

A REVIEW OF THE SOUTHERN AFRICAN SPECIES OF *KINIXYS* BELL (REPTILIA: TESTUDINIDAE)

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Examination of all the *Kinixys* Bell material from Southern Africa south of 22° S available in museum collections has shown that four species occur in this region. On the basis of its poorly developed plastral hinge and gular lip, *K. natalensis* Hewitt is considered the most primitive species in the genus. It has a restricted distribution along the eastern escarpment of South Africa from the Transvaal south to Natal. *Kinixys spekii* Gray seems to be the next most primitive species, but its depressed carapace is an adaptation that enables it to find refuge in rock crevices. It has a very extensive distribution on the central African plateau. *Kinixys belliana* Gray is a larger species with a more convex carapace and a black radial pattern on the shields. Its distribution is restricted to the coastal plain. *Kinixys lobatsiana* Power differs from the other savanna species, and resembles the forest species *K. erosa* (Schweigger) and *K. homeana* Bell, in having the posterior marginal shields recurved and serrated. Its distribution is limited to the Transvaal Bushveld and southeastern Botswana.

Keywords: Southern Africa, systematics, Reptilia, Testudinidae, *Kinixys*.

INTRODUCTION

In the last comprehensive revision of the African hinged tortoises of the genus *Kinixys* Bell Loveridge and Williams (1957) recognized a single savanna species, *K. belliana* Gray.

Broadley (1981) reviewed the populations of *Kinixys* found south of 25° S and east of 30° E, reinstating *K. natalensis* Hewitt as a full species and reviving *spekii* Gray as a subspecies of *K. belliana* Gray. Subsequent examination of more material of savanna *Kinixys* from throughout Africa, including most of the material in United States museums, suggested that *K. spekii* should be treated as a full species and *K. lobatsiana* Power should also be resurrected as a full species (Broadley, 1989). Meanwhile, Boycott and Jacobsen (1988) confirmed the validity of *K. natalensis* and established that its range extends north into eastern Transvaal.

In April 1991 I examined the large collection of *Kinixys* material in the Transvaal Museum. This firmly established the validity of *K. lobatsiana* as a full species with a restricted distribution and with no evidence of sympatry with any other species.

In South Africa I obtained dry shells of *K. lobatsiana* and *K. natalensis* for preparation as skeletal specimens for comparison with similar material of the other species in the genus. This has helped to clarify relationships.

MATERIALS AND METHODS

This study is restricted to populations of *Kinixys* found south of 22° S, i.e., southeastern Botswana,

South Africa, southern Mozambique and Swaziland (there are no records from the Limpopo valley on the Zimbabwe side).

The most useful diagnostic characters are the form of the beak, the shape of the posterior marginals (especially the supracaudal), the dorsal length of the epiplastron in relation to total plastron length, the ratio of shell height to shell length, and carapace pattern.

The ratios used by Laurent (1956, 1962) in his diagnosis of *K. belliana mertensi* were calculated for the southern forms. The measurements were taken with dial callipers. Gular length and width are maximum measurements, but measurements of mid-ventral sulci are average values in the many cases when shield margins are not precisely juxtaposed. Specimens less than 75 mm in shell length have atypical proportions and were not used in the statistical analyses. Shell length to the nearest millimetre between blocks (with carapacial hinge closed) was used as the standard measurement of length, as plastron length is dependent on the very variable development of the gulars. Maximum shell height was also measured between blocks. The nomenclature of bones and shields follows Zangerl (1969).

Two hundred and fifteen specimens were examined from the following institutions (abbreviations preceding catalogue numbers are indicated in parentheses): Albany Museum, Grahamstown (AM); Field Museum of Natural History, Chicago (FMNH); Natural History Museum, London (BM); McGregor Museum, Kimberley (MMK); Museum

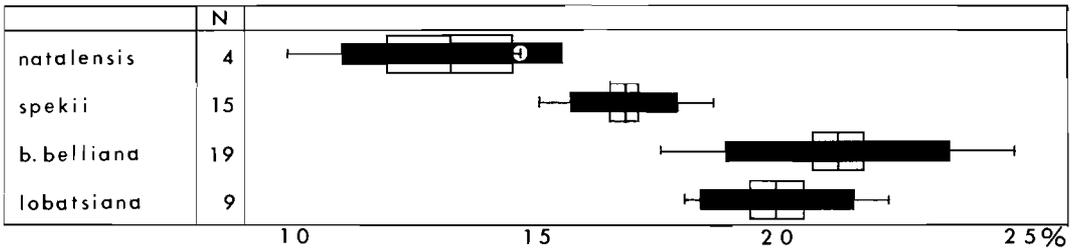


Fig. 1

Variation in the ratio dorsal epiplastron length/plastron midline length in Southern African populations of *Kinixys*. Horizontal line = range, vertical line = mean, solid rectangle = \pm one standard deviation; hollow rectangle = \pm one standard error.

d'Histoire Naturelle, Geneva (MHNG); Natal Museum, Pietermaritzburg (NM); Natural History Museum of Zimbabwe, Bulawayo (NMZB); South African Museum, Cape Town (SAM); Transvaal Museum, Pretoria (TM).

A figure in parentheses after a catalogue number indicates the number of specimens in a series.

CHARACTER ANALYSIS

BEAK. *Kinixys natalensis* has a strongly tricuspid beak, thus differing from all other species in the genus, which have unicuspid beaks.

SHAPE OF POSTERIOR MARGINALS. *Kinixys lobatsiana* has the posterior marginals strongly recurved and serrated like the forest species *K. erosa* and *K. homeana*. In *K. natalensis* the posterior marginals are slightly reverted and feebly serrated (strongly serrated in juveniles). In *K. spekii* and *K. b. belliana* the lateral posterior marginals may be slightly recurved, but they are never serrated.

SHAPE OF SUPRACAUDAL SHIELD AND PYGAL BONE. In the Natal populations of *K. natalensis*, the supracaudal is usually divided, the two halves being separated by a distinct notch; in the Swaziland and Transvaal populations the supracaudal is usually undivided. In *K. spekii* the supracaudal (and underlying pygal bone) is usually distinctly narrowed mesially or proximally excavate. In *K. b. belliana* the supracaudal is not narrowed mesially, but may have a shallow median depression inferiorly, widest proximally. In *K. lobatsiana* the supracaudal is widened mesially, with a distinct longitudinal groove inferiorly, widest proximally.

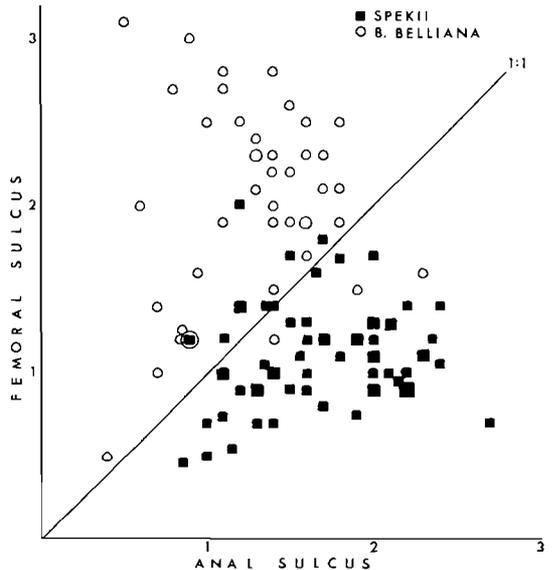


Fig. 2

Scatter diagram of midline length of femoral sulcus and anal sulcus for two Southern African *Kinixys* species. The scale is in cm.

DORSAL EPIPLASTRON LENGTH/PLASTRON MIDLINE LENGTH. In skeletal material, this ratio readily distinguishes *K. natalensis* (10–15 %) from *K. spekii* (15–19 %), *K. b. belliana* (18–25 %) and *K. lobatsiana* (18–22 %). The observed range of variation is shown in Fig. 1.

RATIO SHELL LENGTH/HEIGHT. The range of variation is shown in Table 1. This ratio will usually distinguish *K. spekii* from *K. b. belliana*, the other two species being intermediate.

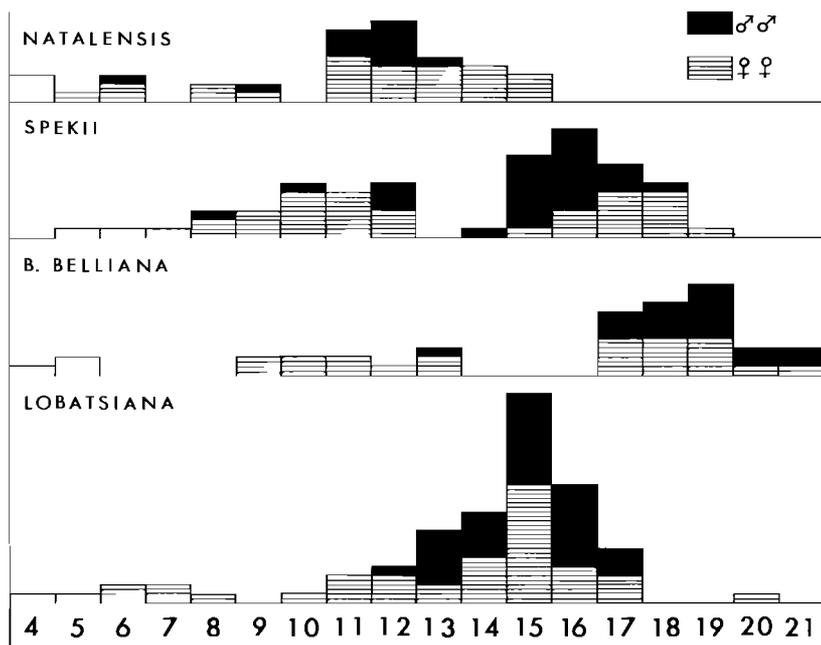


Fig. 3

Histograms showing distribution of specimens by sex in each shell length size class for Southern African populations of *Kinixys*. The horizontal scale is in cm, e.g., Class 12 = 116–125 mm. The smallest vertical division indicates one specimen.

CARAPACE PATTERN. *Kinixys natalensis* and *K. spekii* have a zonary pattern on each dorsal shield, the areolae are dark and are encircled by a pale zone, then a dark zone, often with a ragged or radiate outer margin. The dark markings gradually disappear in adult male *K. spekii* and some male *K. natalensis*. *Kinixys b. belliana* has a radiate pattern on each dorsal shield, the dark areolae are surrounded by a pale zone, and broad black rays (usually six) extending to the margins of each shield. *Kinixys lobatsiana* females usually have a radiate pattern on the dorsal shields, but this is often fragmented or vestigial, while adult males are usually devoid of pattern. Botswana specimens of both sexes are almost devoid of markings.

GULAR LENGTH/WIDTH RATIO. In *K. natalensis* the gular shields (together) are usually more than twice as wide as long, whereas in the other three species they are less than twice as wide (Table 1). *Kinixys spekii* differs from the other species in frequently having the gulars forked anteriorly, especially in males.

PROPORTIONS OF PLASTRAL SHIELDS. Variation in the ratios used by Laurent (1956, 1962) in his diagnosis of *K. belliana mertensi* (considered a synonym of the typical form) in northeastern Zaire and Uganda is shown in Table 1; none are diagnostic. However, southern populations of *K. b. belliana* usually have the median femoral sulcus longer than the anal sulcus, whereas this relationship is reversed in *K. spekii* (Fig. 2).

SIZE AND SEXUAL DIMORPHISM. Shell lengths for the four species are shown in Fig. 3. *Kinixys natalensis* is the smallest species and *K. belliana* the largest. *Kinixys natalensis* females attain a larger size than males and this may also be the case in *K. spekii*. There is no obvious sexual dimorphism in *K. belliana* and *K. lobatsiana*.

CARAPACIAL HINGE. In *K. natalensis* the hinge is restricted to the peripheral bones, there is hardly any intervention of cartilage between the fourth and fifth costal bones, even in the largest adults.

Table 1
Variation in proportions of the shell and various plastral shields in *Kinixys* populations south of 22° S.

	<i>n</i>	Range	Mean	S.D.	C.V.
Shell length/height ratio					
<i>natalensis</i>	33	1,97–2,51	2,18	0,12	5,50
<i>spekii</i>	57	2,17–2,69	2,46	0,13	5,28
<i>belliana belliana</i>	40	1,82–2,34	2,10	0,12	5,71
<i>lobatsiana</i>	68	1,95–2,59	2,28	0,15	6,58
Gular length/width ratio					
<i>natalensis</i>	32	22–65	43,06	10,12	23,50
<i>spekii</i>	57	27–86	59,64	9,48	15,90
<i>belliana belliana</i>	40	40–81	65,20	9,55	14,64
<i>lobatsiana</i>	67	39–94	57,39	10,68	18,61
Gular + humeral sulcus/Plastron width at humero-pectoral sulcus (%)					
<i>natalensis</i>	30	56,0–81,1	68,40	6,40	9,36
<i>spekii</i>	58	54,5–90,6	70,26	8,19	11,66
<i>belliana belliana</i>	40	57,1–84,9	71,54	6,74	9,42
<i>lobatsiana</i>	68	60,7–110,3	76,57	7,22	9,43
Pectoral sulcus/Gular + humeral sulci (%)					
<i>natalensis</i>	32	16,3–40,0	31,17	5,96	19,12
<i>spekii</i>	60	25,9–63,6	41,24	7,80	18,91
<i>belliana belliana</i>	40	28,6–64,7	45,35	9,21	20,30
<i>lobatsiana</i>	68	18,6–57,1	32,30	7,55	23,37
Pectoral sulcus/Abdominal sulcus (%)					
<i>natalensis</i>	33	13,7–38,9	27,26	5,74	21,06
<i>spekii</i>	62	25,8–62,2	39,04	7,31	18,72
<i>belliana belliana</i>	40	30,0–62,9	43,56	7,85	18,02
<i>lobatsiana</i>	66	16,3–58,5	32,89	6,87	20,89

In *K. spekii* the hinge is moderately developed, with cartilage rarely extending more than half-way up the anterior edge of costal 5. In *K. belliana* and *K. lobatsiana* the hinge is well developed, with cartilage extending along the anterior edge of costal 5 and often around the margins of neural 4.

NUMBER OF MARGINALS. *Kinixys natalensis* usually has more than 23 marginals, due to division of the supracaudal and/or insertion of extra marginals on each side. The other species usually have 23 marginals, with rare variations due to fusion or division of individual shields (Table 2).

SYSTEMATICS

KEY TO THE SOUTHERN AFRICAN SPECIES OF KINIXYS

- 1 Beak tricuspid; carapacial hinge poorly developed, not extending beyond the marginals; gulars (together) usually at least twice as wide as long; dorsal epiplastron length less than 15 % of plastron midline length; marginals usually 24 or more, with supracaudal frequently divided, the two halves separated by a deep ventral notch; plastron not concave in males *natalensis*
- Beak unicuspid; carapacial hinge well developed in adults; gulars (together) less than twice as wide as long; dorsal epiplastron more than 15 % of plastron midline length; marginals usually 23, supracaudal not divided; plastron concave in males 2
- 2 Posterior marginals reverted and serrated, underside of supracaudal usually with a longitudinal groove, widest anteriorly *lobatsiana*
- Posterior marginals not reverted or serrated, underside of supracaudal usually smooth or proximally excavate 3

- 3 Carapace distinctly depressed, shell height usually included in length more than 2,3 times; gular lip usually concave above in cross-section, gular scutes often forked; dorsal epiplastron length 15–19 % of plastron midline length; underside of supracaudal narrowed mesially or proximally excavate; median anal suture usually longer than femoral suture; shields of carapace with a basically zonary pattern, adult males often uniform *spekii*
- Carapace convex, shell height usually included in length less than 2,3 times; gular lip usually flat or convex above in cross-section, gular scutes not forked; dorsal epiplastron length 18–25 % of plastron midline length; underside of supracaudal not narrowed mesially or proximally excavate; median femoral suture usually longer than anal suture; shields of carapace with a radial pattern *belliana belliana*

Table 2
Number of marginal shields in *Kinixys* populations south of 22° S.

	<i>n</i>	19	20	21	22	23	24	25	26
<i>natalensis</i>	41	—	—	—	—	11	20	7	3
<i>spekii</i>	61	—	—	—	6	50	5	—	—
<i>belliana belliana</i>	40	—	—	—	—	36	4	—	—
<i>lobatsiana</i>	73	1	—	1	2	64	4	1	—

***Kinixys natalensis* Hewitt, Fig. 5**

Kinixys belliana zuluensis (part) Hewitt, 1931: 475, pl. xxxviii, figs 18–20.

Kinixys natalensis Hewitt, 1935, *Records of the Albany Museum* 4: 353, pl. xxxv, figs 3–4 (type locality: Jameson's Drift, Tugela River, Natal); Broadley, 1981: 204, figs 7–8; Boycott and Bourquin, 1988: 127, pl. 45–47, fig. 28; Boycott, 1988: 90; Lambiris, 1988: 32; Boycott and Jacobsen, 1988: 93, figs 1–4; Branch, 1988: 31, pl. 5; Broadley, 1989: 60, fig. 15; Ernst and Barbour, 1989: 232; Crumly, 1989: 91.

Kinixys belliana belliana (part): Loveridge and Williams, 1957: 384; Wermuth and Mertens, 1961: 180, 1977: 70.

DIAGNOSIS. Beak tricuspid; carapacial hinge not extending beyond marginals; gulars (together) usually at least twice as wide as long; dorsal epiplastron length less than 15 % of plastron midline length; marginals usually 24 or more, with supracaudal frequently divided; plastron not concave in males.

DESCRIPTION. Beak tricuspid; prefrontal longitudinally divided; frontal usually entire, sometimes longitudinally divided; forelimb covered with subimbricate scales, a few enlarged and pointed; five claws on front foot.

Carapace moderately convex (shell length/height ratio 1,97–2,51), often with flat-topped protuberances on vertebrals 4 and 5; anterior margin

not expanded, posterior marginals slightly reverted and feebly serrated in adults (serrated in juveniles); dorsal shields often raised, with well-marked growth annuli; nuchal elongate in adults, often minute dorsally; vertebrals 5, rarely 6 (six specimens); pleurals 4 (five in a hatchling and on one side of three specimens); marginals 23–26, supracaudal usually divided in Natal specimens, the two halves separated by a distinct notch.

Front lobe of plastron truncate anteriorly, not or slightly projecting beyond anterior border of carapace; gulars paired, usually wider than long; pectorals with a narrow median sulcus; axillaries (usually three) small; inguinal large (absent only in AM 6975 G), in contact with or separated from sixth marginal, in contact with femoral; rear lobe short and truncate, with a very shallow posterior notch. Adult males without a concave plastron.

COLOURATION. Carapace with a zonary pattern on each shield, the areolae brown, followed by a broad orange/yellow zone, then a blackish zone which may be broken up into short rays that may extend to the edges of the shield or be followed by another orange/yellow zone. The plastron is yellow with symmetrical blackish markings, a pair of black rings on the abdominal shields being the

most prominent. The colour patterns become broken up and ill-defined in large adults and may disappear completely.

SIZE. Largest male (TM 65799, Hoedspruit, Transvaal) 127 mm long, 89 mm wide, 57 mm high; largest female (AM 6975B, Jameson's Drift, Natal) 155 mm long, 113 mm wide, 70 mm high.

HABITAT. Throughout its range, *K. natalensis* is associated with rocky areas along the eastern escarpment at 300–1000 metres altitude. In the eastern Transvaal it has been found among granite outcrops. The habitat includes valley bushveld in the south, mountain bushveld and mountain thornveld in northern Natal, and arid bushveld and arid lowveld in the extreme north of its range (Boycott and Jacobsen, 1988). During the day these tortoises have been found under rocks on the summit of the Lebombo Range in Swaziland (Boycott, 1988).

DISTRIBUTION. The eastern plateau slopes from the eastern Transvaal at Hoedspruit south to the Natal Midlands at Greytown. Lambiris (1988) has recorded a specimen from Imbali, near Pietermaritzburg, but he concedes (*in litt.*) that it 'was probably an introduced specimen. It had been brought to the Natal Parks Board by an Imbali resident, who found it on the roadside, and there is no independent evidence of a natural population in the area.'

LOCALITIES. (An * indicates sympatry with *K. spekii*, a # indicates sympatry with *K. b. belliana*.) SOUTH AFRICA. *Transvaal*: Bergplaats 25HU TM 69917; Hoedspruit TM 65799; Mananga Kop TM 69915; Manyeleti Game Reserve* (Main Camp) TM 64809; Sabi-Sand/Kruger Nat. Park boundary, S of Tswariri River TM 68250. *Natal*: no locality NMZB 9797–8; Dimane Stream AM – (4); Greytown AM 77, NM 1130; Imbali (Lambiris, 1988); Impanza NM 1143 (2); Itala Game Reserve (Lambiris, 1988) TM 57520; Jameson's Drift AM 6975(12), BM 1934.10.12.1; ± 30 km S of Kranskop (Boycott and Jacobsen, 1988); Manaba# (Hewitt, 1935); Ntambanana (Hewitt, 1931); Othobothini# TM 19346, 69916; Uitkyk, Vryheid Dist. TM 56755; Weenen Nature Reserve NMZB 11071, TM 50682; 'Zululand' NM 1129. SWAZILAND. Big Bend FMNH 224437; Groenpan Farm (photos: J. Culverwell); Mbuluzi Game Reserve* and Mlawula Nature Reserve* (J. Culverwell in Boycott and Jacobsen, 1988); Tshaneni FMNH 224442. MOZAMBIQUE. No locality TM 47208; 10 km SSE of Ressano Garcia* NMZB-UM 30453–4.

Kinixys spekii Gray, Fig. 5

Kinixys spekii Gray, 1863, *Annals and Magazine of Natural History* (3)12: 381 (type locality: Central Africa); Broadley, 1989: 52, fig. 12b.

Kinixys australis Hewitt, 1931: 477, pl. xxxvi, figs 4–6 (type locality: White River, E Transvaal).

Kinixys belliana belliana (not Gray): Loveridge and Williams, 1957: 384 (part); Wermuth and Mertens, 1961: 180 (part); Pienaar, 1966: 127; Switak, 1971: 9; Wermuth and Mertens, 1977: 70 (part); Pienaar, 1978: 213.

Kinixys belliana spekii: Broadley, 1981: 211, figs 11–12; Pienaar *et al.*, 1983: 22, pl. 2; Boycott and Bourquin, 1988: 124 (part), pl. 43–44, fig. 27; Boycott and Jacobsen, 1988: 100; Branch, 1988: 30, pl. 5; Ernst and Barbour, 1989: 230.

DIAGNOSIS. Beak unicuspid; carapacial hinge well developed; gulars (together) usually less than twice as wide as long; dorsal epiplastron length 15–19 % of plastron midline length; marginals usually 23, the supracaudal undivided; carapace depressed, shell height usually included in length more than 2.3 times; plastron concave in males; colour pattern of carapacial shields basically zonary.

DESCRIPTION. Beak unicuspid; prefrontal usually longitudinally divided; frontal entire; forelimbs covered with subimbricate scales, many enlarged and pointed; five claws on front foot.

Carapace depressed (shell length/height ratio 2,17–2,70), highest point frequently on vertebral 1 or 2; dorsal shields relatively flat, areolae of vertebrals usually with a weak longitudinal keel; anterior margin not expanded, lateral posterior marginals slightly reverted, not serrated; nuchal elongate in adults; vertebrals 5 (six in AM 78D only), pleurals 4 (three in TM 58100 and 65800; five in AM 78D and one side of TM 65563 and 65699); marginals 23 (rarely 22 or 24).

Front lobe of plastron truncate anteriorly, projecting well beyond the anterior border of the carapace in both sexes; gulars paired, usually less than twice as broad as long; pectorals with a moderate median sulcus; axillaries two, of moderate size; inguinal large, usually in contact with sixth marginal, in broad contact with femoral; hind lobe short and truncate, with a very shallow posterior notch. Plastron concave in adult males.

COLOURATION. Carapace with a zonary pattern on each shield in juveniles and subadults. This may persist in adult males, but many become uniform olive-brown to buff. In females the dark zones tend to break up into ragged radiations.

The plastral shields usually have ragged circular radiating patterns in subadults and adult females, but these become vestigial or absent in adult males.

SIZE. Largest male (TM 41761, Maputo Elephant Reserve, Mozambique) 181 mm long, 124 mm wide, 79 mm high; largest female (AM 78C, White River, Transvaal: lectotype of *K. australis*) 183 mm long, 115 mm wide, 70 mm high.

HABITAT. This species has a wide range in tropical savannas, and south of the Limpopo it is found in the lowveld areas, including Mopaniveld. Its depressed carapace enables this tortoise to use rock crevices as refuges.

DISTRIBUTION. In South Africa this species inhabits the lowveld areas of the northern and eastern Transvaal, extending south through Swaziland and adjacent Mozambique to Zululand. The southernmost record from north of Mehlwemamba, Hlabisa District, is based on the shell of a juvenile and needs verification.

LOCALITIES. SOUTH AFRICA. *Transvaal*: no locality ('N. Transvaal') TM 12768, 13483-4; Acornhoek TM 66326; Alldays TM 37638; Antioch 240KT TM 64666; Bekaf 650MS TM 52485; De Hoop 203JU TM 42393; Dwaalboom 217KP TM 69898; Hartbees TM 68243; Hilltop, Nelspruit TM 67469; Inkerman 10KQ TM 69899; Jerome 287MT TM 52217; Ka Mininginisi TM 52218; Kruger National Park (localities from Pienaar, 1966, fig. 32); Leamington 207KU TM 65775; Malepo TM 6987; Manyeleti Game Reserve QDS 2431C2 TM 65110, 65699, 66520, 69846, 69890, and QDS 2431D1 TM 65747, 65794, 65800, 65810; Merry Pebble Stream 246KU TM 69896; Mmaboleta Estate TM 42843-4; Mokeetsi-Duiwelskloof TM 21842; Nelspruit TM 67600; Nzulase TM 69894; Ostend 104KT TM 52161; Rolle 235KU TM 69900; S.A. Bantu Trust TM 69901; Seville 224KU TM 65563; The Glen 259 TM 67090; Uitkomst 769LS TM 69895; Vulcanus 584LS TM 69897; White River AM 78(5), 1295. *Zululand*: north of Mehlwemamba TM 64863; Ndumu Game Reserve TM 37895. SWAZILAND. Manzini TM 24205, 42735; 5 km NW of Siphofaneni TM 51023; Tambuji Estates TM 58100; Tshaneni BM 1975.89-91, NMZB-UM 33418. MOZAMBIQUE. Maputo Elephant Reserve TM 41761; Moamba TM 29516-7; 10 km SSE of Ressano Garcia NMZB-UM 30450-1, 30455, 33010; 15 km SSE of Ressano Garcia NMZB-UM 30452.

***Kinixys belliana belliana* Gray, Fig. 6**

Kinixys Belliana Gray, 1831, *Synopsis Reptilium*: 69 (no locality); Bourquin, Vincent and Hitchins, 1971: 21, fig. 12.

Kinixys belliana: Boulenger, 1905: 252, 1907: 428.

Kinixys belliana zuluensis Hewitt, 1931: 471, pl. xxxviii, figs 21-23 (type locality: Richards Bay, Zululand); Hewitt,

1935: 350, pl. xxxv, figs 1-2.

Kinixys belliana belliana: Loveridge and Williams, 1957: 384 (part); Wermuth and Mertens, 1961: 180, 1977: 70 (part); Pooley, 1965: 54, pl. 11; Bruton and Haacke, 1980: 277; Broadley, 1981: 208, figs 9-10; Boycott and Bourquin, 1988: 121, pl. 41; Lambiris, 1988: 32; Branch, 1988: 30; Ernst and Barbour, 1989: 229.

Kinixys belliana zombensis: Broadley, 1989: 50.

DIAGNOSIS. Beak unicuspid; carapacial hinge well developed; gulars (together) usually less than twice as wide as long; dorsal epiplastron length 18-25 % of plastron midline length; marginals usually 23, supracaudal undivided; carapace convex, shell height usually included in length less than 2,3 times; plastron concave in males; colour pattern of carapacial shields radial.

DESCRIPTION. Beak unicuspid; prefrontal entire (but usually cleft anteriorly) or longitudinally divided; frontal large, rarely longitudinally divided; forelimb covered with more or less imbricate scales, many enlarged and pointed, usually five claws on forefoot (four in TM 54828 and on one side of TM 53988 and 55453; six on one side of TM 29400).

Carapace convex (shell length/height ratio 1,82-2,34), highest point usually on vertebral 3 or 4; anterior margin often somewhat expanded, not reverted; posterior marginals not reverted or serrated; dorsal shields with well-marked growth annuli and deep sulci; nuchal elongate in adults; vertebrae 5, pleurals 4 (five on left side of holotype of *K. b. zuluensis*); marginals usually 23.

Front lobe of plastron truncate anteriorly, usually projecting beyond anterior border of carapace, especially in males; gulars paired, usually less than twice as broad as long; pectorals with a moderate median sulcus; axillaries 2-3; inguinal large, usually in contact with sixth marginal, in broad contact with femoral; hind lobe short and truncate with a very shallow posterior notch. Plastron distinctly concave in adult males.

COLOURATION. Carapace yellow, with a bold black radial pattern (4-6 rays on each vertebral and pleural shield). In females the black rays may be almost confluent as in TM 14877 (Hewitt, 1935; pl. xxxv, fig. 1), but at the other extreme is TM 13550 (Hewitt, 1931, pl. xxxviii, fig. 22), with only a few narrow black rays on the vertebrae and pleurals. In males the black pattern is usually less developed and may be obscure in old individuals.

The plastral pattern is very variable. In juveniles the plastron is largely black, except for a broad median band of yellow extending along the median sulci of the pectorals, abdominals and femorals. Thereafter the black is broken up by

yellow intrusions until large adults retain only vestigial black markings, usually in a fragmented radial pattern.

SIZE. Largest male (TM 51378, Candover to Mkuze, Zululand) 211 mm long, 137 mm wide, 90 mm high; largest female (TM 53989, Nkweleni Valley, Zululand) 210 mm long, 136 mm wide, 94 mm high.

HABITAT. In the southern part of its range *K. b. belliana* appears to be restricted to the coastal plain (Coastal Forest and Thornveld), where it is common. Haacke (*in litt.*) has a sight record of specimens in coastal dune forest at Mapelane, south of Lake St Lucia, and a midden of 34 carapaces was found in coastal dune forest near Mbibi (Bruton and Haacke, 1980). TM 51378 was found on a road through savanna thornveld west of the Lebombo Range. Occasionally encountered on the marine beach (Bruton and Haacke, 1980).

DISTRIBUTION. I have earlier (Broadley, 1989) assigned the eastern populations of *K. belliana* to *K. b. zombensis* Hewitt, 1931, with a range extending from coastal Kenya south through Tanzania, Mozambique, southern Malawi and eastern Zimbabwe to Zululand. However, examination of more material makes it difficult to distinguish any subspecies except *K. b. nogueyi* (Latate, 1886) of West Africa. The proportions of the type specimen of *K. belliana* suggest that it originated from Ethiopia and it just falls within the range of variation for *K. b. mertensi* Laurent 1956, (Broadley, 1989). The northern populations of *K. b. belliana* range from northwestern Somalia, through Ethiopia, southern Sudan, western Kenya, Uganda and northeastern Zaire to the western Central African Republic and Cameroon (where there is intergradation with *K. b. nogueyi*); the typical form then extends south through western Zaire to Angola, where the presence of *K. spekii* has not yet been confirmed (the Angolan records in Broadley, 1989: fig. 126, were speculative and based on literature records).

LOCALITIES. SOUTH AFRICA. *Zululand*: no precise locality AM -(2), NMZB 6067-8; Candover to Mkuze TM 51378; False Bay TM 63908; Futululu Forest Station TM 65703; Kosi Bay (Rowe-Rowe, Murray and Daniel, 1968); Hluhluwe Game Reserve (Bourquin *et al.*, 1971); 20 km NNW of Hluhluwe TM 43074-5; 5 km N of Hluhluwe TM 55453; East Shore of Lake St Lucia TM 45828-9; Lake Sibaya Research Station TM 48265; Lala Nek TM 47844; Manaba TM 14877; Manzengwenya

TM 48729-30; Mission Rocks, Lake St Lucia TM 54562; Mkuze Game Reserve (Pooley, 1965); Mtubatuba TM 13544, 13549-50, 53940; Mtubatuba to Hluhluwe TM 57947; Ndumu Game Reserve TM 34678-81; Ndumu Hill (Lambiris, 1988: 32); Nkweleni Valley TM 53986-9; Othobothini TM 19363; Richards Bay NM 1203 (holotype of *K. b. zuluensis*); St Lucia Bay AM -(2); Sodwana Bay TM 64227; Sodwana Bay to Umhlosinga NMZB 6044; Umfolozi Game Reserve (Bourquin *et al.*, 1971); Umfolozi Station BM 1905.3.7.65-66 and 68. MOZAMBIQUE. Chimongo TM 29399-400; Maputo NHMG 65311; Maputo Elephant Reserve TM 41762; Zavora NMZB-UM 28476.

Kinixys lobatsiana Power, Figs 6, 7

Kinixys lobatsiana Power, 1927, *Transactions of the Royal Society of South Africa* 14: 410, pl. xix-xx (type locality: Lobatse, Botswana) and 1931: 46, 49, figs 1-2.

Kinixys lobatsiana: Hewitt, 1931: 488, pl. xxxvii, figs 12-13, text fig. 1e-f, 2; Broadley, 1989: 54, fig. 12b.

Kinixys belliana belliana: (part) Loveridge and Williams, 1957: 384; Wermuth and Mertens, 1961: 180, 1977: 70; Jacobsen, 1977: 15.

Kinixys belliana spekii (not Gray): Auerbach, 1985: 17; Boycott and Bourquin, 1988: 124 (part), pl. 42; Branch, 1988: 30 (part).

Kinixys belliana (part): Auerbach, 1987: 69, pl. 7/1.

DIAGNOSIS. Beak unicuspid; carapacial hinge well developed; gulars (together) usually less than twice as wide as long; dorsal epiplastron length 18-23 % of plastron midline length; marginals usually 23, supracaudal undivided, carapace moderately convex to distinctly depressed; plastron concave in males; colour pattern of carapacial shields radial in some females, but often fragmented, while males are usually uniform.

DESCRIPTION. Beak unicuspid; prefrontal longitudinally divided; frontal large, entire (sometimes transversely divided: Hewitt, 1931, fig. 2); forelimb covered with subimbricate scales, some enlarged and pointed; five claws on front foot (four on one side of TM 4821).

Carapace variable in depth (shell length/height ratio 2,08-2,59 in 33 males: 1,95-2,51 in 32 females), usually level between the centres of vertebrae 1 and 4; dorsal shields relatively flat; anterior margin slightly expanded, posterior marginals strongly reverted and serrated, the supracaudal widened mesially, with a longitudinal groove below; cervical elongate in adults; vertebrae usually 5 (six in TM 4805, 34620, 47207, 69908 and 69914; seven in TM 69963); pleurals 4 (two/three in TM 12760; five in TM 4805, 4826, 34620 and 69908); marginals usually 23 (rarely 19, 21, 22, 24 or 25).

Front lobe of plastron truncate anteriorly, not usually extending beyond the anterior border of carapace; gulars paired, usually less than twice as broad as long; pectorals with a short median sulcus; axillaries 2–3, of moderate size; inguinal moderate to large, usually in contact with sixth marginal and femoral; hind lobe short and truncate, with a shallow posterior notch.

COLOURATION. Subadults and females usually have a fragmented radiate pattern on each carapacial shield, which is red-brown mesially. Males are usually devoid of markings. The plastral shields have a sparse pattern of radiating dark streaks, which usually disappear in adult males. Transvaal tortoises have more distinct markings than those from southeastern Botswana.

SIZE. Largest male (TM 52259, Mamiaanshoek, Waterberg, Transvaal) 172 mm long, 119 mm wide, 74 mm high; largest female (TM 52258, Mamiaanshoek) 200 mm long, 135 mm wide, 86 mm high.

HABITAT. This species inhabits the Transvaal Bushveld and Thornveld (= Middleveld), extending into southeastern Botswana. In the Nylsvley Nature Reserve this tortoise was rarely seen and then mainly in the *Burkea* savanna (Jacobsen, 1977). The type series was taken near Lobatse in the kloofs among the hills (Power, 1931) and in the Transvaal they are mostly found on rocky hillsides (Jacobsen, 1989).

BREEDING. A female from the farm Rietfontein 214JR laid six eggs on 13 April and three of these hatched after 313 days (Jacobsen, 1989).

DIET. One of the types was eating a mushroom when found (Power, 1931). A specimen from the Daspoort Range defaecated the following: largely vegetable matter (leaves of a herb, seeds of a legume *Elphantorrhiza*; two species of tenebrionid beetles, a heliocoprid beetle and a millipede (Jacobsen, 1989). Specimens in captivity in Bulawayo feed avidly on snails (*Achatina* and *Helix*) and millipedes, as do *K. spekii* and *K. b. belliana*.

DISTRIBUTION. The Transvaal bushveld, extending into southeastern Botswana. Two specimens from outside this area require explanation. An adult female from Rochdale Farm, just north of the Soutpansberg, is probably a waif that was swept through the Waterpoort by the Sand River in flood: it is far north of the nearest *K. lobatsiana* localities.

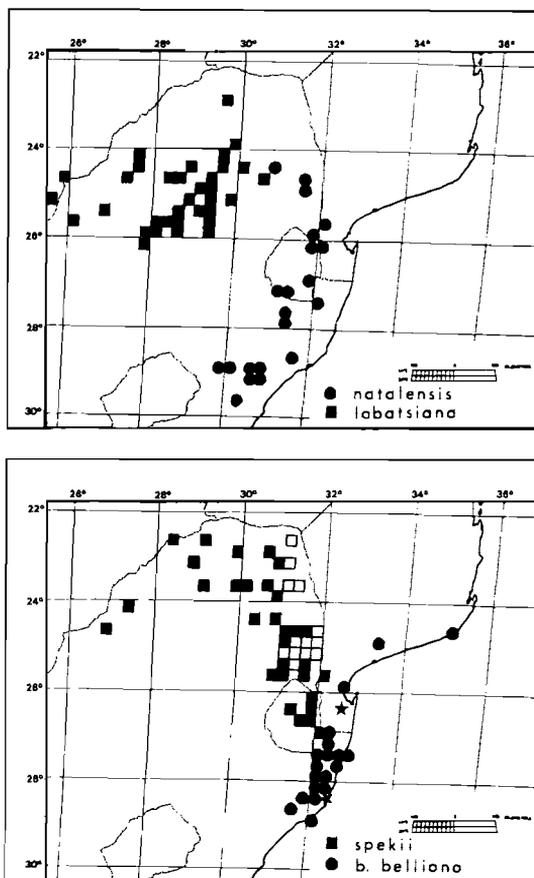


Fig. 4

Distribution of Southern African species of *Kinixys*; top: *K. natalensis* and *K. lobatsiana*., bottom: *K. spekii* and *K. b. belliana*. Open symbols denote literature records; stars denote sympatry of species.

The shell of an adult male was picked up in the Manyeleti Game Reserve in the eastern Transvaal lowveld (which has also yielded nine *K. spekii* and one *K. natalensis*) this specimen was almost certainly translocated from the bushveld and released by a misguided tourist.

LOCALITIES. BOTSWANA. Gaborone (Auerbach, 1987); Lobatse AM -, BM 1947.3.5.72; MMK 209-13, 216-21, 223-4, SAM 43464; Otse (Auerbach, 1987, pl. 7/1)NMZB 11217. **SOUTH AFRICA. Transvaal:** no precise locality TM 12760, 67799, 69963; Boekenhoutskloof Drift 286JR TM 64286; Buffelshoek 351KQ TM 69904; Buffelspoort 421KR TM 69906; Bulge River 198KQ TM 69961; Daspoort Range TM 62795; Die Bron TM 50680;

Goedehoop 749KS TM 69913; Hennops River TM 28663; Klipheuwel 573KS TM 69945; Kloppersdam 187JR TM 63774; Kromdraai NMZB 9877, TM 49863; Leeuwfontein 188JR TM 64362; Loskop Dam TM 48704; Loskop Noord 12JS TM 69909; Lotteringskraal 243JP TM 34620; Malmaniesrivier TM 69983; Mamianshoek TM 52258-9; 'Manyeleti Game Reserve' (translocation) TM 65797; Marble Hall TM 22974; 58 km N of Marble Hall TM 42750; Mooiplaats 242JS TM 69914; Naauwpoort FMNH 17179, TM 13473-5, 13485, 13545-6, 13548; Nylsvley Nature Reserve (Jacobsen, 1977); Orighstad area TM 21329; Pretoria AM -, TM 62810, 65818; Pretoria District NMZB 11072-5, TM 4805, 34666, 34686, 47207; Rietfontein 214JR TM 69962; Rietspruit TM 4821, 4826; Rochdale 700MS TM 36366; Schilderkrans 1041LS TM 69908; Steynsdrift 145JS TM 69944; Syferfontein 178JP TM 69902; Tivoli 98KP TM 69905; Tweefontein 523JQ NMZB 11076; Vlakplaats 354JR TM 69911; Vlakplaats 535KS TM 69946; Vlakplaats 723KS TM 69912; Waterval 297JR TM 69910; Witfontein 521JR TM 69947; Zandspruit 189JR TM 69907; Zonkolol 473JR TM 69903.

RELATIONSHIPS

Until recently the relationships of *Kinixys* to other tortoise genera were obscure (Loveridge and Williams, 1957; Crumly, 1984), but the recent description of the large tortoise *Impregnochelys pachytestis* from the Miocene deposits of Rusinga Island in Kenya (Meylan and Auffenberg, 1985) has revealed a sister genus. Gaffney and Meylan (1988), in their phylogeny of turtles, have included these two genera in an unnamed taxon that is more derived than the tribe Megalochelyini (including *Aldabrachelys*, *Megalochelys*, *Astrochelys*, *Chelonoidis* and *Geochelone*.) but less derived than *Indotestudo* and the tribe Testudinini (including *Testudo*, *Malacochersus*, *Psammobates*, *Homopus*, *Pyxis*, *Acinixys* and *Chersina*).

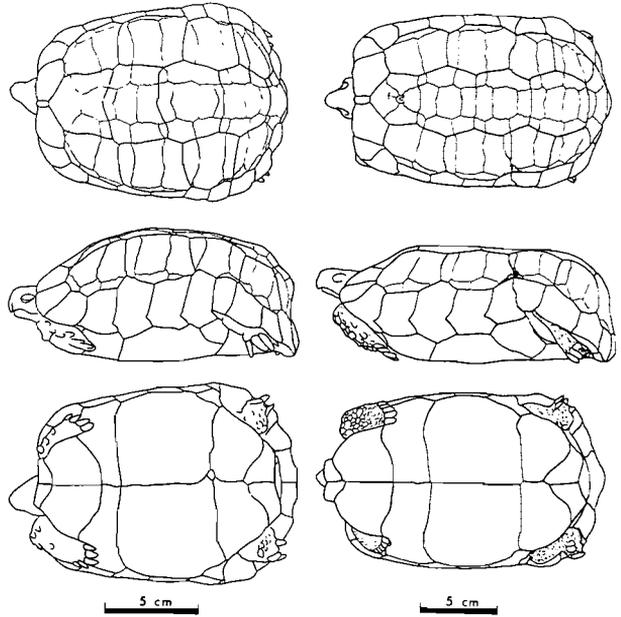


Fig. 5

Dorsal lateral and ventral views of (left) *Kinixys natalensis* (AM -, lectotype female from Dimane Stream, near Jameson's Drift, Tugela Valley, Natal) and (right) *K. spekii* (AM 78C, lectotype female of *K. australis* Hewitt from White River, Transvaal). Thick lines indicate sulci, thin lines indicate sutures between carapacial bones; f = fontanelle.

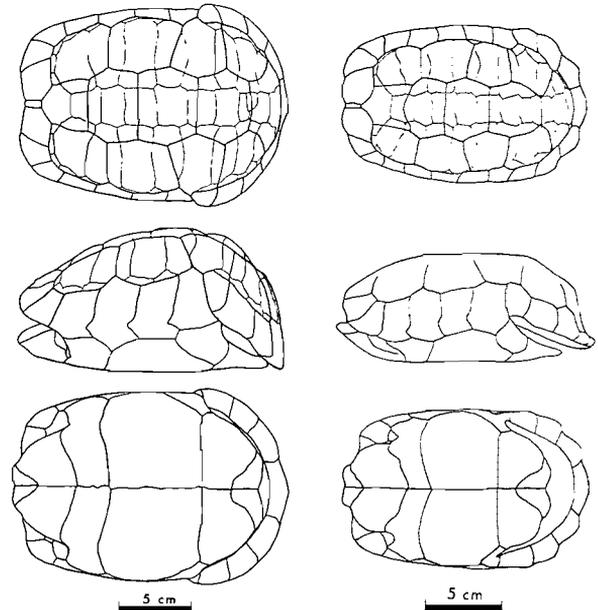


Fig. 6

Dorsal, lateral and ventral views of (left) *Kinixys b. belliana* (TM 34680, female from Ndumu Game Reserve, Zululand) and (right) *K. lobatsiana* (AM -, male from Lobatse, Botswana). Conventions as in Fig. 5.

Kinixys differs from *Impregnochelys* in having a kinetic carapace, and because *K. natalensis* has the most poorly developed hinge (not extending beyond the marginals), it seems a good candidate for the most primitive species in the genus. It frequently displays another primitive feature, i.e., a divided supracaudal with a notch in the posterior carapacial rim separating the two halves. This character is otherwise known only in the Asian genus *Manouria*, considered the most primitive living tortoise genus by both Crumly (1984) and Gaffney and Meylan (1988). In the development of the gular ram (i.e., elongation and thickening of the epiplastra) there is a steady progression from the short epiplastra of *K. natalensis*, via the moderate development in *K. spekii* to the well-developed elongate epiplastra of *K. belliana* and *K. lobatsiana* (even more accentuated in the forest species *K. erosa* and *K. homeana*). *Kinixys lobatsiana* has reverted and serrated posterior marginals like the two forest species, but otherwise seems closer to *K. belliana*.

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I am grateful to the following persons for the loan of material: Dr H. Marx (FMNH), Dr V. Mahner (MHNG) and Mr P. C. Anderson (MMK).

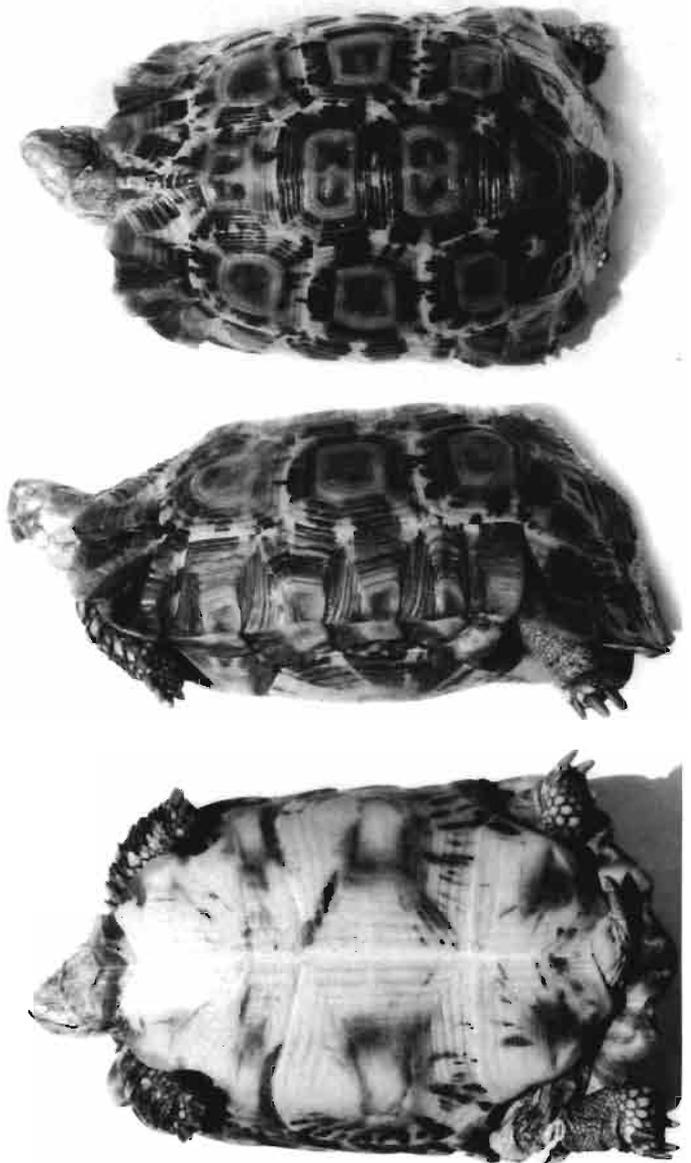


Fig. 7

Dorsal, lateral and ventral views of a distinctly marked female *Kinixys lobatsiana* (NMZB 9877 from Kromdraai Farm, Krugersdorp District, Transvaal).

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