

Osteological Characters of the Shell and Humerus in Hinged Tortoises of the African Genus *Kinixys*

DONALD G. BROADLEY^{1,2}

¹Department of Herpetology, Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe;

²Present Address: Biodiversity Foundation for Africa, P.O. Box FM730, Famona, Bulawayo, Zimbabwe
[Fax: 263-9-540709; E-mail: bfa@coldfire.dnet.co.zw]

ABSTRACT. – Osteological material, consisting of shells, disarticulated shell bones, and humeri, was prepared from all six recognized species of *Kinixys* for comparison with fossil and subfossil chelonian remains from two cave deposits in Zimbabwe. There is much variation, but useful diagnostic features were found in the humerus and xiphiplastron. Comparative views of the carapace, plastron, humerus, and xiphiplastron are provided.

KEY WORDS. – Reptilia; Testudines; Testudinidae; *Kinixys*; tortoise; osteology; morphology; taxonomy; Africa; Zimbabwe

In the most recent phylogeny of the Testudines Gaffney and Meylan (1988) included *Kinixys* in the subfamily Testudininae, associated with the extinct Miocene genus *Impregnochelys*, and placed between the more primitive tribe Megalochelyini and the derived tribe Testudinini.

When the African Cryptodira were revised by Loveridge and Williams (1957) only three species of *Kinixys* were recognized: the forest forms *K. erosa* (Schweigger) and *K. homeana* Bell, and a single savanna hinged tortoise — *K. belliana* Gray. *Kinixys natalensis* Hewitt was revived from synonymy by Broadley (1981) and two more savanna species, *K. spekii* Gray and *K. lobatsiana* Power, were later reinstated (Broadley, 1993a).

Loveridge and Williams (1957) did not thoroughly investigate the osteology of *Kinixys*, mainly discussing the modifications caused by the development of the carapacial hinge, the inferior position of the pleuromarginal sulcus in relation to the costoperipheral suture posteriorly, and the development of the epiplastral lip. The only osteological character in their table of diagnostic features was the development of the postorbital bar in the skull. Crumly (1984) looked at the osteology of the Testudinidae, especially the skull, but the genus *Kinixys* was not investigated in depth.

For the study of several thousand tortoise fragments from cave deposits at Redcliff and Pomongwe in Zimbabwe, comparative osteological material of the shells and humeri of all six species of *Kinixys* was prepared (skulls are too fragile to survive in this harsh environment) and diagnostic features sought. The results are presented below.

MATERIALS AND METHODS

This study was based on material housed in the Natural History Museum of Zimbabwe in Bulawayo. A total of 90 specimens of *Kinixys* was examined. Adequate skeletal material of the two local species *K. spekii* ($n = 41$) and *K. belliana* ($n = 28$) was available and dry shells of the other four species were obtained by donation and exchanges with other museums before being prepared as osteological speci-

mens (*K. natalensis*, $n = 8$; *K. lobatsiana*, $n = 8$; *K. erosa*, $n = 3$; *K. homeana*, $n = 2$). In some cases humeri had to be removed from alcoholic specimens in order to complete the analysis.

RESULTS AND DISCUSSION

Osteological preparations of various portions of the carapace and plastron of the six species of *Kinixys* are illustrated in Figs. 1–6, the humeri of five species are depicted in Fig. 7.

Neurals. — In all species there are normally eight neurals (Fig. 1), with the sulci between vertebral scutes crossing the first, third, fifth, and eighth. The neurals are typically hexagonal and slightly wider posteriorly, with occasional square bones, a derived condition according to Auffenberg (1974), who illustrated the neural pattern of *K. erosa*.

Some *K. spekii* have seven or nine neurals, or even six (NMZB-UM 23498; Razi, Chibi, Zimbabwe) or ten (NMZB 9874; Sengwa Wildlife Research Area, Zimbabwe; this specimen also has eight vertebral shields [Coulson, 1988]).

In *K. homeana* the rear end of the carapace ends abruptly, descending perpendicularly from the eighth neural (i.e., anterior end of the fifth vertebral scute).

Suprapygals and Pygal. — Loveridge and Williams (1957) considered that a single suprapygals was a primitive character within the Testudinidae. However, Crumly (1984) pointed out that the ontogeny of the suprapygals is well demonstrated by *Malacochersus* with its arrested carapacial development: there are two ossifications — a larger subrectangular element and a smaller elliptical one below it. He considered the *Geochelone* pattern (with the superior suprapygals sending down lateral arms to contact the peripherals) to be primitive for the Testudinidae (including *Gopherus*, see Auffenberg, 1976: Fig. 24), while enlargement of the inferior suprapygals or fusion of the two bones represented derived character states. Loveridge and Williams (1957) stated that *Kinixys* had either one or two suprapygals, but they noted that a single bone is unusual, at least in the savanna species.

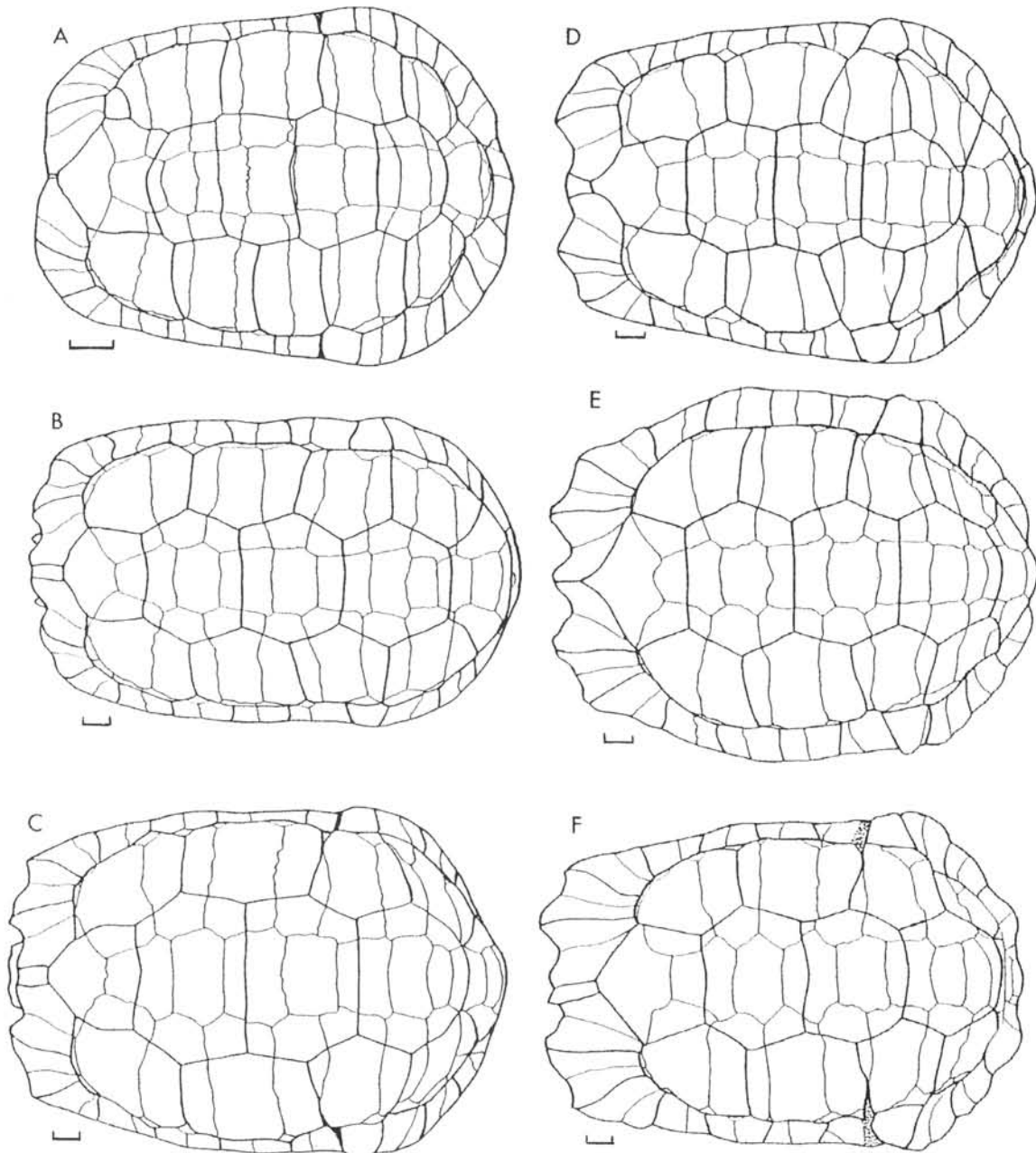


Figure 1. Dorsal views of *Kinixys* carapaces. **A.** *K. natalensis* (NMZB 11071, Weenen Nature Res., Kwazulu-Natal, South Africa); **B.** *K. spekii* (NMZB-UM 20369, Lavingi Pan, Hwange National Park, Zimbabwe); **C.** *K. belliana* (NMZB-UM 32977, Mutare, Zimbabwe); **D.** *K. lobatsiana* (NMZB 11217, Otse, Botswana); **E.** *K. erosa* female (NMZB 9894, Lolodorf, Cameroon); **F.** *K. homeana* (NMZB-UM 33496, Ghana). The line equals 1 cm to scale.

Kinixys natalensis is extremely variable in suprapygal pattern. Two specimens had single bones, four had two, and two had three. This is the only species that may show the *Geochelone* pattern, with a large upper suprapygal in broad contact with the pygal on either side of a small oval inferior bone (Fig. 1A).

In a sample of 41 *K. spekii*, the number of suprapygals was one ($n = 1$), two ($n = 28$), three ($n = 11$), or four ($n = 1$) and in *K. belliana* there were two ($n = 18$) or three ($n = 5$) suprapygals, the individual bones being separated by more or less straight or slightly downwardly curved sutures (Fig. 3A).

Eight *K. lobatsiana* all had two suprapygals, but in NMZB 11074 (Pretoria) the inferior element made contact with the eighth neural on each side of the small superior suprapygal. In two *K. erosa* from Cameroon, the female had a single suprapygal (Fig. 3B) and the male had two, but the upper was fused with the eighth neural.

Kinixys homeana may have the suprapygals irregularly divided horizontally (Fig. 3C), but sometimes also vertically along the median keel, producing six small bones. Pritchard (*pers. comm.*) has supplied diagrams of neural/suprapygal patterns for an additional four specimens: one had a single suprapygal, two had two, and one had three.

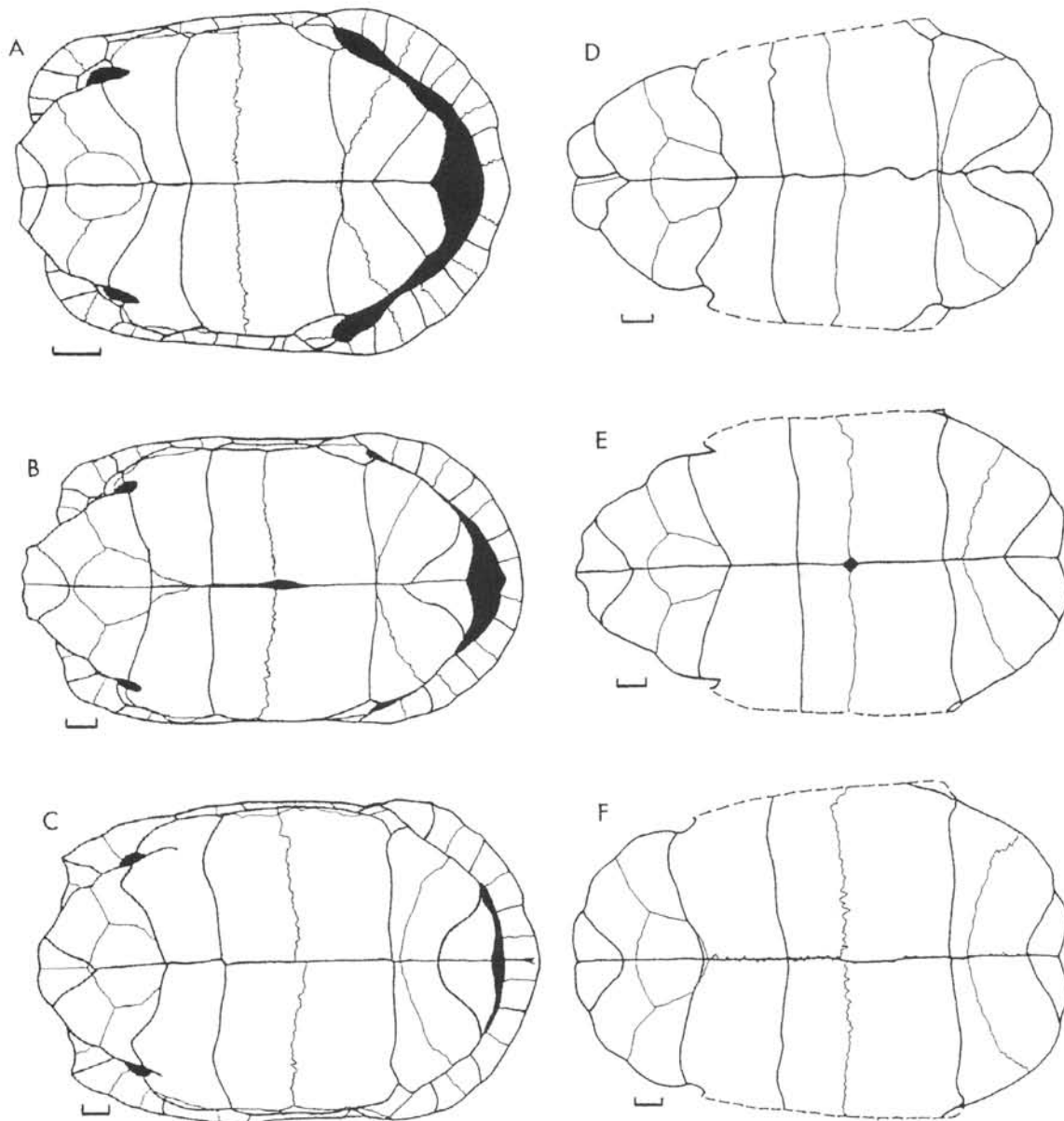


Figure 2. Ventral views of *Kinixys* plastra. Same specimens and sequence as in Fig. 1. **A.** *K. natalensis*; **B.** *K. spekii*; **C.** *K. belliana*; **D.** *K. lobatsiana*; **E.** *K. erosa* female; **F.** *K. homeana*. The line equals 1 cm to scale.

In *K. natalensis* and *K. lobatsiana* the ventral face of the pygal is deeply concave along the midline, in *K. spekii* it is only proximally concave (Fig. 2B), *K. belliana* has a shallow ventral groove, while in *K. erosa* and *K. homeana* the pygal is convex ventrally rather than concave. The pygal shape is reflected by the form of the overlying supracaudal scute (Broadley, 1993a).

A specimen of *K. homeana* is unusual in having the pygal transversely divided (Fig. 3C). In *K. natalensis* there is often a well defined median sulcus on the pygal due to the split supracaudal scute in this species (Fig. 1A).

Pleurals and Peripherals. — All species normally have eight pleurals, with a few specimens having a ninth added posteriorly. However, three out of eight *K. natalensis* have nine pleurals (Fig. 1A). Loveridge and Williams (1957)

remarked upon the nearly complete absence of alternate widening and narrowing at the ends of the pleurals. This feature is quite absent in *K. natalensis* (Fig. 1A), but is slightly developed in *K. spekii* (Fig. 1B).

All species normally have eleven peripherals, with twelve an occasional variant. In the species *K. lobatsiana*, *K. erosa*, and *K. homeana* the peripherals of the posterior hinged section of the carapace are more or less recurved and sinuate, this condition being most developed in *K. homeana* (Figs. 1D, E, F and 3B, C). This development is accentuated with regard to the overlying marginal scutes, which are very strongly reverted and serrated.

Carapacial Hinge. — As indicated by previous authors (e.g., Loveridge and Williams, 1957; Pritchard, 1979; Crumly, 1984), this hinge develops by the gradual ingrowth of

flexible fibrous tissue, initially between the seventh and eighth peripherals, then extending dorsally between the fourth and fifth pleurals and finally between the fourth and fifth neurals (Fig. 4); the suture between the third and fourth neurals may also be replaced by fibrous tissue, so that the fourth neural becomes slightly loose overall, facilitating the action of the hinge.

As previously indicated (Broadley, 1981, 1983a), in the small and primitive *K. natalensis* the hinge is restricted to the peripherals, perhaps due to neoteny. In *K. spekii* the hinge is moderately developed, rarely extending more than half way up the anterior edge of the fifth pleural. In the remaining four species the hinge is fully developed.

Crumly (1984) suggested that the hinge develops earlier in ontogeny in the forest species, in which the flared and serrate eighth peripheral marks the widest point of the shell

(see Siebenrock [1916: Fig. 1] for an internal view of the carapace of *K. erosa*). However Dwight Lawson (*in litt.*) found that in Cameroon some neonates and subadults of *K. homeana* had non-functional hinges, whereas all *K. erosa* neonates had functional hinges.

In a large male *K. erosa* from Cameroon (NMZB 9893) there is partial development of a secondary hinge which, like the primary hinge, originates between the seventh and eighth peripherals, but then continues between the fifth and sixth pleurals and neurals.

Epiplastral Lip. — The development of a thickened epiplastral lip in *Kinixys* was discussed by Loveridge and Williams (1957). This is used by males for shell ramming during courtship (Auffenberg, 1977) and reaches its greatest development in male *K. erosa* (Fig. 5) in contrast to the weak development in the female of this species (Fig. 2E). Similar hypertrophy and development of forked gulars in the male is found in an unrelated west African tortoise, *Geochelone sulcata*, and others outside Africa. I calculated the ratios of dorsal epiplastron length as a percentage of plastron midline length and anterior plastron lobe length as a percentage of width (Table 1). Despite great variability, there is a trend from a weakly developed epiplastral lip in *K. natalensis* to maximum hypertrophy in the two forest species *K. erosa* and *K. homeana*.

Plastron. — As in other tortoises, juvenile *Kinixys* have a large lozenge-shaped fontanelle in the center of the plastron, which gradually closes with growth. As it tends to have

Figure 3. Rear views of *Kinixys* carapaces. **A.** *K. belliana*. **B.** *K. erosa*. **C.** *K. homeana*. Same specimens as Fig. 1. The line equals 1 cm to scale.

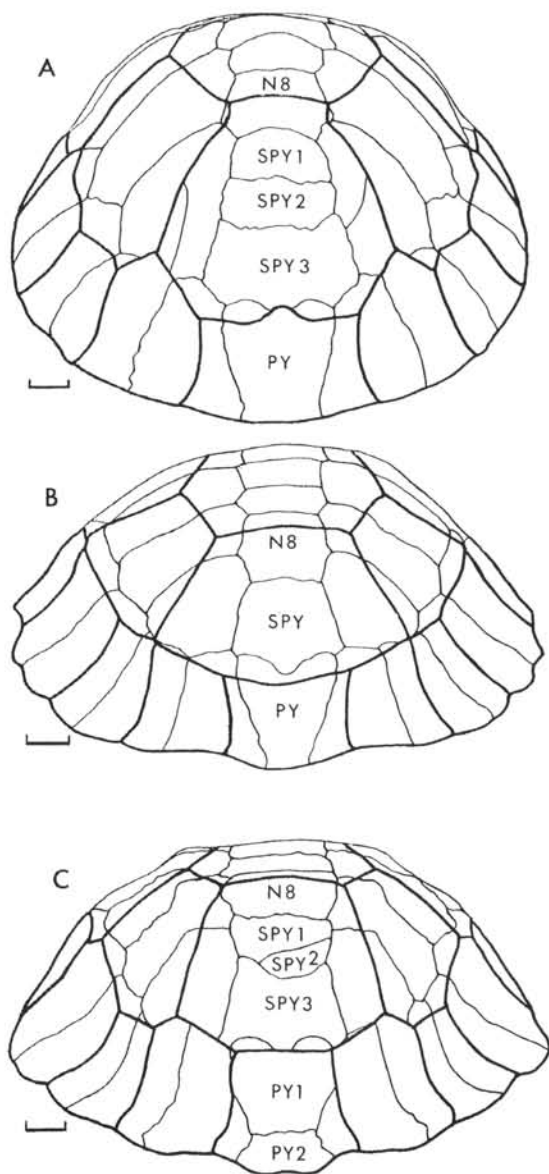
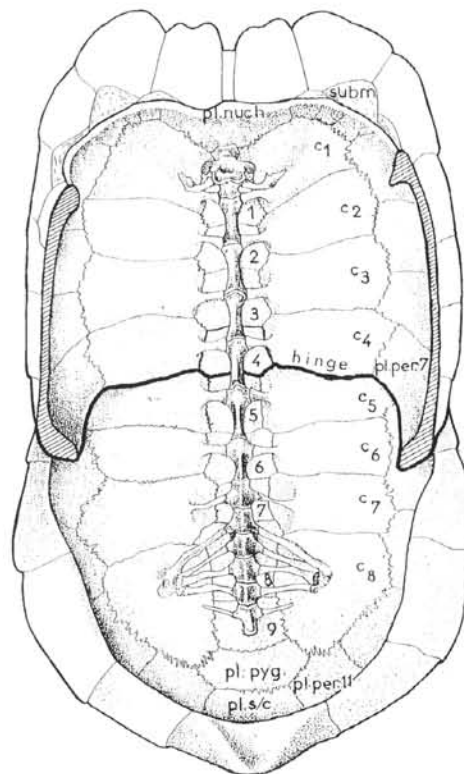


Figure 4. Internal view of the carapace of *Kinixys belliana* (as *Madakinixys domerguei*, after Vuillemin, 1972, pl. vi).



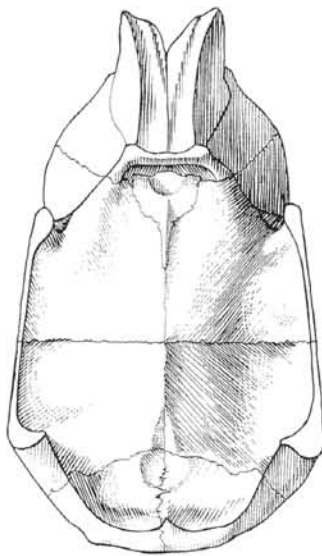


Figure 5. Internal view of the plastron of male *K. erosa* (Yale Mus. 4586, after Loveridge and Williams, 1957).

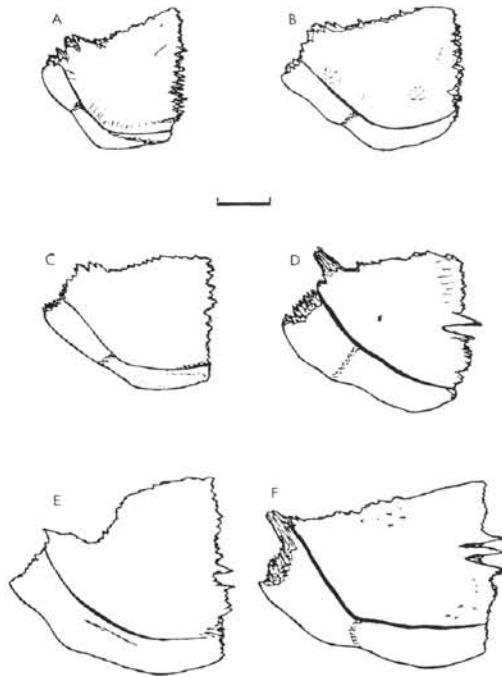


Figure 6. Internal views of *Kinixys* xiphiplastra. **A.** *K. natalensis* (same specimen as in Fig. 1); **B.** *K. spekii* (NMZB 8847, Majoda, Zimbabwe); **C.** *K. belliana* (NMZB-UM 12078, Gonarezhou Nat. Park, Zimbabwe); **D.** *K. lobatsiana* (NMZB 11599, Pretoria, Gauteng, South Africa); **E.** *K. erosa* (same specimen as in Fig. 1); **F.** *K. homeana* (same specimen as in Fig. 1).

thin shell bones, a slit-like fontanelle often persists in adult *K. spekii* (Fig. 2B) and there is a very small square fontanelle in the female *K. erosa* illustrated (Fig. 2E).

Most species of *Kinixys* develop a concave plastron in the adult male, the exception is *K. natalensis*, which may be neotenic.

Xiphiplastron. — The species of *Kinixys* can be divided into two groups on the basis of the degree of development of

Table 1. Variation in length of dorsal epiplastron as a percentage of plastron midline length and anterior plastron lobe length as a percentage of its width in six species of *Kinixys*.

Taxon	n	Dorsal Epiplastron Length Plastron Midline Length			Anterior Plastron Lobe Length/Width		
		Range	Mean	S.D.	Range	Mean	S.D.
<i>natalensis</i>	2	14.3–15.5	14.90	0.85	52.5–58.8	55.50	4.67
<i>spekii</i>	41	14.5–22.7	18.00	2.08	51.9–75.0	62.83	4.85
<i>belliana</i>	28	17.8–25.7	21.35	2.22	47.4–68.1	59.30	5.21
<i>lobatsiana</i>	8	18.6–25.2	21.40	2.31	53.7–67.6	62.30	4.96
<i>erosa</i>	3	22.2–25.9	24.05	2.62	64.3–84.4	74.47	10.05
<i>homeana</i>	2	24.5–24.7	24.60	0.14	63.0–65.0	64.00	1.41

a raised peripheral border on the internal surface of the xiphiplastron (Fig. 6). The less developed condition is found in the species *K. natalensis*, *K. spekii*, and *K. belliana*, where there is only a depressed narrow rim, whereas in *K. lobatsiana*, *K. erosa*, and *K. homeana* there is a broad raised border to the xiphiplastron.

Shell Ankylosis. — This condition has been recorded in two specimens of *K. homeana* from Ghana with carapace lengths (CL) of 189 and 218 mm, but two others (CL 165 and 211 mm) had all sutures distinct (Broadley, 1993b). In an old male (NMZB 9783; CL 188 mm) all sutures in the shell are ankylosed except the carapacial hinge between peripherals 7 and 8, pleurals 4 and 5, and surrounding neural 4, the sutures separating pleurals 5, 6, and 7 from the adjacent peripherals, and also the sutures between the hyoplastra, entoplastron, and epiplastra. Pritchard (*in litt.*) found no indication of ankylosis in six *K. homeana* believed to be from Togo. Complete ankylosis has not been recorded in any other species of Recent tortoise, although common in the terrestrial emydine *Terrapene*, several batagurids (e.g., *Kachuga kachuga*, *Cuora galbinifrons*), and characteristic of the extinct genus *Cylindraspis* of the Mascarene Islands (Crumly, 1984).

Humerus. — Crumly (1984) noted that in *Kinixys* the humerus remains strongly curved in the adult, but while this is true of the savanna species (*K. natalensis*, *K. spekii*, *K. belliana*, *K. lobatsiana*), in the forest species (*K. erosa*, *K. homeana*) humerus curvature apparently decreases in the larger specimens, as Crumly found for tortoises in general.

Crumly (1984) pointed out that in larger tortoises (not *Kinixys*) an entepicondylar foramen develops on the dorsal surface of the distal end of the humerus; this is preceded in development by a prominent entepicondylar groove which marks the course of the radial nerve and blood vessels (Walker, 1973). Crumly listed *Kinixys* as one of the genera that lacks this foramen, but said that large individual specimens may have a groove.

In fact there are marked interspecific differences in the development of an entepicondylar groove and foramen in this genus (Fig. 7). The smallest species, *K. natalensis*, has only a faint groove which fades distally and only a mere trace of a groove can be detected in *K. homeana* and *K. erosa* (the latter being the largest species, for which carapace lengths of 375 mm for a male and 283 mm for a female have been

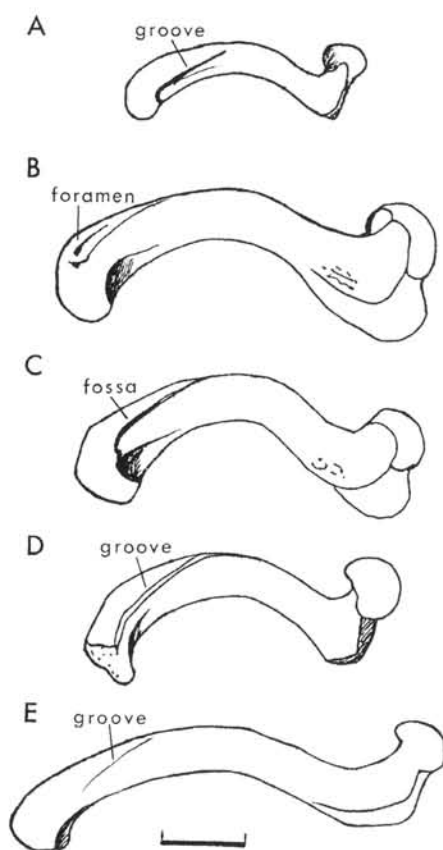


Figure 7. Humeri of *Kinixys*. A. *K. natalensis*. B. *K. spekii*. C. *K. belliana*. D. *K. lobatsiana*. E. *K. homeana*.

recorded in the eastern Congo by Lenglet and Colyn, 1989). *Kinixys lobatsiana* has a groove and in *K. belliana* this becomes a moderate channel or fossa, but never develops into a foramen. *Kinixys spekii* has a well-developed entepicondylar fossa, which in adults usually becomes roofed over with bone distally to produce a foramen (Fig. 7B).

The development of an entepicondylar foramen may be a plesiomorphic character in African Testudinidae; in *Geochelone pardalis* it is even present in hatchlings. The gradual reduction in the expression of this character in *Kinixys* follows the assumed sequence of primitive to derived species based on independent considerations (Broadley, 1983a), with the exception of *K. natalensis*, which may be a neotenic species.

CONCLUSIONS

Diagnostic osteological characters for chelonians are valuable for the identification of fossil or subfossil material. The present study has enabled me to positively identify *Kinixys spekii* from Holocene deposits at Pomongwe Cave in the Matopos National Park in Zimbabwe (Carbon-14 date of 9400 yrs BP) on the basis of a humerus with an entepicondylar foramen.

The xiphoplastron can be a useful diagnostic bone in the northeastern provinces of South Africa, permitting the posi-

tive identification of skeletal material found in the zone where *K. spekii* and *K. lobatsiana* are at least parapatric (Broadley, 1993a).

Acknowledgments

I am grateful to Robstein Chidavaenzi, Curator of Herpetology at the Natural History Museum of Zimbabwe, for facilities granted following my retirement from that institution. My wife Sheila prepared much of the osteological material. Peter Pritchard (Florida Audubon Society) and Dwight Lawson (University of Texas at Arlington) kindly supplied information on *Kinixys homeana*. I thank W.R. Branch, P.C.H. Pritchard, and A.G.J. Rhodin for their valuable comments on an earlier draft of this paper.

LITERATURE CITED

- AUFFENBERG, W. 1974. Checklist of fossil land tortoises (Testudinidae). Bull. Florida State Mus. Biol. Sci. 18:121-251.
- AUFFENBERG, W. 1976. The genus *Gopherus* (Testudinidae): Pt. I. Osteology and relationships of extant species. Bull. Fla. State Mus. Biol. Sci. 20(2):1-110.
- AUFFENBERG, W. 1977. Display behavior in tortoises. Amer. Zool. 17:241-250.
- BROADLEY, D.G. 1981. A review of the populations of *Kinixys* (Testudinidae) occurring in south-eastern Africa. Ann. Cape. Prov. Mus. Nat. Hist. 13:195-216.
- BROADLEY, D.G. 1993a. A review of the southern African species of *Kinixys* Bell (Reptilia, Testudinidae). Ann. Transvaal Mus. 36(6):41-52.
- BROADLEY, D.G. 1993b. Ankylosis in the shell bones of *Kinixys homeana* (Chelonii: Testudinidae). J. Herpetol. Assoc. Afr. 42:20.
- COULSON, I.M. 1988. Variation in shield counts in tortoises of the Sengwa Wildlife Research Area, Zimbabwe. J. Herpetol. Assoc. Afr. 35:9-11.
- CRUMLY, C.R. 1984. The evolution of land tortoises (family Testudinidae). Ph.D. Thesis, Rutgers University.
- GAFFNEY, E.S., AND MEYLAN, P.A. 1988. A phylogeny of turtles. In: Benton, M.J. (Ed.). The Phylogeny and Classification of the Tetrapods, Volume I: Amphibians, Reptiles, Birds. Syst. Assoc. Spec. Vol. 35A:157-219.
- LENGLET, G.L., AND COLYN, M.M. 1989. Note on the maximum length of *Kinixys erosa* (Schweigger, 1812) (Chelonia, Testudinidae). Bull. Inst. Roy. Sci. Nat. Belg. Biol. 59:159-162.
- LOVERIDGE, A., AND WILLIAMS, E.E. 1957. Revision of the African tortoises and turtles of the suborder Cryptodira. Bull. Mus. Comp. Zool. 115(6):163-557.
- PRITCHARD, P.C.H. 1979. Encyclopedia of Turtles. Neptune, NJ: TFH Publ., 895 pp.
- SIEBENROCK, F. 1916. Schildkröten aus dem nördlichen Seengebiet und von Belgisch-Kongo. Ann. Naturhist. Hofmus. Wien 30:1-12.
- VUILLEMIN, S. 1972. Note sur *Madakinixys domerguei* n. gen. n. sp. (Testudinidae). Ann. Univ. Madagascar Ser. Sci. Nat. Math. 9:169-182.
- WALKER, W.F., JR. 1973. The locomotor apparatus of Testudines. In: Gans, C., and Parsons, T.S. (Eds.). Biology of the Reptilia. Vol. 4. Morphology D. New York: Academic Press, pp. 1-100.

Received: 30 November 1996

Reviewed: 23 August 1997

Revised and Accepted: 17 September 1997