patches of dilungu and alluvium. The apparent dearth of endemic fossorial reptiles in the dilungu more likely represents a lack of collecting. The isolation of populations of grassland birds (notably pipits and larks) on these sandy habitats on Katanga's plateaux is attributed to a history of climatic changes in the late Pleistocene. It appears that these Kalahari sands were initially deposited in one or more interpluvials and then isolated in wetter periods (Cotterill in press b).

Lycodonomorphus leleupi isolated on the Kibara and Kundelungu plateaux is hypothesized to represent a relict link to taxa along the East African Rift in east Africa and Malawi. Conversely, *L. upembae* has been isolated in the Upemba depression from its sister species, *L. subtaeniatus*, in the lower Congo basin. The evolutionary history of the other wetland endemic, *Pelusios upembae*, is complicated by its vicariance from *P. bechuanicus*. Speciation of these terrapins has been interwoven with the intricate history of drainage evolution within and around Katanga (discussed below).

This endemism emphasizes the evolutionary significance of different patches (forests, sediments and wetlands) - exemplified by speciation in mushitu. Vicariant speciation of these endemic reptiles illustrates how these patches have functioned as source, as opposed to sink, habitats through evolutionary time. Again, the region's complex physiography has governed these complementary histories in forest, sediments, and wetland. It would be interesting to quantify how these suites of assemblages (e.g., forest) differ from extant populations in their ancestral source habitats (pertinently the Congo lowlands). Phylogeographic studies of

these geographically dispersed lineages should help to elucidate their evolutionary histories.

GEOLOGICAL HISTORY

Tectonic Events in the East African Rift System.—Ultimately, the singular determinant of the diverse topography of Katanga has been activity in the East African Rift system during and after the Miocene. Associated with Africa's rift valley system, tectonic activity in the Pliocene across the south-central African plateau reactivated erosion. Significantly, this was when Katanga's plateaux were uplifted to accentuate the Kamalondo depression. These geologically-recent events account for the varied topography ranging from plateaus and ravines to deep and wide valleys (Dapper 1981; Sebagenzi & Kaputo 2002).

Landscape Evolution in and Around Katanga, and Vicariant Speciation of Aquatic Vertbrates.—Drainage across Katanga has undergone interesting changes and this has influenced biotic evolution profoundly. This history has been intimately interlinked with drainage evolution across the south-central Africa plateau overall, especially the Upper Zambezi and neighbouring systems. Significant events involved shrinkage and expansion of wetlands, with changes in their connections. The most interesting of these events were most likely Plio-Pleistocene. This complex history is still incompletely understood, and its deserving treatment is beyond the scope of this paper. Nevertheless, sufficient biotic and geological evidence points to past connections of wetlands in Katanga with Bangweulu, and with the Upper Zambezi and Okavango systems further south. A model of this recent drainage evolution explains vicariant speciation of lechwe antelopes in south-central Africa - most pertinently the Upemba lechwe (Cotterill in press a, submitted). A synopsis of this drainage evolution, presented below, illustrates this important influence on speciation of vertebrates, notably reptiles, within and around Katanga.

A model of drainage evolution proposed for vicariant speciation of the Upemba lechwe (Cotterill submitted) in the Kamalondo depression centres on past links between the Upper Lualaba-Lufira drainage and the Upper Zambezi through a trans-Katanga drainage system. The first event entailed dispersal by aquatic organisms along a connection, the Palaeo-Kafila; which was then a major river connected to the Palaeo-Chambeshi drainage system. This was when, or soon after, the latter was the principal tributary of Palaeo-Lake Makgadigadi through the Plio-Pleistocene; such that the Palaeo-Chambeshi flowed southwest across the Lukanga depression into Palaeo-Lake Makgadigadi. Large, shallow endoreic lakes played a key role in these dynamics; and especially significant was Palaeo-Lake Lufira, whose recent existence is represented by significant alluvium in the Lufira depression (Cotterill in press a, Fig. 2).

Alternatively, it can be argued that vertebrates dispersed between the Upper-Zambezi and Upper Lualaba across the Congo-Zambezi watershed prior to speciation of *Pelusios upembae*; so that a link between the Palaeo-Chambeshi and the Kamalondo graben via a trans-Katanga drainage system is thus unlikely. The close proximity of the modern Upper Zambezi and Upper Lualaba headwaters is likely geologically recent; and fieldwork by Bell-Cross (1965) discounted the likelihood of fishes dispersing across this watershed.

This favoured explanation for evolution of the endemic terrapin *Pelusios upembae* is supported by interesting congruence in two complexes of wetland birds. The one, its distribution centred on Katanga, entailed vicariant speciation of masked weaver birds (the *Ploceus reichardi* group). These are entirely swamp-dwelling, and dependent on large permanent wetlands,

especially for nesting. This species complex comprises three endemics: with *P. ruweti* Louette & Benson restricted to the Lufira depression; *P. upembae* (Verheyen) in Upemba; and *P. katangae* (Verheyen) occurring along the Luapula River and around Lakes Bangweulu and Mweru. The other species, *P. reichardi* Reichenow is isolated in southeast Tanzania around Lake Rukwa and its drainage system; while the recently discovered *P. burnieri* Baker & Baker is isolated in the Kilombero valley. A congruent pattern is shown by the distribution of Swamp Flycatchers of the *Muscicapa lualabae* (Chapin) complex (Cotterill in press a).

Speciation of endemic fishes in Katanga has been especially prolific. There is an interesting congruence between endemic fishes in the Kamalondo with the water snake *Lycodonomorphus upembae* and Upemba terrapin, *Pelusios upembae*. The zoogeography of these fish faunas also exhibits a significant complementation of Upper Zambezi species. Poll (1963) originally contrasted the aquatic ecology of the lower Congo, which drains and flows under Guineo-Congolian moist forests, with the Upper Lualaba-Lufira, whose tributaries drain a patchwork mosaic of dambos, riparian forests and savanna. These headwaters especially differ in the predominance of cool, fast flowing mountain streams (Banister & Bailey 1979; Teugels & Guégan 1994). Thus, over 600 species of lower Congo fishes do not occur upstream of the Portes d'Enfer; but the fish fauna of the Upper Congo has been augmented by Upper Zambezian species. The relatively high endemism in three ichthyofaunal subregions of Katanga (Upper Lualaba-Lufira, Kamalondo Basin, and Luapula) is especially interesting (Malaisse 1997). This endemicity is illustrated by comparisons of fishes (total endemics/total species richness) of the Kasai-Bushimaie-Lulua (2/77) with the Kamalondo basin (47/183), Upper Lualaba-Lufira (12/87) and Luapula (39/146). The latter also includes Lake Bangweulu and the Upper Chambeshi catchment (Teugels & Guégan 1994; Malaisse 1997).

Congruent patterns of speciation in all these mammals, fishes, birds and reptiles (pertinently *Pelusios upembae*) is most plausibly accounted for by recent drainage evolution. Thus, their vicariant speciation followed on fragmentation of the trans-Katanga drainage system that isolated the Kamalondo depression from the Palaeo-Chambeshi, and thus Palaeo-Lake Makgadikgadi. The history of this huge drainage system, the Palaeo-Chambeshi, is being investigated in detail, with special focus on its former connections with Katanga, to account for past links and fissions. This new model which emphasizes past connections between the Congo and Zambezi drainage systems obviously endorses a radical reconsideration of landscape evolution in south-central Africa (Cotterill 2003, in press a, submitted; F. P. D. Cotterill unpublished data).

CONCLUSIONS

1. The above explanation has focused on the more obvious patterns of endemism, faunal mixing and species persistence exemplified by indicator species in Katanga. The processes responsible for the rich reptile fauna have acted through complimentary, interlinked, and thus complex mechanisms. Proximally, the very diverse physiography and vegetation are combined determinants of high β and γ diversity across Katanga's landscapes. Ultimately, evolution of the region's biodiversity has been driven by a complex history of climatic and geological change.

2. It is unfortunate that knowledge of the biodiversity of this fascinating region (Katanga and northeast Zambia) is so incomplete. The principal herpetological surveys have been very patchy in their focus on protected areas (especially Upemba) and near human settlements

(e.g., Lubumbashi). In particular, we single out Lake Bangweulu, from which very few specimens of any organisms have been collected. Only more thorough faunal surveys of Katanga and surrounding landscapes will provide the necessary data for fascinating phylogeographic studies, and above all quantify zoogeographic patterns more thoroughly.

3. Opportunities for research on Katanga's reptiles, as for all its biodiversity, are practically unlimited. This synthesis provides a framework for further research on this biodiversity hotspot to understand how tectonics, drainage evolution, and climatic change have influenced evolution. This needs to employ phylogeographic studies, with palaeoecological reconstructions that include dating of lake sediments. Phylogeographic comparisons of forest, savanna, wetland and fossorial species, respectively and in comparison, promise to yield fascinating insights into late Tertiary history of the landscape.

4. Notwithstanding deficiencies in data, the distributions exemplified by our current knowledge outline a remarkable history of complex faunal dynamics and speciation. The exceptional species richness and endemism of the reptile fauna of southeast Katanga constitutes a strong argument for the region's conservation. Brooks *et al*. (2001) identified "Upemba Plain" among the top 10 sites for priority conservation in Africa, based on continental patterns of species richness and endemism of amphibians and snakes; but they did not specify the indicator taxa. The global significance of this hotspot of biodiversity is strengthened even more when one acknowledges complementary patterns of other aquatic and terrestrial vertebrates and plants (Cotterill, in press a,b, submitted).

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