The tortoises (Testudinidae) and terrapins (Pelomedusidae) of southern Africa: their diversity, distribution and conservation

W.R. Branch*
Port Elizabeth Museum, P.O. Box 13147, Humewood, 6013 Republic of South Africa

G.A. Benn and A.T. Lombard
Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, 7700 Republic of South Africa

Received 15 February 1995; accepted 21 April 1995

Southern Africa has the richest diversity of land tortoises in the world, as well as an important radiation of pelomedusid terrapins. Total species richness has two epicentres, including the Transvaal lowveld and adjacent KwaZulu/Natal (owing to the prevalence of pelomedusid terrapins) and the Eastern and south-western Cape (owing to small testudinids). The area encompassing Lesotho, Transkei and adjacent regions, lacks testudinids for unknown reasons. Archaeological data indicates that this gap is natural, and not the result of man-induced extinctions. Endemic species are clustered in the Cape, whilst the few threatened species are more widely distributed. The majority of species is well protected in existing reserves. The small number of chelonian species in southern Africa and their relatively well-known distributions, test the efficacy of an iterative reserve selection algorithm. The presence of many allopatric (or nearly so) congeneric species leads to the selection of iterative reserves that protect peripheral populations. To avoid this, marginal records and isolated, peripheral populations should be excluded from the analysis.

Suidelike Afrika het die rykste diversiteit van grondlewende skilpaaie ter wêreld, sowel as 'n belangrike uitstraling van pelomedusiede varswaterskilpaaie. Die totale spesierykheid het twee episentrums, naamlik die Transvaalse laeveld en aangrensende KwaZulu/Natal (te danke aan die oorwig van pelomedusiede varswaterskilpaaie) en die Oos- en suid-westelike Kaap (te danke aan die klein testudiniede soorte). Die gebied wat Lesotho, die Transkei en aangrensende streke insluit, het om onbekende redes geen testudiniede nie. Argeologiese data wys dat hierdie leemte natuurlik is, en nie die resultaat van mens-veroorsaakte uitsterwings. En-demiese spesies is in die Kaap gekonsentreer, terwyl die enkele bedreigde spesies wyer versprei is. Die meeste spesies word binne bestaande bewaringsgebiede goed beskerm. Die klein hoeveelheid cheloniese spesies in suidelike Afrika en hulle betreklik bekende verspreidings, het die doeltreffendheid van die herhalende bewaringsgebiedseleksieprosedure getoets. Die teenwoordigheid van baie allopatriese (of byna) gelyksoortige spesies het veroorsaak dat bewaringsgebiede wat omliggende allopatriese populasies beskerm, geselekteer word. Om dit te voorkom, behoort marginale aantekenings en geïsoleerde omringende populasies van die analise uitgesluit te word.

*To whom correspondence should be addressed

Introduction

Lombard (1995) has noted the likely South African contractual obligations to the Convention on Biological Diversity. This will require the country to develop national strategies, plans or programmes for the conservation and sustainable use of biological diversity. The lack of a national database that inventories the distribution and diversity of the fauna and flora of South Africa threatens this commitment. This is particularly true of South African herpetology, which is presently undergoing somewhat of a renaissance, with burgeoning interest in the diversity of reptiles and amphibians. It has resulted in the recent discovery of numerous new taxa, including obvious novelties (e.g. Bourquin 1991; Mouton & van Wyk 1994; Broadley 1994). The rate of description of new southern African herpetological taxa shows no evidence of decline since Smith's (1838–49) founding studies (Figure 1), and new reptiles and amphibians are currently being discovered or described at a rate of about one new species per month. Despite our incomplete knowledge of herpetofaunal diversity in the subcontinent, it is already evident that reptiles are exceptionally speciose and form a major component of southern African vertebrate diversity, particularly if only endemic species are considered. It should be noted that increasing acceptance of evolutionary species concepts (Frost & Hillis 1990) can be expected to intensify the recognition of taxa with limited geographical range, resulting in new descriptions as well as the revival of taxa previously syno-

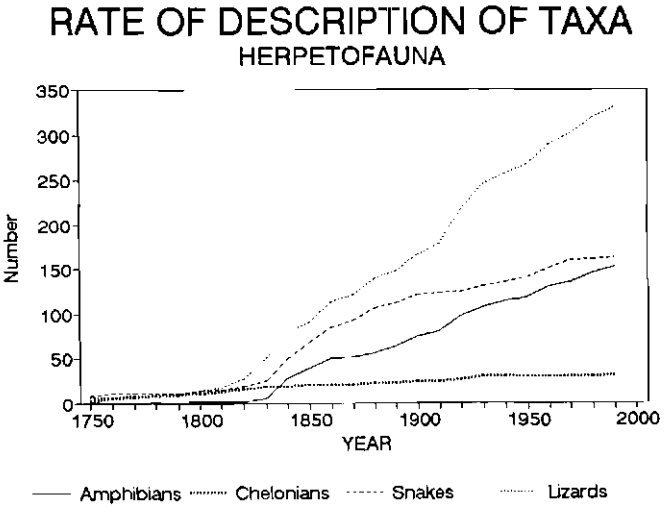

Figure 1 Rate of description of currently recognized southern African herpetofauna. Note that the rate of description of new chelonians is in the plateau phase indicating that local diversity is relatively well-known.

nymized under wide-ranging species (e.g. Broadley 1993).

With the exception of crocodilians (23 species) and rhyncocephalians (2 species), chelonians are the least speciose of extant reptiles, and two main suborders survive. Pleurodirans are primitive aquatic chelonians that withdraw the head sideways. They have a Gondwanaland distribution and are represented in Africa only by the Pelomedusidae. Cryptodiran chelonians withdraw the head straight backwards, and include all land tortoises (family Testudinidae), sea turtles, and aquatic New World terrapins including soft-shelled trionychids. Excluding the Amazonian genera *Podocnemis* (six species) and *Peltocephalus* (one species), pelomedusid pleurodirans are restricted to Madagascar (*Erymnochelys*, one species) and Africa (*Pelusios*, 14 species; *Pelomedusa*, one species). Terrestrial testudinids have a long evolutionary history, with fossils dating from the Middle Eocene (Auffenberg 1974), and an almost cosmopolitan continental distribution in temperate and tropical habitats, with a limited colonization of oceanic islands (e.g. the Aldabra Atoll, Indian Ocean, and the Galapagos Islands, eastern Pacific Ocean), but excluding Australia. However, although numerous fossil species are known (Auffenberg 1974), the extant fauna is relatively depauperate and currently only 42 species, in 11 genera, are recognized (Iverson 1992; Broadley 1993). The surviving species are also patchily distributed and sympatry between even two species is rare.

It has been noted on many occasions (e.g. Greig & Burdett 1976; Branch 1988b, 1989) that southern Africa has a surprisingly rich chelonian fauna. Although comprising only 0,8% of the world's total land surface, South Africa is home to 13 species of tortoise (31% of living species), whilst another (*Homopus* sp.) occurs in adjacent Namibia and may yet be recorded within the Richtersveld area. Generic diversity is even higher, with five (45,5%) of the eleven recognized genera present. The diversity of other chelonians in the subcontinent is less remarkable, but by no means insignificant. It includes two soft-shelled trionychids, six side-necked pleurodirans, and five sea turtles (Branch 1988a; Broadley 1993). Although part of this diversity has been summarized in recent popular reviews (e.g. Branch 1988a; Boycott & Bourquin 1988), the detailed diversity, distribution and conservation status of chelonians in the region has not previously been reviewed.

Before an objective analysis of the conservation status of any group can be undertaken it is necessary to have a sound understanding of its taxonomic diversity and distribution. These criteria are not easily met for southern African reptiles. Lombard, Nicholls & August (1995) applied an iterative reserve selection algorithm to South African snakes, using the base maps of Broadley (1990). They concluded that most of the snake species in South Africa were adequately protected. However, knowledge of the current composition and distribution of other southern African squamates, particularly lizards, is so poor that it is impossible to objectively assess their diversity or conservation status. Fortunately, chelonians are better known with relatively well-documented distributions. The rate of description of new taxa has stabilized, relative to other groups in the region (Figure 1), and they therefore offer a suitable reptilian study group. Our studies, detailed below, address the following questions:

(i) Where are the centres of diversity for
  (a) tortoises and terrapins
  (b) endemic species, and
  (c) threatened species?
(ii) Are southern African tortoises and terrapins adequately protected in existing reserves?
(iii) Where are the 'ideal' reserves for protecting southern African chelonians?
(iv) What new reserves are required to fully protect southern African chelonians?

An analysis of habitat association and zoogeography of southern African chelonians will be presented elsewhere (Branch & Benn in prep.)

Methods

Taxonomy

Chelonian diversity for the region was compiled from the reviews of Branch (1989), Boycott (1989), Broadley (1989, 1993), and Iverson (1992). Analysis was restricted to the families Testudinidae and Pelomedusidae. Owing to their marine or marginal occurrence, sea turtles and fresh-water trionychid terrapins have been excluded. The latter have only two representatives in southern Africa. The Nile soft-shell terrapin (*Trionyxs triunguis*) occurs only in the lower Cunene River, downstream of the Ruacana Falls, whilst the Zambezi soft-shelled terrapin (*Cycloderma frenatum*) is known from the Sava River in Mozambique and the Sabi-Lindi river confluence in eastern Zimbabwe (Branch 1988a). Even though five species of sea turtle have been recorded from South African coastal waters (Branch 1988a), most are considered vagrant or marginal vistors. In contrast to the global situation, where most sea turtles are threatened by exploitation or indirect mortality (Frazier 1992), they are considered well protected in South Africa. Only two species, the loggerhead turtle (*Caretta caretta*) and leatherback turtle (*Dermochelys coricaea*), are known to utilize Maputaland beaches for breeding (Hughes 1974a, b). These fall in well-protected areas and the breeding populations of both are rising. Isolated records of nesting leatherbacks on Eastern Cape beaches (Mullins 1984) may reflect expansion of the Maputaland colony, as this species is known to show the least site fidelity to its natal beaches.

Subspecies have been described for only a few southern African chelonians, although trinomials are required for some species with extralimital races: *Kinixys belliana nogueyi* is restricted to West Africa, whilst the typical race is found in East Africa and the subcontinent (Broadley 1993); *Pelusius subniger parietalis* and *Pelusios castanoides intergularis* are restricted to the Seychelles, with the typical races of both species occurring in the subcontinent (Bour 1983). Chelonians with subspecific differentiation within the subcontinent include the following.

Marsh terrapin (*Pelomedusa subrufa*)

In a footnote, Bour (1986) provisionally recognized two races within southern Africa. *P. s. nigra*, is considered to be restricted to KwaZulu-Natal, Free State and adjacent Eastern Cape (Iverson 1992), whilst typical *P. s. subrufa* extends from Somalia and Ghana through the central and western regions of the subcontinent, to Cape Town. A fuller analysis of the situation has not been published, and the

matter requires further attention.

Mountain tortoise (*Geochelone pardalis*)

Broadley (1989) continues to recognize a dwarf northern race (*G. p. babcocki*) extending throughout most of eastern and southern Africa; typical *G. p. pardalis* is considered to be restricted to the Eastern Cape, with relict populations on the southern Namibian escarpment. This arrangement has been questioned by Boycott & Bourquin (1988) and Bauer, Branch & Haake (1993), the latter considering the large size of the 'typical' race to be an ecotypic response to the relatively moist and temperate climate of the Eastern Cape region.

Speckled padloper (*Homopus signatus*)

Boycott (1986) validated the southern race, *H. s. peersi*, that was later (Bour 1988) placed in the synonymy of *H. s. cafer*. Although both races appear well defined morphologically, there is a large area of intergradation in the Calvinia - Loeriesfontein region, at the junction of Western Mountain Karoo and Succulent Karoo vegetation types.

Karoo tent tortoise (*Psammobates tentorius*)

Following their monographic revision, Loveridge & Williams (1957) reduced all 16 taxa described by Hewitt (1933, 1934) within this complex to synonymy, and recognized only three races (*P. t. tentorius*, *P. t. trimeni* and *P. t. verroxii*), all of which are restricted to the Cape provinces and adjacent Namibia. Nonetheless the races remain poorly defined, with massive areas of intergradation (see Greig & Burdett 1976). The complex is in urgent need of a modern taxonomic revision, and may yet be found to contain cryptic taxa.

Distribution data base

Although for many specimens point locality data were available, a significant number of early records had less detailed provenance. Analysis of distribution was therefore limited to quarter-degree grid squares (QDS). The data base was derived from a variety of sources, including the following.

(a) Published literature

A number of recent provincial and national herpetofaunal surveys have published up-dated point locality maps of the chelonian fauna (e.g. Transvaal — Jacobsen 1989; Orange Free State — Bates 1992; Swaziland — Boycott 1993; Botswana — Auerbach 1987). These have been compiled into the current data base. Recent taxonomic revisions (e.g. *Pelusios*, Broadley 1981; and *Kinixys*, Broadley 1993) were also incorporated.

(b) Museum collections

The extensive Cape tortoise collections made by Greig & Burdett (1976) have been consolidated into the South African Museum (SAM) and Port Elizabeth Museum (PEM), both of which are fully computerized and readily accessible, and already contained significant chelonian collections. In addition, the tortoise holdings of the Albany Museum, including the historically important collections of Hewitt and Duerden, have also been incorporated into the PEM collection. Owing to the paucity of Cape terrapin records, additional records from the Transvaal Museum were also included. Although a number of major collections were not fully surveyed (e.g. the Transvaal Museum, Pretoria, and the Natural History Museum of Zimbabwe, Bulawayo), many of their chelonian records have been incorporated from the published literature. The lack of the remaining material is not believed to have seriously limited the following analysis.

A number of unusual complications may attend tortoise records in museum collections. Tortoise shells formed a common cultural artefact of indigenous peoples (e.g. 'buccu' pouches), and as such were often acquired by early European explorers and subsequently deposited in museum collections. The accompanying locality data may be very vague (e.g. the type localities of: *Psammobates oculifer*, Cape; *G. pardalis*, Cape of Good Hope) or reflect the locality of the individual from which it was acquired. Another common complication is that of human translocations. The popular appeal of tortoises results in them often being illegally collected and subsequently released in localities distant from their natural distribution. The distribution maps of Greig & Burdett (1976) reflect this with the frequent use of '?' symbols, and such a translocation misled Pooley (1965) into including the angulate tortoise (*Chersina angulata*) as part of the Natal herpetofauna. Many questionable records were deleted from the analysis to avoid possible skewing of reserve selection.

The presence of tortoises and terrapins in protected areas was determined from published and unpublished sources (see references in Table 1). Threatened species were taken to be those listed in the most recent South African Red Data Book (RDB) — Reptiles and Amphibians (Branch 1988b).

Data analysis for iterative reserve (IR) selection, congruence with existing protected areas, and hotspot analysis were performed with the geographic information system (GIS) ARC/INFO ver. 6.1.1 (Environmental Systems Research Institute, Redlands, California) using the methodology detailed in Lombard (1995). On some occasions, analyses were re-run with the removal of marginal records or those of questionable status.

Results and Discussion

Centres of diversity in southern Africa

All tortoises and terrapins

Generalized range maps for all southern African chelonians have been included in several recent popular guides to the subcontinent's reptiles (Branch 1988a; Boycott & Bourquin 1988). However, only one previous attempt has been made to prepare detailed point locality maps for the region's chelonians (Greig & Burdett 1976). This, however, was restricted to land tortoises and did not include freshwater terrapins (trionychids or pelomedusids) or sea turtles.

The final data base for pelomedusids and testudinids comprises a total of 1997 records. Individual species maps will be presented elsewhere in a fuller analysis of habitat association and zoogeography of southern African chelonians (Branch & Benn in prep.). Geographic coverage of chelonians in southern Africa is not uniform, and large areas have few or no chelonian records (Figure 2). For the central Kalahari regions and Namibia this reflects, in part, poor collecting, although it is also obvious that chelonian diversity is low in these regions. The paucity of records from Zimbabwe is an artefact as the large herpetological collections amassed by Dr Broadley in Zimbabwe and housed in Bulawayo were not incorporated.

Table 1 Chelonians recorded within major reserves in southern Africa

Species	Reserves	Reference
Geochelone pardalis	1, 2, 3, 4, 6, 10, 11, 12, 13, 14	a, b, c, d,
	15, 26, 27, 28, 36, 37, 38, 41, 42,	f, i, j, k,
	44, 45, 48, 49, 50, 51, 52, 53, 54,	l, p, q, v,
	55, 56, 58, 59, 61, 63, 64, 65, 66,	w, x
	67, 72, 73, 74, 76, 77, 78, 81, 83,	
	84, 85, 86	
Chersina angulata	2, 3, 5, 8, 26, 27, 28, 29, 30, 31,	b, c, e, h,
	36, 87	k, l, m, n,
		o, y
Homopus areolatus	3, 5, 8, 26, 30, 31, 32, 33, 34, 35	c, e, h, n, o
Homopus boulengeri	2, 36	b, k
Homopus signatus	7, 29	g, m
Homopus femoralis	2, 4, 26 (?)	b, d, j
Homopus sp.		
Kinixys belliana	9, 10, 11, 12, 13, 16, 17, 24	r, z
Kinixys spekii	1, 10, 37, 40, 42, 43, 44, 50, 72,	a, q, r
	73, 76, 77, 81, 82, 84, 85	
Kinixys lobatsiana	41, 44, 55	r
Kinixys natalensis	1, 14, 15, 45, 73, 74, 75	r
Psammobates tentorius	2, 26, 29, 36	b, j, m, p
Psammobates geometricus	31, 32, 33, 34, 35	o
Psammobates oculifer	6, 53, 55, 58, 59, 66, 69	q, s
Pelomedusa subrufa	1, 2, 3, 4, 5, 6, 8, 11, 12, 13, 14,	a, b, c, d,
	15, 18, 19, 20, 21, 27, 28, 36, 37,	e, f, h, i,
	38, 40, 41, 43, 44, 46, 47, 48, 49,	k, l, p, q,
	50, 51, 53, 55, 56, 57, 58, 59, 60,	v, w, x
	61, 62, 63, 65, 66, 67, 68, 72, 76,	
	83, 84, 86	
Pelusios sinuatus	1, 9, 10, 11, 12, 13, 14, 24, 37, 45,	a, i, q, v,
	49, 50, 73, 76, 77, 78, 79, 81, 82,	w, z
	83, 84, 85	
Pelusios subniger	1, 76, 77, 81, 84, 85	a, w
Pelusios castanoides	9, 10, 17, 24	i, w
Pelusios rhodesianus	9, 22, 23, 24, 25, 79	i, w
Pelusios bechuanicus	70, 71, 83	t, w

Reserve Legends

National Parks. 1, Kruger NP; 2, Karoo NP; 3, Addo Elephant NP; 4, Mountain Zebra NP; 5 , Bontebok NP; 6, Kalahari Gemsbok NP; 7, Richtersveld NP; 8, Langebaan NP.

Natal Reserves. 9, St Lucia GR; 10, Ndumu GR; 11, Mkuzi GR; 12, Hluhluwe GR; 13, Umfolozi GR; 14, Itala GR; 15, Weenen NR; 16, Kosi Bay NR; 17, Sodwana Bay NP; 18, Tugela Drift NR; 19, Umtamvuna NR; 20, Oribi Gorge NR; 21, Kranzkloof NR; 22, Bluff NR; 23, Charters Creek NR; 24, Mapelane NR; 25 Umlalazi NR.

Cape Reserves. 26 Anysberg NR; 27, Andries Vosloo Kudu and Sam Knott NR; 28, Thomas Baines NR; 29, Goegap NR; 30, De Hoop NR; 31, Elandsberg PNR; 32, Voelvlei NR; 33, J.N. Briers-Louw NR; 34, Harmony Flats NR; 35, Riverlands NR; 36, Karoo NR.

Transvaal Reserves. 37, Blydesrivierpoort NR; 38, Bronkhorstspruit Dam NR; 39, Cynthia Letty FR; 40, Jerico Dam NR; 41, Loskop Dam NR; 42, Lillie FR; 43, Nooitgedacht Dam NR; 44, Ohrigstad Dam NR; 45, Pongola NR; 46, Suikerbosrand NR; 47, Vaal Dam NR; 48, Doomdraai Dam NR; 49, Fanie Botha Dam NR; 50, Hans Merensky NR; 51, Hans Strydom Dam DR; 52, Happy Rest NR; 53, Langjan NR; 54, Messina NR; 55, Nylsvley NR; 56, Percy Fyfe NR; 57, Abe Bailey NR; 58, Barberspan NR; 59, Bloemhof Dam NR; 60, Boskop Dam NR; 61, Hartebeestpoort Dam NR; 62, Marievale NR; 63, Roodeplaat Dam NR; 64, Rustenburg NR; 65, Rust-der-Winter Dam NR; 66, S.A. Lombard NR; 67, Vaalkop Dam NR; 68, Wolwespruit NR.

Free State Reserves. 69, Sandveld NR.

Botswana Reserves. 70, Moremi WR; 71, Chobe NP.

Swaziland Reserves. 72, Hlane GR; 73, Mlawula NR; 74, Ndzindza NR; 75, Mbuluzi GR.

Zimbabwe Reserves. 76, Gonarezhou NP; 77, Chizariri NP; 78, Lake Kyle RP; 79, McIlwaine RP; 80, Matobo NP; 81, Matusadona NP; 82, Ngezi RP; 83, Victoria Falls - Zambezi NP; 84, Hwange NP; 85, Mana Pools NP.

Namibia Reserves. 86, Ethosha NP; 87, Sperrgebiet Diamond Area 1.

Reference legends

a, Pienaar, Haacke & Jacobsen 1983; b, Branch & Braack 1989; c, Branch & Braack 1987; d, Grobler & Bronkhorst 1981; e, Braack 1981; f, Haacke 1984; g, Branch, unpubl. obs.; h, G. Thomsett, unpubl. obs.; i, Bourquin 1990; j, Burger 1993; k, Burger unpubl obs.; l, Burger & Branch 1994; m, Branch, unpubl. obs; n, Hensley, pers. comm.; o, Baard 1993a; p, Branch, unpubl. obs.; q, Jacobsen, Newberry & Petersen 1986; r, Broadley 1993; s, Bates 1992; t, Auerbach 1987; u, Broadley 1981; v, Boycott 1993; w, Broadley & Blake 1979; x, Hoffmann 1989; y, Branch 1994; z, Haagner & Els 1986.

However, only two testudinids (*Kinixys spekii* and *G. pardalis*) are widespread in the country, although a number of pelomedusids (e.g. *Pelomedusa subrufa* and *Pelusios sinuatus*) are also common.

Despite these collection artefacts, it is evident that one large, well-collected region is depauperate in chelonians. It extends through the eastern regions of the Eastern Cape (Transkei), Lesotho, the KwaZulu-Natal midlands, north-eastern Free State and the North West Province. The only species occurring in this large region, albeit known from only a few isolated records, is the Cape terrapin (*Pelomedusa subrufa*). The absence of major river systems precludes other terrapins (*Pelusios* spp.), but it is not obvious why land tortoises should be absent. Although a large part of the region is montane grassland, the mountain tortoise (*G. pardalis*) occupies similar habitat in the southern Free State, and its absence in the lowlands of the old Transkei region is inexplicable. Local extinction, via human agency, is possible as mountain tortoise are known to have been readily eaten by early man. Although Greig & Burdett (1976) considered tortoises to be '...now extinct in the Transkei, and nearly so in Lesotho', there is no supportive evidence that they were either present throughout the region, or that any extinctions resulted directly, or even indirectly, from anthropomorphic factors.

Insight into the topic may be gained from studies at archaeological sites. Although tortoise remains are often noted in reports of faunal assemblages from such sites, they are rarely determined to species level. In a noteable exception, during study of two sites (Edgehill and Welgeluk) on the Konaap River near Adelaide in the Eastern Cape, Hall (1990) recorded four taxa (*G. pardalis, Pelomedusa subrufa, C. angulata* and *Homopus areolatus*) in levels from 6000 years BP to the present. Tortoises were present in numbers inversely related to their size (which may be a reflection of the ease of transport and/or the amount of meat present on a carcass). All four species are still common in the region. Further north, on the border of the area presently lacking tortoises, Welbourne (in Derricourt 1977) analysed faunal

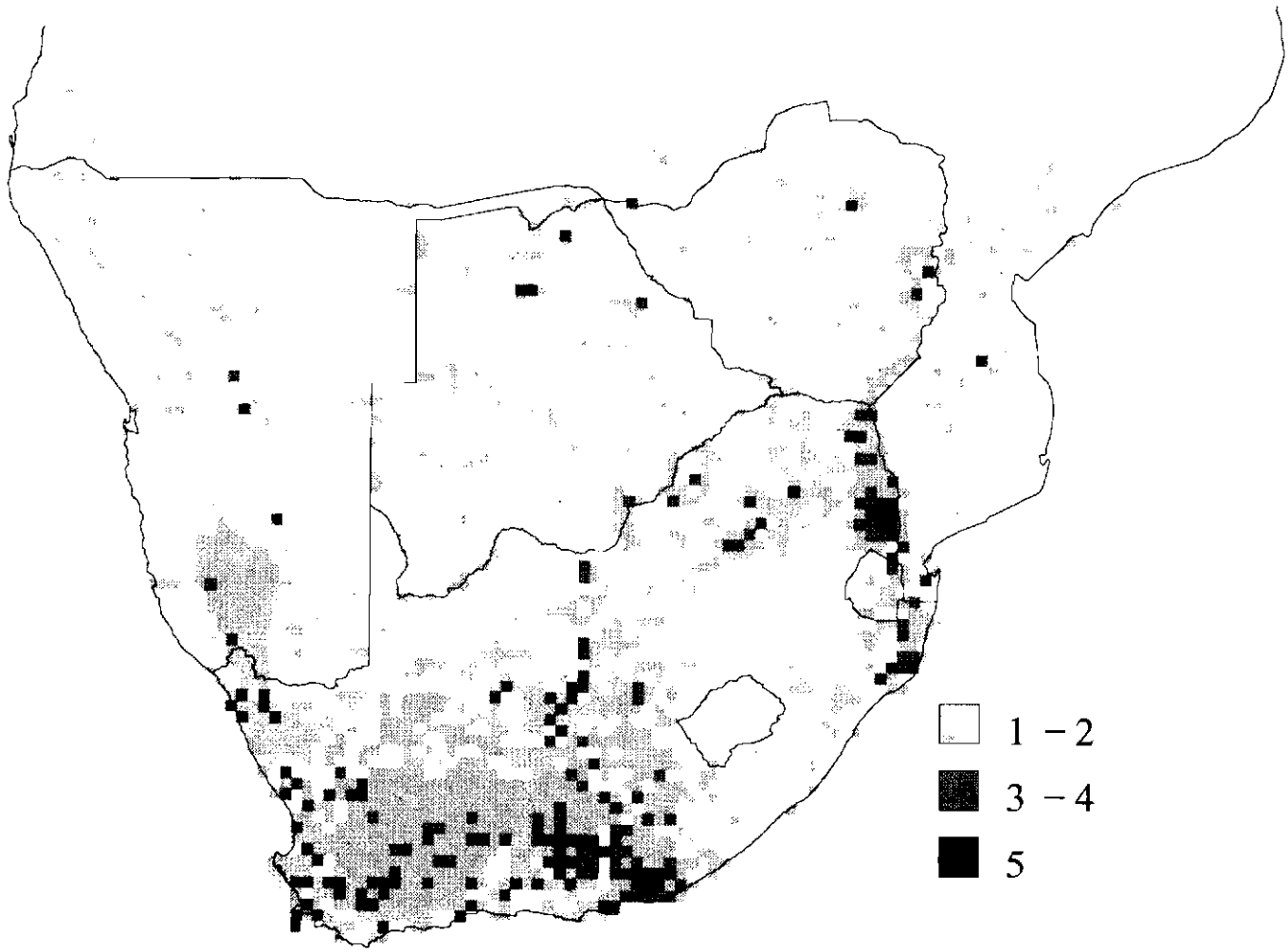

Figure 2 Density map showing areas of land tortoise and pelomedu-sid terrapin species richness in southern Africa.

remains from a late Stone Age site at Oakleigh, near Queenstown, recording *Testudo* sp. (probably *Geochelone*) shell fragments only from recent strata (levels 3 and 4, 500–400 years BP). The paucity and even absence of chelonian remains in archaeological sites in the tortoise-free area is confirmed by other studies. At the Sehonghong Rockshelter (29°44'S; 29°47'E, Qacha's Nek District, western Lesotho) only a single tortoise fragment was noted in a layer dating from 1400±50 BP. No tortoise remains occurred in older layers, *c.* 7000 to 32000 BP. At two other large sites in eastern Lesotho no tortoises were recovered from levels broadly contemporary with the upper Sehonghong specimen (Carter, Mitchell & Vinnicombe 1988). Similarly, only two tortoise fragments were found from a layer dated to 6140±100 BP at Tloutle (29°28' S; 27°46'E) in north-western Lesotho (Mitchell 1993a), and only a single fragment from 260 to 330 BP was found at Hololo Crossing (28°44'S; 28°27'E) (Mitchell, Parkington & Yates 1994). In the same paper, a fairly large faunal assemblage from the site Bolahla (30°04'S; 28°24'E; at the confluence of the Bolahla River and the Senqu/Orange River) contained no tortoises at all. The few tortoise remains in all these sites may be San hunter-gatherer artefacts as tortoise carapaces were used as bowls and a fragment from such an artefact would be indistinguishable from an animal eaten and discarded. Artefacts could be traded in from quite a distance and thus not be representative of the immediate site catchment (Yates, pers. comm).

The only Lesotho site from which tortoise records are too numerous to be artefacts is Ntloana Tsoana in north-western Lesotho (29°19'S; 27°49'E) where 58 unidentified tortoise fragments were collected from four levels dated to between 8780±80 BP and 12110±120 BP (Mitchell 1993b). Their identity was undetermined, however, and they may be referable to the terrapin *Pelomedusa subrufa*, which is known from the area. In the eastern Free State, Plug & Engela (1992) recorded no chelonians in their detailed study of the Rose Cottage Stone Age site near Ladybrand, whilst Esterhuysen, Behrens & Harper (1994) recorded only a few tortoise pieces from the Leliehoek Shelter, another Holocene sequence from the eastern Free State. Unfortunately, the latter are not specifically identified. Together these archaeological records support the historical absence of tortoises in the region until at least 32000 BP, and do not support Greig & Burdett's (1976) contention that tortoises in the region were exterminated. Studies on archaelological sites in lowland regions of the Transkei, however, are required to confirm the situation throughout the region. Although Greig & Burdett (1976) also considered the mountain tortoise to '... have been exterminated in the western Cape coastal areas, largely for food', this again remains conjecture. *Chersina angulata* remains are common in archaeological sites from the western Cape, but *G. pardalis* has not been identified (Klein, pers. comm.), and

there is therefore no confirmation that the species was previously present.

Within the subcontinent two general epicentres of chelonian diversity are evident (Figure 2). The first, centred in the lowveld regions of the Eastern and Northern Transvaal and northern Maputaland, includes both tortoises and terrapins. Previous analysis (Greig & Burdett 1976) considered the region relatively depauperate in testudinid diversity, but the recent study by Broadley (1993) recognizes four species of southern African hingeback tortoises whereas only a single species was thought to be present by Greig & Burdett (1976). Both the Kruger National Park and Northern Transvaal localities with five taxa include the two common pelomedusids (*Pelomedusa subrufa* and *Pelusios sinuatus*). Only a single pelomedusid enters the Cape provinces, and the high tortoise diversity in this second epicentre results from a dramatic radiation in testudinids. Of these, only the mountain tortoise is not endemic to the subcontinent. Numerous QDSs record the presence of five taxa, but the Cape terrapin is present in all with varying arrangements of four testudinids. These are discussed in fuller detail in the following section.

Endemic species

Chelonian endemicity is mainly restricted to the Cape region (Figure 3), where the testudinid genera *Chersina, Homopus* and *Psammobates* have their evolutionary centre. Along with Madagascan *Pyxis*, these are considered the most derived testudinid lineages (Gaffney & Meylan 1988). The rich chelonian diversity in the Kruger National Park region comprises wide-ranging species with tropical affinities (e.g. *G. pardalis*, *K. spekii*, and *Pelusios* spp.). Their exclusion leaves only two endemic testudinids (*Kinixys lobatsiana* and *K. natalensis*), which have mutually exclusive ranges in the west and east of the Transvaal, respectively. The two species are not sister taxa within *Kinixys; K. lobatsiana* shows affinities with *K. belliana* and the Central and West African forest species *K. erosa* and *K. homeana*, whilst *K. natalensis* is more similar to *K. spekii* (Broadley 1993).

Within the Cape provinces, the ranges of the three *Psammobates* species are mainly exclusive, with *P. geometricus* restricted to the south-western Cape, and *P. oculifer* occurring north of the Orange River. The geometric tortoise lives in well-established sympatry with two other tortoises (*C. angulata* and *H. areolatus*) in a number of sites in the southern Western Cape (Figure 3; Beard 1990). The only well-established region of sympatry within *Psammobates* occurs between *P. tentorius* and *P. oculifer* in West Griqualand (Power 1932). As Grieg & Burdett (1976) noted, the record of *P. oculifer* from the Aus region (Mertens 1955), where it would occur in sympatry with *P. t. verroxii*, should be treated with circumspection, as no recent records confirm the presence of this species in the area. Similarly, a number of other species also reputed to have been collected at Aus (Mertens 1955), e.g. *H. signatus* and *C. angulata*, have not been subsequently collected in the region.

The angulate tortoise (*C. angulata*) is distributed in a wide belt through coastal habitats from East London to the Orange River, with scattered inland populations. These probably represent relict populations surviving in moister, more vegetated habitats associated with localized high rainfall in the escarp-

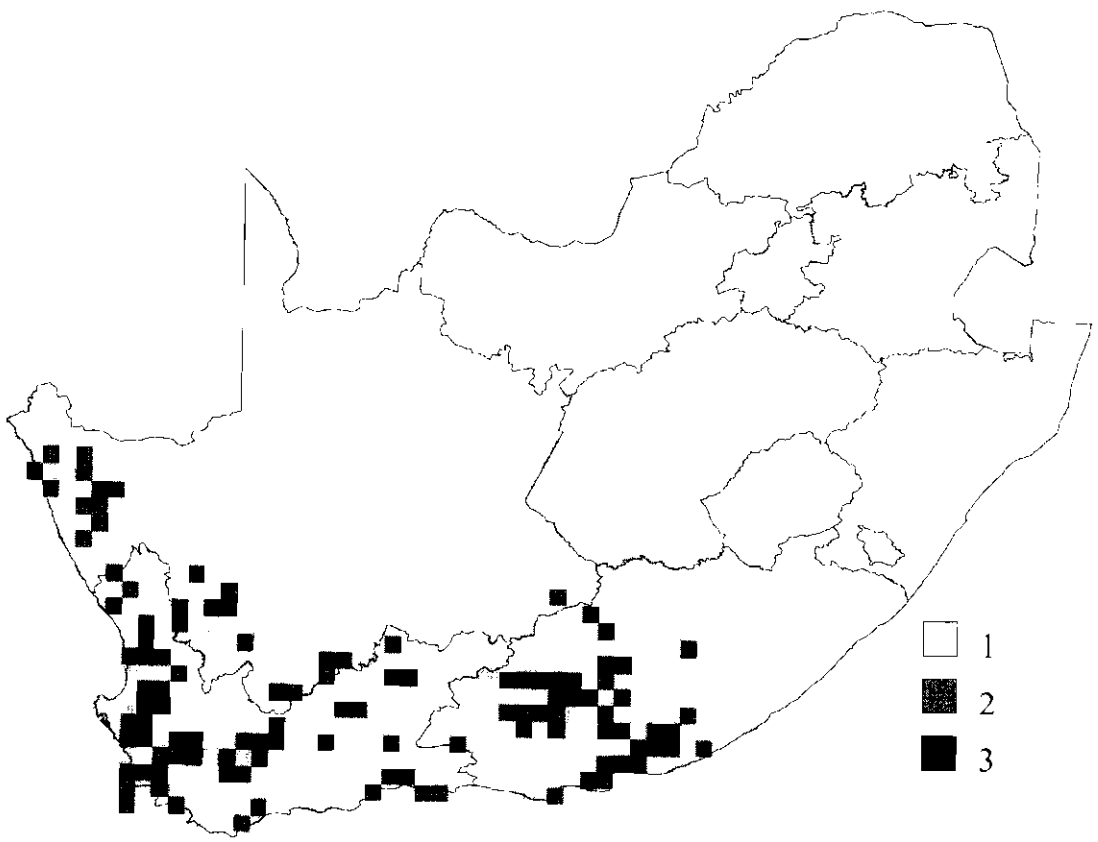

Figure 3 Density map showing areas of endemic land tortoise and pelomedusid terrapin species richness in South Africa.

ment mountains (Branch 1990). The species occurs in high densities in many Cape coastal regions (Branch 1984), and is commonly translocated as a pet (e.g. Pooley 1965). Many isolated northern records in Namibia (Greig & Burdett 1976) probably arise in similar fashion, and the most northerly confirmed record is within the northern part of the Obib dune sea in the southern Sperrgebiet (Branch 1994). The species has also been introduced and subsequently formed large populations on a number of offshore islands, e.g. Dyer and Dassen islands (Branch 1991).

With the exception of Griqualand *Psammobates*, the only other regions of sympatry between congeneric tortoises involve padlopers (*Homopus* spp.). Greig & Burdett (1976) note the extension of the range of the parrot-beaked tortoise (*H. areolatus*) inland into the Cradock region, where it overlaps the range of the greater padloper (*H. femoralis*). However, these species do not occur syntopically, *H. femoralis* being restricted to montane grassland on the summit plateaus whilst *H. areolatus* occurs in relict populations inhabiting the well-vegetated lower slopes. The presence of *C. angulata, Psammobates tentorius, G. pardalis* and *Pelomedusa subrufa* in the region means that it is theoretically possible to find up to six chelonians in a single QDS, although only five have as yet been recorded. A similar mixture of relict, montane, and mesic- and xeric-adapted species occurs in the Karoo National Park, Beaufort West. The park straddles the arid southern plain of the Great Karoo, and the foothills and summit plateau of the Nuweveld Mountains. The mosaic of habitats generated by edaphic and elevational variation, including localized high rainfall on the summit plateau, supports a rich chelonian fauna including six species (Branch & Braack 1989). These are identical to those found around Cradock, with the exception that *H. areloatus* does not occur as a mesic-adapted relict, but is replaced on the dolerite outcrops by *Homopus boulengeri*. The presence of another relict population of *H. areolatus* in the poorly surveyed region on the Roggeveld Mountains around Middelpos (Greig & Burdett 1976), may reflect another minor centre of diversity.

Two specimens of *H. boulengeri* (PEM specimens 3976 & 3981) from the Hantam Mountains, north-west of Calvinia (3119BC) represent new distribution records for the species and are the first records of sympatry between this species and the speckled padloper (*H. signatus*). Greig & Burdett (1976) discuss confusion over a *H. boulengeri* specimen doubtfully recorded from Piketberg (3218DC), whilst Mertens' (1955) report of both species from the Aus area in southern Namibia can also be discounted. The records of *H. boulengeri* are now known to be referable to a new species (Branch 1992), whilst the *H. signatus* specimen appears to have been obtained from elsewhere. Reported sympatry between *H. signatus* and *H. boulengeri* in the Calvina region is of importance, as these sister species are sometimes placed in a separate subgenus *Chersobius* (Cooper & Broadley 1990), and have similar ecologies. The presence of *C. angulata* and *P. tentorius* in the Hantam Mountains indicates another minor centre of diversity in the western escarpment region.

Threatened species

A map of the distributions of RDB species (Figure 4) shows a single 'hotspot' in Natal. This results from the inclusion of

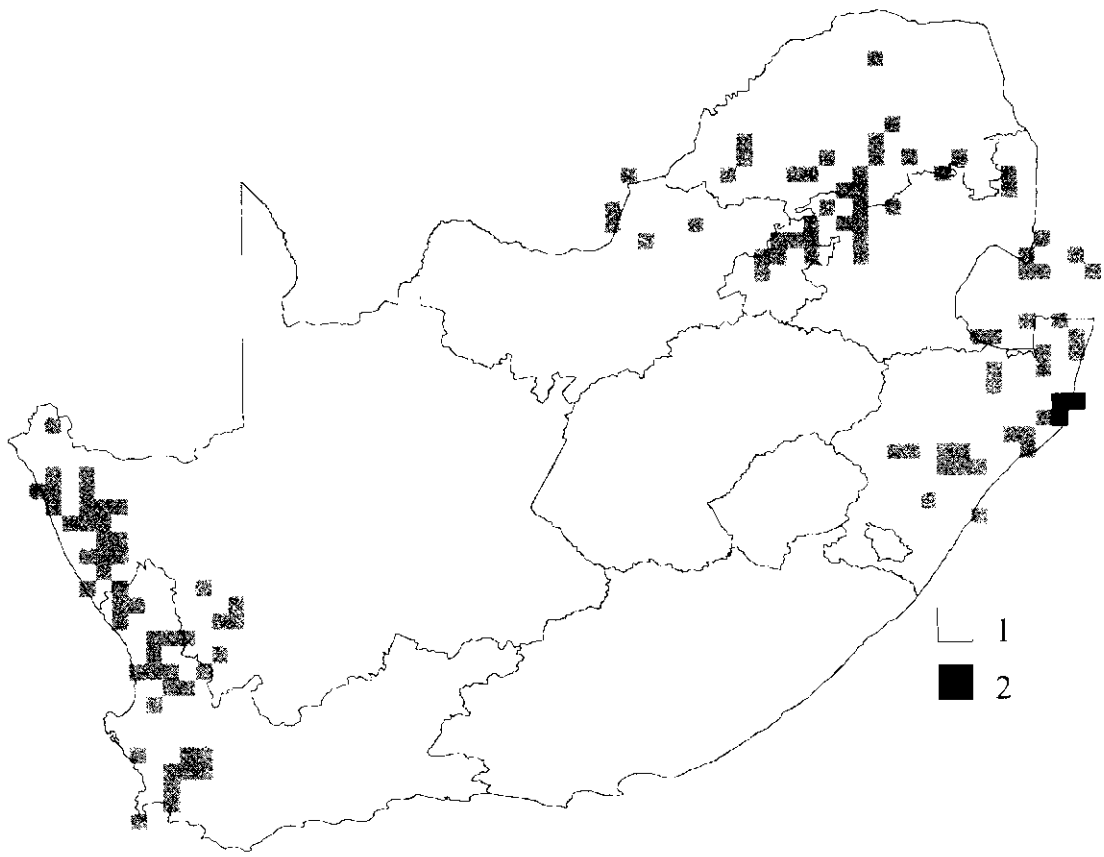

Figure 4 Density map showing areas of threatened land tortoise and pelomedusid terrapin species richness in South Africa.

two terrapins (*Pelusios castanoides* and *P. rhodesianus*). However, both are listed only as 'Peripheral' in the RDB and have large distributions in Mozambique, and Mozambique and northern Zimbabwe, respectively, throughout most of which they are unthreatened. The remaining species, *Psammobates geometricus* (Endangered), *K. natalensis* (Rare) and *Homopus signatus cafer* (Restricted), have non-overlapping ranges. Analysis of the distributions of all species, including RDB species, was performed at the species level resulting in the full range of *H. signatus* being illustrated. In fact, the race *H. signatus cafer* has a much more restricted range and is restricted to the the Picketberg-Klawer region (Boycott 1986). The conservation of the geometric tortoises has been well addressed (Beard 1990, 1993a, b), and it is well protected in all possible existing reserves in the south-western Cape.

Table 2 The eight iterative reserves that protect all Southern African land tortoises and pelomedusid terrapins

Number	QDGS	Species protected
1	2832AD	*Kinixys belliana (belliana), Pelusios rhodesianus, Pelusios castanoides, Pelusios sinuatus*
2	2716DD	*Chersina angulata, Psammobates tentorius (verroxii), Homopus* sp. nov *('bergeri')*
3	3319CB	*Homopus areolatus, Psammobates geometricus, Pelomedusa subrufa*
4	1823DA	*Pelusios subniger, Pelusios bechuanicus*
5	2431DA	*Kinixys spekii, Geochelone pardalis (babcocki), Kinixys natalensis*
6	3119BC	*Homopus boulengeri, Homopus signatus*
7	2425DB	*Psammobates oculifer, Kinixys lobatsiana*
8	2823CC	*Homopus femoralis*

Subspecies shown in brackets

Southern African tortoises and terrapins in existing reserves

The results of a survey of tortoises and terrapins in existing protected areas in southern Africa is summarized in Table 1. Relatively few protected areas have prepared faunal inventories of the species they are designed to protect. Siegfried (1989) notes the presence of 582 statutory nature reserves in South Africa alone, but we were able to find reports (published and unpublished) of chelonians in only 87 southern African reserves (i.e. less than 15%). Despite this poor documentation, however, it is evident that most species are already recorded from at least one exisiting protected area (Table 1). Ideally, for maintenance of genetic diversity and protection from localized disasters (natural and man-induced), all species should be protected in a number of separated reserves (populations). Tortoises and terrapins recorded from only a few reserves (number shown in brackets) include: *H. boulengeri* (2); *H. femoralis* (3); *Homopus* sp. (0); *K. lobatsiana* (3); *Psammobates tentorius, Pelusios castanoides* (4) and *P. bechuanicus* (3).

Iterative reserves

A total of eight iterative reserves (IRs) were determined to represent all southern African non-trionychid chelonians at least once. These, along with the species they 'protect', are detailed in Table 2, and their distribution shown in Figure 5.

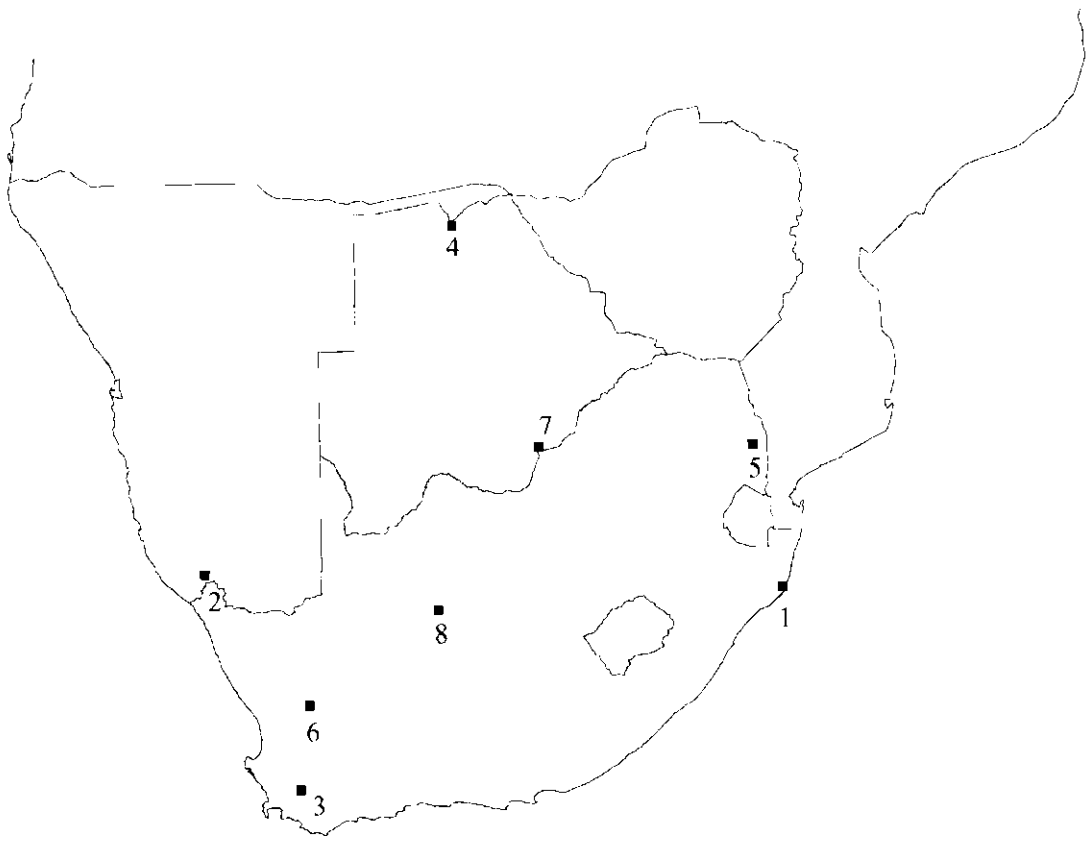

Figure 5 Distribution of Iterative Reserves conserving all land tortoises and pelomedusid terrapins in southern Africa.

Table 3 Existing reserves falling within selected Iterative Reserves

Reserve	Existing Reserve	Owner
1 (2832AD)	Mhlatuze State Forest	Natal Parks Board
	Mihobi Nature Res.	State Forest (KwaZulu)
	Hell's Gate Military Area	National Defence Force
	Cape Vidal State Forest	Natal Parks Board
	Dukuduku State Forest	Natal Parks Board
	Mapelane Nat. Res.	Natal Parks Board
	Nyalazi State Forest	Natal Parks Board
	St. Lucia Game Reserve	Natal Parks Board
2 (2716DD)	No reserves	
3 (3319CB)	Matroosberg State Forest	Western Cape Nat. Cons.
	Karoo Nat. Botanical Garden	Nat. Botanical Gardens
4 (1823DA)	No reserves	
5 (2431DA)	Kruger NP	National Parks Board
	Manyeleti Game Reserve	N.Tvl Environment and Tourism
	Sabie-Sand Game Reserve	?
6 (3119BC)	Akkerendam Nat. Res.	Local authority: Calvinia
7 (2425DB)	No reserves	
8 (2823CC)	No reserves	

Existing protected areas falling within the same QDS as an IR are listed in Table 3.

It is desirable that reserve selection analysis should be restricted to localities taken from within the centre of a species' range. This was not done in the present study. Isolated or peripheral records may not represent viable populations, and are more likely to represent translocated specimens or inaccuracies in distribution data. In addition, marginal populations may not protect maximum genetic diversity for the species concerned.

With these caveats in mind, how well do the determined IRs (Table 2) protect the species under discussion?

IR 1 (2832AD)

No less than eight protected areas fall within the IR, and the four species targeted for protection by the IRs (i.e. *Kinixys belliana* (*belliana*), *Pelusios rhodesianus*, *P. castanoides*, and *P. sinuatus*) are all recorded from at least one of these reserves (Table 1). The conservation status of these species in the area is considered good.

IR 2 (2716DD)

As the IR is not in South Africa, no statutory protected reserves are listed in the data base as occurring in the QDS. However, the region borders the southern Sperrgebiet, a wilderness region currently inaccessible owing to mining activites, but that is under consideration for proclamation as a Namibian reserve. Of the three species that the IR is targeted to protect [i.e. *C. angulata*, *Psammobates tentorius* (*verroxii*), and *Homopus* sp. nov ('bergeri')], the population of *C. angulata* is at least marginal and may even be a translocation (Branch 1994). The IR is also marginal for the new *Homopus* sp. (whose main distribution is centred around Aus), and protects only the northern race (*P. t. verroxii*) for the tent tortoise.

IR 3 (3319CB)

Although targeted for three species (i.e. *H. areolatus*, *Psammobates geometricus*, and *Pelomedusa subrufa*), the proposed IR is now only marginal for the endangered geometric tortoise. Although three existing protected areas fall within the QDS it contains none of the four viable reserves for this species listed by Baard (1993a). It does, however, contain viable populations for the remaining target species, as well as the angulate tortoise (*C. angulata*).

IR 4 (1823DA)

The IR is extralimital but borders protected areas in northern Botswana, i.e. Moremi WR and Chobe NP, from which one of the targeted terrapins (*Pelusios bechuanicus*) is recorded. Viable populations of the other target species, *Pelusios subniger*, are protected in numerous Zimbabwe reserves (Table 1).

IR 5 (2431DA)

Fortunately the QDS contains three well-established reserves (e.g. Kruger NP) from which all three target species (i.e. *K. spekii*, *G. pardalis* (*babcocki*), and *K. natalensis*) have been recorded. However, the IR is marginal for *K. spekii* and protects only the northern race (*G. p. babocki*) of the mountain tortoise.

IR 6 (3119BC)

The only existing reserve (Akkerendam NR) in the QDS belongs to a local authority. The IR is marginal for both target species (i.e. *H. boulengeri* and *H. signatus*) and, moreover, protects only an intergrade population between the two races of *H. signatus* (Boycott 1986)

IR 7 (2425DB)

No existing protected areas occur in the QDS. The IR is well situated for conserving the Kalahari tent tortoises (*Psammobates oculifer*), but is unsuitable for *K. lobatsiana* as it occurs at the western extreme of its range.

IR 8 (2823CC)

No existing protected areas occur in the QDS, and the IR is also marginal for the greater padloper (*H. femoralis*), occurring at the western limit of northern populations.

What new reserves are required to fully protect southern African chelonians?

If marginal locality records are not excluded from the iterative reserve selection analysis, the analysis is often biased. This is particularly problematic with tortoises that show little sympatry among congeneric species. As noted earlier, the ranges of the three species of *Psammobates*, four hingeback tortoises (*Kinixys* spp.), and five *Homopus* species are mainly allopatric, with only marginal overlap with that of congeners. However, it is these areas (as illustrated by the selection of IRs 5 and 6) that are preferentially selected by the algorithm in its search to minimize the number of IRs required to fully protect members of the group.

Of the eight IRs selected to conserve the 20 species of southern African land tortoises and pelomedusid terrapins, only the first (QDS 2832AD) can be considered ideally situated to protect all four target species. The remaining seven IRs only poorly protect their target species, either including peripheral populations or conserving only limited genetic diversity within the species (particularly in polytypic species). In addition, the IRs 2, 4, 7 and 8 have no existing protected

Table 4 Existing major reserves protecting the majority of southern African land tortoises and pelomedusid terrapins

Reserve	Species protected (M = marginal)
Karoo National Park	*Homopus femoralis, H. boulengeri, Geochelone pardalis, Psammobates t. tentorius, Pelomedusa subrufa, Chersina angulata (M)*
Elandsberg PNR*	*Psammobates geometricus, Homopus areolatus, Chersina angulata*
St Lucia Game Reserve	*Kinixys belliana, Pelusios castanoides, P. rhodesianus, P. sinuatus*
Kruger National Park	*Kinixys natalensis, K. spekii (M), Geochelone pardalis, Pelusios sinuatus, P. subniger, Pelomedusa subrufa*
Goegap Nature Reserve	*Homopus s. signatus, Psammobates tentorius trimeni*
Kalahari Gemsbok NP	*Psammobates oculifer*
Moremi Wildlife Reserve	*Pelusios bechuanicus, P. subniger*

*Private nature reserve, but the largest and only viable population of the endangered geometric tortoise.

reserves within their borders. Analysis of Table 1 reveals that most species are already adequately protected in existing reserves, of which only seven are required to conserve 17 (85%) of the region's tortoises and terrapins (Table 4). The outstanding species, not protected in these reserves, are given below.

Kinixys lobatsiana

The species is currently recorded from only three reserves, including Loskop Dam NR, Nylsvley NR, and Ohrigstad NR (Table 1). Twenty-seven of the other QDS recorded for this species include (at least in part) a number of statutory protected areas, of which the most important (over 10 000 ha) are: Kransberg National Park (2427CB, National Parks Board, NPB) and Blyde River Canyon NR (2430DA, Eastern Transvaal Nature Conservation). The latter is at the extreme east of the species range.

Homopus sp.

A new species restricted to the highlands around Aus, and isolated rocky mountains in the Namib Desert near Luderitz, where the species is currently afforded protection in the northern parts of the Sperrgebiet. Proclamation of a reserve in the Aus vicinity would safely protect this species, as well as the northern race (*P. t. verroxii*) of the tent tortoise.

Within the Cape, the following two endemic species are relatively poorly protected.

Homopus boulengeri

Currently recorded only from the Karoo NP (NPB) and Karoo NR (Eastern Cape Nature Conservation).

Homopus signatus

Currently recorded from the Goegap NR (Northern Cape Nature Conservation) and Richtersveld NP (NPB). Only a single record is known from the latter, where its presence is also marginal.

In order to identify a more appropriate set of reserves, we recommend that, (i) all species currently protected, and (ii) all marginal locality records, should be excluded from the database. A re-run of the iterative algorithm would then provide more appropriate recommendations for the protection of currently unprotected species.

Final comments

This study has shown that the rich chelonian fauna of southern Africa is relatively well protected in existing reserves. The small number of chelonian species in southern Africa and their relatively well-known distributions test the efficacy of the iterative algorithm developed by Rebelo & Siegfried (1992). Owing to the presence of many allopatric (or nearly so) congeneric testudinid species, many of the selected reserves protect only peripheral populations. Seven of the eight iterative reserves selected by the algorithm were considered unsuitable to protect the target species. By their nature these may represent relict, non-viable populations in decline, owing to either natural or man-induced environmental changes. They may also more readily represent translocations or mistakes in the recording of distributional data. Peripheral populations may also partially protect genetic diversity within a species, particularly where polytypic species are involved. This aspect was compounded in the iterative reserve analysis which was performed only at the species level. We recommend that peripheral populations of all species should be excluded from iterative reserve selection procedures.

The study revealed that several tortoise species are inadequately protected. These include two Cape endemic padloper species (*H. signatus* and *H. boulengeri*) which are amongst the smallest extant testudinids and which are subject to increasing illegal collecting for the international pet trade. It is recommended that consideration be given to proclaiming further reserves in the succulent Karoo biome.

Acknowledgements

We thank Dr O. Bourquin (Natal Parks Board), Marius Burger (Eastern Cape Conservation), and Jenni Hensley (Western Cape Conservation) for information relating to chelonians in reserves in their regions. Wulf Haacke supplied locality data for *Pelomedusa* in the Transvaal Museum collection, and Gerald Haagner willingly analysed data in the PEM herpetological database. Denise Drinkrow extracted data from the SAM database. The SAM collection incorporates the former herpetological collection of Cape Nature Conservation, which is gratefully acknowledged. Professor R. Klein (Stanford), Dr R. Yates (University of Cape Town) and Dr Simon Hall (University of the Witwatersrand) quickly answered queries relating to tortoise remains in archaeological sites. ATL and GAB acknowledge financial support from the Department of Environmental Affairs and Tourism, and the Foundation for Research Development.

References

AUERBACH, R. D. 1987. The Amphibians and Reptiles of Botswana, Mokwepa Consultants (privately published), Gaborone, 295 pp.

AUFFENBERG, W. 1974. Checklist of fossil land tortoises (Testudinidae). *Bull. Fla St. Mus.* 18: 120–251.

BAARD, E. H. W. 1990. Biological aspects and conservation status of the geometric tortoise, *Psammobates geometricus* (Linaeus, 1758) (Cryptodira: Testudinidae). Ph.D. thesis, University of Stellenbosch.

BAARD, E.H.W. 1993a. A conservation strategy for the geometric tortoise, *Psammobates geometricus*, in the south-western Cape Province, South Africa. Internal report 11, Cape Nature Conservation, Stellenbosch, 64 pp.

BAARD, E.H.W. 1993b. Distribution and status of the geometric tortoise, *Psammobates geometricus*, in South Africa. *Biol. Conserv.* 63: 235–239.

BATES, M.F. 1992. The herpetofauna of the Orange Free State, with special emphasis on biogeographical patterning. M.Sc. thesis, Univ. Natal, 420 pp.

BAUER, A.M., BRANCH, W.R. & HAAKE, W.D. 1993. The herpetofauna of Kamanjab and adjacent Damaraland, Namibia. *Madoqua* 18: 117-145.

BOUR, R.H. 1983. Trois populations endémiques du genre *Pelusios* (Reptilia, Chelonii, Pelomedusidae) auxîles Seychelles; relations avec les espèces africaines et malagaches. *Bull. Mus. natn. Hist. nat. Paris 4 ser.* 5(A1): 343–382.

BOUR, R.H. 1986. Note sur *Pelusios adansonii* (Schweigger, 1812) et sur une nouvelle espece affine du Kenya (Chelonii, Pelomedusidae). *Stud. Palaeochelon.* 2: 23–54.

BOUR, R.H. 1988. Taxonomic and nomenclatural status of *Homopus signatus* (Gmelin 1789): Reptilia: Chelonii. *J. Herpetol. Assoc. Afr.* 35: 1–6.

BOURQUIN, O. 1990. Presence, distribution, population sizes, survival requirements, threats to and importance values of chelonids in Natal. Internal report, Natal Parks Board, 50 pp.

BOURQUIN, O. 1991. A new genus and species of snake from the Natal Drakensberg, South Africa. *Ann. Transvaal Mus.* 35: 199–203.

BOYCOTT, R.C. 1986. A review of *Homopus signatus* (Schoepff) with notes on related species (Cryptodira: Testudinidae). *J. Herpetol. Assoc. Afr.* 32: 10–16.

BOYCOTT, R.C. 1989. Species status reports (*Homopus boulengeri, H. signatus,* and *Psammobates oculifer*). pp 78–79, 82–84, 88–90. In: The Conservation Biology of Tortoise, (eds.) I.R. Swingland and M.W. Klemens, Occ. Pap. IUCN Species Survival Commission (SSC) 5.

BOYCOTT, R.C. 1993. A herpetofaunal survey of Swaziland. M.Sc. thesis, Univ. Natal, 175 pp., 43 figs.

BOYCOTT, R.C. & BOURQUIN, O. 1988. The South African Tortoise book. A guide to South African tortoises, terrapins and turtles. Southern Book Publ., Johannesburg, 148 pp.

BRAACK, H.H. 1981. Lower vertebrates of the Bontebok National Park. *Koedoe* 24: 67–77.

BRANCH, W. R. 1984. Preliminary observations on the ecology of the angulate tortoise (*Chersina angulata*) in the Eastern Cape Province, South Africa. *Amphibia-Reptilia* 5: 43–55.

BRANCH, W.R. 1988a. Field guide to the snakes and other reptiles of southern Africa, Struik Publishers, Cape Town, 326 pp.

BRANCH, W.R. (Ed.). 1988b. South African Red Data Book — Reptiles and Amphibians. *S. Afr. Nat. Sci. Prog. Rep.* 151, 241 pp.

BRANCH, W.R. 1989. Species Status reports (*Chersina angulata, Homopus areolatus, H. bergeri, H. femoralis,* and *Psammobates tentorius*). pp 68–77, 91–93. In: The Conservation Biology of Tortoise, (eds.) I. R. Swingland and M.W. Klemens, Occ. Pap. IUCN Species Survival Commission (SSC) 5.

BRANCH, W.R. 1990. Herpetofauna of the Cape Province, South Africa: New distribution records and zoogeography. *J. Herpetol. Ass. Afr.* 37: 17–44.

BRANCH, W.R. 1991. The herpetofauna of the offshore islands of South Affica. *Ann. Cape Prov. Mus.* 18: 205–225.

BRANCH, W.R. 1992. *Homopus 'bergeri'* — A wrong name for a new tortoise from southern Namibia (abst.). In: Proc. 2nd HAA conference. (Eds.) W.R. Branch, G.V. Haagner and R.C. Boycott. *J. Herpetol. Assoc. Afr.* 40: 11.

BRANCH, W.R. 1994. Herpetofauna of the Sperrgebeit region of southern Namibia. Herpetol. Na,t. Hist. 219: i-ii.

BRANCH, W.R. & BRAACK, H.H. 1987. The reptiles and amphibians of the Addo Elephant National Park. *Koedoe* 30: 61–112.

BRANCH, W.R. & BRAACK, H.H. 1989. Reptiles and Amphibians in the Karoo National Park: A surprising diversity. In: Proceedings of the First H.A.A. Conference, (ed.) W.R. Branch. *J. Herpetol. Ass. Afr.* 36: 26–35.

BROADLEY, D.G. 1981. A review of the of the genus *Pelusios* Wagler in southern Africa (Pleurodira: Pelomedusidae). *Occ. pap. Natl. Mus. Rhod. B. Nat. sci.* 6: 633–686.

BROADLEY, D.G. 1989. Species Status reports (*Geochelone pardalis*, pp. 43– 44; *Kinixys* sp., pp. 49–61). In: The Conservation Biology of Tortoise, (eds.) I.R. Swingland and M.W. Klemens, Occ. Pap. IUCN Species Survival Commission (SSC) 5.

BROADLEY, D. G. 1990. FitzSimons' Snakes of southern Africa. rev. ed. Delta Books, Johannesburg, 376 pp. + 10 pp. addendum.

BROADLEY, D.G. 1993. A review of the southern African species of *Kinixys* Bell (Reptilia: Testudinidae). *Ann. Transvaal Mus.* 36: 41–52.

BROADLEY, D.G. 1994. The genus *Scelotes* Fitzinger (Reptilia: Scincidae) in Mozambique, Swaziland and Natal, South Africa. *Ann. Natal Mus.* 35: 237– 259.

BROADLEY, D.G. & BLAKE, D.K. 1979. A check list of the reptiles of the national parks and other conservation areas of Zimbabwe Rhodesia. *Arnoldia Rhod.* 8(35): 1–15.

BURGER, M. 1993. The herpetofauna of Anysberg Nature Reserve, Cape Province, South Africa. *J. Herpetol. Assoc. Afr.* 42: 1–12.

BURGER, M. & BRANCH, W.R. 1994. Tortoise mortality caused by electrified fences in the Thomas Baines Nature Reserve, Eastern Cape. *S. Afr. J. Wildl. Res.* 24: 32–37.

CARTER, P.L., MITCHELL, P.J. & VINNICOMBE, P. 1988. Sehonghong: The Middle and Later Stone Age industrial sequence at a Lesotho rock-shelter. BAR International Series 406, Oxford

COOPER, M.R. & BROADLEY, D.G. 1990. A new species of fossil *Homopus* (Cryptodira: Testudinidae) from South Africa. *Stud. Palaeochelon.* 2: 41–55.

DERRICOURT, R.M. 1977. Prehistoric Man in the Ciskei and Transkei, C. Struik, Cape Town. 284 pp.

ESTERHUYSEN, A. B., BEHRENS, J. & HARPER, P. 1994. Leliehoek Shelter: a Holocene sequence from the eastern Orange Free State. *S. Afr. Archaeol. Bull.* 49: 73–78.

FRAZIER, N.B. 1992. Sea turtle conservation and halfway technology. *Conserv. Biol.* 6: 1791–84.

FROST, D.R. & HILLIS, D.M. 1990. Species in concept and practise: Herpetological applications. *Herpetologica* 46: 87–104.

GAFFNEY, E.S. & MEYLAN, P.A. 1988. A phylogeny of turtles. pp. 157–219. In: The Phylogeny and Classification of the Tetrapods. Vol. 1., (Ed) M.J. Benton, Clarendon Press, Oxford.

GREIG, J. C. & BURDETT, P.D. 1976. Patterns in the distribution of southern African terrestrial tortoises. *Zool. Afr.* 11: 249–273.

GROBLER, J. H. & BRONKHORST, P.J. 1981. A preliminary checklist of the reptiles and amphibians in the Mountain Zebra National Park. *Koedoe* 24: 193–197.

HAACKE, W.D. 1984. The herpetology of the southern Kalahari domain. *Koedoe* (suppl). 1984, 171–186.

HAAGNER, G.V. & ELS, R.E. 1986. The reptiles of Mapelane. *Lammergeyer* 37: 14–21.

HALL, S. 1990. Hunter-gatherer-fishers of the Fish River Basin: A

contribution to the Holocene prehistory of the Eastern Cape. Ph.D. thesis (unpubl.), University of Stellenbosch.

HEWITT, J. 1933. On the Cape species and subspecies of the genus *Chersinella*, Gray. Part I. *Ann. Natal Mus.* 7: 255–293.

HEWITT, J. 1934. On the Cape species and subspecies of the genus *Chersinella* Gray. Part 2. *Ann. Natal Mus.* 7: 303–349.

HOFFMANN, L.A.C. 1989. An annotated list of amphibian and reptile observations from the Etosha National Park. *Madoqua* 16: 87–92.

HUGHES, G. R. 1974a. The sea turtles of south-east Africa. I. Status, morphology and distributions. *Oceanog. Res. Inst. Invest. Rep.* 35: 1–144.

HUGHES, G. R. 1974b. The sea turtles of south-east Africa. II. The biology of the Tongaland Loggerhead turtle *Caretta caretta* L. with comments on the Leatherback turtle *Dermochelys coriacea* L. and the Green turtle *Chelonia mydas* L. in the study region. *Oceanog. Res. Inst. Invest. Rep.* 36: 1–96.

IVERSON, J. 1992. A revised Checklist with Distribution Maps of the Turtles of the World, privately published, Richmond, Indiana, 363 pp.

JACOBSEN, N.H.G. 1989. A herpetofaunal survey of the Transvaal. Ph.D. thesis, Univ. Natal, 1621 pp.

JACOBSEN, N.H.G., NEWBERY, R.E. & PETERSEN, W.L. 1986. A checklist of the herpetofauna of the Transvaal Provincial Nature Reserves. Transvaal Nature Conservation Division, Pretoria, 38pp.

LOMBARD, A.T. 1995. Introduction to an evaluation of the protection status of South Africa's vertebrates. *S. Afr. J. Zool.* 30: 63–70.

LOMBARD, A.T., NICHOLLS, A.O. & AUGUST, P.V. 1995. Where should nature reserves be located in South Africa? A snake's perspective. *Conserv. Biol.* (in press).

LOVERIDGE, A. & WILLIAMS, E.E. 1957. Revision of the African tortoises and turtles of the suborder Cryptodira. *Bull. Mus. comp. Zool.* 115: 163–557.

MERTENS, R. 1955. Die Amphibien und Reptilien Südwestafrikas. *Abh. senckenb. naturforsch. Ges.* 490: 1–172.

MITCHELL, P.J. 1993a. The archaeology of Tloutle rock-shelter, Maseru District, Lesotho. *Navor. Nat. Mus. Bloemfontein* 9: 77–132.

MITCHELL, P.J. 1993b. Archaeological investigations at two Lesotho rock-shelters: Terminal Pleistocene/ early Holocene assemblages from Ha Makatoko and Ntloana Tsoana. *Proc. Prehist. Soc.* 59: 39–60.

MITCHELL, P.J., PARKINGTON, J.E. & YATES, R. 1994. Recent Holocene archaeology in western and southern Lesotho. *S. Afr. Archaeol. Bull.* 49: 33–52.

MOUTON, P. le F.N. & VAN WYK, J.H. 1994. Taxonomic status of geographical isolates in the *Cordylus minor* complex (Reptilia: Cordylidae). *J. Herpetol. Assoc. Afr.* 43: 6–18.

MULLINS, A. J. 1984. Leatherback turtle (*Dermochelys coriacea*), breeding on the Bathurst coast. *The Naturalist* 28: 14.

PIENAAR, U. de V., HAACKE, W.D. & JACOBSEN, N.H.G. 1983. The Reptiles of the Kruger National Park, Nat. Pks. Board, Pretoria, 236 pp.

PLUG, I. & ENGELA, R. 1992. The macrofaunal remains from recent excavations at Rose Cottage Cave, Orange Free State. *S. Afr. Archaeol. Bull.* 47: 16–25.

POOLEY, A.C. 1965. A preliminary checklist of the reptiles found within the Mkuzi and Ndumu Game Reserves in northern Zululand. *Lammergeyer* 3: 12–40.

POWER, J.H. 1932. *Testudo verreauxii* Smith: a study in variation. *S. Afr. J. Sci.* 29: 466–472.

REBELO, A.G. & SIEGFRIED, W.R. 1992. Where should nature reserves be located in the Cape floristic region, South Africa? Models for the spacial configuration of a reserve network aimed at maximising the protection of floral diversity. *Conserv. Biol.* 6: 233–252.

SIEGFRIED, W.R. 1989. Preservation of species in southern African nature reserves. pp. 186–201. In: Biotic Diversity in southern Africa, (ed.) B.J. Huntley, Oxford University Press, Cape Town.

SMITH, A. 1838–49. Illustrations of the Zoology of South Africa consisting chiefly of figures and descriptions of the objects of Natural History collected during an Expedition into the Interior of South Africa in the years 1834, 1835 and 1836. *Reptilia*. London, pls. i–xxviii) pp 1–28.