Description of an anomalous tortoise (Reptilia: Testudinidae) from the Early Holocene of Zimbabwe

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An anomalous subfossil tortoise is described from a Holocene cave deposit at Pomongwe in the Matobo Hills, southwest Zimbabwe (Carbon 14 date 9400 ±100 yrs BP). This specimen appears to be unique in its truncated and depressed anterior carapace with loss of the normal second peripheral, but agrees with *Kinixys* Bell and *Impregnochelys* Meylan & Auffenberg in having numerous auxiliary scales. It may lack the carapacial hinge of *Kinixys.* The epiplastron appears most similar to that of a female *Chersina angulata* Gray.

Keywords: *Kinixys spekii* (?), Testudinidae, osteology, Holocene, Zimbabwe, Africa.

INTRODUCTION

The extensive deposits in Pomongwe Cave in the Matobo Hills were excavated in 1960/61 (Cooke 1963). Beneath a superficial layer of dust (Level 1) was a thin deposit of red soil (Level 2), which had been imported during the 1920s by the current curator in an attempt to stabilize the white ash (Level 3) on the floor of the cave for the benefit of visitors to the cave paintings. The bone recovered from Level 3 included many fragments of tortoise bones (Brain 1981), some identified as *Stigmochelys* (ex *Geochelone*) *pardalis* and *Kinixys spekii* (Broadley 1993, 1997), but eight more or less complete bones possibly represent an undescribed taxon. Tortoise bones from later excavations in the same cave (Walker 1995) were also examined, but did not yield additional material of this unusual form. As no further excavations are planned in this cave, it was decided to describe this tortoise on the basis of the limited available material.

MATERIALS AND METHODS

Comparative material of all African tortoise species except *Geochelone sulcata* (Miller) was available in the Herpetology Department of the Natural History Museum of Zimbabwe in Bulawayo (NMZB) (see Appendix 1). Nomenclature for bones and epidermal shields follows Zangerl (1969), while nomenclature for limb bones follows Walker (1973). In the figures, thin black lines denote bone margins, sutures and fractures, while thick white (subfossil) or black (other genera) lines denote sulci between epidermal shields.

SYSTEMATIC PALAEONTOLOGY

Order Testudines Linnaeus, 1758 (=Chelonii Brongniart 1800)
Suborder Casichelydia Gaffney, 1975
Infraorder Cryptodira Cope, 1868
Superfamily Testudinoidea Batsch, 1788
Family Testudinidae Batsch, 1788
Subfamily Testudininae Batsch, 1788

Genus (?) *Kinixys* Bell, 1827

Type species: *Kinixys castanea* Bell (=*Testudo erosa* Schweigger 1812), by original designation.

(?) ***Kinixys spekii*** Gray, 1863: 381, Figs 1–4

Locality and horizon. Pomongwe Cave, Matobo National Park, southwest Zimbabwe. Excavated by C.K. Cooke in 1960/61. Level 3 (Pomongwe Industry), Carbon 14 dated at 9400 ± 100 yrs BP (Cooke 1963), i.e. early Holocene. These bones are stained red-brown, so were presumably at the surface of Level 3 in contact with the red soil of Level 2.

Diagnosis. This specimen differs from all known forms of Testudinidae in the truncated anterior carapace with apparent fusion of the second and third peripherals, the third marginal scute is restricted to the dorsolateral surface of the carapace and the peripheral bone shows clear sulci demarcating three axiliary scales (submarginals of Loveridge & Williams 1957) on its anteroventral surface (Fig. 1). The epiplastron most closely resembles that of a female *Chersina angulata* (Fig. 2), but is truncated laterally, while the upper surface is slightly concave in cross-section instead of sloping steeply away towards the hyoplastral suture. The gulars may have been even longer than in *Chersina.* However, it should be noted that elongate thickened epiplastra are even better developed in male *Kinixys erosa,* although in this case they are deeply forked (Loveridge & Williams 1957: fig. 49; Broadley 1997: fig. 5).

Material. NMZB 14473A, an almost complete right second + third peripheral, with associated first costal (NMZB 14473B), and NMZB 14473C, a partial right epiplastron; NMZB 14473D, a complete fourth neural; NMZB 14475A, a right humerus, lacking the head, and NMZB 14475B , a right femur lacking the head. NMZB 14471A, outer portion of a left hypoplastron (level 2); NMZB 14474, right costal 8 (level 1).

Description

The most diagnostic bone (NMZB 14473A) apparently represents the fused second + third peripherals, with a distinct angular 'shoulder'. This bone has maximum dimensions of 26 mm long by 22 mm wide (Fig. 1A,C). The

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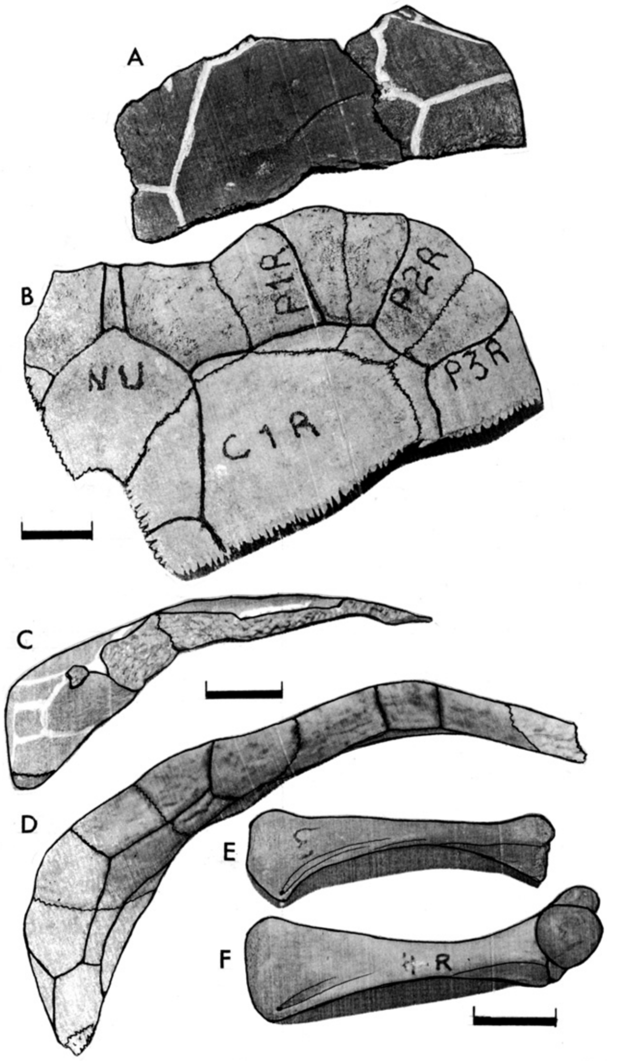

Figure 1. (?) *Kinixys spekii,* NMZB 14473A+B: **A**, dorsal and **C**, anterior views of right peripherals 2 + 3 and right costal 1; **E**, dorsal view of right humerus to show ectepicondylar fossa (note white spot in the shadow below it). *Kinixys spekii*: NMZB 8847: **B**, dorsal and **D**, anterior views of nuchal, right costal 1 and right peripherals 1–3; **F**, dorsal view of right humerus of NMZB 11925. Scale bars = 1 cm.

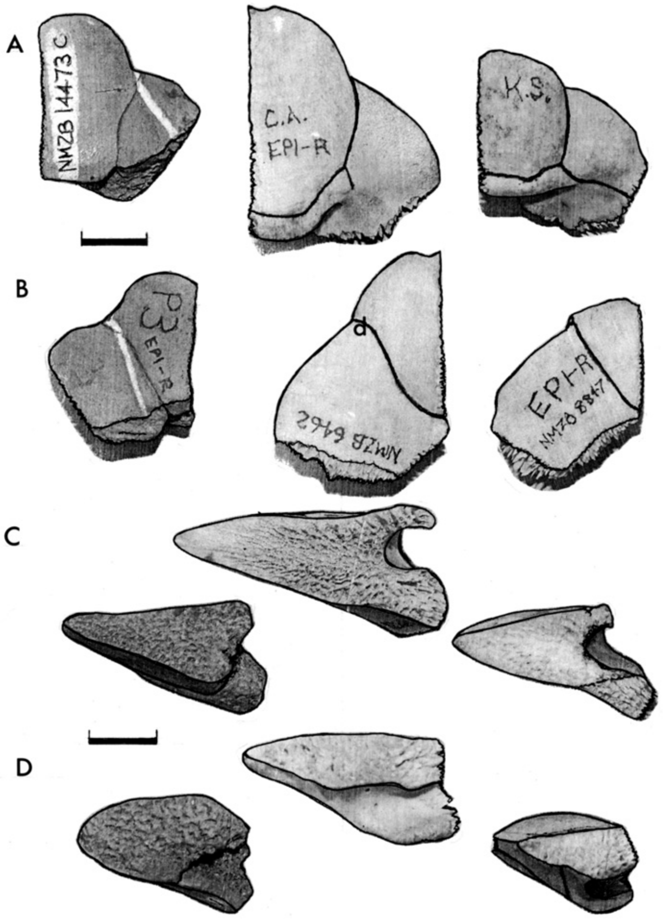

Figure 2. Right epiplastron of, from left to right: (?) *Kinixys spekii* NMZB 14473C; *Chersina angulata* NMZB 6492; *Kinixys spekii* NMZB 8847. **A**, dorsal views; **B**, ventral views; **C**, interepiplastral suture; **D**, epiplastral/hyoplastral suture. Scale bars = 1 cm.

sulci marking the lateral margins of the first pleural cross the inner anterior corner, and wedge into the inner posterior corner to meet the sulcus separating the second and third marginals. The rounded anterior edge of the bone is bordered by two large axillary scales, with a smaller rectangular one wedged between them and the second marginal, which is dorsally subtriangular in shape. On the inner anterior edge of the bone is a small projection terminating in a sutural face quite distinct from the adjacent one to accommodate the first peripheral, suggesting the presence of an independent epithecal ossification. The internal suture with the hyoplastral buttress apparently terminated at the point where the first and second peripherals meet the first costal. The African species showing least anterior expansion of the first three peripherals is *Psammobates oculiferus,* but the form of the enigmatic peripheral of this specimen seems closest to *Kinixys.*

The associated first costal (NMZB 14473B) is subrectangular and has a maximum width of 38 mm and length of 22 mm (Fig. 1A,C), the bone is very thin. The sulci marking the borders of the first and second vertebrals cross the dorsal third. A shallow depression marks the areolus, a curved groove extends from it laterally to the second marginal and a shallower one extends anteriorly to the first marginal. The intact suture between the peripheral and the first costal indicates that the carapace was strongly depressed.

The partial epiplastron (NMZB 14473C) is 25.5 mm wide, with a lip 26.5 mm long and 13 mm deep, but the bone is broken caudad, so it is not known if there was a posterior excavation of the epiplastral lip (Fig. 2). The dorsal surface is slightly concave mesially. Ventrally the gular sulcus diverges towards the gular/hyoplastral suture, suggesting that it will reach the entoplastron.

The hexagonal fourth neural (NMZB 14473D) is the same size and shape of the corresponding bone of *Kinixys spekii,* but dorsally it has shallow depressions on each side of the midline, while ventrally the vertebral scar is weak.

A right humerus (NMZB 14475A) lacks the head (estimated length 44 mm, Fig. 1E). It resembles that of *Kinixys spekii,* with a well-defined fossa culminating in a foramen, but the bone is more slender (maximum width at distal end 11 mm, maximum width of shaft 3.5 mm) than a comparable sized *K. spekii* humerus from the same level (12.8 and 4 mm, respectively). It also differs in having a sharp keel lateral to the ectepicondylar fossa and also a pronounced ventral keel.

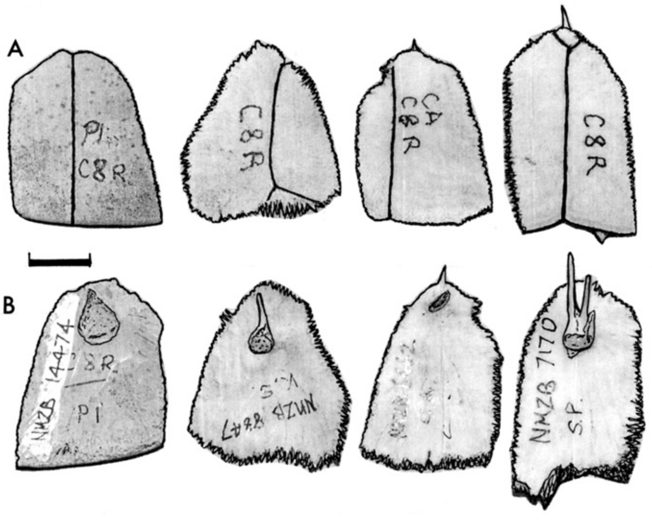

Figure 3. Right costal 8 of, from left to right: (?) *Kinixys spekii* NMZB 14474; *Kinixys spekii* NMZB 8847; *Chersina angulata* NMZB 6492; *Stigmochelys pardalis babcocki* NMZB 7170. **A**, dorsal views; **B**, ventral views. Scale bars = 1 cm.

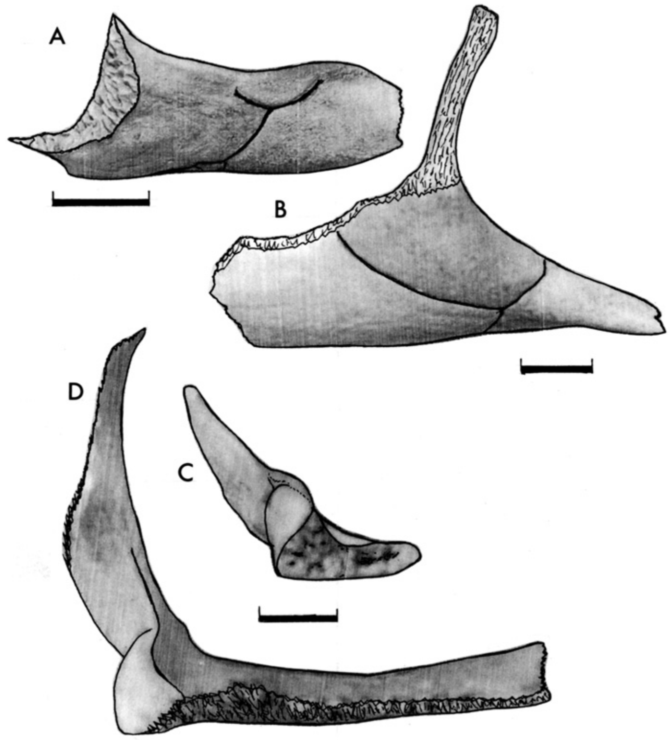

Figure 4. (?) *Kinixys spekii* NMZB 14471A, outer portion of left hypoplastron: **A**, lateral view: **C**, rear view. *Kinixys spekii* NMZB 8847, left hypoplastron: **B**, lateral view, **D**, rear view. Scale bars = 1 cm.

A right femur (NMZB 14475B) lacks the head and is shorter than the humerus. It resembles that of *K. spekii*, but the tibial condyle is wider, while the dorsal surface lacks the shallow terminal depression of the latter species.

Right costal 8 NMZB 14474 (Level 1), height 30 mm, width at lower edge 25 mm (Fig. 3). The sulcus between the fourth pleural and fifth vertebral is straight, the suture between costals 7 and 8 is gently curved and that between costal 8 and the suprapygal is straight. The subtriangular iliac scar is quite large. The lower edge shows a smooth curve but is somewhat worn (?from use as a scraper), but the costo-peripheral suture may not have closed.

Outer posterior portion of left hypoplastron NMZB 14471A (Level 2), height 18 mm (Fig. 4). There is no development of the long incurving buttress beneath the hinge found in *Kinixys spekii*, instead the superior projection slopes steadily outwards and posteriorly the outer margin of bone bordering the xiphiplastron is much higher.

This specimen was initially suspected to represent a new genus and species, but because it was sympatric with *Kinixys spekii*, there remains the possibility that it represents a highly anomalous specimen of the latter species, which it resembles in size. I described a Recent specimen of *Pelusios sinuatus* which had numerous fusions of bones in both carapace and plastron, resulting in an almost circular shell, but this terrapin was caught as an adult and lived for many years in captivity (Broadley 1997b). So the truncated anterior carapace may not have been a major handicap to the 'mongrel' Matobo tortoise.

PALAEOECOLOGY

The habitat in the vicinity of Pomongwe cave has been illustrated by Brain (1981: fig. 24). It is an extensive area of rugged granite hills with intervening areas of woodland and very limited areas of grassland (Walker 1995: plates 2–5). The tortoises eaten by the Stone Age people and represented in the cave deposits are *Stigmochelys pardalis* and *Kinixys spekii.*

The only tortoise carapace examined which shows a suggestion of a 'shoulder' on peripherals 2 and 3 is from the steppe tortoise *Testudo horsfieldi,* which has a broad, somewhat depressed shell, but not truncated anteriorly. However, it seems that the 'shoulder' may be better developed in the 'saddlebacked' races of *Chelonoidis nigra* on the Galapagos Islands. A photograph of the adult male holotype of *C. n. hoodensis* (Van Denburgh 1914: plate 53, fig. 2) shows this well (see also Pritchard 1979: 340). The raised anterior carapace and narrow anterior plastron give the saddleback tortoises more freedom for their forelimbs and neck, allowing them to negotiate rugged terrain, as illustrated by a photograph of an adult *C. n. ephippium* on Pinzon (= Duncan) Island (King 1968: 17). Molecular data indicates that *Chelonoidis* is sister to *Kinixys* (Le *et al.* 2006). Gerlach (1999) has shown that the saddleback giant tortoise, *Aldabrachelys arnoldi,* of the Seychelles shows adaptations of the deep jaw and humerus musculature enabling it to browse efficiently. An extinct saddleback giant tortoise, *Cylindraspis vosmaeri,* is also known from Rodrigues, the easternmost of the Mascarene Islands (Bour 1984), so the saddleback adaptation can appear in unrelated giant tortoises inhabiting isolated islands which lack predators.

The present specimen differs from all the saddlebacked giant tortoises in its small size, depressed carapace and African mainland distribution. The reduced anterior carapace and plastron could have made this tortoise more agile and fast moving in a rocky habitat. It may have had a life style similar to that of *Malacochersus tornieri,* spending most of the time wedged in rock crevices and emerging for short spells of activity in the vicinity of its retreat (Ireland & Gans 1972). This unusual specimen apparently belongs in the *Chelonoidis/Kinixys* clade (Le *et al.*, 2006),

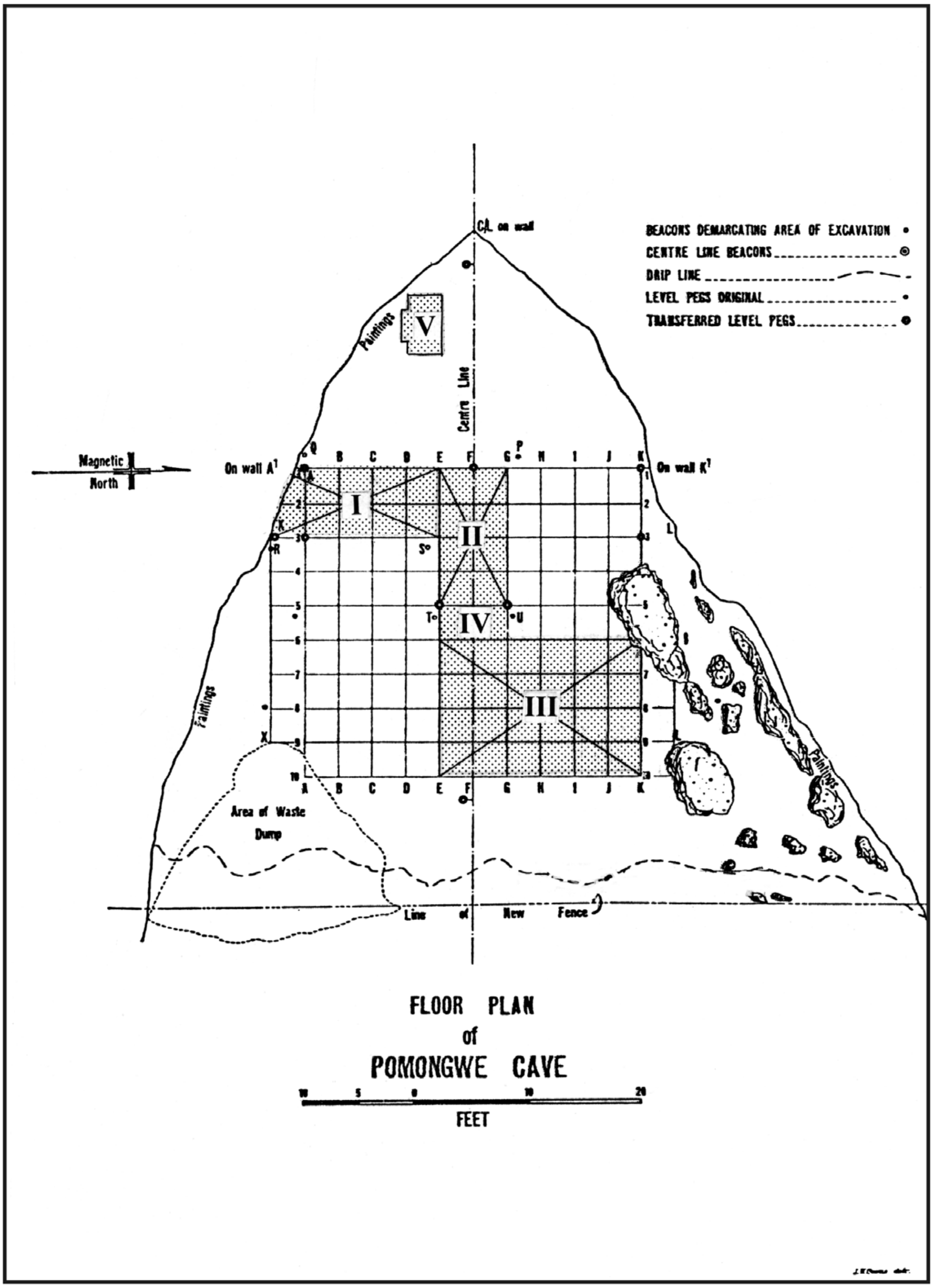

Figure 5. Floor plan of Pomongwe Cave (modified from Cooke 1963: fig. 1). The excavated areas are stippled. Trenches I to III were excavated by Cooke in 1960/61 and trenches IV and V by Walker (1995). The grid is of one metre squares.

having numerous axillary scales like the latter genus and *Impregnochelys* of the Miocene of Africa (Meylan & Auffenberg 1986).

DISCUSSION

C.K. Brain analysed the 17 756 bone fragments from C.K. Cooke's excavations at Pomongwe Cave in 1960/61 and recorded a total of 1357 fragments of tortoise carapace and plastron (Brain 1981: table 9). Of these, 321 fragments came from level 3, and apart from the six bones that are assigned to the specimen under consideration, I have assigned 55 fragments to the leopard tortoise *Stigmochelys pardalis* (the genus *Stigmochelys* Gray was reinstated by Lapparent de Broin, 2000) and 24 to *Kinixys spekii*, the remainder are unidentified. Two additional bones assigned to the unusual specimen came from levels 1 and 2, but may have been brought towards the surface by burrowing rodents or beetles. The fact that the eight diagnostic bones are in relatively good condition suggests that they were not subject to trampling on the open floor of the cave, but may have been excavated from among the boulders of the rock fall to the right of the cave (Fig. 5). If in the future a fresh excavation is made between the end of Cooke's Trench III and the rock fall, more of the missing bones of the carapace and plastron may be found. It is also possible that this tortoise was not eaten, but took refuge between the rocks during a drought and died there, which would also account for the bones not being scattered. The corner of the metre square J6 where this strange tortoise may have been found is illustrated in Cooke (1963: plates XIX A & B). Bone is not normally preserved in the acidic granite-derived sand of the Matobo Hills, so tortoise bones are only likely to be found in dry caves.

I am indebted to C.K. ('Bob') Brain (Transvaal Museum) for painstakingly sorting the thousands of bone fragments excavated in Pomongwe Cave by Cran Cooke in 1960/61. I am grateful to the late Barbara Bennefield, who prepared most of the comparative skeletal material used in this study prior to her untimely death in 1986. I also thank John and Moira FitzPatrick for photographing the bones and making the prints from which the images in Figs 1–4 were prepared. Robert Drewes (California Academy of Sciences) kindly supplied me with photographs of the type material of *Chelonoidis nigra hoodensis* (Van Denburgh). I thank Peter Pritchard and Bill Branch for their advice regarding the interpretation of this strange tortoise.

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APPENDIX 1. Comparative material.

Kinixys natalensis, NMZB 11071, Weenen Nature Reserve, KwaZulu-Natal, South Africa
Kinixys spekii, NMZB 8847, Majoda, Zimbabwe
Kinixys spekii, NMZB 11925, Matobo National Park, Zimbabwe
Kinixys belliana, NMZB 12078, Gonarezhou National Park, Zimbabwe
Kinixys nogueyi, NMZB 9708, Ngaoundere, Cameroon
Kinixys erosa, NMZB 9894, Lolodorf, Cameroon
Kinixys homeana, NMZB-UM 33496, Ghana
Chersina angulata, NMZB 6462, Port Elizabeth, Eastern Cape Province, South Africa
Stigmochelys pardalis babcocki, NMZB 7170, Bulawayo, Zimbabwe
Psammobates geometricus, NMZB 6565, Elandsberg Nature Reserve, Voëlsvlei, Western Cape Province, South Africa
Psammobates oculiferus, NMZB-UM 12755, 250 km S of Mamono, Botswana
Psammobates tentorius, NMZB 7070, Karoo National Park, Eastern Cape Province, South Africa
Homopus boulengeri, NMZB 7178, Sutherland, Western Cape Province, South Africa
Homopus femoralis, NMZB 6651, Molteno, Eastern Cape Province, South Africa
Testudo horsfieldi, NMZB 7764, 'southern U.S.S.R.'
Malacochersus tornieri, NMZB-UM 33658, Dodoma, Tanzania