

Original article

A new species of tortoise of the genus *Homopus* (Chelonia: Testudinidae) from southern Namibia

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Abstract.—*Homopus bergeri* Lindholm 1906 was based on a single partial shell from Namibia. No other *Homopus* were recorded from the country until a population of *Homopus* was discovered in the Aus region, southern Namibia, in 1955. It was originally referred to *H. boulengeri* Duerden 1906, and then inaccurately to *H. bergeri*. Inspection of the type of *H. bergeri* Lindholm 1906 shows that it is a junior synonym of *Psammobates tentorius verroxii* (A. Smith 1839). The Aus *Homopus* is morphologically distinguishable from all other *Homopus* and is described as a new species, *Homopus solus*. Morphological variation, distribution and biology in *H. solus* are described. The use of the combinations *Homopus 'solos'* by Devaux (2003) and *Homopus bergeri (solos)* (Lindholm, 1906) by Bonin *et al.* (2006) have no nomenclatural standing.

Key words.—Testudinidae, *Homopus*, new species, Namibia, *Homopus bergeri*

For some years a population of unusual small tortoises has been known from rocky habitats in southern Namibia. They have caused considerable taxonomic confusion. Mertens (1955) was the first to discuss this population on the basis of live specimens supplied to him by Mr Erni from his Farm Plateau near Aus. He referred them to *Homopus boulengeri* Duerden 1906, an unusual range extension for this Karoo species. With no supportive material at hand, Loveridge & Williams (1957) treated the record with caution. However, subsequent material from the vicinity of Aus (Farms Plateau and Augustfelde) and Udabipberge (Witpuetz), confirmed the presence of *Homopus* in Namibia, which Mertens (1971) continued to refer to *H. boulengeri*. Greig & Burdett (1976) assessed the distribution of South African tortoises, and although they extended the known range of *H. boulengeri* within the Cape region a large disjunction remained between the known Cape distribution and Mertens' (1971) Namibian records. They

considered the occurrence of *H. boulengeri* in Namibia as “unlikely”.

Due to concern with the validity of the Aus material, Greig stimulated searches for fresh material of *Homopus* in the region, and this led to the discovery of additional specimens. Differences in the colour pattern and morphology of this population, compared with typical *H. boulengeri* from the Cape, led Greig to speculate that a new species of *Homopus* was involved. Provisionally, and informally, this was referred to *Homopus bergeri* Lindholm 1906, although the type was unobtainable and had for many years been considered a junior synonym of *Psammobates tentorius verroxii* (Mertens 1955, Loveridge & Williams 1957). Despite this the name *H. bergeri* prematurely entered popular usage for the Aus tortoise (Boycott 1986, Newbery & Jacobsen, 1986; Branch, 1988, 1989; Branch *et al.*, 1988). Branch (1992) discussed the confused taxonomic status of the Aus tortoise and noted that

the application of the name *Homopus bergeri* had been premature. A further analysis of tortoise distributions in the subcontinent (Branch *et al.* 1995) confirmed that *H. boulengeri* was restricted to South Africa, with the known Namibian records being referable to '*H. bergeri*'. The inapplicability of this name was iterated by Karl & Tichy (1999), and much recent literature has referred to the Namibian population as *Homopus* sp. (e.g., Boycott & Bourquin 1988, Branch 1998, Cunningham & Simang 2007). However, taxonomic confusion remains in the international literature (e.g., David 1994, Bonin *et al.* 1996, Rogner 1996, Schleicher & Loehr 2001, Vetter 2002, Devaux 2003).

Resolution of the taxonomic status of the Aus *Homopus* requires three problems to be addressed:

1. Is the Aus tortoise referable to the genus *Homopus*?
2. If so, is the type of *H. bergeri* Lindholm 1906 referable to the Aus *Homopus*?
3. If not, is it conspecific with *H. boulengeri* or any other member of the genus, or does it represent an un-named taxon?

A detailed description of the type of *Homopus bergeri* Lindholm 1906 is given below and its identity, and thus nomenclatural availability for the Aus *Homopus*, addressed. The morphology of the Aus *Homopus* is then compared with that of other tortoises to confirm whether or not it is referable to *Homopus*, and then with other *Homopus* species to see whether it is conspecific with any extant or fossil species.

MATERIALS AND METHODS

Measurements (mm): CLS, carapace length straight - anterior edge of nuchal to posterior edge of supracaudal, at midline (in most tortoises, including *Homopus*, the gulars do not

extend beyond the nuchal and CLS = total length, TL); CLC, carapace length curved - anterior edge of nuchal to posterior edge of supracaudal, at midline; CWMS, carapace width middle straight - greatest carapace width, bridge to bridge, at midbody; CWMC, carapace width middle curved - greatest carapace width, bridge to bridge, at midbody; CWPS, carapace width posterior straight - greatest width, marginal to marginal, of carapace at level of hind limb openings; GL, gular length - straight midline contact between paired gulars; PL, plastron length - straight midline distance between anterior junction of gulars and posterior junction of anals; PW, plastron width - horizontal width of abdominal at level of suture marginals 5-6; AN, anal notch - midline length between posterior fusion of anals and inner edge of supracaudal; AW, anal width - horizontal width between posterior tips of anals; Depth - maximum height of shell at middle of carapace.

The terminology of shell scutes and bones follows Loveridge & Williams (1957). Specimens of all species examined were housed in the collections of: Port Elizabeth Museum (PEM, now Bayworld) and Transvaal Museum (TM, now Northern Flagship Institute), South Africa; State Museum, Windhoek, Namibia (SMWH), and Museum Wiesbaden Naturhistorische Landessammlung, Germany (MWNH).

RESULTS AND DISCUSSION

Generic assignment of the Aus tortoise

The genus *Homopus* Dumeril & Bibron 1835 (genotype *Testudo areolata* Thunberg 1787; designation by Dumeril & Bibron 1835, not Fitzinger 1843, see Bour 1988) comprises small African tortoises with the triturating surfaces of maxilla and premaxilla without ridges; maxillary not entering roof of palate; prootic narrowly exposed dorsally; quadrate enclosing stapes; centrum of third cervical biconvex;

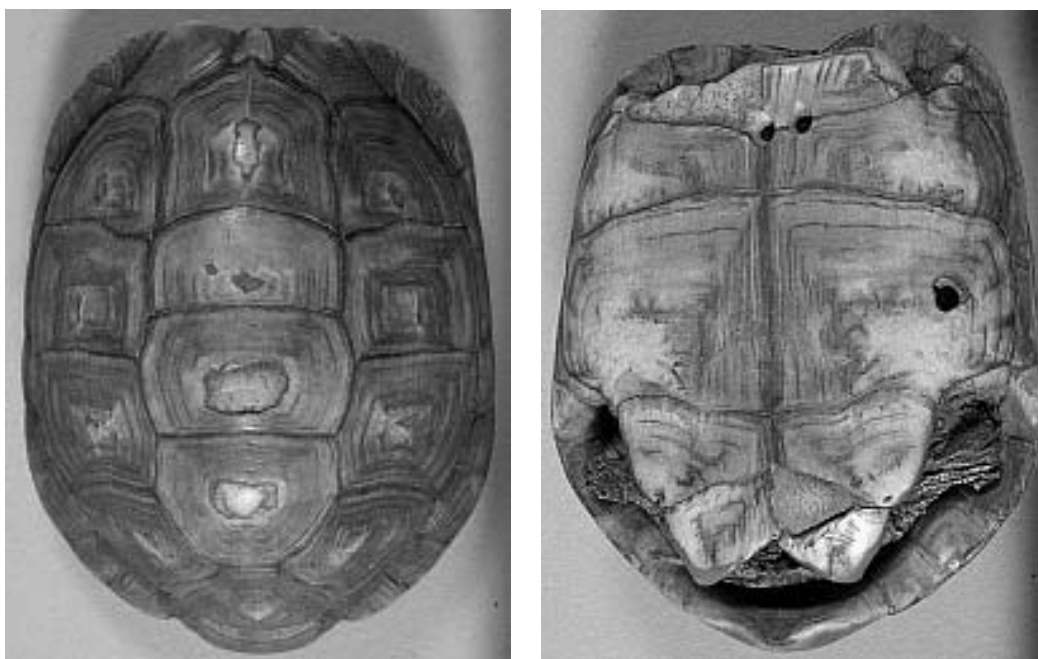


Figure 1. Dorsal (left) and ventral (right) views of the holotype of *Homopus bergeri* Lindholm 1906 (MWNH 711), showing the rounded shell shape, smooth marginals, and plain carapace and plastron coloration.

carapace without hinge; no submarginal scutes; gulars divided; and gular region only slightly thickened (Auffenberg 1974). In addition to these features, the Aus tortoise possesses the following suite of characters that confirm its generic assignment to *Homopus*, and distinguish it from other tortoises in southern Africa: carapace depressed, with a distinct nuchal (c.f. *Stigmochelys*), paired gulars (c.f. *Chersina*) that are broader than long (c.f. *Psammobates*), and without a carapace hinge (c.f. *Kinixys*).

Homopus bergeri Lindholm 1906

The type (MWNH 711) of *Homopus bergeri* is a partial shell with attached dried hind limbs and tail (Fig. 1). It bears the label “*Testudo bergeri* (Ldh) (male sign) Type”. A small natural puncture occurs on the plastron at the outer edge of the left abdominal. As is typical for

Khoisan “buccu” pouch artifacts, the plastron anterior to the humeral-pectoral sulcus has been removed, and two holes (usually for leather thongs) have been drilled in the plastron just posterior to the humeral-pectoral suture. Detailed colour views of the type shell can be viewed at <http://www.nws-wiesbaden.de/coll116.html>.

Scutes.—Carapace domed, with the each vertebral (V) polished and with emergent bone at the centre of V1-4; vertebrals 5, without depressed areolae; costals 4/4, without depressed areolae; 4th smallest; nuchal large and broad, 6.0 mm long, 6.3 mm wide posteriorly; marginals 11/11, non-serrate, only marginals 10-11 with slightly recurved edges; 1st marginal much wider posteriorly and making broad contact with 1st costal on each side, and excluding on left the 2nd marginal from contact with the 1st

costal (on right just in contact); marginals 1-5 in contact with 1st costal (1, 3-5 on left), 5-7 in contact with 2nd costal, 7-8 in contact with 3rd costal, and 9-11 in contact with 4th costal; supracaudal large and recurved, suggesting the shell is of a male; axillaries 2, 1st smallest and in contact with marginals 3-4, 2nd largest and in contact with marginals 4-5; inguinal 1, in contact on both sides with marginals 7-8; tail longish (suggesting it is a male), extending 19.5 mm at right angles to midline and just reaching marginal 10; both thighs with a single large buttock tubercle, each ringed at base with 3 enlarged scales. Plastron broken, portion anterior to the humeral-pectoral sulcus lost; without plastral concavity; outer edges of femorals in contact with marginals 6-7 on both sides, abdominals in contact with marginals 5-6 on both sides; bridge with obvious ridge; growth rings obvious on vertebrae and costals, 8-9 rings on 4th costal.

Measurements (mm).—Total - CLS 87.7 (91 in type description), CLC 115.0, PW 62.0, CWMS 66.7, CWMC 102, CWPS 69.6, AN 12.6, AW 20.0, Depth 43.9 (43.5 in type description). Vertebrae - length midline (1-5 respectively) 22.4, 12.5, 14.9, 20.4, 20.6; vertebral suture widths, 1st - 2nd 22.4, 2nd - 3rd 23.6, 3rd - 4th 21.6, 4th - 5th 6.6, 5th - supracaudal 17.4. Vertebrae-costals (right-left): V1-C1 16.6, 16.6; V1-C2 both in tip contact; V2-C2 9.7, 8.8; V2-C3 5.4, 5.3; V3-C3 9.0, 9.3; V3-C4 7.4, 6.8; V4-C4 12.5, 13.3. Plastral sutures (midline), anal 8.8, femoral 6.1, abdominal 28.0, pectoral 7.4.

Colouration.—Carapace golden brown to light brown on polished vertebral centres; no radiating or areola pattern; plastron patternless, uniform light brown merging to honey-brown at midline; mummified hindlimbs and tail dirty light brown.

Taxonomic history and identity of *Homopus bergeri* Lindholm 1906

Homopus bergeri has a confused and complicated taxonomic history. This confusion stems, in part, from the fragmented nature of the single type. Although obtained in Gibeon, southern Namibia, Lindholm (1906) noted that it could have originated from “deeper in South Africa”.

Soon after its description, Siebenrock (1909a) transferred *H. bergeri* to *H. boulengeri*, but within the same year he transferred it to the *tentorius* group of *Testudo* (Siebenrock, 1909b). Perhaps he was influenced by a footnote in Duerden (1907), who considered *H. bergeri* only doubtfully referable to the genus *Homopus*. Werner (1910) obtained an additional shell from Hereroland that he referred to *Testudo bergeri*. It is well-illustrated (Werner 1910, Fig. 14a-c) and conforms closely to Lindholm’s type. Until the present, Siebenrock’s decision has been followed in principle by all subsequent workers, although as the generic status and interrelationships of the *tentorius* group has evolved, the synonymy of *bergeri* has increased, e.g., *Testudo bergeri* by Siebenrock (1909a); *Chersinella verroxii bergeri* by Hewitt (1934); *Testudo verroxii bergeri* by Mertens (1955); *Testudo smithi bergeri* by Mertens & Wermuth (1955); *Psammobates tentorius verroxii* by Loveridge & Williams (1957); and *Testudo tentorius verroxii* by Mertens (1971).

The type of *Homopus bergeri* Lindholm 1906 is clearly not referable to the Aus *Homopus*, as has been noted earlier by Branch (1992) and iterated by Karl & Tichy (1999). The shell is more domed (CLS/Depth = 2.0) than that of the Aus *Homopus* (range 2.24-2.98, avg. 2.61, SD = 0.26, n = 18), more rounded in dorsal aspect, and there are also too few marginals (10-11), which are also non-serrate. The pale light brown colouration (although possibly faded) is

unlike that of the Aus *Homopus* (which usually has an areolar carapace pattern, and dark anterior and central plastral sutures; see below), and the obvious buttock tubercle on each hind limb is typical in *Psammobates tentorius verroxii*, but usually absent in the Aus *Homopus*. Finally, the shell appears to be from an adult (based on the number of growth rings) and a male (based on the length of the tail) and yet lacks the plastral concavity that is present in adult male Aus *Homopus*.

It should be noted that Mertens (1955) did not consider *bergeri* as being available for the Aus *Homopus*. In fact, he used it for a plain brown tortoise from Klein Windhoek that he called *Testudo verroxii bergeri*, and which was later referred to *Psammobates tentorius verroxii* (Loveridge & Williams, 1957). The status of *bergeri* as a possible northern race of *P. tentorius* remains unresolved, however, and awaits a modern revision of that species (Branch 2006).

Relationship of the Aus *Homopus*

Homopus comprises four named extant species (*H. areolatus*, *H. femoralis*, *H. boulengeri* and *H. signatus*), one (*H. signatus*) with a southern race (*H. s. cafer*) whose taxonomic status requires a modern reappraisal. Loveridge & Williams (1957) discussed the early assignment of chelonian fossils to *Homopus* and discussed their subsequent reinterpretation. A single fossil species, *H. fenestratus* Cooper & Broadley 1990, is currently known from a single partial body cast from uncertain horizon in the Albany District, Eastern Cape Province, South Africa. The living species are restricted mainly to the Cape region of South Africa, with one species extending northeast into the adjacent regions of the North West and Free State provinces (*H. femoralis*). Records of one species (*H. signatus*) from extreme southern Namibia remain problematic. Mertens (1955) noted that some early records of *H. signatus* (Boettger 1893; Fleck 1894) were due to misidentified *Psammobates oculifer*, but con-

tinued to recognise Werner's (1910) record from Keetmanshoop. However, this has not been supported by recent material (Branch *et al.* 1995), and although the distribution of *H. signatus* has been extended into the Richtersveld (Bauer & Branch 2001), it remains unknown from Namibia. All recent records of Namibian *Homopus* (Schleicher & Loehr 2001, Griffin 2002, Schleicher 2004, Cunningham & Simang 2007) are referable to the Aus population, whilst earlier records of other species (*e.g.*, *H. boulengeri* Werner 1910; *H. signatus* Mertens 1955) are probably based on incorrect locality data. Ernst & Barbour's (1989) 'verified' records of *H. boulengeri* from near Aus simply re-iterate Merten's (1955, 1971) confusion.

Hewitt (1932) was the first to discuss intrageneric relationships within *Homopus*, contrasting the characters of the four recognised species. He identified two "well-defined" groups consisting of *areolatus-femoralis* and *signatus-boulengeri* and proposed the new genus *Pseudomopus* to accommodate the latter group. Later Hewitt (1937) realised that his new genus was a junior synonym of *Chersobius* Fitzinger 1835. Although subsequent authors (*e.g.*, Loveridge & Williams, 1957; Boycott, 1986; Cooper & Broadley 1990) have acknowledged the differences enumerated by Hewitt, his partition into two genera has not been followed. Other behavioural and penial characters (Branch, unpub. obs.) also support Hewitt's groupings, and a molecular reappraisal of intrageneric relationships within *Homopus* is needed to resolve whether or not *Chersobius* is a valid genus.

The Aus *Homopus* falls into the '*Chersobius*' group, and is easily distinguished from *areolatus* and *femoralis* by possessing five claws on each forelimb, an obvious plastral concavity in mature males, a single inguinal and 11-12 marginals. Its relationship to *H. boulengeri* and *H. signatus* requires fuller analysis.

Morphological comparison of the Aus
Homopus with *H. signatus* and *H.*
boulengeri

Beak.—The Aus *Homopus* usually has a well-developed tricuspid beak, usually with a serrated lateral edge (Fig. 2). In some adults the beak may become rounded, presumably with wear (e.g., PEM R17048). In *H. boulengeri* the beak is rounded, although it may appear bicuspid in aged specimens as the beak becomes ragged with wear. In *H. signatus* the beak is usually distinctly bicuspid, although it may rarely appear weakly tricuspid due to a small central cusp. It also has ragged lateral edges.

Prefrontal.—The prefrontals are usually fragmented in the Aus *Homopus*, with few specimens having identical arrangements (Figs 2 & 3). In *H. boulengeri* and *H. signatus*, however, the prefrontal condition is more consistent, being usually elongate and longitudinally divided, sometimes with a horizontal suture forming single or paired anterior prefrontals.

Nuchal.—The nuchal in both the Aus *Homopus* and *H. boulengeri* is always longer than broad, and always reaches its greatest length in the midline. It is, however, relatively larger in *H. boulengeri* than in the Aus *Homopus*. The nuchal is largest in *H. signatus*, where it is often as broad as long, and may appear almost divided due to serration of the suture margins.

Marginals.—Most Aus *Homopus* have 11 marginals on each side (16 of 27, 59.2%), with a third of individuals having 12 marginals (9, 33.3%), and a few with unequal counts (11/12 in 2, 7.4%). There are usually more marginals in *H. boulengeri*, with 12 marginals on each side being normal (13 of 19, 68.4%), but with 13 marginals on each side occurring frequently (5 of 19, 26.3%). There are usually 12 (16 of 19, 84.2%), less frequently 11 (3 of 19, 15.8%), marginals in *H. signatus* (Fig. 4). Although the anterior and posterior marginals in the Aus

Homopus are distinctly serrate, they never reach the spiny, recurved nature found in typical *H. s. signatus*.

Bridge.—The bridge usually involves marginals 4-8 in the Aus *Homopus* and bears an obvious to prominent horizontal ridge. The bridge of *H. signatus* also bears a prominent ridge, whilst in *H. boulengeri* the bridge is usually rounded and lacks a prominent ridge. The usefulness of this feature for the identification of empty shells or shell fragments has been discussed by Branch & Bauer (1995).

Axillaries and Inguinals.—All Aus *Homopus* studied had a single large inguinal in contact with the femoral on each side, but usually had two axillaries (15 of 25 specimens, 60.0%), with a single axillary on each side in eight specimens (32.0%), whilst the remaining two specimens had 2/3 axillaries. All *H. boulengeri* studied had both a single axillary and inguinal, as did the great majority of both races of *H. signatus*. Although many reviews (e.g., Loveridge & Williams 1957, Boycott & Bourquin 1988, 2000) indicate only a single axillary occurs in *H. signatus*, a few individuals (2 of 19, 10.5%) of the typical race may have two axillaries.

Buttock tubercles.—Enlarged buttock tubercles in the Aus *Homopus* are usually absent in both sexes, although a small patch of enlarged scales, some taking the form of small tubercles, is often present in both sexes on the posterior edge of the thigh close to the tail base (Fig. 5). In some males (e.g., PEM R17048) it may form a small buttock tubercle. Although most previous reviews state that buttock tubercles may be present or absent in *H. boulengeri* (e.g., Loveridge & Williams 1957, Boycott & Bourquin 1988, 2000), it has not previously been noted that the expression of this feature is sexually dimorphic in the species. Most mature males have a single, prominently enlarged conical buttock tubercle on the posterior surface of each thigh. Usually the buttock tubercle is sur-



Figure 2. Tricuspid beak, serrated jaw and prefrontal condition in *Homopus solus*. Holotype PEM R8754 (left), allotype PEM R8765 (right).

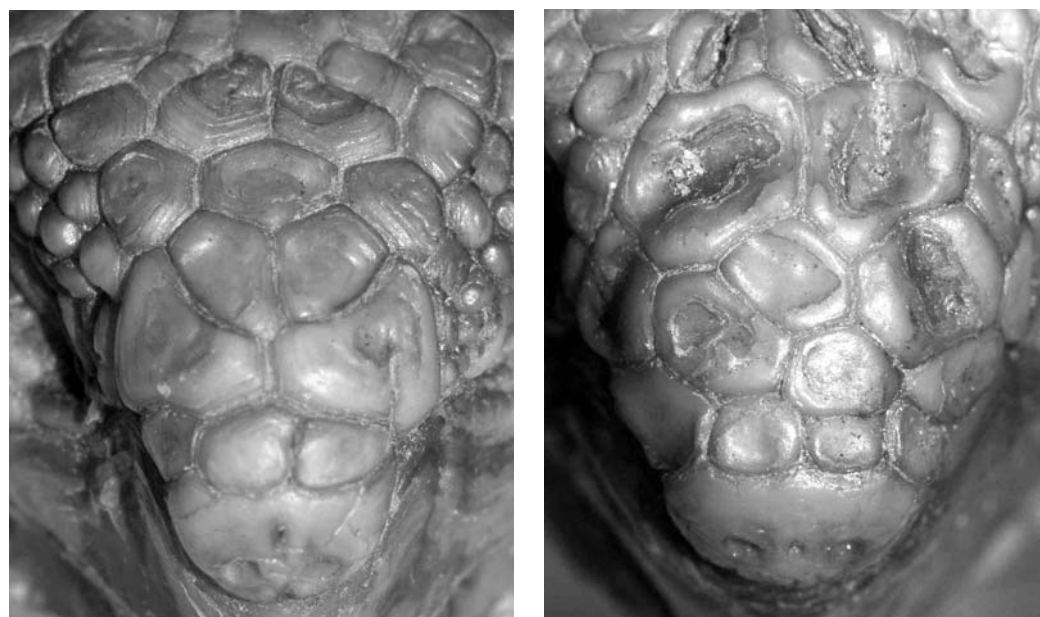


Figure 3. Prefrontal condition in *Homopus solus*. PEM R17046 (left), PEM R8764 (right).

rounded by a single (sometimes double) ring of smaller tubercles. Duerden (1906) notes the absence of a buttock tubercle in one male. Buttock tubercles are usually absent in females (uniquely present in PEM R10309), but may be represented by a small patch of large, but flattened tubercles. This patch is present in immature males (<55mm CLS), but without enlargement of the main tubercle. The development of

buttock tubercles in *H. signatus* is not sexually dimorphic, and prominently enlarged conical buttock tubercles are present on the posterior surface of each thigh in juveniles and in all mature males and females. Usually the buttock tubercle is the most prominent of a ridge of enlarged scales that run across the posterior face of the thigh from the knee to the tail base.

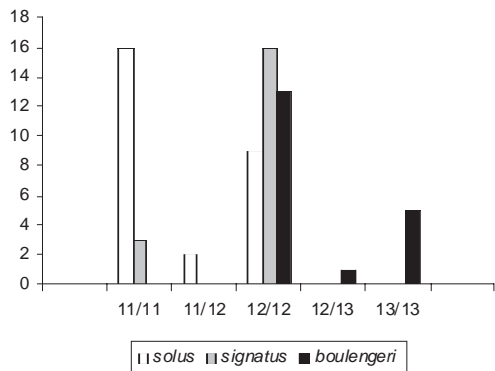


Figure 4. Number of marginal scutes in *Homopus solus*, *H. signatus* and *H. boulengeri*.

Scale rows on forelimbs.—Loveridge & Williams (1957) considered that the number of longitudinal rows of enlarged scales on the front surface of the forelimbs differed between *Homopus* species, with *H. areolatus* and *H. femoralis* having very large scales in 3-4 rows, *H. boulengeri* having 4-5 rows, and *H. signatus* 5-6 rows. The exact number of rows of large, imbricating scales on the forelimb is difficult to determine accurately. Boycott (1986) noted variability in this feature, even though it had been used by Hewitt (1935) to distinguish the subspecies *H. signatus peersi* (= *H. s. cafer*, Bour 1988), and no consistent difference in the relative size of forelimb scales in *H. boulengeri*, *H. signatus* and the Aus *Homopus* (which all occur in 4-5 rows) could be found during this study. However, in agreement with the observation of Loveridge & Williams (1957), the forelimb scales are relatively smaller than those in *H. areolatus* and *H. femoralis* and consequently are arranged in more longitudinal rows.

Plastron midline sutures.—All three *Homopus* have broadly similar arrangements of plastron midline sutures (Table 1), with the abdominal suture the longest, followed by that of the humeral. In the Aus *Homopus* and *H. signatus*, the abdominal sulcus is usually twice the length

of the humeral sulcus, whilst it is slightly shorter in *H. boulengeri* (Table 1). The gular, pectoral, femoral and anal are approximately subequal in length, but the femoral is shorter than the anal in the Aus *Homopus* and *H. signatus*. In contrast, in *H. boulengeri* the femoral is longer than the anal and also proportionately longer relative to the abdominal (Table 1).

Shell proportions.—There is no difference in the relative width of the shell between the three species. However, the shell of the Aus *Homopus* is significantly shallower (CLS/Depth) than that of *H. boulengeri*, but not of *H. signatus* (Table 2). Shell proportions also differ between the sexes, with females having relatively deeper and wider shells in all three *Homopus* species (Table 2).

Carapace fenestra.—All adult extant *Homopus*, except the Aus species, have completely ossified shells. In the Aus *Homopus*, however, large fenestra are present in the carapace of juveniles (e.g., PEM R8763, CLS 60 mm; R8766-67, mummified young, CLS 36-38 mm) and retained even in relatively large adults (e.g., PEM R8768, CLS 87 mm, Fig. 6). The reduced ossification of the dorsal shell elements occurs in the neurals and pleurals underlying the central region of the overlying vertebrals and costals, respectively.

Colour pattern.—The Aus *Homopus* usually has an areolar carapace colour pattern. The pale brown carapace scutes have a dark brown (sometimes stippled) edge that is usually less than a third of the scute width. The marginals and plastron scutes are also usually dark-edged, with the dark border wider on, or usually restricted to the anterior edge. Colouration on the plastron scutes may be greatly faded in some specimens. *H. boulengeri* never has an areolar carapace pattern, with the carapace always uniformly coloured, although this may vary from olive green, pale brown or rust red. The plastron is also generally uniform in colour



Figure 5. Posterior thigh area of *Homopus solus* (allotype PEM R8765) showing the patch of enlarged scales without obvious buttock tubercle.



Figure 6. Internal view (head left) of dry, distorted carapace of *Homopus solus* (PEM R8768) showing the reduction of ossified dorsal shell elements (white network of bone). The dark areas are gaps in the bone revealing the overlying keratin cover of the carapace scutes. Due to the reduced ossification the carapace has curled inwards along the vertebral axis.

Table 1. Three ratios of plastral midline suture measurements (mm) for three species of *Homopus*.

	<i>H. solus</i>	<i>H. boulengeri</i>	<i>H. signatus</i>
Femoral/anal			
Average	0.80	1.57	0.74
Maximum	1.25	2.33	1.29
Minimum	0.56	0.97	0.43
SD	0.17	0.33	0.20
Number	18	19	18
Abdominal/femoral			
Average	3.77	2.56	3.46
Maximum	5.30	4.57	4.75
Minimum	2.62	1.77	2.28
SD	0.71	0.66	0.75
Number	18	19	18
Abdominal/humeral			
Average	2.14	1.89	2.10
Maximum	2.93	2.96	2.62
Minimum	1.72	1.49	1.73
SD	0.30	0.33	0.28
Number	18	19	18

Table 2. Ratios of carapace length (CLS) to shell depth and carapace width (middle, straight) in females (F) and males (M) of three species of *Homopus*.

	<i>H. solus</i>		<i>H. boulengeri</i>		<i>H. signatus</i>	
	F	M	F	M	F	M
CLS/Depth						
Average	2.50	2.76	2.17	2.44	2.49	2.78
Maximum	2.98	3.42	2.59	2.75	2.80	3.06
Minimum	2.24	2.34	1.96	2.18	2.25	2.57
SD	0.25	0.34	0.20	0.20	0.19	0.18
Number	13	10	8	10	10	7
CLS/Width						
Average	1.25	1.39	1.29	1.36	1.33	1.40
Maximum	1.41	1.51	1.37	1.45	1.39	1.48
Minimum	1.10	1.30	1.19	1.23	1.28	1.18
SD	0.09	0.08	0.05	0.08	0.04	0.11
Number	13	10	8	11	5	6

(and usually of a lighter tone than that of the carapace), although in some males it may be darkly speckled. The colouration of *H. signatus* is more complicated, with regional variation and a southern race, *H. s. cafer*, that is characterized by reduced speckling. Relative to other *Homopus*, however, the carapace of *H. signatus* is always speckled, sometimes with an underlying areola and/or rayed pattern, and usually darker, with more rays and fewer speckles in females (Loehr *et al.* 2006).

Conclusions.—In many features of its morphology the Aus *Homopus* differs from both *H. boulengeri* and *H. signatus* (summarized in the *Diagnosis* below), and is thus not conspecific with either. Its relationship to fossil *H. fenestratus* (Cooper & Broadley 1990) remains more problematic as the latter is known from a single, incomplete type. Although both share fenestra in the bony elements of the shell, those in the Aus *Homopus* occur extensively on the carapace, unlike the plastral fontanelle of *H. fenestratus*. Moreover the ‘bun-shaped’ shell of the latter is subcircular in outline, unlike the subrectangular shape of the Aus *Homopus*. These differences indicate that the Aus *Homopus* cannot be confidently assigned to the extinct *H. fenestratus*, which is also geographically well separated. As the Aus *Homopus* is well-differentiated morphologically from all extant and extinct species, opportunity is taken to describe it below.

SYSTEMATICS

(Reptilia: Chelonia: Testudinidae)

Homopus solus **Branch sp. nov.**

Homopus boulengeri - Mertens 1955, 33; Mertens 1971, 24; Greig & Burdett 1976, 270.

Homopus bergeri - Boycott 1986, 10; Newbery & Jacobsen 1986 (poster); Branch *et al.* 1988, 5; Branch 1989, 75; Boycott 1989, 78; Pritchard 1990, 603; Iverson 1992, 264; David

1994, 50; Bonin *et al.* 1996, 136; Rogner 1996, 81; Anon (Red Data Animals Africa) 2000, 114.

Homopus ‘bergeri’ - Branch 1992, 11.

Homopus sp. - Branch 1998, 28; Boycott & Bourquin 2000, 180; Cunningham & Simang 2007, 129.

Homopus sp. (“*Homopus bergeri*”) - Schleicher 2004, 3.

Homopus “Namibian form” - Vetter 2002, 47.

Homopus ‘solos’ - Devaux 2003, 40.

Homopus bergeri (solos) - Bonin *et al.* 2006, 227.

Common name - Nama padloper. (inappropriate name = Berger’s padloper, Branch 1988, 1989)

Nomenclatural note.—The use of the combinations *Homopus ‘solos’* by Devaux (2003) and *Homopus bergeri (solos)* (Lindholm, 1906) by Bonin *et al.* (2006) may have caused confusion. Both descriptions are accompanied by illustrations of the Aus *Homopus*, and note that they are based on a proposed (manuscript) name by W. R. Branch that is described here. Fortunately both names have no nomenclatural standing; the first is a *nomen nudum* as the diagnosis is inadequate and the inclusion of the name in inverted commas indicates that the author did not consider it a formal name. The presentation of latter name also does not present a formal name, and it is therefore yet another synonym of the Aus *Homopus*. In addition, the name ‘solos’ is not homonymous with *Homopus solus* and therefore the problematic usage does not conflict with description of the latter. Their use, however, illustrates the nomenclatural dangers of using manuscript names.

Holotype.—PEM R8754 (CDNEC 6381), Figs. 2, 7-8, an adult female collected in the vicinity of Aus, Luderitz District, Namibia (2616Da), by Peter Mostert during June 1982.

Allotype.—PEM R8765 (CDNEC 6382), Figs. 2, 5, 9, an adult male with everted penis, collected from the Kowie Mountains, Luderitz District, Namibia (2615Cb) by P. Mostert during June 1982.

Paratypes.—12 specimens, comprising 3 subadult females, 5 adult males and 4 adult females: PEM R8755 (CDNEC 6370), subadult female, hills at Aus (2616Cb), November 1981, Mrs. Steenkamp; PEM R8756 (CDNEC 6371), subadult female, Aus (2616Cb), November 1981, P. Mostert; PEM R8757 (CDNEC 6372), subadult female, Aus (2616Da), December 1981, P. Mostert; PEM R8758 (CDNEC 6373), adult male, Aus (2616Cb), March 1982; P. Mostert, PEM R8760 (CDNEC 6375), adult male, Farm Plateau, Aus District (2616Cb), April 1982, P. Mostert; PEM R8761 (CDNEC 6377), adult male, 'Heinrichsfelde', Aus District (2616Ca; 26°48'S, 16°10'E), May 1982, P. Mostert; PEM R8764 (CDNEC 6378), adult female, Aus (2616Cb), June 1982, P. Mostert; PEM R9415, adult male, Farm Weldevrede, 45.2km E Luderitz (2616Da, 26°36'S, 16°41'E), 28 March 1992, P. Freed; PEM R17046 (CDNEC 6379), adult female, Farm Plateau, Aus District (2616Cb), June 1982, P. Mostert; PEM R17047 (CDNEC 6376), small adult female, headless, Aus (2616Da), April 1982, P. Mostert; PEM R17048 (CDNEC 6380), adult male, same details as R17046; PEM R17049 (CDNEC 6383), adult female, Farm Plateau, Aus District (2616Cb), August 1982, P. Mostert.

Additional material.—PEM R8759 (CDNEC 6374), Aus (2616Cb), April 1982, P. Mostert.

PEM R8763, 22 km SE of Rosh Pinah (2816Bb), halfway up slopes of Megakop, June

1989, J. Hensley; PEM R8766-67, two mummified juveniles collected in vicinity of Aus (2615Cb) in early July 1982, P. Mostert; PEM R8768 (carapace only), Jakkalskop 180, Luderitz District (2616Da), on top of flat-topped hill in dwarf shrub savannah, 1 October 1989, D. Clark; PEM R8769, Kowiesberg, Luderitz District, October 1988, W. R. Branch (forepart of plastron with left forelimb collected in brown hyena den); SMWH 6604, Witputz (juvenile carapace); SMWH 6605-6, 6608, 7455, Aus; SMWH 6607, 45km E of Luderitz; SMWH 8190, "Oranjemund area"; TM 55040, Rosh Pinah, 27°58'S, 16°46'E (2716Dd), 21 May 1981, I. Pehleman; mummified female; TM 56974-75, 1 km W Aus, 26°40'S, 16°16'E (2616Cb), A. de Kock, November 1981.

Etymology.—The specific epithet *solus* is Latin for alone or lonely, describing both the separation of the species' range from that of all other members of the genus, as well as the desolate, sparsely-populated habitat in which the tortoise lives. In addition, the name alludes phonetically (sol) to the sun and the heat of the Namib Desert.

Diagnosis.—A small *Homopus* that forms part of the '*Chersobius* group', and thus differs from *H. areolatus* and *H. femoralis* by possessing five claws on each forelimb, an obvious plastral concavity in mature males, a single inguinal and 11-12 marginals. Among the '*Chersobius* group' it differs from *H. signatus*, its nearest geographical neighbour, and from *H. boulengeri*, to which it was originally referred (Mertens 1955, 1971), by having an areolar carapace colour pattern (usually speckled in *signatus* and patternless in *boulengeri*); usually lacking prominent buttock tubercles in both sexes (present in both sexes in *signatus*, but usually only in males in *boulengeri*); having two axillaries (usually single in both *signatus* and *boulengeri*); a tricuspid beak (usually bicuspid in *signatus* and rounded in *boulengeri*); a small, narrow nuchal (broad in *signa-*

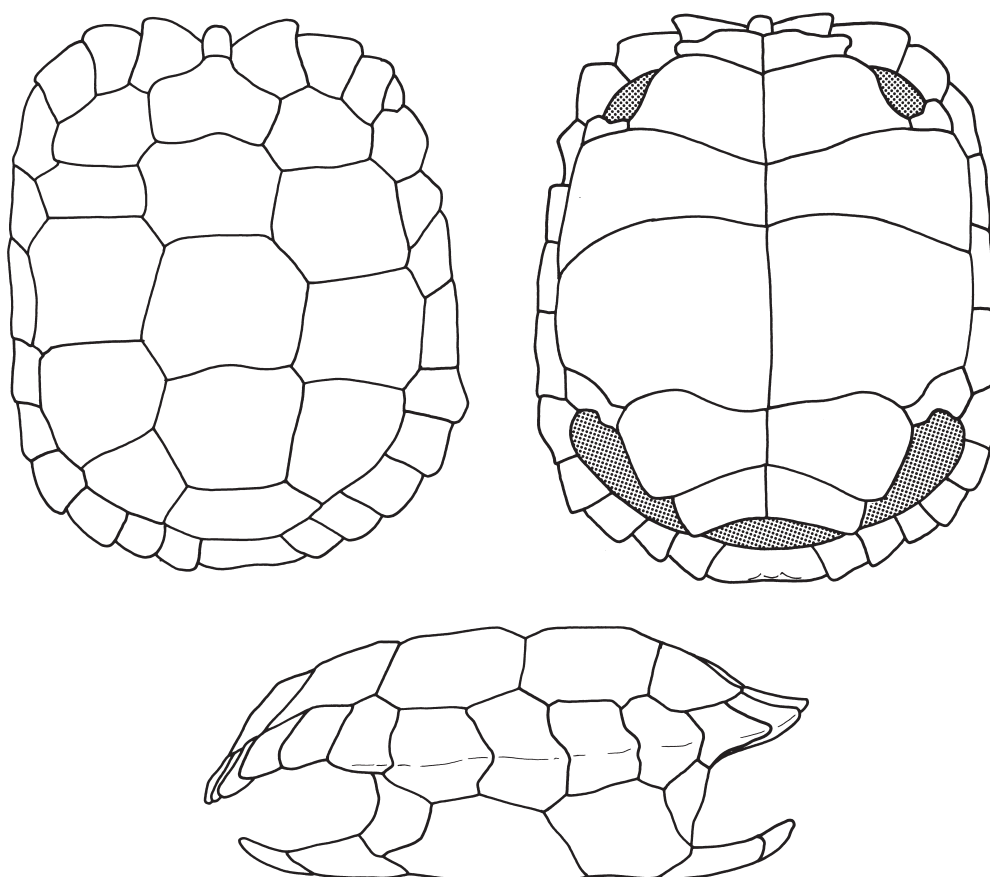


Figure 7. Shell of Holotype (PEM R8754) *Homopus solus*, dorsal (top left), Ventral (top right) and lateral (bottom) views. Scale is 1 cm.

tus); a relatively shallower shell; fragmented prefrontals (usually more elongate and longitudinally divided in *signatus* and *boulengeri*); usually having 11 marginals (mainly 12 in *signatus* and always 12 or more in *boulengeri*); having a well-defined ridge on the bridge (rounded in *boulengeri*); and having the anal midline suture longer than the femoral (femoral suture longer than the anal in *H. boulengeri*).

Description of the Holotype.—An adult female with neck and limbs extended, and mouth slightly open; growth rings obvious on all scutes; carapace flattened, slightly widened posteriorly; vertebrals 5, with faintly depressed areolae, largest V3, smallest V1, widest V5; costals 4/5 (C1 on left side divided), with slightly depressed areolae; C1 smallest, C2-3 largest; nuchal large, slightly longer (5.0 mm) than broad (4.7 mm); marginals 12/12, with non-recurved edges; marginals

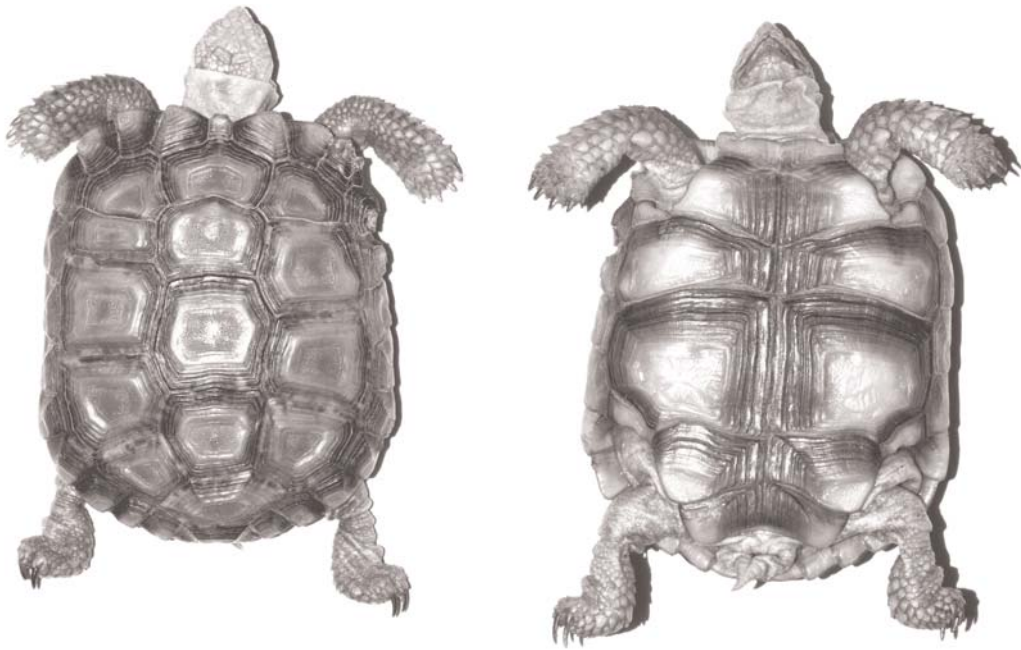


Figure 8. Holotype (PEM R8754) *Homopus solus*, dorsal (left) and ventral (right) views.

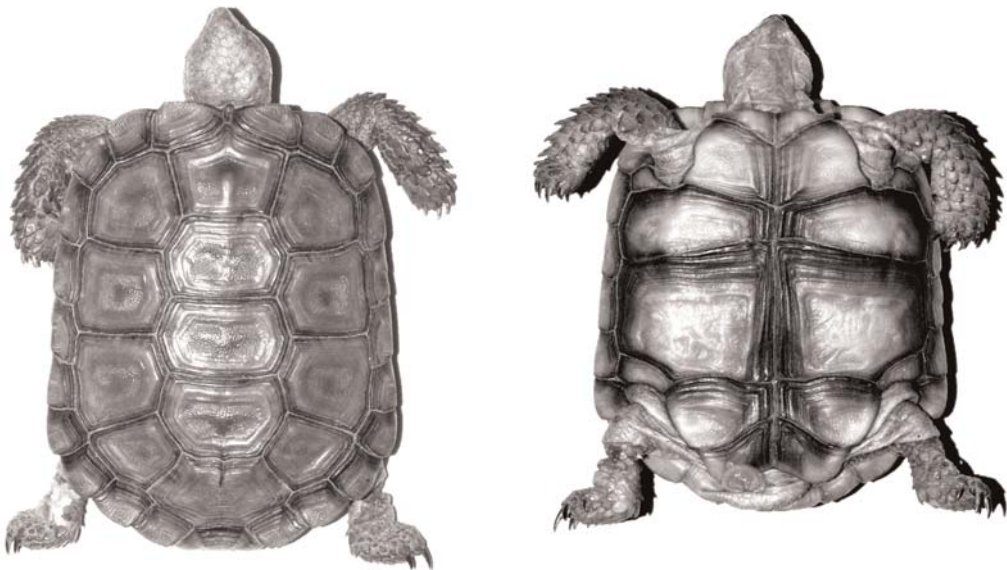


Figure 9. Allotype (PEM R8765) *Homopus solus*, dorsal (left) and ventral (right) views.

1-3 and 8-12 slightly serrated; 1st marginal much wider posteriorly and making broad contact with 1st costal on each side; marginals 1-4 in contact with 1st costal, 4-6 in contact with 2nd costal (right side), 6-8 in contact with 3rd costal, and 8-11 in contact with 4th costal; supracaudal medium, not recurved; axillaries 1/1; inguinals large, 1/1, in contact on both sides with marginals 7-8; bridge long (marginals 4-8) with obvious ridge just below midline of marginals; plastron slightly depressed along midline sutures, but without plastral concavity; plastron midline suture lengths (mm) - gular 7.7, humeral 14.2, pectoral 9.6, abdominal 27.2, femoral 7.9, anal, 9.3; gulars paired and much wider (combined width 25 mm) than long (midline suture 7.7 mm); humerals broader than long, and abutting on each side a single large axillary that is in contact with marginals 3-4; pectorals much wider than long, midline suture narrower than contact with marginals (4-6); abdominals very large, central suture only slightly smaller than abdominal-pectoral suture, and in contact with marginals 6-7 on both sides; femorals broader anteriorly, separated from marginals by large inguinal, that is in broad contact with marginals 7-8; anals broader than long, rounded at tips.

Head small, snout somewhat pointed; upper beak strongly tricuspid, lower beak unicuspid; upper and lower jaw margins serrated laterally (Fig. 2); head scalation not uniform; nostrils placed anteriorly, surrounded by soft, fleshy nasorostral, bordered posteriorly by 4 scales, outer largest; prefrontals fragmented, with 5 scales roughly symmetrically arranged (Fig. 2); crown of head (frontal/frontoparietal region) roughly triangular, partially fragmented and pitted, bordered on sides by enlarged row of scales, that are in turn separated by 2-3 rows of smaller scales from the eye; crown demarcated posteriorly by two enlarged, broad parietals, and laterally on each side by an elongate temporal above the ear; neck covered with soft, flexible skin with small, flattened granules.

The forelimbs have 5 claws and are covered anteriorly with 4-5 longitudinal rows of large, overlapping scales, the largest in line with claw 4; the hind limbs each have 4 claws; the upper part of the limbs are covered in soft skin with scattered small scales; these become larger and more juxtaposed on the lower limbs; both thighs with a cluster of 15-18 enlarged scales on posterior surface, the largest centrally placed and tubercular; the soles of all limbs are covered in elongate, spiny scales whose tips are orientated towards the claws; tail short (extending to only 12th marginal) and lacks a terminal spine.

Carapace with areolar pattern; vertebral and costal centres dirty brown with light yellowish brown edge, in turn bordered by dark brown border that sometimes has paler blotches or darker rays (*e.g.*, V3); marginals, nuchal and supracaudal tipped in pale brown, with a wide, dark brown margin on anterior and inner borders; plastron scutes brown centred, with extensive dark brown borders (except for posterior edges); limbs with yellow brown scales and paler (dirty cream) skin on the upper limbs, tail and neck; claws on hind limbs dark brown; head pale yellow-brown, slightly darker on crown and labial area.

Description of the Allotype (where different from holotype).—An adult male with neck and limbs extended, mouth slightly open, and no incisions (Fig. 9); vertebrals 5, with faintly depressed areolae, largest V3, smallest V1, widest V5; costals 4/4, with slightly depressed areolae; C4 smallest, C1-3 subequal; nuchal tiny; marginals 11/12, with non-recurved edges; marginals 1-2 and 8-12 slightly serrated; plastron with shallow plastral concavity deepest at level of abdominal-femoral suture; plastron midline suture lengths (mm) - gular 7.8, humeral 11.2, pectoral 6.1, abdominal 26.6, femoral 5.8, anal, 9.7. Head scalation not uniform; prefrontals fragmented, with six scales symmetrically arranged (Fig. 2); crown of head

(frontal/frontoparietal region) roughly triangular, fragmented and pitted, bordered on sides by enlarged row of scales; parietals at back of crown fragmented; elongate temporal divided into 3 scales on right, 2 on left. The posterior surface of the thigh is covered with a patch of flattened scales, with only one scale forming a weak buttock tubercle (Fig. 5); tail slightly elongate (extending to anterior edge of last marginal), without terminal spine but with penis partially everted. Colouration similar to holotype, except brown scute margins on carapace and plastron narrower, vertebral and costal scute centres dirty brown, and limbs and head slightly darker brown.

Paratype variation (including exceptional features in additional material).—As in other *Homopus* there is a frequent tendency for irregular scutellation, particularly on the carapace where 7 of 26 specimens have supernumary costals and 5 of 26 specimens have supernumary vertebrae. Specific abnormalities include: PEM R8763 - supernumary vertebral between 4-6, both nuchal and supracaudal divided; PEM R8755 - supernumary vertebrae between V3-V4 & V4-5, supracaudal divided; PEM R17048 - V5 divided longitudinally; PEM R17049 - V3-4 fragmented into 3 vertebrae, V5 partially divided; PEM R8761 - V2 divided, 5 left costals; TM 56974 - supernumary vertebral (V6) between V5 and supracaudal, and extra costal between RC4 and V6. The nuchal is always longer than broad and its size usually varies from small to medium, however it is very large (subequal to 2nd marginal) in PEM R 8768; fragmented axillaries (2/3) in R9415 and SMWH 6607; an enlarged temporal scale is present, but is divided in the allotype and PEM R9415; the beak is tricuspid in nearly all specimens, but is rounded in PEM R17048; enlarged scales on the posterior surface of the thigh are absent in hatchlings and subadults, but slightly enlarged and raised tubercles are visible in some specimens >65mm CLS, and may even form small buttock

tubercles in some mature males (e.g., PEM R17048).

Measurements for the type series are shown in Table 3.

Colouration is relatively constant; typically the carapace is red-brown, often with an olive tinge in old adults. Each dorsal scute usually has a pale areola and a dark border that is usually rich red-mahogany in colour and may be irregularly flecked. The plastron is similarly patterned, although the dark border is often more extensive, particularly on the anterior and lateral margins. The head and limbs are pale to dirty brown. Very large females, in which growth has presumably slowed, become more uniform in colouration with dark scute margins limited only to the sutures and dark margins of plastron becoming more blotched; subadults are pale brown in colour with dark brown borders very reduced and limited just to the sutures; as in *H. boulengeri*, the ventrum of mature males may become infused with darker blotches (e.g., PEM R9415). Typical, well-coloured individuals are illustrated in colour in Branch (1988), Bonin *et al.* (1996), Boycott & Bourquin (2000), Devaux (2003), and Schleicher (2004).

Sexual Dimorphism.—Colouration is not known to be sexually dimorphic. Sexual dimorphism in colouration within *Homopus* is known only in *H. areolatus* (Branch 1998) and *H. signatus* (Loehr *et al.* 2006). Adult males have a relatively shallow plastral concavity and a longer tail, and the shell is also shallower (CLS/Depth, males - mean 2.76, range 2.34-3.42, standard deviation 0.34, n= 10; females - mean 2.50, range 2.24-2.98, standard deviation 0.25, n=13) and narrower (CLS/CWMS, males - mean 1.39, range 1.30-1.51, standard deviation 0.08, n=10; females - mean 1.25, range 1.10-1.41, standard deviation 0.09, n=13). Females also grow larger, with three females studied exceeding 100 mm CLS, whilst only two males exceed 90 mm CLS.

Table 3. Measurements (mm) for type series of *Homopus solus* (see Materials and Methods for abbreviations)

Status	PEM R	Sex	CLS	CWMS	CWPS	PL	PW	GL	Depth
Holotype	8754	F	88	71	73.5	76	66	8	38
Allotype	8765	M	79	59	61	67	54	7	28
Paratype	8755	F	44	38	37	37	32.5	3	19.5
Paratype	8757	F	46	42	41.8	41.8	38	4	20.5
Paratype	8756	F	66	52	55	59.5	46.2	6.5	28
Paratype	17047	F	77	60	64.5	66.5	54.5		32.5
Paratype	17046	F	85	66	69	75	60.5	9	32
Paratype	17049	F	94.5	73.3	77.2	81.3	68.8	7.6	38.3
Paratype	8764	F	104	82	84	90	77	9	41
Paratype	8760	M	74	57	60	63	51	6.2	30
Paratype	8758	M	77	59	61.5	66	53	4	28
Paratype	17048	M	83	59.5	61.8	68	54	7.1	29
Paratype	9415	M	86.5	59	63.3	70.5	54.5	7.2	34.5
Paratype	8761	M	89	59	62	70	57	7	29

Size.—Maximum length; female (PEM R8764) CLS 104 mm, 240g; male (SMWH 7455) CLS 96 mm. Smallest specimens are two mummified (perhaps slightly shrunken) juveniles, 36 and 37 mm CLS, collected near Aus in early July 1982. Schleicher (2004) notes a maximum size for a female of 114 mm shell length (not stated how measured), with males reaching only “8-9 cm” in shell length. A wild hatchling measured TL 32.5 mm (Cunningham & Simang 2007), but hatchlings average slightly larger (36.2 mm TL) in captivity (Schleicher & Loehr 2001).

Distribution.—Endemic to southern Namibia (Fig. 10), with the main distribution centred around the escarpment mountains near Aus, but with scattered records from other isolated mountains in the sand and gravel plains of the southern Namib Desert, *e.g.*, the Kowiesberg near Luderitz, low granite hills 4-5 km SW from Tschaukaib siding (2615Da), and 2-3 km SE from Haalenberg siding (2615Cb) (W. Wendt pers. comm.). The most southerly records are from Witputs on the Huib Plateau

near Rosh Pinah, with an undocumented sight record of *Homopus* shell fragments from the eastern rim of the Fish River Canyon opposite Ai-Ais (M. Griffin pers. comm.). Schleicher (2004) notes a shell found 50 km north of Aus on the plateau of the Rooirand Mountains.

Habitat.—Restricted to barren mountains, with sparse and succulent vegetation in the Namib Desert and with grassland on the Aus escarpment. Populations on the Kowiesberg in the Namib Desert near Luderitz are subject to extreme aridity (often <10 mm rainfall p.a.) and must obtain most of their water from their food and/or advective fog from the offshore, cold Benguela Current. Rainfall at Aus is higher (80-100 mm p.a.) and falls mainly from January to June. Maximum temperatures may exceed 40°C (March); minimum temperatures at Luderitz may drop to 0°C (June) and well below freezing at Aus, where winter snowfalls are common. Mendelsohn *et al.* (2002) note that the dominant rock types in the area form part of the Namaqua Metamorphic Complex, with resultant shallow, coarse-textured lithic

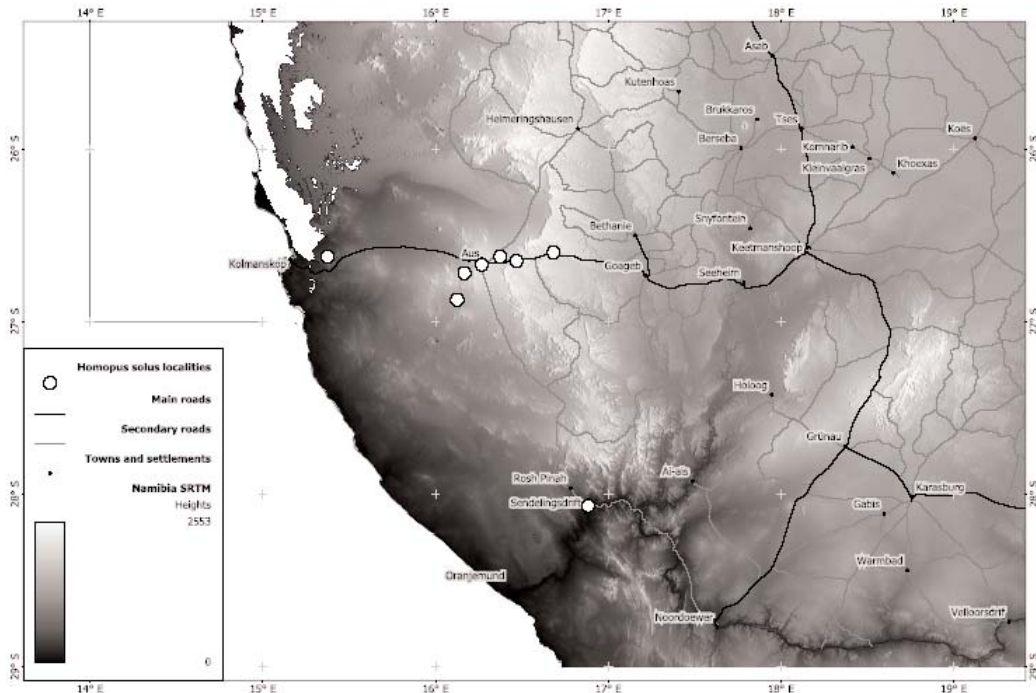


Figure 10. Distribution of *Homopus solus* in southern Namibia (based on material examined).

leptosol soils. Photographs of typical habitat in the Aus region are shown in Devaux (2003) and Schleicher (2004).

Conservation Status.—All tortoises are protected by national legislation in Namibia. The species was listed as Endemic and Indeterminate in Namibia (Griffin 2002), but as Vulnerable (VU C2a) in the 2006 IUCN Red List of Threatened Species (as *Homopus bergeri*). *Homopus solus* has a very restricted distribution and remains poorly known. However, there is no formal data indicating that it is threatened, either by habitat destruction or illegal collecting, or that its range or numbers have declined. The species is known to occur in a number of protected areas, including Namib-Naukluft National Park (marginally), National Diamond Coast Recreation Area, the Sperrgebiet, and the Ai-Ais/Hunsberg Reserve (Griffin 2002).

Biology.—The species is rock-living and inhabits very arid, rocky terrain, although it may forage in sand gullies between rock outcrops. It has been reported to shelter under rock slabs and to be particularly active during and after winter rains (Mertens 1955). Captive specimens have been noted to readily climb steep rock faces (Schleicher 2004). It has been observed drinking from rock pools, and tortoises on the Kowiesberg and other adjacent very arid mountains may obtain sufficient moisture from the regular fogs that are characteristic of the coastal regions of the Namib Desert. Possible food plants on the sparsely vegetated Kowiesberg include *Grielum sinuatum*, *Wahlenbergia erophiloides*, *Pellaea frutescens*, *Zygophyllum dregeanum*, *Heliochrysum* sp., *Limeum* sp. (M. Müller, pers. comm.). Cunningham & Simang (2007) note that lichens are also grazed, and give further details of ecology and habitat use. Reproduction in

captive populations is relatively well-studied (Schleicher & Loehr 2001; Schleicher 2004). It is unknown whether the species is very rare in the region, or rarely seen due to infrequent activity. During seven years (1969-1976) of archaeological research in the Kowiesberg region only two tortoises were observed (W. Wendt pers. comm.).

Aspects of shell morphology, including the flattened shell and large fenestra in the bone elements, are possibly adaptations to reduce shell weight, enabling it to climb steep rock faces and to shelter in rock cracks. The pancake tortoise (*Malacochersus tornieri*) is another African tortoise that inhabits rocky terrain, in Tanzania, and shows similar morphological adaptations. Whether these features represent convergence between the two taxa, or are indicative of a close phylogenetic relationship remains unknown. Similar reduction in the osteological elements of the shell also occur in the unique type of the fossil tortoise, *Homopus fenestratus* (Cooper & Broadley 1990), but fuller fossil material is required before the significance of these features can be assessed.

The reduced ossification of the shell may mean that the species is more susceptible to predation. A broken plastron fragment from a large female (PEM R8769) was found high on the summit rocks of the Kowiesberg in a rock overhang used by a brown hyena. This large predator could easily crush and consume adult tortoises. An adult male shell (CDNEC 6375) has damage to marginals 6-12 on the left bridge, which are similar to canine gnaw marks, possibly from a black-backed jackal, which is also common in the region. Avian predators, such as crows and kelp gulls, occur in the region and are also known to kill hatchling and juvenile tortoises (Branch & Els 1990).

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