

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3040, 37 pp., 33 figures, 1 table
May 6, 1992

The Transylvanian Turtle, *Kallokibotion*, A Primitive Cryptodire of Cretaceous Age

EUGENE S. GAFFNEY¹ AND PETER A. MEYLAN²

ABSTRACT

Repreparation and redescription of the Late Cretaceous turtle, *Kallokibotion*, from Sinpetru, Romania (Transylvania), allows a reassessment of its phylogenetic position. *Kallokibotion* is a cryptodire because it has the otic trochlea synapomorphy of cryptodires, and it is a member of the Selmacryptodira because it has a posterior pterygoid process under the middle ear. It lacks the posterior temporal emargination synapomorphic of the Daiocryptodira and lies outside that group. We interpret *Kallokibotion* as the sister group of

all other Selmacryptodira. In *Kallokibotion* the foramen caroticum basisphenoidale is entirely formed by the basisphenoid and the division between the palatine artery and the internal carotid artery is neither embedded in nor covered by bone, both conditions primitive with respect to selmacryptodirans.

As *Kallokibotion* is not a baenid, European records of baenids based on *Kallokibotion* or similar taxa, are invalid. Baenids are restricted to western North America.

INTRODUCTION

Franz Baron Nopcsa von Felső-Szilvas was an enigmatic and erratic paleontologist, producing a number of papers on fossil reptiles in the early part of this century. As a Transylvanian noble he worked on dinosaurs and other fossils found in the region, although most of his specimens were deposited in the Natural History Museum, London. Nopcsa's fascinating life has been related by Colbert (1968), who has documented such stories as Nopcsa's life as a spy during World War I and his efforts to lead an invasion of Albania.

But one of the more interesting stories and one relevant to the turtle described here, was the ending of Nopcsa's life. To quote from Colbert: "Bajazid, the secretary who lived with Nopcsa for many years, was more than a secretary; he was a lover. Indeed, Nopcsa maintained two Albanian homosexual boy-friends, who participated in his strange and unreal life. In his lucid periods he directed his brilliant mind to research on dinosaurs and other fossil reptiles, and in the study of ethnology, archaeology, and geography of Al-

¹ Curator, American Museum of Natural History.

² Research Associate, American Museum of Natural History.

bania. At other times his activities tended to run to bizarre extremes.

"On the 25th of April, 1933, something cracked inside Nopcsa. He gave to his friend Bajazid a cup of tea heavily laced with a sleeping powder. He then murdered the sleeping Bajazid, shooting him in the head with a pistol" (Colbert, 1968: 118). Nopcsa then killed himself with the same pistol. It is interesting to note that the turtle described here was named by Nopcsa (1923a), *Kallokibotion bajazidi*, apparently in honor of his friend.

The dinosaurs that make up most of the Upper Cretaceous Transylvanian fauna contemporary with *Kallokibotion* are discussed in Nopcsa (1923a), see also Chure and MacIntosh (1989) for later references. A geologic study of the locality and surrounding area is given in Grigorescu (1983) and Weishampel et al. (1991).

Kallokibotion was described by Nopcsa in two papers: 1923a and 1923b. He argued that this turtle was relatively primitive compared with recent forms and placed it in the "Amphichelydia," now recognized as a wastebasket taxon of fossil turtles not clearly allied to any particular recent group (Gaffney, 1975a, 1984). No new material on *Kallokibotion* has come to light since Nopcsa's day, but the three partial skulls described by him have been reprepared, resulting in new information. Because of inconsistencies and ambiguities in Nopcsa's descriptions (Nopcsa, 1923b) and the fragmentary nature of the material, *Kallokibotion* has been difficult to compare with other turtles. This paper uses the new cranial information and reexamines all available material to place *Kallokibotion* in a cladistic framework of turtle relationships (Gaffney and Meylan, 1988). Nonetheless, the relatively poor preservation; very difficult matrix; and lack of preparation of most of the specimens is a serious problem that has restricted our ability to determine the osteology of *Kallokibotion*.

Although our conclusions are hampered by the poor state of preservation of the material, we argue that *Kallokibotion* is a relatively primitive cryptodire and of considerable interest in elucidating the early phylogenetic history of the group, thus substantiating

Nopcsa's general conclusions. Its appearance in the fossil record in the Late Cretaceous is a good deal later than would be expected (there are more advanced turtles in the Late Jurassic), but this is not an unusual occurrence in paleontology.

In addition to Gaffney and Meylan (1988), the reader is referred to Gaffney (1979a) for turtle skull morphology in general, to Gaffney (1979b) for descriptions of *Glyptops* and other primitive cryptodires, to Evans and Kemp (1975) for *Pleurosternon* (*Mesochelys*) skull morphology, to Gaffney (1983) for *Meiolania* skull morphology, and to Gaffney et al. (1987) for *Kayentachelys* descriptions.

ACKNOWLEDGMENTS

It would have been impossible to complete this paper without the close cooperation of specialists at Natural History Museum, London, particularly Dr. Angela Milner, Mr. Cyril Walker, and Ms. Sandra Chapman. The skulls were skillfully prepared by Otto Simonis, formerly of the American Museum of Natural History. The figures are the work of Frank Ippolito of AMNH. We thank Dr. D. Brinkman and Dr. H. Hutchison for reading a number of drafts, making useful comments, and considerably improving the paper. Dr. France de Broin very kindly made available undescribed specimens that she is currently studying. We are extremely grateful to Dr. Dan Grigorescu for reading the manuscript and correcting a number of errors.

INSTITUTIONAL ABBREVIATIONS

AMNH American Museum of Natural History

BMNH Natural History Museum, London

ANATOMICAL ABBREVIATIONS

<i>Skull</i>		pal	palatine
		pf	prefrontal
bo	basioccipital	pm	premaxilla
bs	basisphenoid	po	postorbital
epi	epipterygoid	pro	prootic
fr	frontal	pt	pterygoid
ju	jugal	qj	quadratojugal
mx	maxilla	qu	quadrate
na	nasal	so	supraoccipital
op	opisthotic	sq	squamosal
pa	parietal	vo	vomer

Shell bones

co costal
 ent entoplastron
 epip epiplastron
 hyo hyoplastron
 hypo hypoplastron
 me mesoplastron
 ne neural
 nu nuchal
 pe peripheral
 pg pygal
 sp suprapygal
 xip xiphiplastron

Shell scales

ab abdominal
 an anal
 ce cervical
 fe femoral
 gu gular
 hu humeral
 in intergular
 m marginal
 pe pectoral
 pl pleural

SYSTEMATICS

ORDER TESTUDINES

GIGAORDER CASICHELYDIA

MEGAORDER CRYPTODIRA

CAPAXORDER SELMACRYPTODIRA

FAMILY KALLOKIBOTIONIDAE

Genus *Kallokibotion* Nopcsa 1923a

TYPE SPECIES: *Kallokibotion bajazidi* Nopcsa 1923a.

DISTRIBUTION: Late Cretaceous, Maas-trichtian (fide Grigorescu, 1983), Sînpetru (formerly, Szentpeterfalva), Romania (Transylvania, which has been part of Romania since 1918).

DIAGNOSIS: A selmacryptodiran turtle with no temporal emargination of the daiocryptodiran type, a long parietal-squamosal contact probably present, parietal relatively elongate; prefrontal forming large lappet on skull roof as in *Kayentachelys*, not meeting on midline; nasal forming internarial process; triturating surfaces very narrow as in *Glyptops*; lower jaws very deep as in *Kayentachelys*; foramen caroticum basisphenoidale formed entirely by basisphenoid; canalis caroticus lateralis opens on ventral surface at a foramen formed by basisphenoid and pterygoids; pterygoids with very narrow medial extension to midline, unlike any other turtle; palatine with parasagittal grooves on ventral surface; incisura columellae auris enclosing eustachian tube and stapes in bone.

Cervical vertebrae amphicoelous with high postzygapophyses posteriorly, narrow centra,

and a low ventral keel; caudal vertebrae amphicoelous with tightly fitting zygapophyses concave anteriorly unlike those in other turtles; first thoracic vertebra facing directly anteriorly; nuchal bone small and rectangular; eight neurals probably present; two suprapyals, anterior one larger; plastron with short, rounded anterior lobe; full set of plastral scales; paired intergular (= gular of Hutchison and Bramble, 1981) scales unequal in size and extend onto entoplastron, gular (= extragular of Hutchison and Bramble, 1981) scales limited to epiplastron; large, triangular mesoplastra separate hyoplastron and hypoplastron for most of their width but mesoplastra do not meet in the midline (as a possible variant, they may meet in midline).

Kallokibotion bajazidi Nopcsa 1923a

TYPE SPECIMEN: Designated lectotype BMNH R4916. Consists of most of carapace, posterior lobe of plastron, pelvis, and a caudal vertebra.

DIAGNOSIS: Same as for genus.

SYNONYMY: *Kallokibotion magnificum* Nopcsa 1923b, designated lectotype BMNH R4930.

REFERRED SPECIMENS: Most of the specimens used in this study were purchased by the BMNH from Baron Nopcsa before or soon after the publication of his 1923b paper.

BMNH R4886 – Carapace fragment; the only specimen differing in data from the rest: “Szentpeterfalva, collid. & presd. by Lady Woodward, 1923,” (label).

BMNH R4916 (figs. 23, 24) – Lectotype of *Kallokibotion bajazidi*. Most of a carapace (Nopcsa, 1923b: fig. 1 in part, pl. 1, fig. 18; pl. 4, fig. 1), posterior lobe of plastron; pelvis (ibid., pl. 2, figs. 4–6), and a caudal (Nopcsa, 1923b: pl. 1, figs. 23–25).

BMNH R4917 – Posterior half of a small shell, poorly preserved (Nopcsa, 1923b: pl. 3, fig. 13).

BMNH R4918 (figs. 2–4, 28) – A partial shell (Nopcsa, 1923b: fig. 2) with skull and jaws (Nopcsa, 1923b: pl. 1, figs. 1–3). This specimen contains the most complete skull but nearly all of the surface bone has been damaged during preparation. The visible sutures are mostly within the bone and vary from the original surface position. The skull was separated from the matrix by breaking through the bone layer. The actual surface of the skull is still in the matrix

TABLE 1
Comparison of Criteria Used by Nopcsa (1923b)
to Distinguish Two Species of *Kallokibotion*

	<i>K. bajazidi</i>	<i>K. magnificum</i>
Nuchal scute	broad	narrow
Ratio of length to breadth of third vertebral scute	10:23	10:20
Posterior outline of last verte- bral scute	slightly concave	strongly con- vex
Mesoplastra meet in mid- line	no	yes
Intergular scutes	short	short
Included speci- mens	B, C, D, E (R4918, R4916, R4921, R4919, R4917, R4922)	A (R4930) & ?

attached to the shell. During preservation most of the bone was broken and distorted to a varying degree but only the palate has been subjected to large-scale distortion. It was hoped that because most of the palate had not been prepared, new preparation of it would yield better information. However, it became apparent that the palate was broken and dislocated by roughly longitudinal fractures resulting in a state of preservation that gives relatively little morphological information.

BMNH R4919 (figs. 21, 22) – Anterior margin of carapace (Nopcsa, 1923b: fig. 1) with thoracic vertebrae (Nopcsa, 1923b: pl. 2, fig. 1); according to Nopcsa this and BMNH R4921 are the same individual.

BMNH R4920 – Posterior part of carapace (Nopcsa, 1923b: fig. 5) plus some shell fragments.

BMNH R4921 (figs. 5–13, 29–31) – Partial skull and jaw (Nopcsa, 1923b: pl. 1, figs. 7–9), six cervicals (Nopcsa, 1923b: pl. 1, figs. 10–17), seven caudals (Nopcsa, 1923b: pl. 1, figs. 20–22, 26–29), sacral rib (Nopcsa, 1923b: pl. 1, fig. 30), partial pelvis, partial right and left scapulocoracoid (Nopcsa, 1923b: pl. 3, fig. 12), right and left humerus (Nopcsa, 1923b: pl. 3, figs. 1–3, 5, 6), left femur (Nopcsa, 1923b: pl. 3, fig. 8). In this specimen the bone is best preserved of all the *Kallokibotion* skulls. Removal of almost all the matrix and separation of the skull roof from the braincase yielded good results. Unfortu-

nately, almost all the palate and snout are missing and most of the remaining areas are damaged due to breakage. Nonetheless, sutures are generally good on this specimen and information from the skull roof and braincase is significant.

BMNH R4922 – Anterior margin of plastron (Nopcsa, 1923b: fig. 2).

BMNH R4923a – Ilium (Nopcsa, 1923b: pl. 2, fig. 7).

BMNH R4923b – Femur (Nopcsa, 1923b: pl. 3, fig. 4).

BMNH R4924 (fig. 31) – Femur (Nopcsa, 1923b: pl. 3, figs. 7, 9, 10).

BMNH R4925 (figs. 14–16) – An eroded braincase and otic region (Nopcsa, 1923b: pl. 1, figs. 4–6). Good sutures are seen on this skull, but it is relatively incomplete.

BMNH R4926 – Pubis and acetabulum (Nopcsa, 1923b: pl. 2, fig. 8).

BMNH R4927 – Fragment of central portion of carapace.

BMNH R4928 – First two thoracic vertebrae.

BMNH R4929 – Ilium.

BMNH R4930 (figs. 25–27) – Lectotype of *Kallokibotion magnificum*. Plastron (Nopcsa, 1923b: fig. 4; pl. 4, fig. 2), steinkern of nearly complete shell, and external mold of carapace (Nopcsa, 1923b: fig. 3) with some fragments of posterior peripherals, thoracic vertebrae, and shell fragments.

BMNH R4931 – Posterior portion of carapace.

BMNH R4932 – Partial shell of largest individual, largely unprepared.

BMNH R4953 – Distal end of right humerus (Nopcsa, 1923b: pl. 3, fig. 11).

BMNH R5815 – Shell fragments.

BMNH R9379 – Distal end of left humerus.

BMNH R9380 – Humeral fragment.

BMNH R9381 – Right ilium.

BMNH R9382 – Glenoid area of scapulocoracoid.

BMNH R11176 – Shell fragments in matrix block.

BMNH R11177 – Pelvis, hind limb fragments, vertebrae, shell fragments.

BMNH R11178 (figs. 19, 20) – Partial shell showing sutures.

BMNH R11179 – Shell fragments in matrix block.

BMNH R11180 – Carapace fragment.

BMNH R11181 – Carapace fragment.

DISCUSSION: Although Nopcsa did not specifically designate type specimens for his two species in either paper (1923a, 1923b), the British Museum material includes clearly identified type specimens. BMNH R4916 is labeled as the type of *Kallokibotion bajazidi* Nopcsa and BMNH R4930 is labeled as the type of *Kallokibotion (Kallokibotium) mag-*

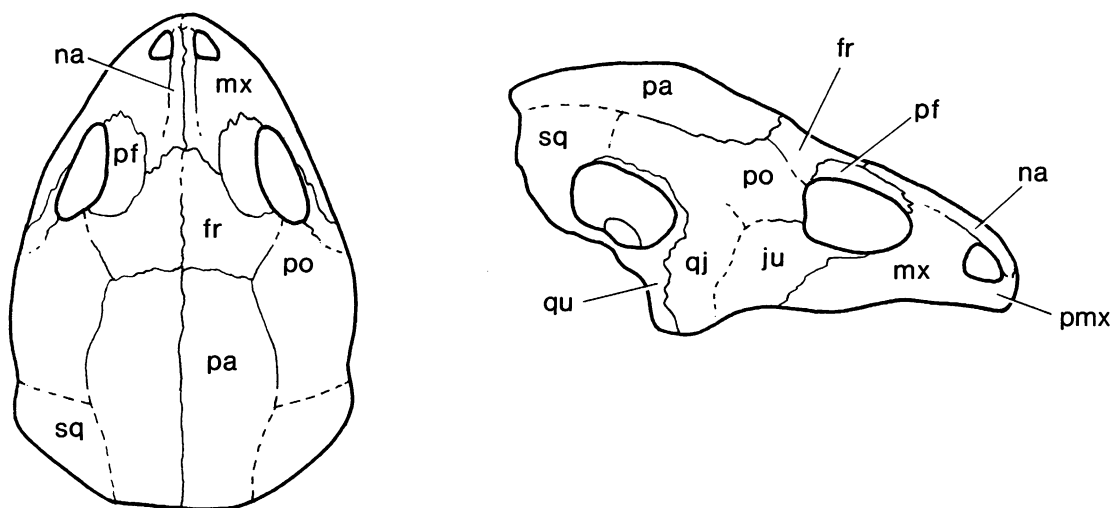


Fig. 1. *Kallokibotion bajazidi*. Dorsal and lateral views of reconstruction of skull. See figure 8 for palate. Based on BMNH R4918 and BMNH R4921. Abbreviations on p. 2.

nificum Nopcsa. This is consistent with Nopcsa's intentions as we interpret them from Nopcsa (1923b) and is legitimized here by designating these specimens as lectotypes.

Nopcsa (1923b: 24) distinguished two species from the same horizon and locality: *Kallokibotion bajazidi* (Nopcsa, 1923a) and *Kallokibotion magnificum*, n. sp. Table 1 compares the characters used by Nopcsa to identify these taxa along with the specimens included. Examination of these characters in the broader context of variation within recent species gives little support for the recognition of two taxa. The limits of what Nopcsa identified as the cervical (nuchal) scute in BMNH R4919 is clear and it is unusually broad; however, the scute markings in BMNH R4930 are not clear in the nuchal area and Nopcsa's figure 3 overstates the detail visible on this specimen. The two vertebral scute characters are visible in the two types, but involve only minor differences in shape and are the type of character that commonly varies within recent species. The mesoplastra certainly do not meet in the midline in BMNH R4918 and BMNH R11178. Because both specimens are about the same size or larger than BMNH R4930, in which they may meet in the midline, it is unlikely that this is due to differences in stage of growth. However, as discussed below, the evidence for medially

meeting mesoplastra in BMNH R4930 is ambiguous. Even if it is present, individual variation in this character does occur in baenids (Gaffney, 1972). The intergular scute character is listed by Nopcsa as the same in both species, presumably in error, but comparing BMNH R4930 with the isolated anterior plastral margin, BMNH R4922, reveals no particular difference. In the absence of any other features distinguishing the two supposed taxa, only one species is recognized here.

CRANIAL MORPHOLOGY

Figures 1–16

NASAL

The region of the nasals (figs. 1–4) is preserved only in BMNH R4918, the surface of the bone is gone, and the area is distorted and broken. Limits of the nasals are dubious but some features are visible. From the material preserved, Nopcsa's (1923b) description is accurate. There are two long nasal bones that extend anteriorly from the frontals to reach the premaxillae and separate the paired nares. The position of the premaxilla-nasal contact, however, could be at any one of a number of breaks, but the most likely position is one with a fairly short dorsal process on the premaxilla. The posterior area of the nasals

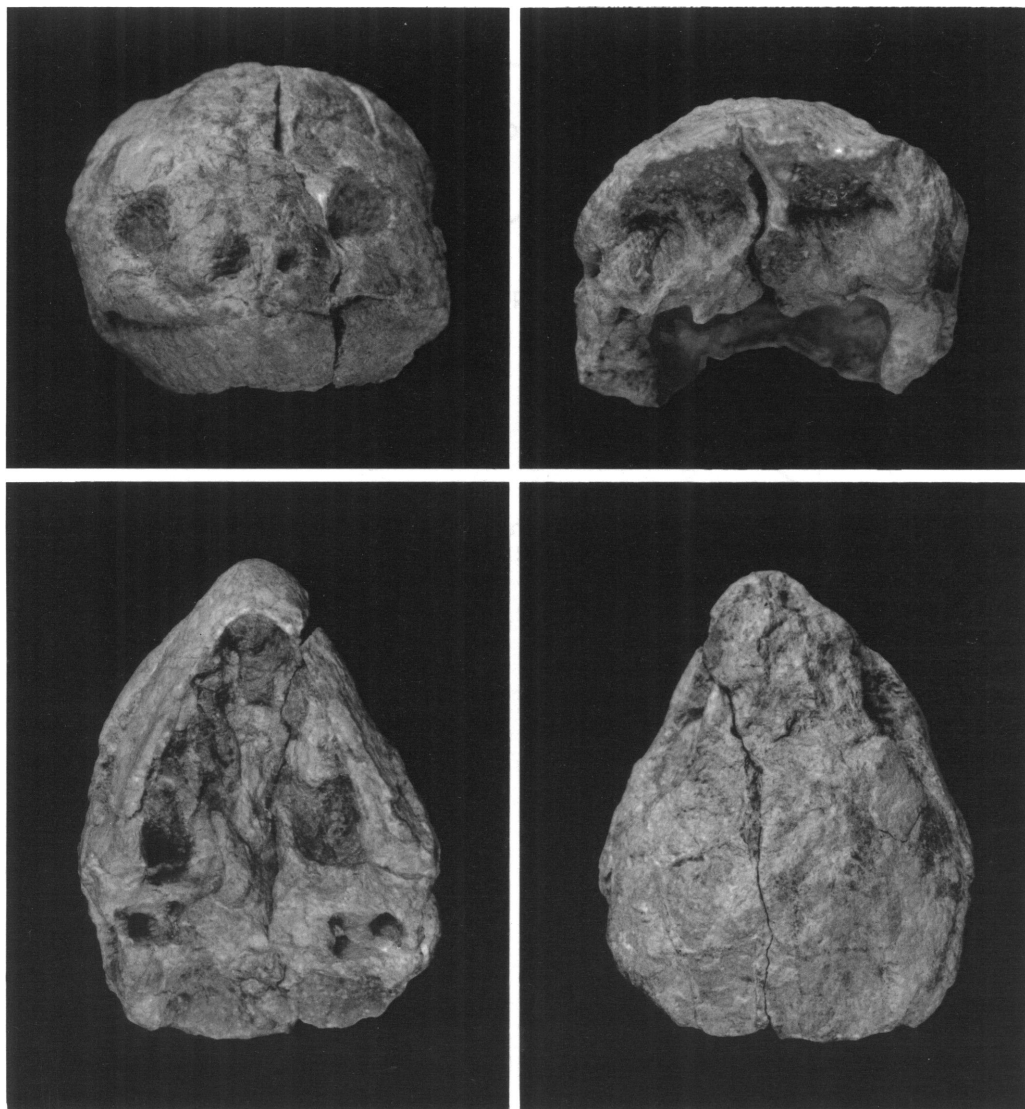


Fig. 2. *Kallokibotion bajazidi*. Skull of BMNH R4918. Upper left, anterior view; upper right, posterior view; lower left, palatal view; lower right, dorsal view.

is not well preserved but a nasal-prefrontal contact seems unlikely. Only the ventral surface of the nasals is preserved; the dorsal surface was probably somewhat wider.

PREFRONTAL

Prefrontals are preserved on the left side of BMNH R4921 and on both sides of BMNH R4918 (figs. 1–6). The former appears to lack the ventral portion but the dorsal piece is well

preserved. In BMNH R4918 the bones are cracked, have ambiguous limits, and lack their dorsal surface. The dorsal process of the prefrontal is much as described by Nopcsa; it is relatively large and forms the anterodorsal margin of the orbit. The prefrontal is separated from the midline by the frontal and contacts the maxilla anteriorly. There does not appear to be a nasal contact. The frontal lies behind the prefrontal and prevents a prefrontal-postorbital contact. The ventral sur-

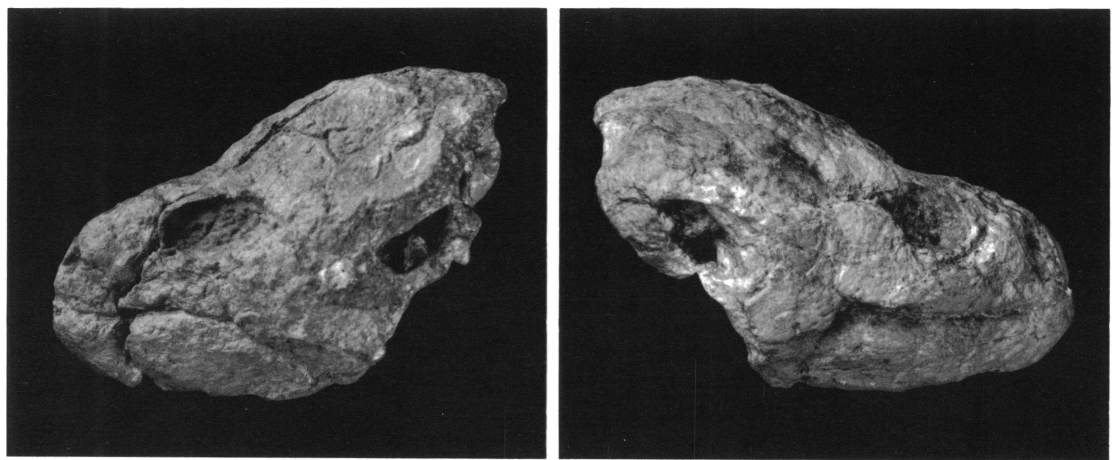


Fig. 3. *Kallokibotion bajazidi*. Skull of BMNH R4918. Left, left lateral view; right, right lateral view.

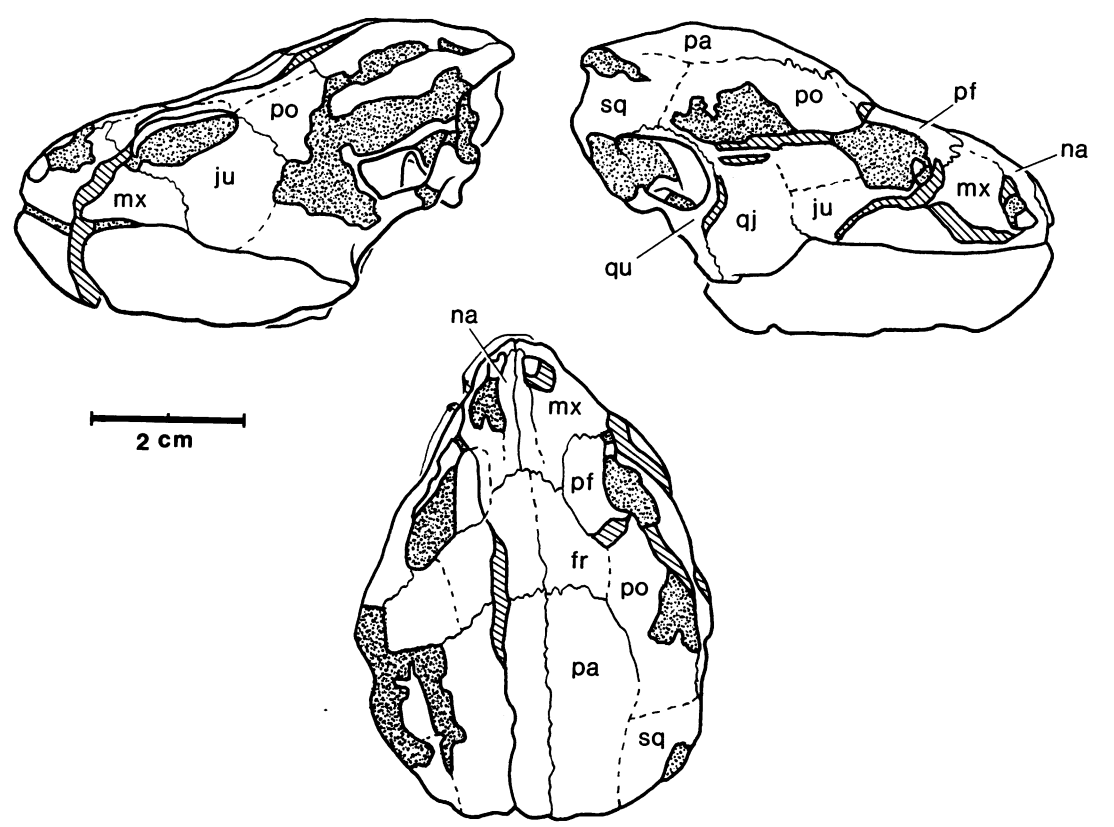


Fig. 4. *Kallokibotion bajazidi*. Skull of BMNH R4918. Key to figures 2, 3. Upper left, left lateral view; upper right, right lateral view; lower, dorsal view. Differential crushing has produced asymmetrical sutures. Cracks that may be sutures are represented by dashed lines. Abbreviations on p. 2.

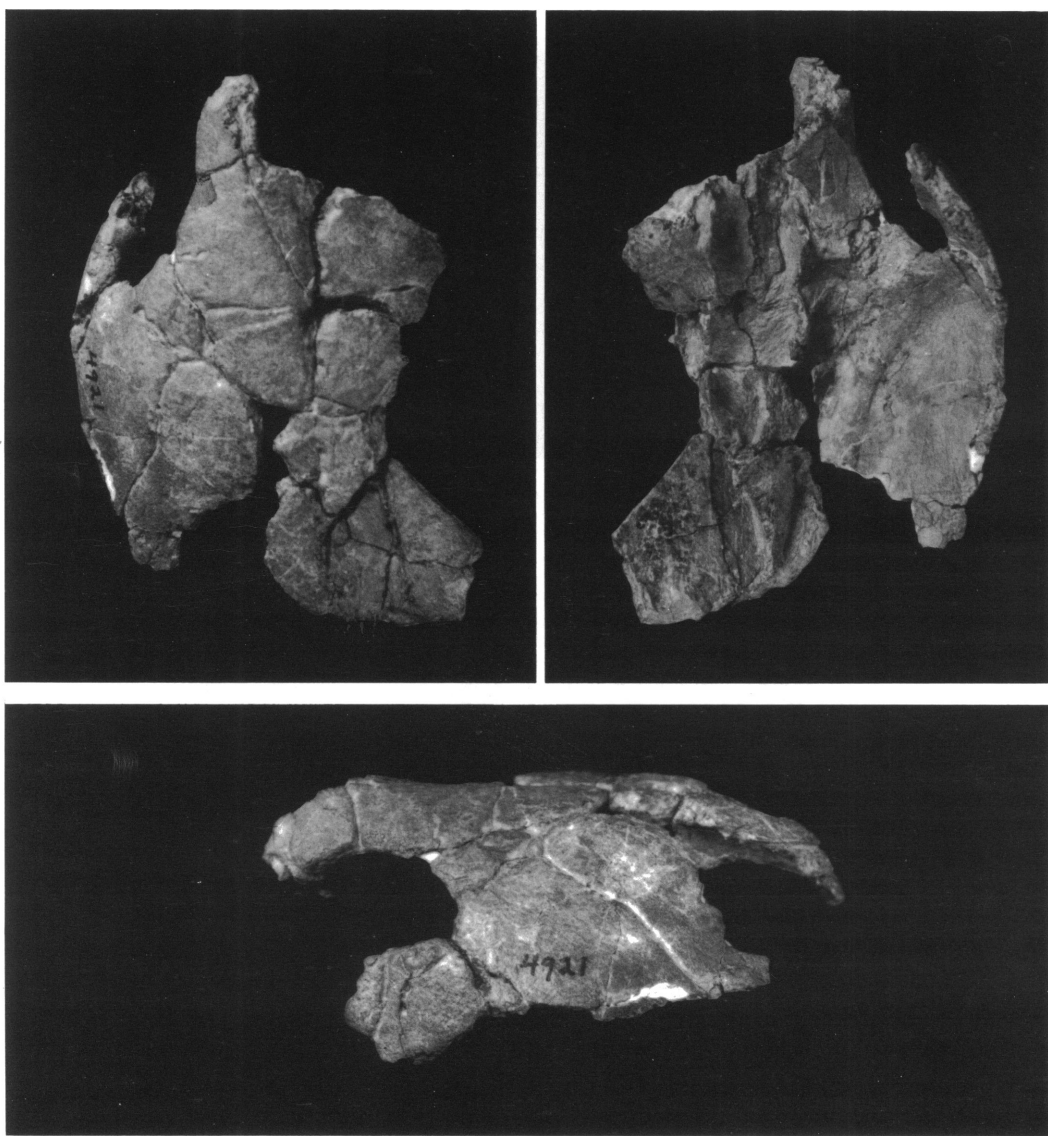


Fig. 5. *Kallokibotion bajazidi*. Skull roof of BMNH R4921. Upper left, dorsal view; upper right, ventral view; lower, left lateral view.

face of the left side of BMNH R4921 shows a narrow extension of the frontal reaching the orbit (fig. 6).

In the parasagittal break in BMNH R4918 some of the ventral process of the prefrontal can be seen but its contacts are not clear. There is what can be interpreted as a vomer-prefrontal contact and the visible morphology is consistent with that of other cryptodires.

The left prefrontal preserved in BMNH

R4921 shows the internal morphology of this bone anterior and medial to the orbit. Just anterior to the contact with the frontal there is a lateral indentation, or sinus, opening medially into the posterior part of the fossa nasalis. This structure is similar to the large, posterior portion of the fossa nasalis in *Proganochelys*. It is part of the fossa nasalis itself rather than a separate sinus formed by the maxilla and nasal as in *Meiolania*.

In *Kallokibotion* the fissura ethmoidalis is

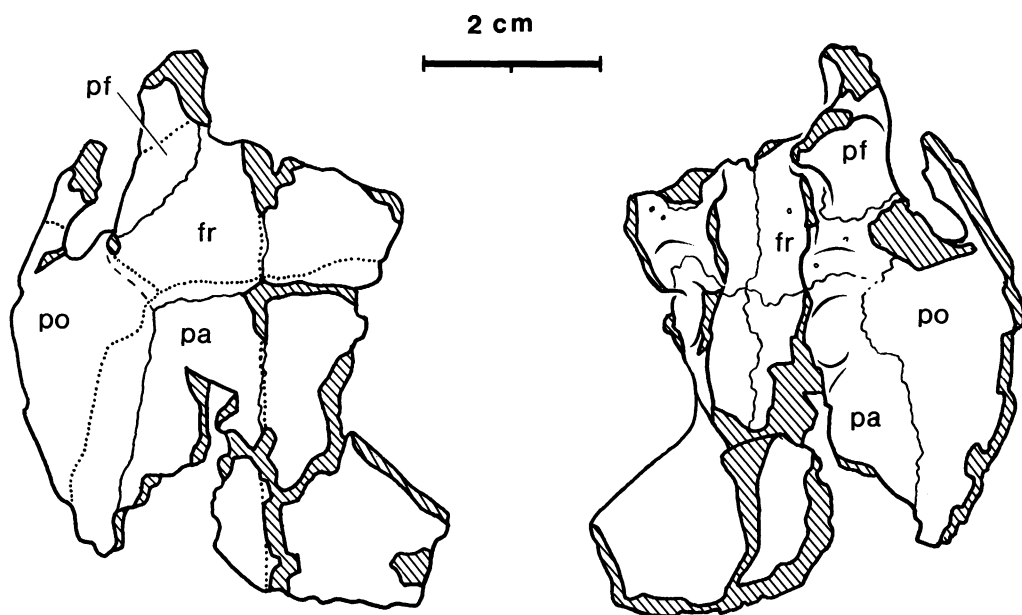


Fig. 6. *Kallokibotion bajazidi*. Skull roof of BMNH R4921. Key to figure 5. Left, dorsal view; right, ventral view. Dotted lines show scale sulci, preserved only on this specimen. Abbreviations on p. 2.

very wide, the fossa nasalis openly communicating with the rest of the cavum cranii.

FRONTAL

Frontals are preserved on both sides of BMNH R4921 and BMNH R4918 (figs. 1–6) but their limits are not entirely clear. In BMNH R4918 the frontal contacts the nasal anteriorly and the prefrontal anterolaterally but whether the maxilla reaches the frontal or if a nasal-prefrontal contact prevents this is not determinable. Posteriorly there is a transverse contact with the parietal visible on both specimens and posterolaterally the frontal reaches the postorbital, although this contact is not entirely clear on any specimen. On the ventral surface of the left side of BMNH R4921 a suture is visible at this location and the reconstruction is based on this contact even though it cannot be followed on the dorsal surface.

The ventral surface of the frontal is visible on both sides of BMNH R4921. The sulcus olfactorius is very broad, much as in baenids rather than eucryptodires.

One of the *Kallokibotion* skulls, BMNH R4921, has scale sulci on it (fig. 6), showing that *Kallokibotion* had cranial scales, as in *Proganochelys* and a number of other turtles.

The pattern of the scales in *Kallokibotion* shows two large paired scales roughly overlying frontals and parietals and meeting on the midline. This pattern is not particularly close to any other cranial scale pattern.

PARIETAL

Parts of the parietal (figs. 1–6) are preserved in all three specimens but it is not complete in any of them. The parietal has a transverse suture anteriorly with the frontal and presumably contacts the postorbital anterolaterally and to some extent laterally. Although the lateral edge of the parietal is discernible, the limits of the postorbital and quadratojugal in this area are not. The lateral margin of the parietal is a long, parasagittal suture that runs to the posterior margin of the skull. The parietal contacts the squamosal along the posterior part of its lateral margin. We interpret this contact as being relatively extensive. The squamosal-quadratojugal contact is based on the right side of BMNH R4921 where a small portion of this suture appears to be present.

The parietal of *Kallokibotion* is a relatively elongate element, without lateral expansions, contrary to Nopcsa's (1923b) description, that lacks any temporal emargination. It is thus

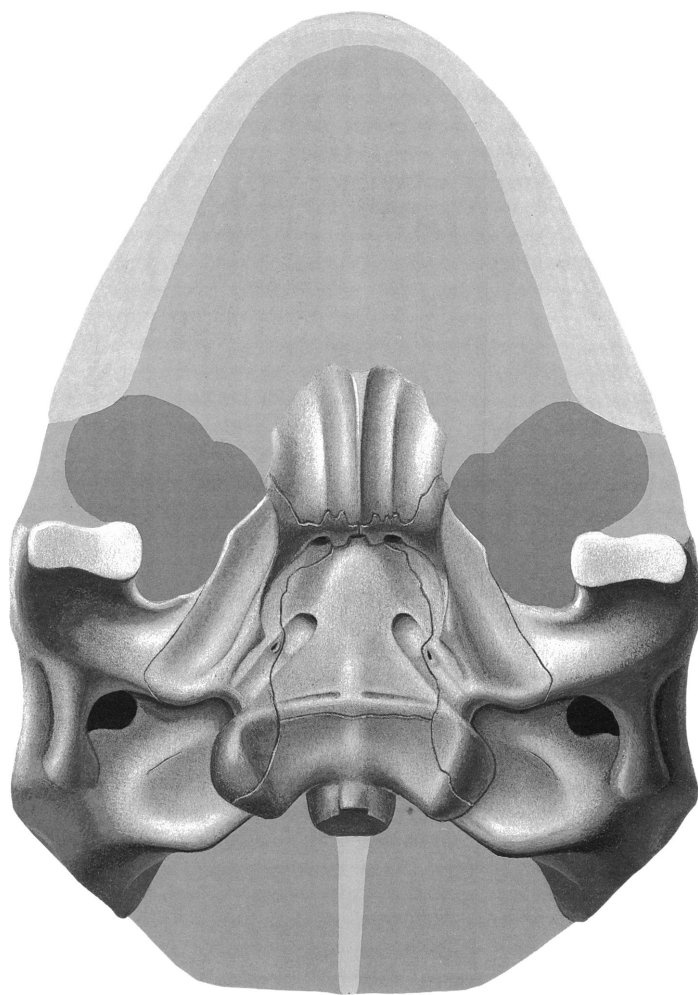


Fig. 7. *Kallokibotion bajazidi*. Composite restoration of skull in ventral view, based primarily on BMNH R4921, with additions from BMNH R4918 and BMNH R4925.

similar to the hypothesized primitive cryptodiran condition as seen in *Pleurosternon* (*Mesochelys*).

The processus inferior parietalis (fig. 16) is preserved in part in all three *Kallokibotion* skulls but sutures showing its contacts are not clear. The processus contacts the prootic posteriorly and forms the anterodorsal portion of the foramen nervi trigemini (fig. 16). Ventrally the processus reaches the epipterygoid as seen in BMNH R4925.

JUGAL

The region of the jugal is preserved in BMNH R4921 and BMNH R4918 (figs. 1–

4) although few of the sutures are clear. In BMNH R4918 the jugal-maxilla suture can be made out and it slopes posteroventrally from the ventral margin of the orbit. The posterior limits of the jugal are not preserved in BMNH R4921 while in BMNH R4918 only the dorsal contact with the postorbital on the left side is clear. Cracked areas in BMNH R4918 obscure the quadratojugal-jugal contact and the reconstruction indicates one possible position of the suture. The orbital floor is not visible in any specimen and the palate is too poorly preserved to allow identification of the medial process of the jugal. It does seem clear, however, that the

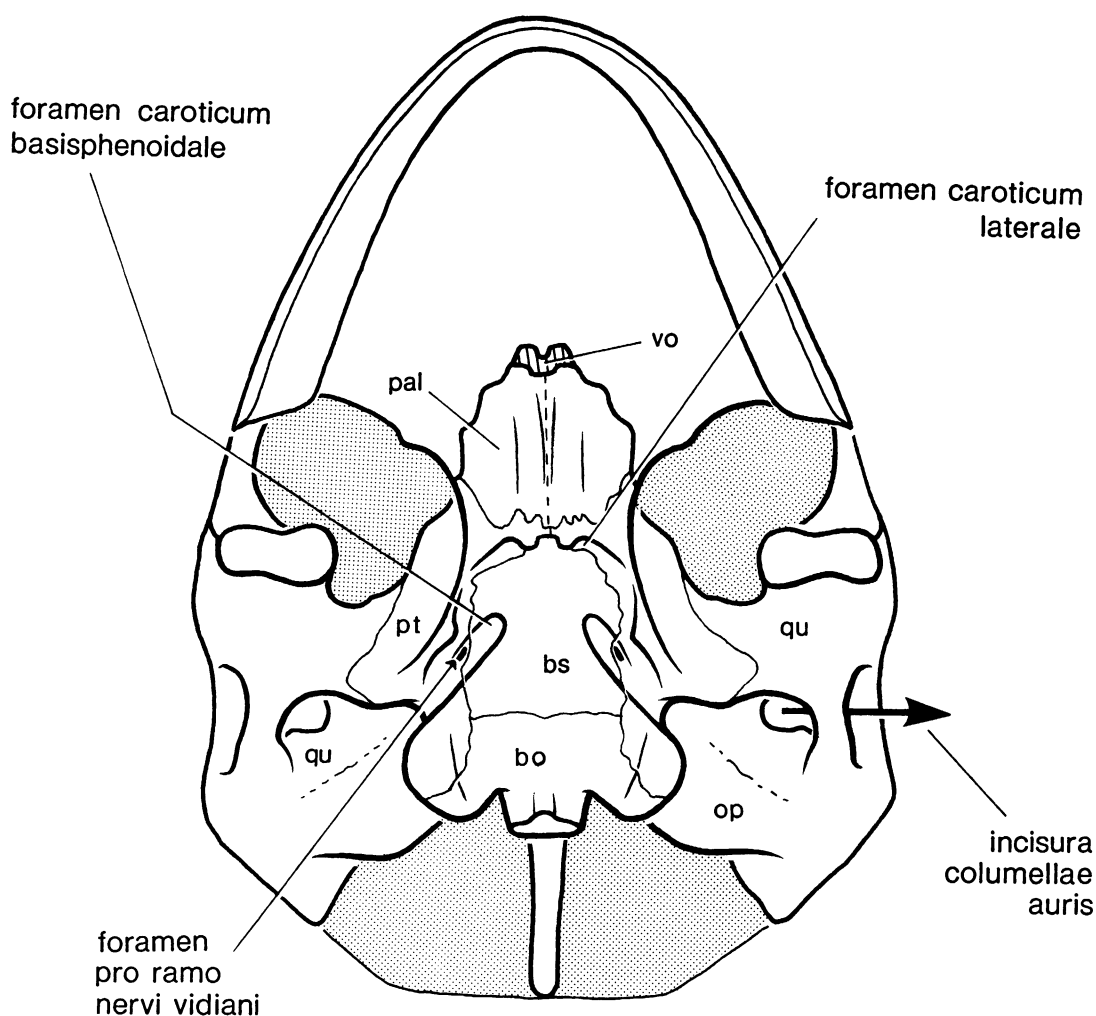


Fig. 8. *Kallokibotion bajazidi*. Restoration of skull, key to figure 7. Abbreviations on p. 2.

jugal has some exposure along the ventral margin of the skull.

QUADRATOJUGAL

Portions of the quadratojugal are preserved in BMNH R4921 and BMNH R4918 (figs. 1–4) but the best area is on the right side of BMNH R4918. Here the ventral half of the quadratojugal is present and shows the usual chelonian semicircular suture with the quadrate posteriorly. Anteriorly there is a questionable suture with the jugal while dorsally the presumed contact with the postorbital cannot be clearly seen on any specimen. Similarly, possible contacts with the parietal and squamosal cannot be ruled out.

SQUAMOSAL

The squamosal is preserved in BMNH R4921 and BMNH R4918 (figs. 1–4) but its contacts are not clear on any specimen. It is very likely that the squamosal has a relatively long parasagittal suture with the parietal on the posterior portion of the skull roof based on interpretations of broken areas in BMNH R4918. The anterior margin of the squamosal on the skull roof presumably contacts the postorbital but this suture cannot be made out on any of the specimens.

The antrum postoticum of *Kallokibotion* is a well-developed cavity in the posterodorsal region of the cavum tympani, as in most tur-

ties. The posterior margin of the squamosal continues the posterior margin of the parietal and turns ventrally and anteriorly around the outer opening of the cavum tympani. Ventrolateral to the incisura columellae auris the squamosal is interpreted as contacting the quadrate (see Quadrate). The medial contacts of the squamosal with the otic chamber elements cannot be made out.

POSTORBITAL

The region of the postorbital is preserved in part in BMNH R4921 and BMNH R4918 (figs. 1–6) but few of its contacts are identifiable. At least part of the parasagittal parietal-postorbital contact is visible in both skulls and the jugal-postorbital contact is visible in BMNH R4918. On the left side of BMNH R4918 the jugal-postorbital suture is visible but crushing of the dorsal margin of the orbit has altered its position. In the restoration (fig. 1) the presumed original position of the suture is shown. It would be of some systematic significance if it could be determined whether *Kallokibotion* had a relatively large and long postorbital, such as in *Mesochelys*, or if it was more similar to the reduced postorbital of *Meiolania*. Unfortunately, this cannot be definitely determined, although the former is more likely based on the positions of other elements.

PREMAXILLA

The region of the premaxilla is preserved only in BMNH R4918; the bone surface is badly broken. The margin forming the triturating ridge is damaged but there does not appear to be a strong premaxillary hook or notch. The apertura narium externa is divided medially by bone but most of the separation appears to be by the nasals, although some premaxillary contribution is possible. The nasal-premaxillary suture is interpreted as lying at the ventral margin of the apertura narium externa, but its position is not entirely clear (figs. 1, 4). The palatal portion of the premaxilla is visible, although poorly preserved, and indicates that the triturating surface at this point is relatively narrow. A paired foramen praepalatium can be made out at the anterior portion of the premaxilla, but breakage prevents identification of vomerine or other sutures.

MAXILLA

The maxilla is preserved only in BMNH R4918 (figs. 1–4); most of its surface and ventral margin is damaged. As preserved, the labial ridge in *Kallokibotion* is straight and moderately high. The dorsal portion of the maxilla occupies the region between nares and orbit and the maxilla forms the anteroventral margin of the orbit. Contrary to Nopcsa's (1923b) assertion, there is no evidence for a lacrimal bone or lacrimal duct in *Kallokibotion*.

The palatal surface of the skull is not preserved well enough to identify maxillary sutures (other features of the palate are discussed under Vomer). The lower jaws are still attached to the skull in BMNH R4918 (fig. 2) and the triturating surface cannot be seen directly. However, a break in the skull on the left side provides a cross section showing that the triturating surface is relatively narrow in comparison to that of *Chelydra* and is similar to that of *Glyptops*. The free lower jaws of BMNH R4921 are also narrow and consistent with this observation.

VOMER

The area of the vomer is preserved in part in BMNH R4921 and BMNH R4918 (figs. 2, 7–13). In BMNH R4918 (fig. 2) the entire palate is visible but it is badly broken up and distorted. This specimen shows that a secondary palate was not present and that the maxillary triturating surfaces were narrow and lacked accessory ridges as seen in *Meiolania*. One feature that the palate does have in common with *Meiolania* is the parasagittal choanal grooves separated by a median ridge. However, in *Meiolania* (Gaffney, 1983) the vomer forms the sagittal region of the palate while in *Kallokibotion* the palatines seem to dominate (fig. 8). These grooves and the ridges limiting them laterally are best seen in BMNH R4921 (figs. 7–9), although only the posterior part of the palate is preserved. In BMNH R4918 the foramen palatinum posterius can be identified on both sides. It is relatively small in diameter (in contrast to such forms as *Chelydra* but similar to *Meiolania*) and lies close to the lateral margin of the palate, a further indication of the narrowness of the triturating surface.

If the condition of the right side of the

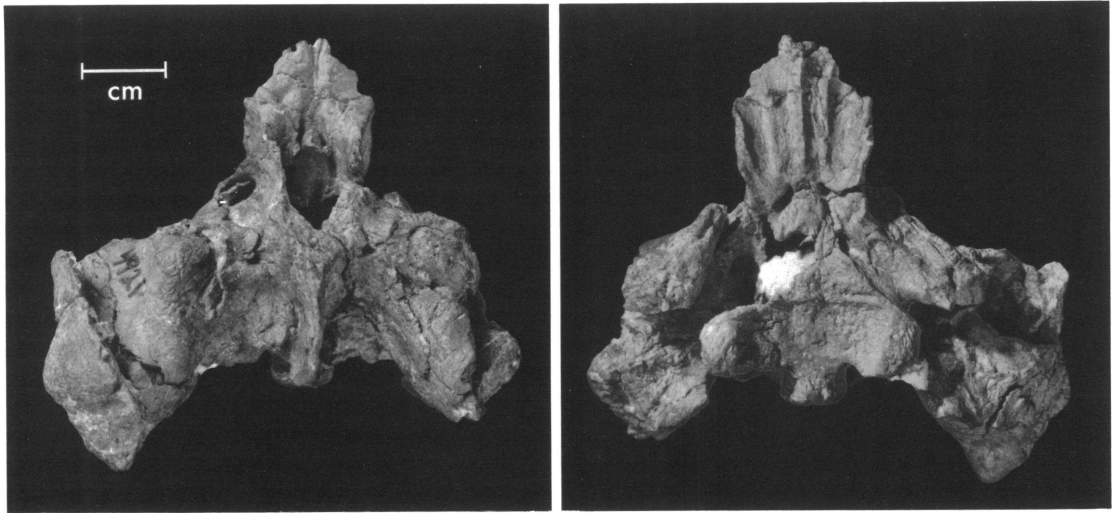


Fig. 9. *Kallokibotion bajazidi*. Braincase of BMNH R4921 in dorsal (left) and ventral (right) views. See figures 7, 8.

palate in BMNH R4918 is assumed to be largely accurate (the left side has much of the bone missing) then the paired apertura narium interna are separated by a relatively wide expanse of bone, presumably vomer. The degree of separation would be comparable to that seen in *Meiolania* and greater than that seen in *Chelydra*. The right side of the palate in BMNH R4918 also shows parasagittal ridges, a more medial one in the anterior part of the palate and a more lateral one farther posterior, but these have been deformed and broken and are probably the result of post-mortem damage. The ridges seen on the better preserved BMNH R4921 do not agree with the ones in BMNH R4918 in position or degree of development.

In BMNH R4921 the posterior part of the palate preserves portions of the vomer, palatines, pterygoids, and basisphenoid (figs. 7–13). Sutures can best be seen on the dorsal surface where the vomer lies between the palatines and barely contacts the pterygoids. These sutures are overlapping to a variable extent but clear limits for the vomer on the ventral surface are not visible. It is clear that on the ventral surface the vomer makes up at least the anterior part of the median ridge, but it is unlikely that it extends posteriorly to completely separate the palatines, as is primitive for turtles. As in *Meiolania*, *Kallokibotion* has two pairs of troughs in this part

of the palate separated by a median ridge and a pair of parasagittal ridges. In *Meiolania* the more medial troughs end blind at the triturating surfaces anteriorly while the more lateral ones lead into the internal nares. To the extent that this is determinable in *Kallokibotion*, it appears to be the same. In *Meiolania* the medial troughs are the more dorsal while in *Kallokibotion*, the lateral pair are more dorsal. In *Meiolania* these troughs do not extend posteriorly onto the region of the intrapterygoid slit so that there is a relatively flat surface in the posterior part of the palate. In *Kallokibotion* this flat surface is not developed and the troughs become indistinct at the anterior margin of the pterygoid (i.e., the pterygoid-vomer and pterygoid-palatine suture).

PALATINE

See Vomer for discussion.

QUADRATE

Portions of the quadrate are preserved in all three *Kallokibotion* skulls (figs. 1–4, 7–11) but the bone is not complete in any of them. As in most turtles the quadrate forms the major portion of the cavum tympani and the incisura columellae auris. The cavum tympani in *Kallokibotion* is of the “normal” cryp-

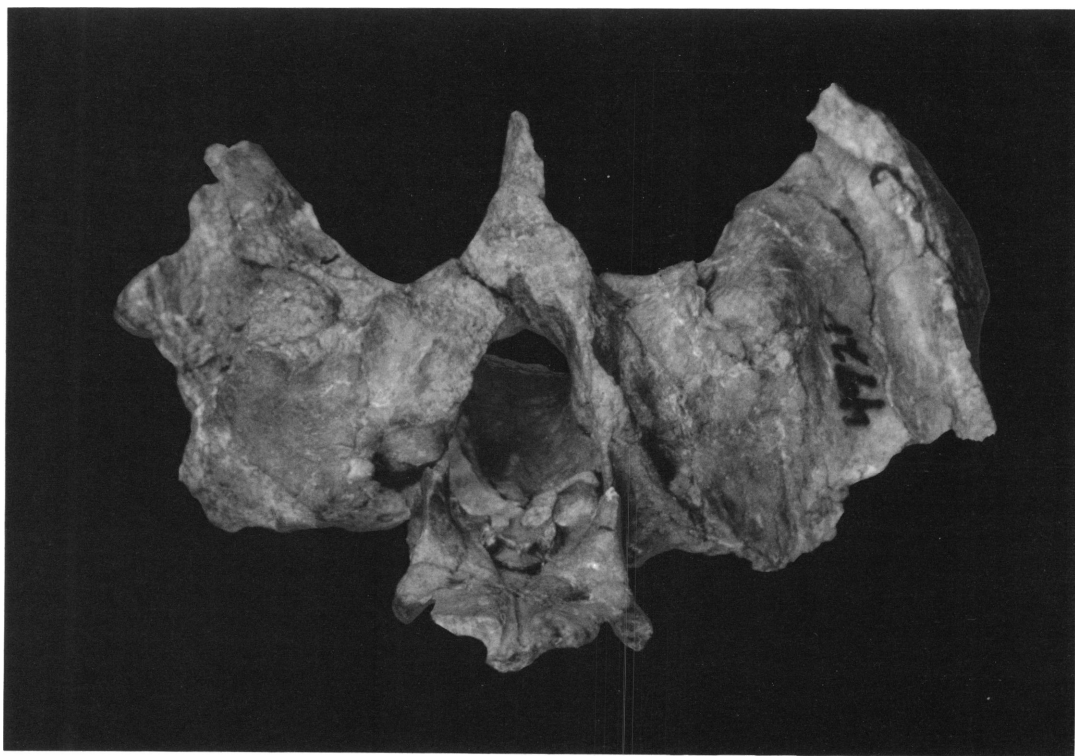


Fig. 10. *Kallokibotion bajazidi*. Braincase of BMNH R4921 in anterior view.

todiran type, such as that seen in baenids and chelydrids. It is C-shaped with a well-developed antrum postoticum and without accessory concavities. The squamosal-quadrate suture is not discernible. The incisura columellae auris is of interest because it is completely enclosed on both sides of BMNH R4918. It is of the type seen in baenids, meiolaniids, and pleurodires, in which the stapes and eustachian tube are enclosed together in an oblong incisura rather than being separated by bone as in many eucryptodires.

The medial contacts of the quadrate are best seen in BMNH R4925 on the dorsal surface of the otic chamber (figs. 11, 14, 15). The quadrate forms the lateral half of a well-developed foramen stapedio-temporalis and contacts the prootic anterior to the foramen. The prootic-opisthotic suture is not discernible but the posteromedial region of the quadrate contacts the opisthotic. Anteriorly the quadrate reaches the posteroventral margin of the foramen nervi trigemini (fig. 16). On

the ventral side of the skull the quadrate reaches the pterygoid and runs posterolaterally along the side of the pterygoid as in most cryptodires. The quadrate bears most, if not all, of the processus trochlearis oticum, which is moderately developed in *Kallokibotion* to about the extent seen in *Chelydra*. The processus articularis of the quadrate is preserved only in BMNH R4918 where it is still articulated to the lower jaw.

The foramen stapedio-temporalis is best seen in BMNH R4925 although it is also present, but crushed, in BMNH R4921. The foramen leads into the canalis stapedio-temporalis which cannot be probed in any of the available specimens. In BMNH R4921 the aditus canalis stapedio-temporalis in the roof of the cavum acustico-jugulare is visible but sutures are not clear in this region. Presumably the quadrate makes up the lateral portion of the aditus and the canalis stapedio-temporalis. In BMNH R4925 and BMNH R4921 the foramen stapedio-temporalis ap-

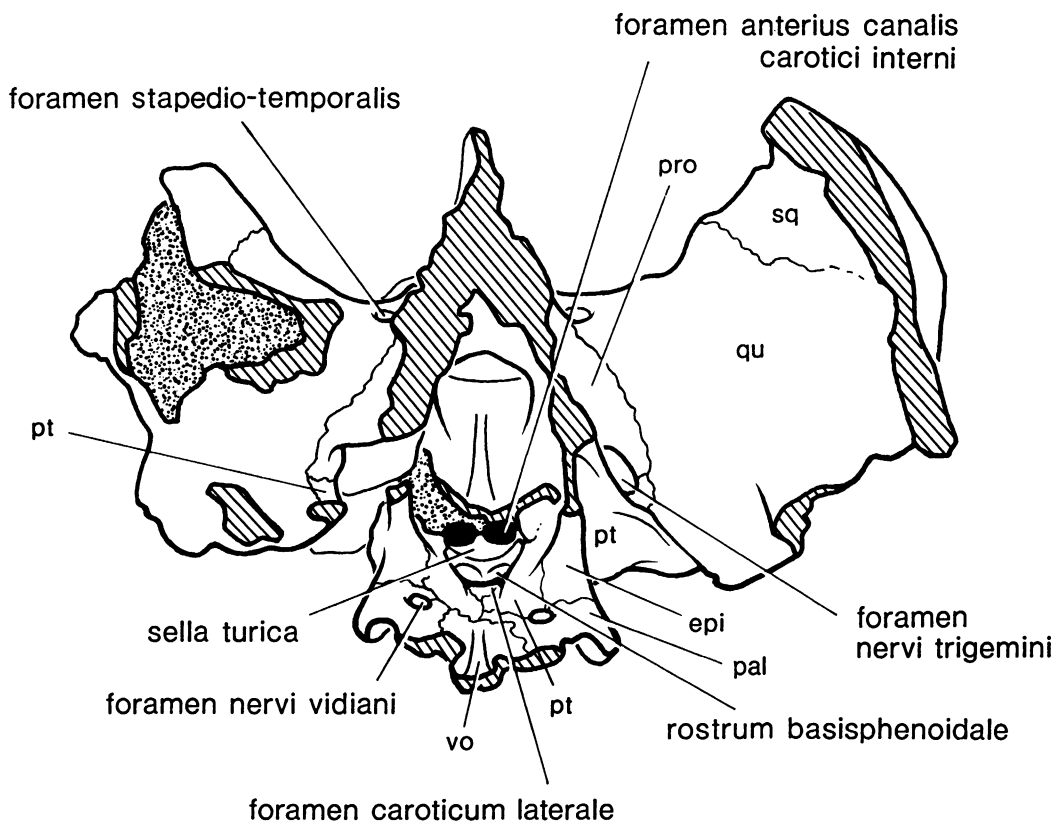


Fig. 11. *Kallokibotion bajazidi*. Braincase of BMNH R4921 in anterior view. Key to figure 10. Foramina anterius canalis carotici interni restored. Sutures differ slightly from figure 13 due to foreshortening. See figures 9, 12, 13. Abbreviations on p. 2.

pears to be about the same diameter as the foramen posterius canalis carotici interni.

EPIPTERYGOID

The epipterygoid is preserved in part in BMNH R4921, BMNH R4925, and BMNH R4918 (figs. 10–16). The bone is relatively large and has an expanded ventral “foot” that widens where it contacts the pterygoid. Although the epipterygoid of *Meiolania* is also relatively large, it does not have this feature. A prominent foramen is developed in the suture between epipterygoid and palatine with the pterygoid forming part of the foramen margin (fig. 13). This foramen presumably contains the vidian nerve. The dorsal edge of the epipterygoid contacts the parietal. The epipterygoid appears to form the ventral margin of the foramen nervi trigemini.

PTERYGOID

Portions of the pterygoid are preserved in all three *Kallokibotion* specimens (figs. 7–16). The bone is best seen in BMNH R4921 on both dorsal and ventral surfaces. Posteriorly the pterygoid contacts the basioccipital posteromedially and the basisphenoid medially. It forms the ventral margin of the fenestra postotica and contacts the quadrate laterally. These relations are consistent with cryptodires such as baenids that have an open fenestra postotica. The pterygoid bears a groove extending posterolaterally from the foramen caroticum basisphenoidale in BMNH R4925 and BMNH R4921.

Anteriorly, on the ventral surface (fig. 8), the pterygoids meet on the midline between the basisphenoid and palatines. The contact of the pterygoids is very narrow and occurs

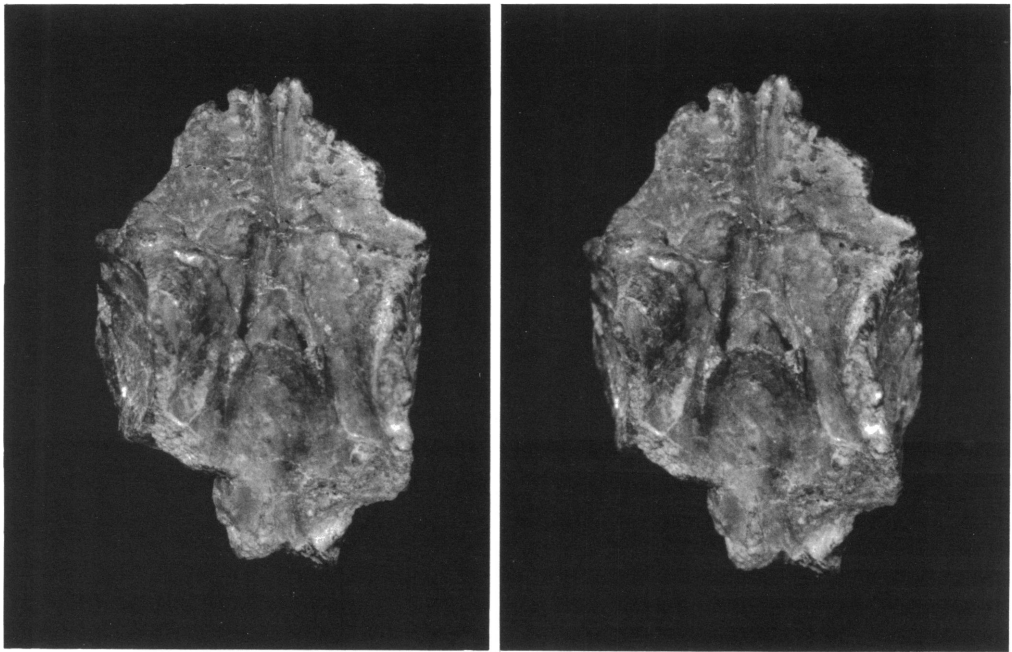


Fig. 12. *Kallokibotion bajazidi*. Stereophotograph of anterior portion of basicranium of BMNH R4921 in dorsal view.

at the posterior end of the median palatal ridge. The anterior margin of the pterygoid is a suture that is roughly transverse medially and angles sharply in an anterior direction as it goes laterally. This shape of the anterior margin of the pterygoid differs from most turtles, but is similar to that seen in *Meiolania*. However, the medial contact of the pterygoids is more extensive in *Meiolania*, which has a well-developed intrapterygoid slit, a space separating the pterygoids and basisphenoid, and through which the palatine artery apparently travels. In *Kallokibotion* there is no intrapterygoid slit and the palatine artery is contained in a paired canalis caroticus lateralis that enters the skull at the basisphenoid-ptyergoid contact. This contact area, however, is developed into a steplike condition in *Kallokibotion* so that the basisphenoid is at a more dorsal level than the pterygoids. If the posterior edge of this step were extended posteriorly and if the pterygoids and basisphenoid separated from each other, then the *Meiolania* condition would be approximated. This area in *Kallokibotion* is seen only in BMNH R4921 (figs. 7, 8); the foramina and some sutures are present in

BMNH R4925 (figs. 14, 15) but most of the surface bone has been eroded off and the remaining bone is all at the same level, deeper than the original surface. BMNH R4918 yields no useful information in this area.

The vertical separation of basisphenoid and pterygoids is accentuated by a groove running posteriorly and slightly laterally from the foramen for the palatine artery. This groove runs just lateral to the foramen caroticum basisphenoidale and presumably reflects the division of the cerebral carotid, which would enter the foramen caroticum basisphenoidale from the palatine artery. The palatine artery would travel anteriorly and enter the skull via the foramen in the basisphenoid-ptyergoid suture. Other than *Proganochelys* and *Kayentachelys*, there are no other turtles described as having the palatine artery branching off the internal carotid before the internal carotid enters the skull, nor is there a case of the palatine artery entering the skull via its own foramen without any connection with the canalis caroticus internus. In *Solnhofia* (Gaffney, 1975b) there is a posterior opening of the canalis caroticus internus and it is possible that the palatine artery branched off the

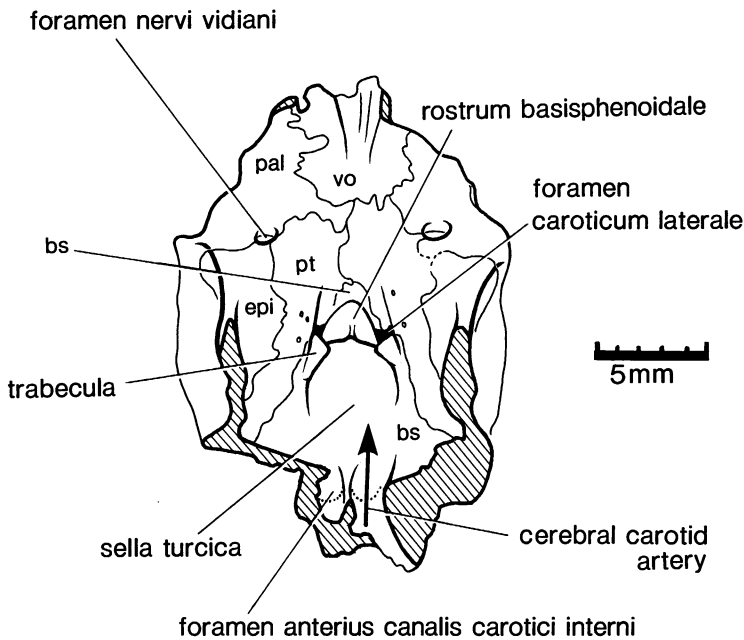


Fig. 13. *Kallokibotion bajazidi*. Anterior portion of basicranium of BMNH R4921 in dorsal view. Key to figure 12. See figures 9–11. Abbreviations on p. 2.

cerebral carotid artery before entering the skull. However, in *Solnhofia* there is a definite internal connection between the canalis caroticus lateralis and the canalis caroticus internus. In baenids (Gaffney, 1982) the canalis caroticus lateralis branches off the canalis caroticus internus inside the skull. The canalis caroticus lateralis as such does not exist in *Proganochelys* or *Kayentachelys* because the palatine artery presumably extends anteriorly in the interpterygoid space persistent in these two taxa. *Kallokibotion*, although not a perfect morphologic intermediate, could be interpreted as advanced over the *Proganochelys*-*Kayentachelys* stage in having a closed interpterygoid vacuity, but primitive with respect to all other cryptodires in not having the palatine artery enclosed or embedded in bone where it branches off the internal carotid. The advanced condition (taxon X in fig. 33) would be a canalis caroticus lateralis that branched off the canalis caroticus internus within the bone, either pterygoid or pterygoid plus basisphenoid. In some eucryptodires, usually referred to the Sinydidae/Macrobaenidae, the foramen basisphenoidale is entirely formed by the basi-

sphenoid and the palatine-internal carotid division is widely open ventrally. The canalis caroticus internus and the canalis caroticus lateralis in *Kallokibotion* are about the same diameter, indicating that the internal carotid and the palatine artery are also the same size.

The anterolateral limits of the pterygoid in *Kallokibotion* are missing in BMNH R4925 and BMNH R4921 while in BMNH R4918 the area is damaged and lacks clear sutures. The pterygoid is covered dorsally by the epipterygoid and palatine, seen in BMNH R4921, as in most cryptodires. A poorly preserved processus pterygoideus externus can be made out on the right side of BMNH R4918 (fig. 2) and it appears to be developed as in such cryptodires as *Chelydra*.

On the dorsal surface much of the pterygoid can be seen in BMNH R4921 (figs. 10–13). The crista pterygoidea is largely covered dorsally by the epipterygoid which has an expanded ventral portion. Medially the pterygoid contacts the basisphenoid and just anterior to the basisphenoid is a median contact of both pterygoids. Anteriorly the sutures are overlapping with palatine and vomer but the right pterygoid at least reaches the vomer al-

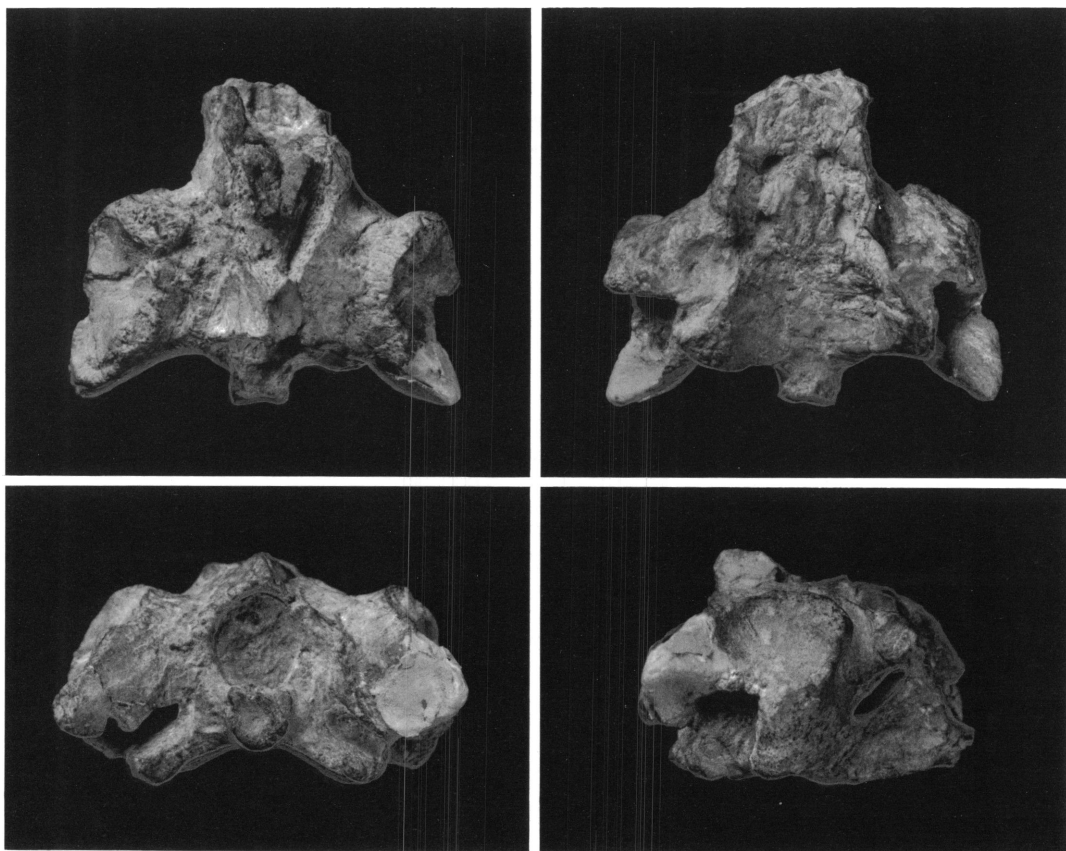


Fig. 14. *Kallokiboton bajazidi*. Braincase of BMNH R4925. Upper left, dorsal view; upper right, ventral view; lower left, posterior view; lower right, right lateral view.

though the left one seems to be prevented from this contact by a palatine-right pterygoid contact. On both sides of BMNH R4921 the pterygoid forms the medial margin of the foramen nervi vidiani. On the dorsal surface the pterygoid is exposed in a relatively narrow strip in the floor of the sulcus cavernosus between the epipterygoid and the basisphenoid.

SUPRAOCCIPITAL

Portions of the supraoccipital are preserved in all three skulls but sutures are indistinct and none of the specimens have a complete supraoccipital.

The ventral portion has contacts that are best seen on the right side of BMNH R4925 (figs. 14, 15). Here the supraoccipital contacts the exoccipital posteriorly; lateral to the fo-

ramen magnum it contacts the opisthotic posterolaterally and seems to form at least part of the foramen stapedio-temporale. The prootic contact is not clear. The participation of the supraoccipital in the cavum labyrinthicum is not visible.

The crista supraoccipitalis extended at least to the posterior margin of the parietal, this can be seen in BMNH R4921 and BMNH R4918. The edges preserved are broken but thin and probably did not extend beyond the skull roof. Anteriorly and dorsally the supraoccipital contacts the parietal; there does not appear to be any exposure of the supraoccipital on the dorsal surface of the skull roof.

EXOCCIPITAL

The exoccipital is preserved in BMNH R4925 (figs. 14, 15) with some sutures visi-

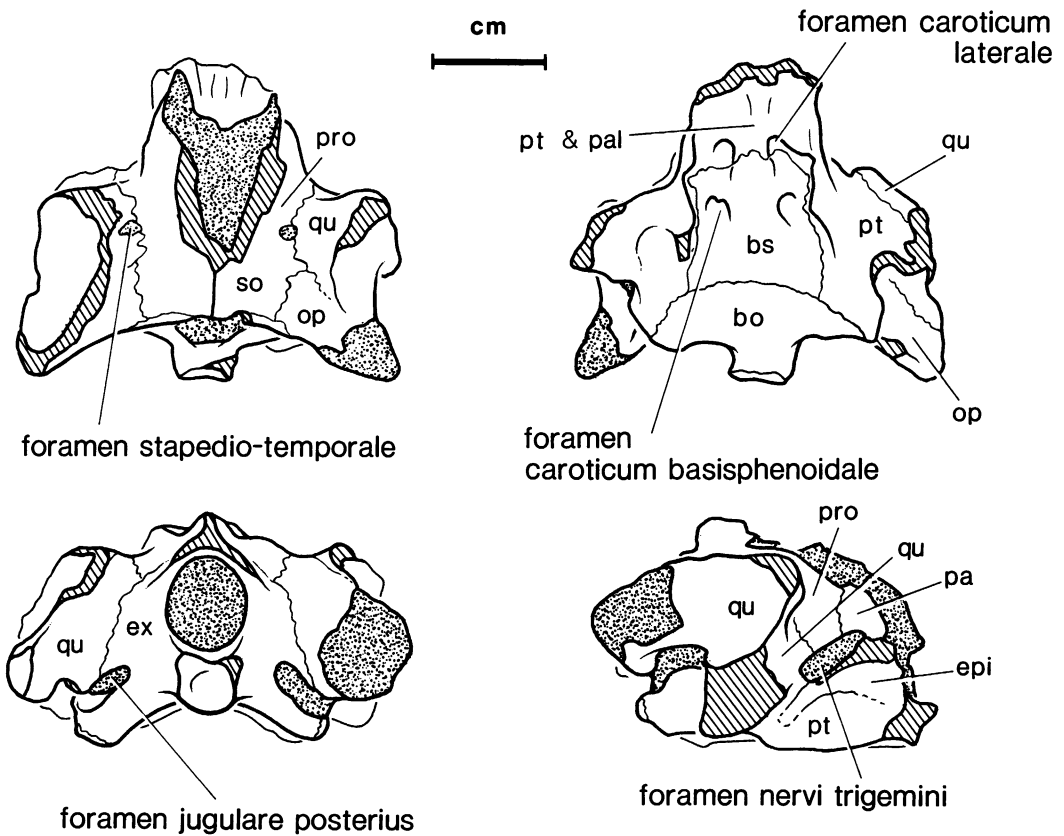


Fig. 15. *Kallokibotion bajazidi*. Braincase of BMNH R4925. Key to figure 14. Upper left, dorsal view; upper right, ventral view; lower left, posterior view; lower right, right lateral view. Abbreviations on p. 2.

ble, as well as in BMNH R4921 but in the later the bone is crushed and distorted. The exoccipital of *Kallokibotion* has the standard chelonian shape forming the lateral margins of the foramen magnum. The supraoccipital forms the dorsal margin of the foramen magnum preventing the exoccipital from meeting in the midline. It cannot be determined how much of the condylus occipitalis is formed by the exoccipitals as the contact with the basioccipital is not clear on any specimen. The foramen jugulare posterius is confluent with the fenestra postotica, as in baenids. At least one foramen nervi hypoglossi is visible although others may have been present.

BASIOCCIPITAL

The basioccipital is present in all three specimens but BMNH R4918 is too poorly

preserved in this area to convey useful information. The basioccipital of *Kallokibotion* (figs. 7–9, 14, 15) has a long, transverse suture with the basisphenoid anteriorly and meets the pterygoid laterally. The basioccipital-exoccipital suture is not visible and the degree to which the condylus occipitalis is made up of basioccipital is not determinable. *Kallokibotion* has well-developed tubercula basioccipitales, comparable to those seen in such baenids as *Chisternon*.

PROOTIC

The region of the prootic is preserved in all three skulls but sutures delimiting the bone are almost completely absent. From BMNH R4925 (figs. 15, 16) the prootic appears to form the posterodorsal portion of the foramen nervi trigemini and to contact the quad-

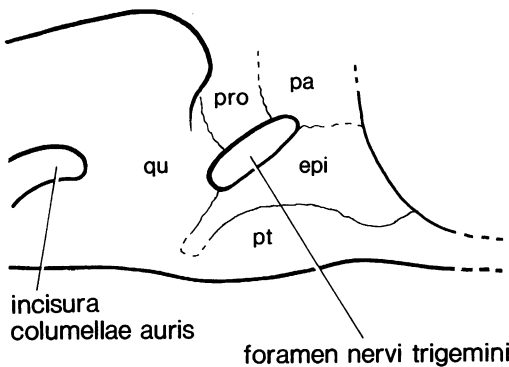


Fig. 16. *Kallokibotion bajazidi*. Lateral view of right sidewall of braincase, reconstruction based primarily on BMNH R4925 with additions from BMNH R4921. Abbreviations on p. 2.

rate laterally and the parietal anteriorly. The prootic does not form a significant portion of the processus trochlearis oticum. The medial surface of the prootic is exposed in BMNH R4921 but sutures are not visible and crushing has obscured the fossa acustico-facialis.

OPISTHOTIC

The opisthotic (figs. 14, 15) is preserved in all three skulls but very little information is available from BMNH R4918. The opisthotic contacts the quadrate anterolaterally and the supraoccipital anteromedially. Medially the exoccipital borders the opisthotic in occipital view. The processus paroccipitalis of the opisthotic is well developed and comparable to the condition in *Chelydra*. The opisthotic forms the dorsal margin of the fenestra postotica and the roof of the cavum acustico-jugulare. Although portions of the cavum are visible in BMNH R4921 and BMNH R4925, little of systematic value is apparent.

BASISPHENOID

The basisphenoid is preserved in all three specimens but the preservation is so poor in BMNH R4918 that nothing useful can be obtained. Much of the dorsal surface is preserved in BMNH R4921 and sutures on the ventral surface can be seen in both BMNH R4921 and BMNH R4925.

Beginning in ventral view (figs. 7, 8, 14, 15), the basisphenoid of *Kallokibotion* is a

roughly triangular element contacting the pterygoids anteriorly and laterally and bordered by the basioccipital posteriorly. The lateral margins are subparallel rather than forming a straight-sided triangle. Although there is a vague, rounded convexity in the center of the basisphenoid, there is no separate parasphenoid ossification as reported by Nopcsa (1923b).

The foramen caroticum basisphenoidale (figs. 7, 8, 15) is a prominent paired structure situated about midway along the length of the basisphenoid. This foramen is preserved on both sides of BMNH R4925 (figs. 14, 15) but the bone surface is badly eroded and it is likely that the original margins of the foramen were situated slightly more posteriorly. In BMNH R4921 (figs. 7–9) the foramen caroticum basisphenoidale is preserved only on the left side. In this specimen there is a very small foramen in the lateral wall of the sulcus leading into the foramen caroticum basisphenoidale, and this small foramen is probably the foramen pro ramo nervi vidiani. A distinct sulcus is formed on the ventral surface of the basisphenoid that begins posteriorly at the notch formed near the pterygoid-basioccipital suture and extends anteromedially into the foramen caroticum basisphenoidale and presumably held the internal carotid artery.

Anterior to the foramen caroticum basisphenoidale the basisphenoid has another sulcus on its ventral surface, less well defined than the carotid sulcus, that extends anteromedially into the posterior opening of what is here termed the canalis caroticus lateralis. This paired opening (described in more detail under pterygoid) lies just beyond the anterior edge of the basisphenoid although it is possible that the basisphenoid enters the margin of the foramen to some extent.

The foramen caroticum basisphenoidale leads anteromedially into the canalis caroticus internus which can be examined for almost all of its length in BMNH R4921. There is no indication of any canal or foramen joining the canalis along its relatively short passage into the cavum cranii. The diameter of the canalis caroticus internus is at least twice that of the canalis caroticus lateralis in *Kallokibotion*. Only a small part of the canalis caroticus internus is preserved on the right

side of BMNH R4921, but on the left side it is complete except for a small part of its medial wall anteriorly. The canalis opens into the cavum cranii at the foramen anterius canalis carotici interni.

In *Kallokibotion* the paired foramina anterius canalis carotici interni (figs. 10, 11) lie very close together and are separated only by a narrow bar of bone. The foramina enter the sella turcica at its posterior edge beneath the dorsum sellae. The sella turcica and dorsum sellae are visible only in BMNH R4921 (figs. 12, 13); the sella turcica is well preserved and complete but the dorsum sellae is preserved only on the left side where the anterior edge is broken. As preserved, the dorsum barely overhangs the foramen anterius canalis carotici interni but even if only a small amount of bone is missing, the dorsum would distinctly overhang the foramen to a greater extent than seen in *Chelydra*. From the portion of the dorsum sellae preserved, it is clear that it was very close to the foramen anterius canalis carotici interni and that the broad extent of bone separating those structures in *Meiolania* and chelonoids is absent. This condition of the dorsum sellae, sella turcica, and foramen anterius canalis carotici interni of *Kallokibotion* is similar in baenids, such as *Eubaena*, as described by Gaffney (1982). The lateral margin of the foramen anterius canalis carotici interni, however, extends farther anteriorly than the wall of bone separating the foramina on the midline, so that with an overhanging dorsum sellae there would be a single, common opening for both foramina, much as seen in *Solnhofia*.

The basisphenoid of BMNH R4921 has only part of one processus clinoides and it is an anterolateral continuation of the dorsum sellae. Its original extent is unknown. Below the processus there is a well-developed paired concavity lateral to the foramen anterius canalis carotici interni. The anterior foramen nervi abducentis opens into this concavity. Posteriorly the foramen nervi abducentis opens on the dorsal surface of the basisphenoid, back from the dorsum sellae.

The rostrum basisphenoidale (figs. 12, 13) of *Kallokibotion* has paired trabeculae that do not meet in the midline but reach anteriorly to a greater degree than in baenids. The trabeculae have unfinished ends implying

cartilaginous extensions during life. In *Meiolania* and baenids the sella turcica has an ill-defined anterior margin but in *Kallokibotion* the basisphenoid has a semicircular lip that is separated from a more anterior and ventral extension of the basisphenoid (labeled rostrum basisphenoidale in fig. 13). This anterior extension has paired troughs laterally and a midline ridge that would appear to form a space for the anterior continuation and medial confluence of cartilaginous extensions of the trabeculae. It is an unusual structure not known in other turtles.

Equally unusual is the dorsal opening of the foramen caroticum laterale (figs. 12, 13) of *Kallokibotion* which lies just ventral to the bony termination of the trabecula in the rostrum basisphenoidale. This paired foramen lies at the posterolateral end of a curved cleft running down the midline. The cleft is formed within the basisphenoid rather than between basisphenoid and pterygoid as in the intra-ptyergoid slit of *Meiolania*.

LOWER JAWS (figs. 2, 3)

Lower jaws are preserved in BMNH R4918 and BMNH R4921. In BMNH R4918 the jaws are complete but still attached to the skull, making it impossible to see the dorsal surfaces. In BMNH R4921 only the posterior half of the right ramus is preserved. Neither lower jaw is well preserved and only a few sutures are apparent.

The lower jaws in *Kallokibotion* are clearly narrow and deep in comparison to those of baenids but similar to those of *Kayentachelys*. The triturating surface is visible only posteriorly in BMNH R4921 but BMNH R4918 also shows that it is narrower than in any baenid. At least posteriorly there are both labial and lingual ridges separated by a shallow trough. From BMNH R4921, it seems likely that the lingual ridge disappears anteriorly. This condition of a deep, narrow jaw with low triturating ridges and an anteriorly absent lingual ridge occurs in *Kayentachelys*, and *Neurankylus* and is probably primitive for cryptodires.

The medial surface of the lower jaw is damaged in both specimens and the position and extent of the foramen intermandibularis medius and the presence or absence of a

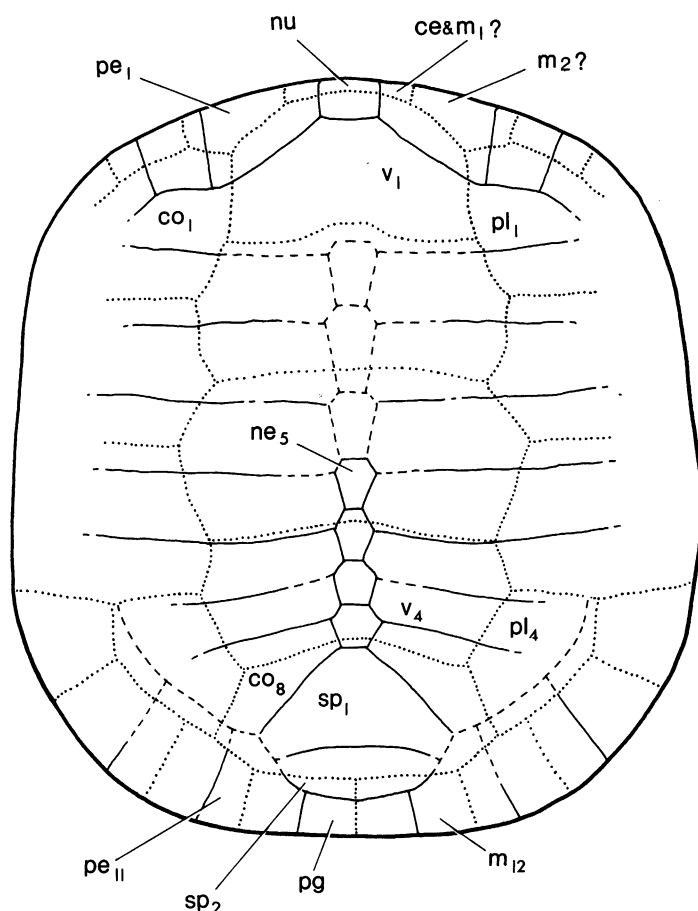


Fig. 17. *Kallokibotion bajazidi*. Composite reconstruction of carapace based on all available specimens. Bones labeled on left, scales labeled on right. Abbreviations on p. 3.

splenic is not determinable. The area articularis mandibularis is similar to that of other cryptodires but it is inclined vertically to a greater degree than in baenids. A retroarticular process seems to be absent. The coronoid bone can be differentiated from the dentary in the region of the processus coronioideus. All of the processus is formed by the coronoid, and it extends posterodorsally as a distinct process.

POSTCRANIAL MORPHOLOGY

CARAPACE (figs. 17, 19–25)

Kallokibotion is not represented by a well-preserved carapace from one individual, and most of the partial carapaces are fragmentary and poorly preserved. The restoration (fig.

17) is a composite that must be considered tentative.

Although sutures are hard to make out on many of the *Kallokibotion* specimens, this is interpreted as the result of poor preservation rather than fusing, as in many baenids. Some of the largest specimens (i.e., BMNH R4916 and BMNH R11178) of *Kallokibotion* have open sutures in the shell. Nopcsa's (1923b) published drawings of the carapace appear to be based on BMNH R4919 (anterior margin) and BMNH R4916 (most of carapace) in Nopcsa, 1923b: figure 1, BMNH R4930 in figure 3, and BMNH R4917 in figure 5. In general, the drawings are accurate but some parts are inconsistent with our observations and these are noted below.

The nuchal region is best preserved in

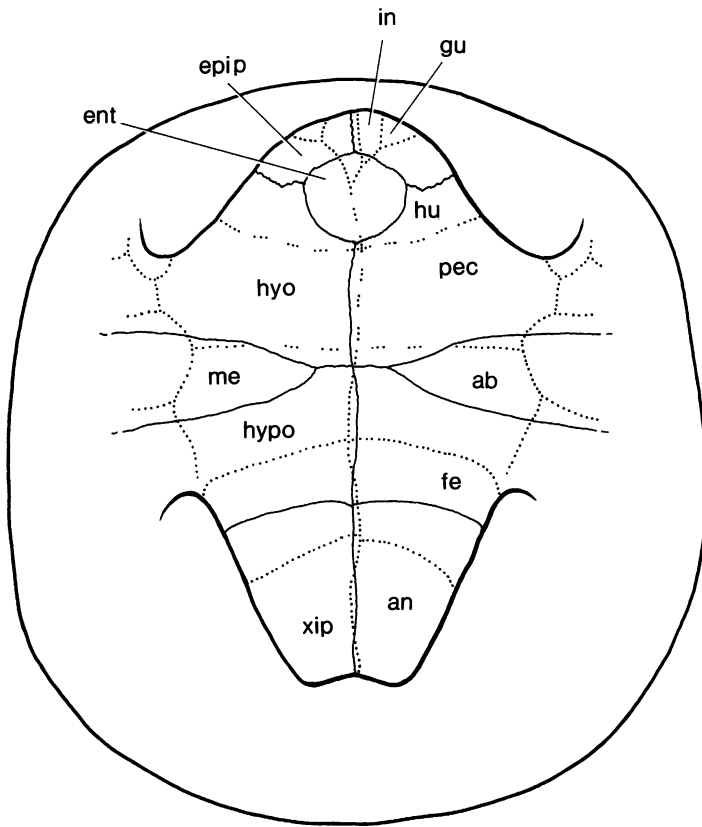


Fig. 18. *Kallokibotion bajazidi*. Composite reconstruction of plastron based on all available specimens. Bones labeled on left, scales labeled on right. Abbreviations on p. 3.

BMNH R4919 (figs. 21, 22). The sutures present indicate a nuchal bone that is relatively small compared with those of other turtles and nearly square—an unusual shape, as most turtle nuchals are wider posteriorly as in *Glyptops* and *Pleurosternon*. None of the other specimens seem to preserve the nuchal sutures to substantiate or contradict BMNH R4919. However, the sutures are present on both dorsal and ventral surfaces of this specimen and we accept this shape for *Kallokibotion*.

The neural bones are not well preserved in *Kallokibotion*. The best specimen is BMNH R11178 (figs. 19, 20). This shell shows neurals 2–8 and gives some indication of their shape but many of the sutures are damaged. Neurals 2–5 appear to be the typical “coffin-shaped,” six-sided neurals seen in most turtles. Neurals 7 and 8 are also six-sided. Two other specimens, BMNH R4917 (Nopcsa,

1923b: pl. 3, fig. 13) and BMNH R4920 (Nopcsa, 1923b: fig. 5) preserve the posterior part of the carapace and agree with this pattern, although neither specimen is well preserved. None of the specimens have a first neural clearly delimited.

There are eight pairs of costal bones in *Kallokibotion*; Nopcsa's (1923b: fig. 1) interpretation of nine pairs is incorrect. The intercostal sutures can be seen in BMNH R11178, BMNH R4918, and BMNH R4916. From a reexamination of these it is apparent that Nopcsa's suture in this figure between his first and second costals is actually between the peripherals and the first costal. Presumably the neural sutures in this figure are based on BMNH R4920 because none are apparent in BMNH R4916. The proximal and distal contacts of the costals are preserved best in BMNH R4920 but only for the posterior costals.

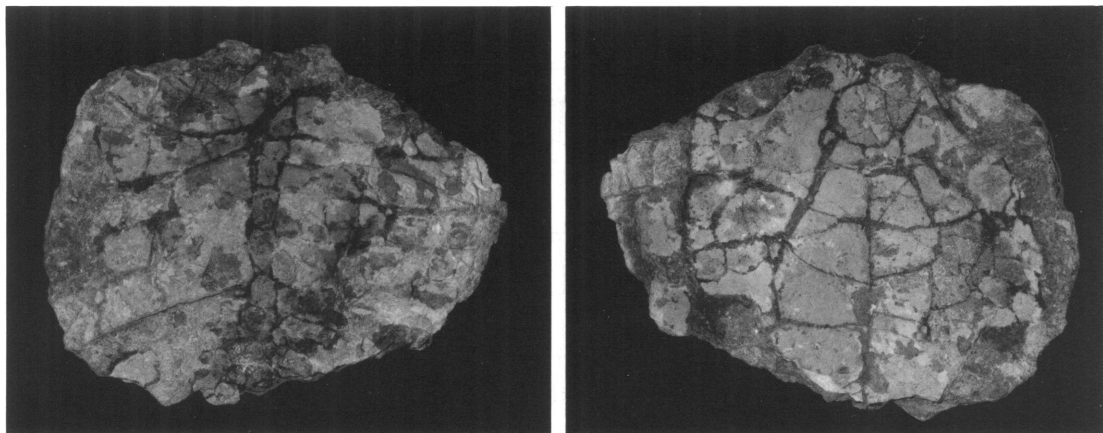


Fig. 19. *Kallokibotion bajazidi*. Shell of BMNH R11178 in dorsal (left) and ventral (right) views.

The peripheral bones of *Kallokibotion* are also poorly preserved. The first three peripherals can be seen in BMNH R4919. Some of the bridge peripherals are present in BMNH R4918, and posterior peripherals are in BMNH R4916. Few of these, however, are preserved well enough to develop a complete restoration. There appear to be the usual 11 pairs of peripherals; the posterior ones are curved upward. Guttering on the bridge peripherals is not determinable.

Based primarily on BMNH R4916 (figs. 23, 24), there are two suprapygals, an anterior one that is larger and nearly triangular in shape, and a posterior one that is quadrilateral and broad, similar to those seen in *Glyptops*. The pygal is rectangular and narrower than the suprapygals.

The carapacial scales in the nuchal region of *Kallokibotion* are preserved only in BMNH R4930. Nopcsa (1923b) interpreted this specimen as having a very wide, divided cervical scale. The midline is damaged in this specimen and we have been unable to verify the presence of a sagittal sulcus.

However, Dr. H. Hutchison (personal commun.) has brought to our attention the fact that if this interpretation of a large cervical scale is accepted, then the peripheral-marginal relationship seen in nearly all other turtles would be different in *Kallokibotion*. One test of this situation would be the total number of marginal scales but, unfortunately, this is not determinable. Dr. Hutchison

has suggested as an alternative which we have adopted in figures 17 and 22, that the first and second marginals are fused (or possibly not fused if Nopcsa's "divided cervical" is correct). Another possibility is the presence of a very small cervical scale entirely on the nuchal bone but obscured by poor preservation. In any case, the small nuchal bone in *Kallokibotion* requires some departure from the more common cervical scale relations seen in other turtles.

Kallokibotion has the usual five vertebral scales and these are relatively wide—wider than in *Glyptops*, but not as wide as in *Kayentachelys*. The last vertebral scale does not separate the last marginal scales. The pleural scales of *Kallokibotion* are not preserved laterally, but there are the usual four and they have comparable positions in *Glyptops*. The pleural scales overlap onto the peripheral bones as in *Glyptops*, *Kayentachelys*, and most non-eucryptodires, but in contrast to *Pleurosternon* and *Adocus* in which the marginal scales overlap onto the costal bones.

PLASTRON (figs. 18–20, 26–28)

The best plastron of *Kallokibotion* is BMNH R4930 (fig. 27), but it is incomplete and most sutures are obscured. This specimen, however, provides the outline and most of the scale pattern seen in the restoration (fig. 18), while most of the sutures are from BMNH R4922 (anterior lobe) and BMNH

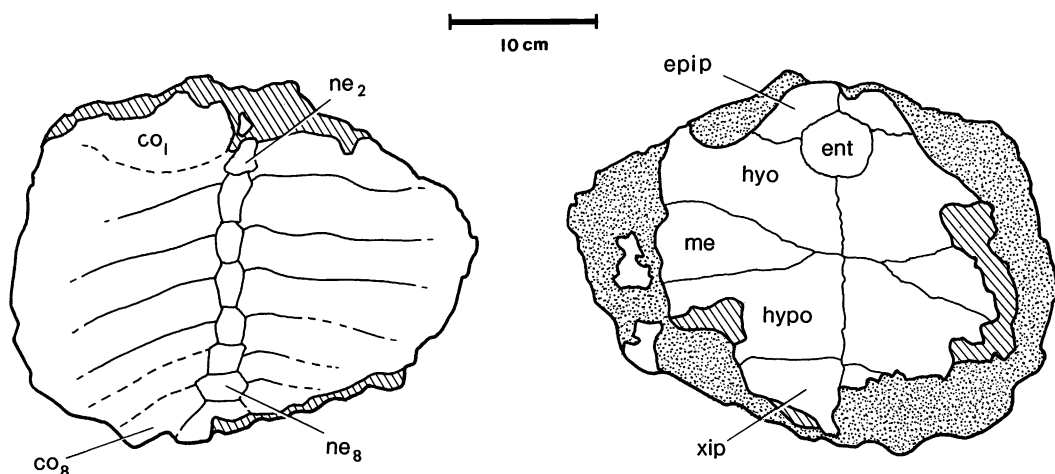


Fig. 20. *Kallokibotion bajazidi*. Shell of BMNH R11178 in dorsal (left) and ventral (right) view. Abbreviations on p. 3.

R11178 (figs. 19, 20). The figures of the plastron published by the Transylvanian baron show some errors. The line drawings (Nopcsa, 1923b: figs. 2, 4) show that the entoplastron is placed much too far posteriorly and some of the sutures cannot be substantiated. Based on comparison with specimens, figure 2 (Nopcsa, 1923b) seems to be based on BMNH R4922 for the anterior part of the anterior lobe, and the rest is based on BMNH R4918. Figure 4 in Nopcsa (1923b) is based on BMNH R4930 and we agree with the outline and most of the sulci but the sutures are questionable. Nopcsa's other plastron figure is plate 4, figure 2, which shows the dorsal (internal) surface of BMNH R4930. The surface morphology shown agrees with the specimen but the sutures, which are drawn in, are questionable in most areas.

The anterior lobe of the plastron in *Kallokibotion* is distinctly shorter than the posterior lobe, in contrast to *Glyptops* and *Pleurosternon*. In BMNH R4922 the anterior edge is relatively straight transversely; in BMNH R4930 the intergular (gular of Hutchison and Bramble, 1981) scale areas are slightly protuberant. The entoplastron is completely enclosed on both dorsal and ventral surfaces by the medially meeting epiplastra, in contrast to *Kayentachelys* but as in *Glyptops* and *Pleurosternon*. The ento-epiplastron sutures can be seen in part in BMNH R4922 but only in BMNH R11178 (figs. 19, 20) are all the limits

of the entoplastron visible. The shape of the entoplastron is roughly circular, being slightly wider than long.

On the dorsal surface of the anterior lobe, the epiplastra-entoplastron contacts are distinct in BMNH R4922 and interpretable in BMNH R4930 (fig. 27). The posterior limits of the entoplastron, i.e., the contacts with the hyoplastra, are not preserved in either specimen. The figure of BMNH R4930 in Nopcsa (1923b: pl. 4, fig. 2) shows a simple, curved suture between entoplastron and epiplastra, but BMNH R4922 shows that this interpretation is probably wrong. As in *Pleurosternon*, the entoplastron of *Kallokibotion* has a short, anterior process on the midline slightly separating the epiplastra, but only on the dorsal surface. The anterior margins of the epiplastra form a raised edge just in front of a shallow trough, all visible in Nopcsa's figure (1923b: pl. 4, fig. 2). The entoplastron and the contact area of entoplastron-epiplastra bear a pair of rugose ridges in the positions of the dorsal processes of the epiplastra seen in *Proganochelys* and *Kayentachelys*. These ridges in *Kallokibotion* are not the bases of actual processes—there is no indication of continuing bone in the steinkern of BMNH R4930.

In BMNH R11178 (figs. 19, 20) there are clear epiplastron-hyoplastron sutures and these are in the typical positions for generalized cryptodires. The hyoplastron forms the

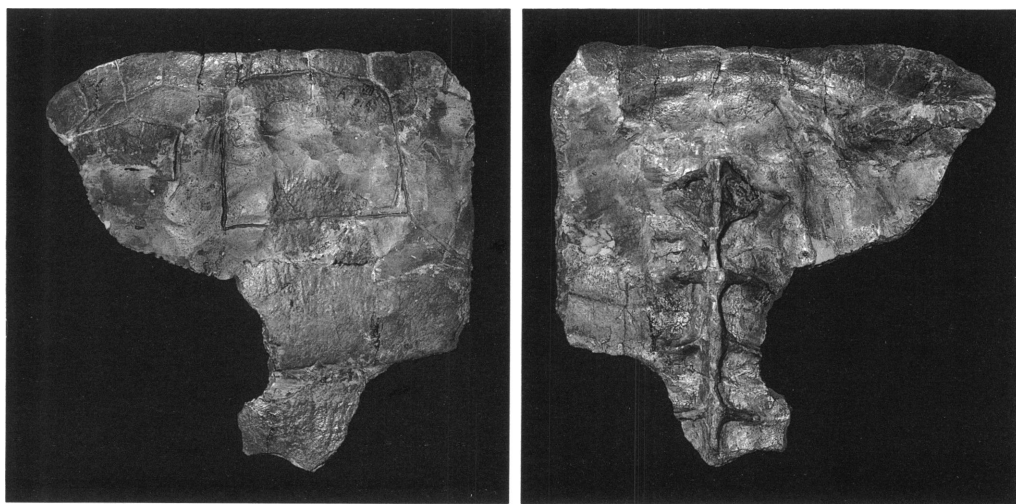


Fig. 21. *Kallokibotion bajazidi*. Anterior carapace fragment BMNH R4919 in dorsal (left) and ventral (right) views.

axillary buttress which is well developed in *Kallokibotion* and extends anteriorly to reach the middle of the second peripheral and extends onto the costals (seen in BMNH R4919). The hyoplastron and hypoplastron are partly separated by a pair of mesoplastra. In BMNH R4918 and BMNH R11178 the mesoplastra are large, triangular bones, much wider than long, that do not meet in the midline. The hyoplastra and hypoplastra contact each other on either side of the midline. In BMNH R4930 (figs. 26, 27) the medial areas of both mesoplastra are ambiguous, although Nopcsa (1923b: fig. 4; pl. 4, fig. 2) has drawn them as meeting on the midline. The steinkern of BMNH R4930 has markings that may be sutures and they do indicate medially meeting mesoplastra, although some similar markings on the same steinkern do not appear to be sutures. It is possible that both conditions occur in *Kallokibotion*, but, if so, they are not likely to be the result of growth differences. BMNH R4930 is about the same size as BMNH R4918 and actually smaller than BMNH R11178, but it should be larger than the other two, if they are to be interpreted as juveniles. No other cryptodire is known to have large mesoplastra not meeting in the midline in adults, although there is a presumed juvenile *Baena* (Gaffney, 1972) that has a similar morphology.

The hypoplastron of *Kallokibotion* has a well-developed inguinal buttress contacting costals 5 and 6. The posterior lobe of the plastron tapers posteriorly and the width of the hypoplastra and xiphiplastra narrows conspicuously. Although the posterior lobe does not taper in *Glyptops*, it does in *Pleurosternon* and *Kayentachelys*.

Our use of the "conventional" terminology of plastral scales needs to be qualified. Hutchison and Bramble (1981) questioned the homology of some of these scales, particularly between certain trionychids and other cryptodires. Some of their conclusions also affect the scale terminology of relatively primitive turtles, like *Kallokibotion*. The scales in question are the two most anterior pairs, usually called intergulars and gulars, which Hutchison and Bramble (1981) proposed to call gulars and extragulars, respectively. However, they use as their primary criteria "postulates" that rely on the recognition of general evolutionary trends and functional scenarios. These postulates are interesting and thought provoking but seem to us to be too speculative to be the sole basis for homology arguments. We do agree with one of their conclusions: the conventional scheme of plastral terminology "... cannot be uncritically applied to all turtles" (Hutchison and Bramble, 1981: 84). The homologies of the anterior

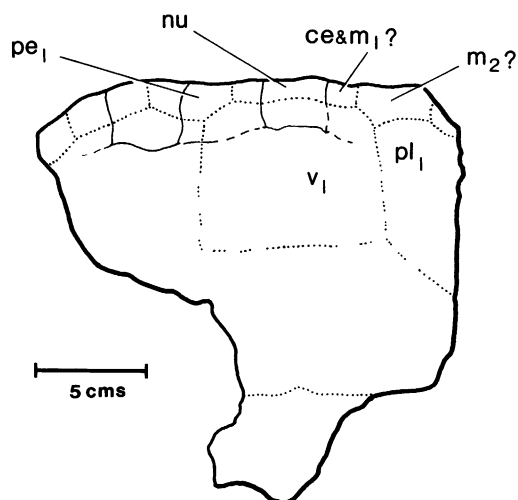


Fig. 22. *Kallokibotion bajazidi*. Anterior carapace fragment BMNH R4919 in dorsal view. Abbreviations on p. 3.

scales in particular are unresolved and we agree that the identification of gular scales in primitive turtles does not mean that these are homologous with the gular scales of testudinoids. On the other hand, we do not see compelling evidence for another conclusion

of Hutchison and Bramble, that the intergulars (conventional sense) of primitive turtles are the homologs of the gulars of testudinoids. Therefore, we use the conventional terminology but restrict the homology to casichelydians with seven pairs of plastral scales. We do not see convincing criteria for establishing homology in cases where anterior plastral scales have been reduced in number.

The scale pattern of the plastron in *Kallokibotion* (fig. 18) generally agrees with the pattern seen in other relatively primitive cryptodires. There are paired intergular scales widely separating smaller, paired gular scales. The left intergular scale is distinctly smaller than the right in the two specimens that preserve the area: BMNH R4922 and BMNH R4930. The gular scales are entirely on the epiplastra and the intergulars extend onto the anterior part of the entoplastron, much as in *Glyptops* and other primitive cryptodires. The humeral-pectoral sulcus lies entirely on the hyoplastron. The pectoral-abdominal sulcus lies largely on the mesoplastra laterally but its medial extent is unclear due to poor preservation. The abdominal-femoral sulcus is at the base of the posterior plastral lobe, as in



Fig. 23. *Kallokibotion bajazidi*. Dorsal view of carapace of BMNH R4916.

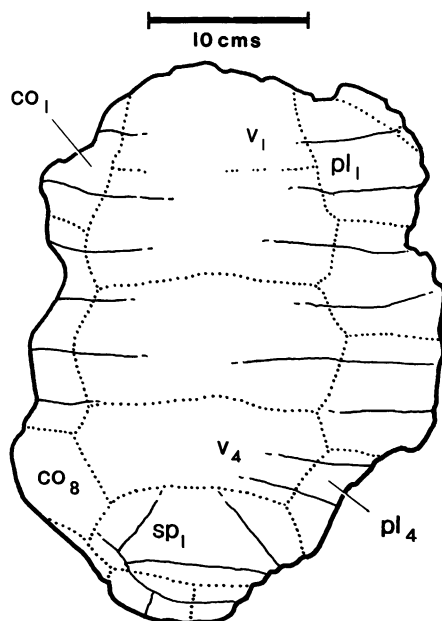


Fig. 24. *Kallokibotion bajazidi*. Dorsal view of carapace of BMNH R4916. Abbreviations on p. 3.

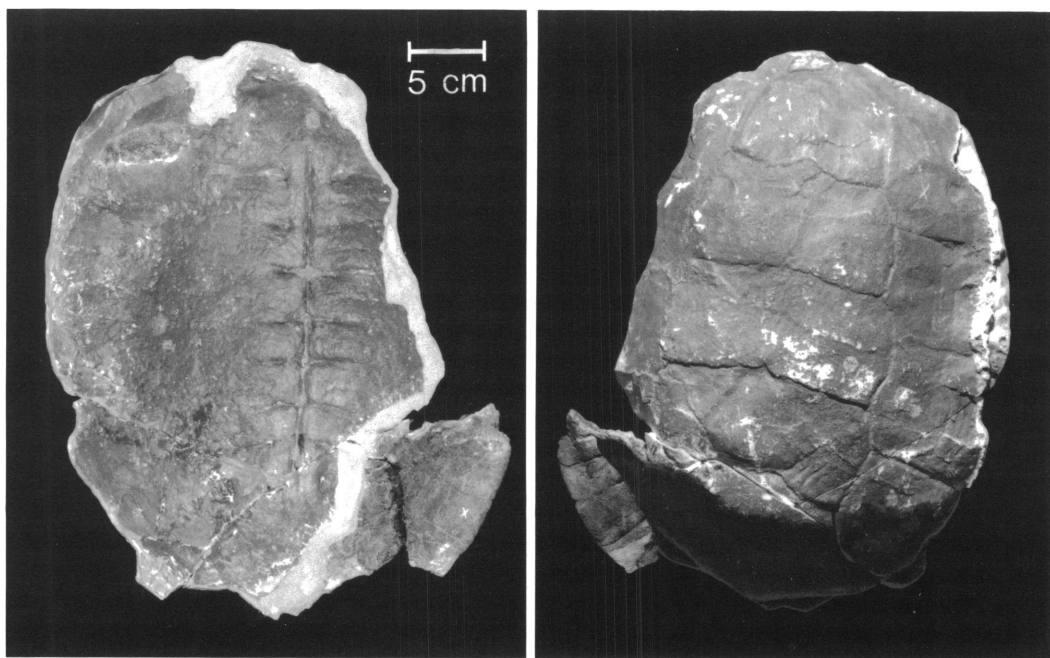


Fig. 25. *Kallokibotion bajazidi*. Ventral (left) and dorsal (right) views of plaster cast of carapace of BMNH R4930 (left posterior peripherals are real).

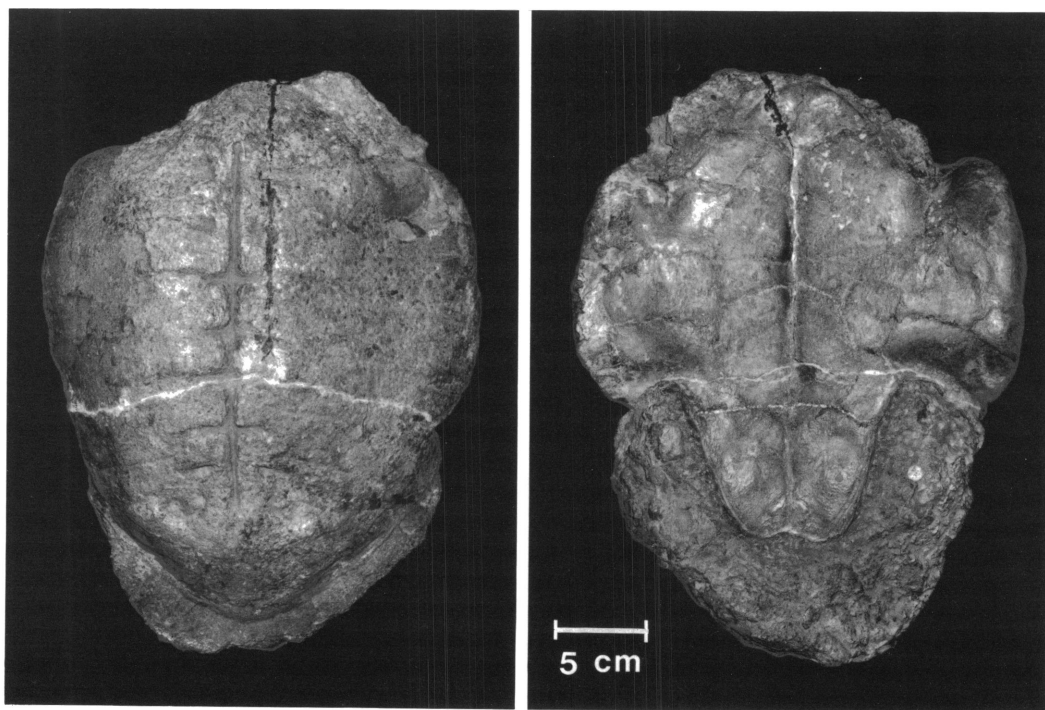


Fig. 26. *Kallokibotion bajazidi*. Steinkern (internal mold) of shell of BMNH R4930 in dorsal (left) and ventral (right) views.

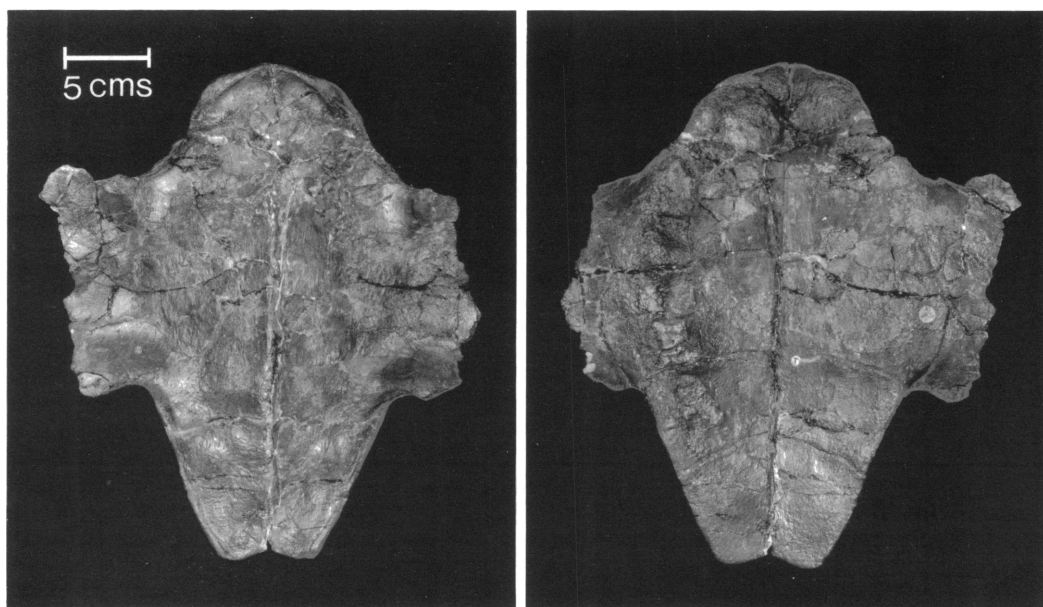


Fig. 27. *Kallokibotion bajazidi*. Dorsal (left) and ventral (right) views of plastron of BMNH R4930.

most turtles, and the femoral-anal sulcus is entirely on the xiphiplastron, again a common position. There are four inframarginal scales, the two more anterior ones being smaller than the two more posterior ones. These scales are not clearly delimited, particularly laterally.

The shell of *Kallokibotion* can be considered reasonably well known and the features that are preserved are consistent with the pattern seen in other non-eucryptodires. The few features interpretable as advanced do not ally the form with other taxa known at present.

CERVICAL VERTEBRAE

Two specimens of *Kallokibotion* have cervicals preserved. BMNH R4916 has cervicals 6–8 in situ with the ventral areas free of matrix, but the dorsal surfaces are not accessible. In BMNH R4921 there are parts of six cervicals, which, as identified by Nopcsa (1923b: 8) are numbers 3, 5–8, and a questionable second cervical. There is no indication of the basis for his identifications, and he refers to them (*ibid.*) as “isolated.” Only his cervical 3 has zygapophyses; the rest consist of little more than a centrum. On the basis of comparisons with *Glyptops* and baenids, it seems

more likely that his cervical 3 is more posterior, probably 6, 7, or 8.

All of the preserved cervicals are amphicoelous to a marked extent, as in *Kayentachelys*, *Glyptops*, *Pleurosternon*, and plesiochelyids. The cervicals are similar to those of *Glyptops* and baenids in having high, narrow centra, being particularly narrow in the middle of the centrum, and continuous with a low ventral keel. There are short transverse processes without evidence of cervical ribs, although this is hard to determine due to poor preservation.

The so-called cervical 3 (BMNH R4921) of Nopcsa (1923b) is most likely a posterior cervical, being particularly similar to posterior cervicals of *Glyptops*. This cervical compares very closely with cervicals 6–8 in BMNH R4916, which is not prepared enough to reveal differences among them. The postzygapophyses are farther apart than the prezygapophyses. Both articulations are at about 45° from the horizontal. There is no neural spine and the highest part of the cervical is the bone connecting the postzygapophyses. The cervicals of *Kallokibotion* are consistent with those seen in other primitive cryptodires.

CAUDAL VERTEBRAE (fig. 32)

Nopcsa (1923b) indicated that caudals were found with two specimens, BMNH R4916 and BMNH R4921, but at present, only the seven caudals of BMNH R4921 are available. The caudals of BMNH R4921 are in three series, as described and figured by Nopcsa (1923b: 10) from anterior to posterior: figures 20–22, figures 19 and 29, figures 26–28. All these centra articulate well together and are probably a natural series, caudals 1–6.

The caudals of *Kallokibotion* are quite different from the caudals seen in other primitive cryptodires. In *Kallokibotion* the caudals are low and wide, the neural spine is only a low ridge. The centra are amphicoelous except for the platycoelous articulation of the sacral. The zygapophyses are unusual in being tightly fitting and broadly curved, concave anteriorly in dorsal view. Transverse processes are mostly broken but one of the more anterior caudals has moderately developed processes, less extensive than in baenid anterior caudals. Hemal spines were presumably present, but all are now represented by broken edges or articular facets.

SHOULDER GIRDLE

BMNH R4921 has parts of the right and left scapula and coracoid preserved (Nopcsa, 1923b: pl. 2, figs. 2, 3). Nopcsa figured the right scapula which is the most complete, retaining the scapular process, the glenoid and the bases of the acromion process, and the coracoid. The left scapula also consists of the glenoid and only part of the scapular process.

The scapula of *Kallokibotion* differs from that of most turtles in being short, robust, and with a thickened distal end. A web of bone connects the acromion and the scapular process, extending up the scapular process. Only the base of the coracoid is preserved.

The shoulder girdle of *Kallokibotion* is unusual and does not show close similarities to that of any other turtle.

PELVIS

Parts of the pelvis are preserved in a number of *Kallokibotion* specimens, but the best one is BMNH R4916, figured accurately by Nopcsa (1923b: pl. 2, figs. 4–6). This pelvis



Fig. 28. *Kalkokibotion bajazidi*. BMNH R4918 in ventral view showing position of skull in relation to plastron.

is somewhat deformed, having been crushed anteroposteriorly. Other specimens provide supplemental information, particularly BMNH R4926, a pubis and acetabulum, and BMNH R11177, a pelvis, lacking the ilia. BMNH R4921 is an incomplete but uncrushed pelvis and BMNH R4923a are ilia.

The pelvis of *Kalkokibotion* is what would be expected in a generalized cryptodire. It is most similar to the pelvis in baenids and *Glyptops* (the pelvis being poorly known at present in *Kayentachelys* and *Pleurosternon*). The pelvis of *Kalkokibotion* has a long and well-developed epipubis, similar to *Baena arenosa*, AMNH 5907 and *Chisternon undatum*, AMNH 5904. But *Kalkokibotion* differs from baenids and nearly all other cryptodires in having small thyroid fenestrae. This is primitive for cryptodires, as these foramina are small in *Proganochelys* (Gaffney, 1990). *Kalkokibotion* has well-developed lateral pubic processes as in baenids and most other cryptodires. The posterior iliac process of

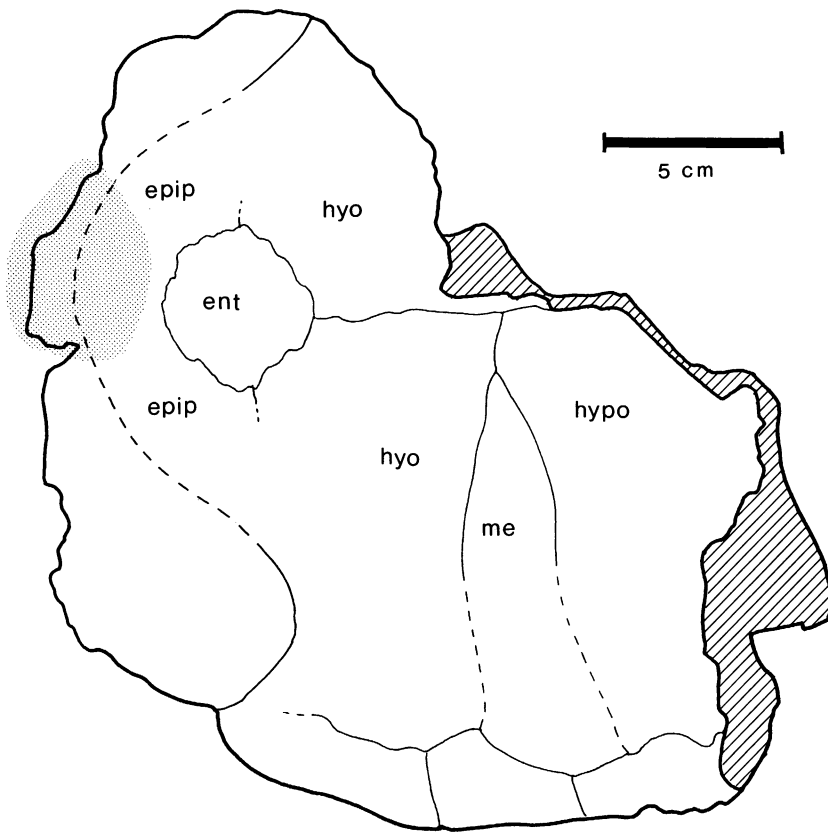


Fig. 29. *Kallokibotion bajazidi*. Key to figure 28. BMNH R4918 in ventral view, skull is shown in stipple in ventral view, anterior toward top of page. Abbreviations on p. 3.

Kallokibotion is less developed than in baenids and much smaller than in *Proganochelys*, but it is similar to those in more advanced cryptodires, although this is a variable feature.

HUMERUS (fig. 30)

BMNH R4921 and BMNH R4923b provide good humeri for *Kallokibotion*. These are figured by Nopcsa (1923b: pl. 3, figs. 1–6) and are accurate. The humerus in *Kallokibotion* is similar to those in baenids and chelydrids and is what would be expected in a generalized cryptodire. The head of the humerus has a shoulder adjacent to the lateral process, a condition common among the more generalized turtles but less common among more advanced turtles. The humeral shaft is curved, to a somewhat greater extent than in baenids and chelydrids. The medial process

is much larger than the nearly absent lateral process, much as in chelydrids but in contrast to baenids and *Proganochelys* where there is a distinct lateral process. The systematic significance of this feature is not apparent. The distal end is widened, again as in chelydrids, and a completely formed ectepicondylar foramen is present, in contrast to the open foramen of chelydrids.

The humerus of *Kallokibotion* most resembles those of primitive cryptodires except for the reduced lateral process, although the distribution of this feature is not clear at present.

FEMUR (fig. 31)

The femur of *Kallokibotion* is best seen in BMNH R4924 and BMNH R4923b, figured accurately by Nopcsa (1923b: pl. 3, figs. 7–10). The femur is not drastically different from that in baenids but the trochanter major and

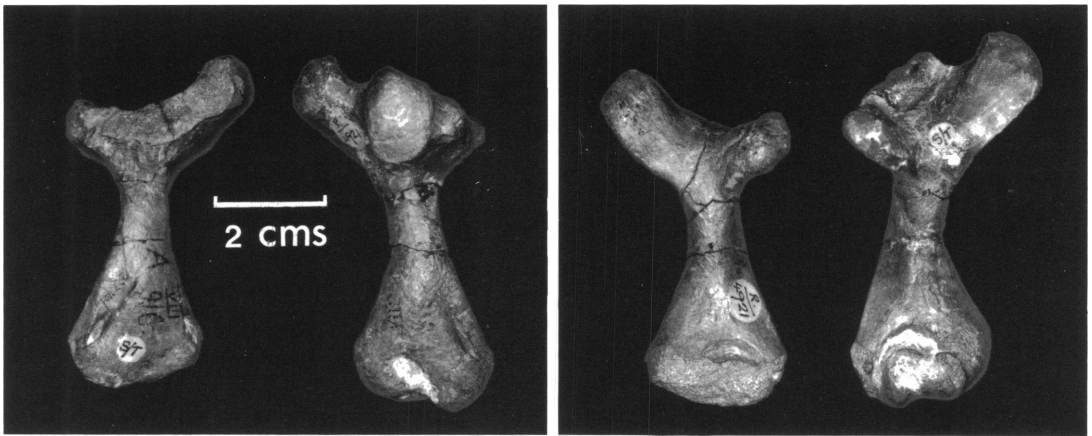


Fig. 30. *Kallokibotion bajazidi*. Right and left humeri of BMNH R4921.

trochanter minor are connected by a bony web, similar to testudinids and some chelonoids but in contrast to baenids and other primitive cryptodires. The shaft of the femur in *Kallokibotion* is strongly curved in contrast to the straighter shaft of the femur in baenids and most turtles. The significance of these differences is not clear, but the femur of *Kallokibotion* does not match what would be expected in a primitive cryptodire.

A fragment of a tibia (BMNH R4921), a sacral rib (BMNH R4921), some indeterminate bones in a large shell (BMNH R4932), and unprepared postcranial elements are also present in the collection.

RELATIONSHIPS

Nopcsa (1923b) was correct in arguing that *Kallokibotion* was a relatively primitive turtle, not closely related to any living groups. He placed it in the "Amphichelydia," a wastebasket taxon commonly used by his contemporaries for extinct groups of turtles (Gaffney, 1984). It is now possible to place *Kallokibotion* in a better tested system of turtle relationships that includes more taxa, living and extinct, and relies on the analysis of derived character distributions to form groups (Gaffney and Meylan, 1988). The methods used here are more thoroughly discussed and referenced in Gaffney and Meylan (1988) and Gaffney (1984).

Following the order of treatment in Gaffney and Meylan (1988: 169), *Kallokibotion*

can be placed in the megaorder Cryptodira because it has the prootic and quadrate thickened to form a processus trochlearis oticum, a synapomorphy of that group. *Kallokibotion* is advanced over *Kayentachelys* and is in the capaxorder Selmacryptodira because it has these synapomorphies:

1. Posterior process of the pterygoid floors middle ear
2. Pterygoid teeth absent
3. Interpterygoid space closed

The hyperorder Daiocryptodira is diagnosed by:

1. Posterior temporal emargination separates or nearly separates, parietal and squamosal bones
2. Dorsal process of epiplastron absent

Kallokibotion does not have a well-preserved posterior part of the skull roof, but it is clear that temporal emargination of any kind is virtually absent, and a long squamosal-parietal contact is very likely. *Kallokibotion* does not have a dorsal process of the epiplastron, but this process is also absent in *Glyptops*, so its distribution is ambiguous in the groups proposed by Gaffney and Meylan (1988). A well-developed squamosal-parietal contact does occur in some daiocryptodires, such as *Baena* and *Meiolania*, but there is morphologic evidence supporting the argument that this is secondary (Gaffney, 1972; Gaffney and Meylan, 1988). The contact in *Kallokibotion*, however, does not seem to be

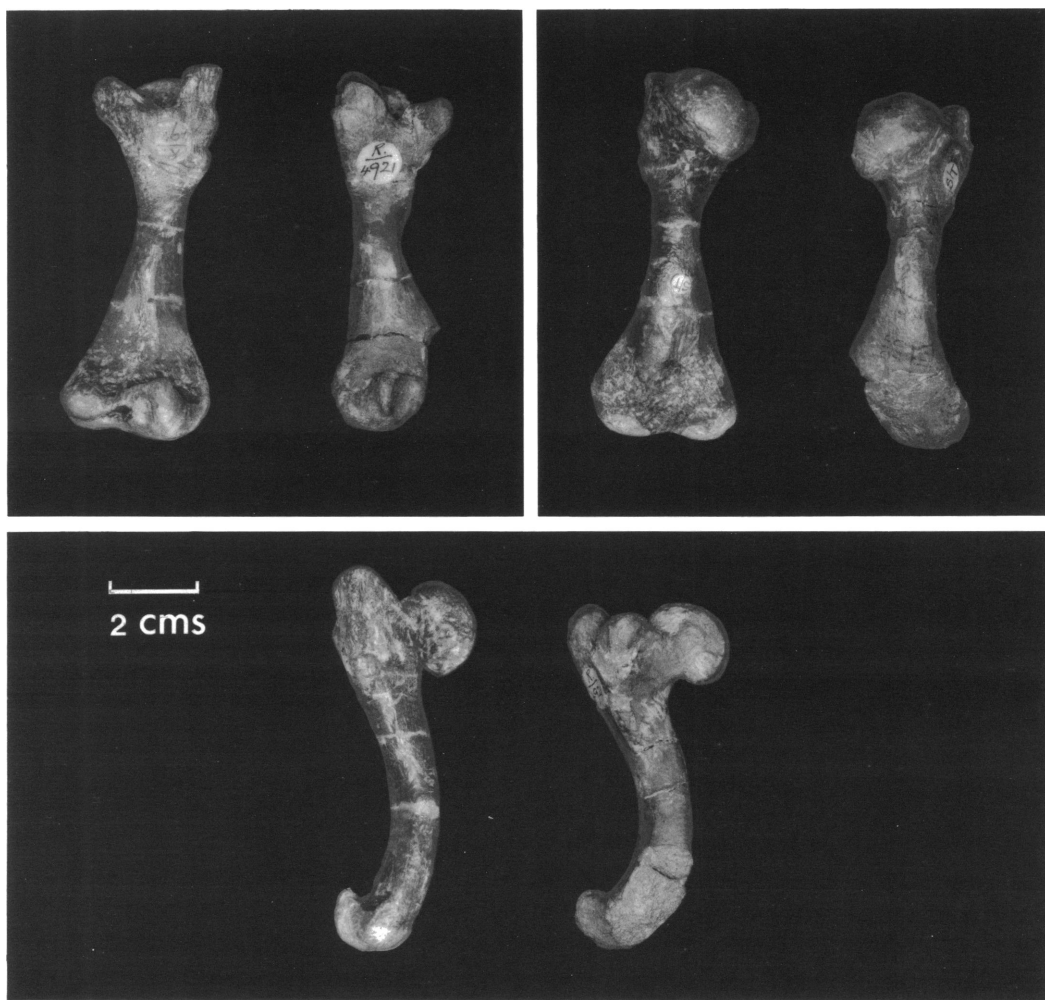


Fig. 31. *Kallokibotion bajazidi*. Femora of BMNH R4924 (left-hand specimen in each figure) and BMNH R4921 (right-hand specimen in each figure).

secondary and it is interpreted here as the primitive condition for Cryptodira.

Kallokibotion is clearly excluded from the Eucryptodira, on the following characters:

1. Foramen posterius canalis carotici interni not situated at the posterior margin of pterygoid
2. Mesoplastra present

In addition *Kallokibotion* retains the following primitive characters absent in most eucryptodiran groups:

1. Vertebrae amphicoelous
2. First thoracic vertebra faces anteriorly

Although a number of taxa, such as *Neurankylus*, *Pleurosternon*, and *Naomichelys*, are poorly known but important in determining relationships of primitive cryptodires, a useful assessment of *Kallokibotion*'s relationships can be made. *Kallokibotion* is clearly not a eucryptodire; it lacks all the diagnostic characters of that group. Baenids plus eucryptodires are the Daiocryptodira, diagnosed principally by having some degree of temporal emargination. *Kallokibotion* has a well-developed temporal roof with no emargination and thus lies outside the Daiocryptodira. However, temporal roofing and emargination vary considerably in turtles, although

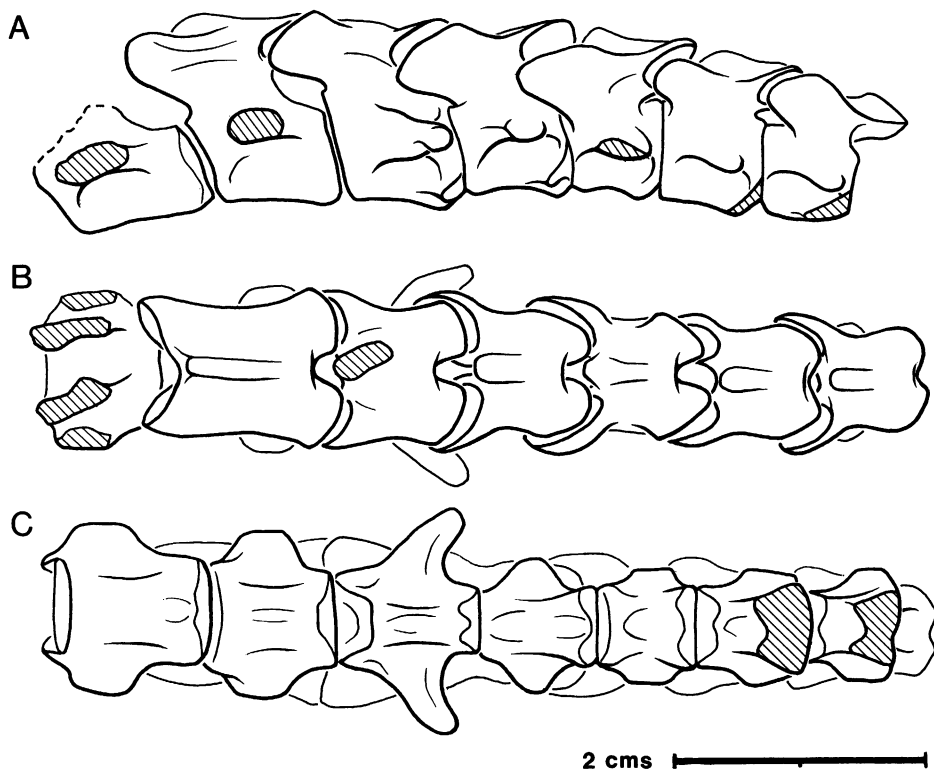


Fig. 32. *Kallokibotion bajazidi*. Last sacral vertebra and caudals 1-6 of BMNH R4921. A, Left lateral view; B, dorsal view; C, ventral view. Anterior to the left.

there is no reason to think that the *Kallokibotion* condition is not primitive. *Kallokibotion* does lie within the Selmacryptodira, the group consisting of all cryptodires except the early Jurassic *Kayentachelys*. It is very likely, then, that the relationships of *Kallokibotion* are with the most primitive of the cryptodires. The carotid arterial system is an important source of characters within cryptodires at this level and *Kallokibotion* has this area preserved. In *Kallokibotion* the medial branch (cerebral) of the internal carotid enters the basisphenoid with little or no contribution from the pterygoid, the primitive condition for amniotes and also found in *Proganochelys* and *Kayentachelys*. In all other cryptodires (with the exception of a skull from the Early Cretaceous of China [Gaffney and Ye, in prep.]) the pterygoid forms part or all of the canal or foramen for the internal carotid medial branch. This feature would make *Kallokibotion* the sister group of all other selmacryptodires. Also in contrast to all other

selmacryptodires, *Kallokibotion* lacks a bony connection between the canalis caroticus lateralis and the canalis caroticus internus, indicating that the division between the palatine artery and the internal carotid was entirely outside the skull, as in *Proganochelys* and *Kayentachelys*. In all other selmacryptodires the palatine artery-internal carotid division is either embedded in or covered by bone. Based on these synapomorphies we conclude that *Kallokibotion* is best hypothesized as the sister group to all other Selmacryptodira, but we do not consider this to be a particularly well-tested hypothesis because of the relatively poor preservation of the material.

OTHER OCCURRENCES OF *KALLOKIBOTION*

De Broin (1977: 5, 325, 329) reported the presence of "les baenoidea" in the Paleocene of Cernay and Menat in France. Two tentative identifications were made, one taxon

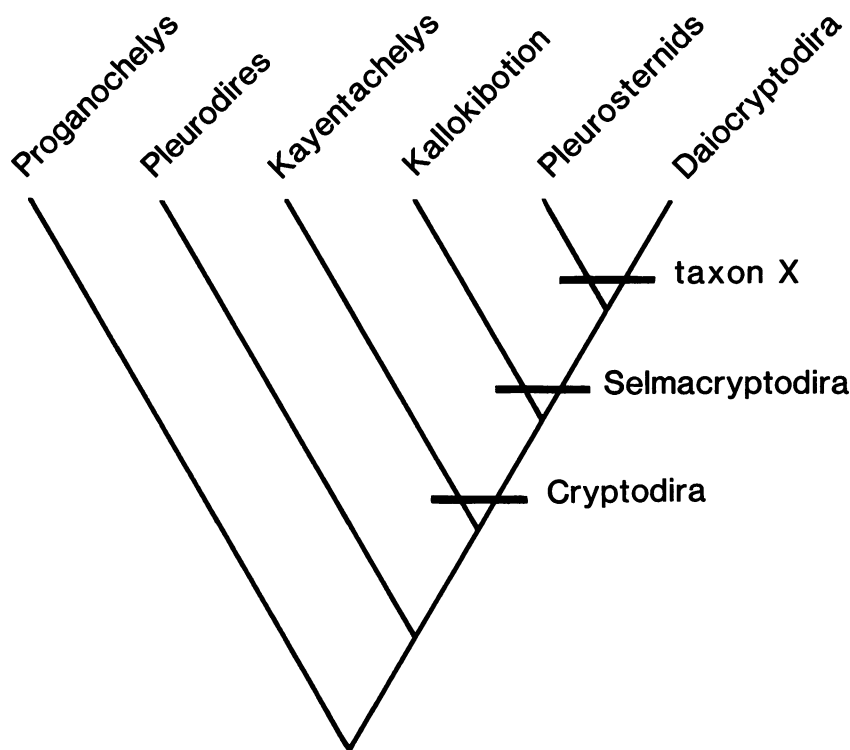


Fig. 33. Cladogram showing relationships of *Kallokibotion* among primitive turtles.

similar to *Compsemys* and one similar to *Kallokibotion*. Thanks to the graciousness of Dr. de Broin I have been able to examine this material. The *Kallokibotion*-like material is all from Cernay and nearly all of it consists of disarticulated cranial and postcranial elements referable to a number of undescribed cryptodires. Some of this material does have features found in *Kallokibotion*. The most similar are a series of squamosals and a braincase. The squamosals (Paris museum numbers BR 13358, BR 15064, and BR 2545) indicate a skull roof with no temporal emargination and a posterior margin well posterior to the postotic antrum (visible on the internal surfaces of the squamosals). This morphology would agree closely with that of *Kallokibotion* as described here. However, squamosals this extensive, although somewhat rare in turtles, are not limited to *Kallokibotion*. The chelid *Pseudemydura* (Gaffney, 1979a), the baenid *Baena* (Gaffney, 1979a), and meiolaniids also have large squamosals and a completely covered skull roof

posteriorly. Ckhikvadzé (1987) figured a skull he identified as *Yumenemys inflatus* which also has a completely unemarginated skull roof very similar to that of *Kallokibotion* in general shape, but no sutures are indicated. Although the squamosals from Cernay are certainly suggestive of *Kallokibotion*, they alone are not diagnostic.

Another Cernay specimen, Paris museum number BR 12460, may be more significant in identifying a possible near relative of *Kallokibotion*. This partial skull consists of the otic chambers, occiput, and braincase but no dermal roofing elements. This braincase is the only other specimen that we are aware of that agrees with *Kallokibotion* in having the primitive condition of the foramen caroticum basisphenoidale combined with a ventrally opening foramen caroticum laterale, just anterior to the foramen caroticum basisphenoidale. Unfortunately, sutures are not readily apparent, so it cannot be determined whether or not the foramen caroticum basisphenoidale is formed by the basisphenoid

alone, but the foramina can be identified by directly following them into the cavum cranii. This braincase is nearly three times the size of comparable elements in *Kallokibotion* and differs from that form in a number of features, including having both pairs of foramina closer to the midline and closer to each other than in *Kallokibotion*. The presence of an open palatine artery is best interpreted as primitive for cryptodires, but *Kallokibotion* is nonetheless the only other turtle with this particular condition. The best that can be said of Paris museum number BR 12460 at present is that it is a selmacryptodiran below the level of taxon X in figure 33, as in *Kallokibotion*.

Also in the Cernay turtle fauna are plastra, unassociated with other elements, that have medially meeting mesoplastra (as well as the unique presence of epiplastra consisting of three separate ossifications) and could also be associated with either squamosals or braincase or both. In any case, the Cernay Paleocene material could belong to near relatives of *Kallokibotion*, but they do not have synapomorphies supporting this. Further study by Dr. de Broin may clarify the relations of this material.

The taxon from Cernay that is similar to *Compsemys* is very fragmentary and not really identifiable. In any case, *Compsemys*, as currently understood, is not a baenid.

It is worth noting at this point that Groesens-van Dyck (1983, 1984) identified baenids in the Paleocene of Belgium based on the resemblance of the Belgian material to the Cernay specimens. The figured and described Belgian specimens, however, have no diagnostic features in common with baenids or *Kallokibotion*.

As we interpret the relationships of *Kallokibotion*, it is not a baenid, and it has none of the derived characters of baenids (fide Gaffney and Meylan, 1988). The European records of baenids based on *Kallokibotion* or *Kallokibotion*-like taxa can be discarded. As far as we can determine, the Baenidae is restricted to western North America and does not occur in Europe or Asia.

Mlynarski (1966) described more *Kallokibotion* material from Sinpetru, the type locality. He figures the internal surface of a car-

apace (pl. 15, fig. 3) which agrees with the BMNH material but is hardly diagnostic. He also lists more carapace fragments, humerus, femur, and shoulder girdle fragment. None of these specimens have been seen by us.

REFERENCES

- Chure, D., and J. McIntosh
1989. A bibliography of the Dinosauria. Museum of Western Colorado Paleontology Series no. 1, pp. 1-226.
- Ckhikvadze, V. M.
1987. Sur la classification et les caractères de certaines tortues fossiles d'Asie rares et peu étudiées. *Stvdia Palaeocheloniologica* 2(3): 55-86.
- Colbert, E. H.
1968. Men and dinosaurs. New York: E.P. Dutton, 283 pp.
- de Broin, F.
1977. Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé supérieur et du Tertiaire de France. *Mém. Mus. Nat. Hist. nat., Paris Sér. C*, 38: 1-366.
- Evans, J., and T. S. Kemp
1975. The cranial morphology of a new lower Cretaceous turtle from southern England. *Palaeontology* 18: 25-40.
- Gaffney, E. S.
1972. The systematics of the North American family Baenidae (Reptilia, Cryptodira). *Bull. Am. Mus. Nat. Hist.* 147(5): 241-320.
1975a. A phylogeny and classification of the higher categories of turtles. *Bull. Am. Mus. Nat. Hist.* 155(5): 387-436.
1975b. *Solnhofia parsonsi*, a new cryptodiran turtle from the Late Jurassic of Europe. *Am. Mus. Novitates* 2576: 25 pp.
1979a. Comparative cranial morphology of recent and fossil turtles. *Bull. Am. Mus. Nat. Hist.* 164(2): 65-375.
1979b. The Jurassic turtles of North America. *Bull. Am. Mus. Nat. Hist.* 162(3): 91-136.
1982. Cranial morphology of the baenid turtles. *Am. Mus. Novitates* 2737: 22 pp.
1983. Cranial morphology of the extinct horned turtle, *Meiolania platyceps*, from the Pleistocene of Lord Howe Island. *Bull. Am. Mus. Nat. Hist.* 175(4): 361-480.
1984. Historical analysis of theories of chelonian relationship. *Syst. Zool.* 33(3): 283-301.

1990. The comparative osteology of the Triassic turtle *Proganochelys*. Bull. Am. Mus. Nat. Hist. 194: 263 pp.
- Gaffney, E. S., and P. A. Meylan
1988. A phylogeny of turtles. In M. J. Benton (ed.), The phylogeny and classification of tetrapods, pp. 157–219. Oxford: Clarendon Press.
- Gaffney, E. S., J. H. Hutchison, F. A. Jenkins, Jr., and L. J. Meeker
1987. Modern turtle origins: the oldest known cryptodire. Science 237: 289–291.
- Grigorescu, D.
1983. A stratigraphic, taphonomic and paleoecologic approach to a “forgotten Land”: the dinosaur-bearing deposits from the Hateg Basin (Transylvania-Romania). Acta Palaeontologica Polonica 28(1-2): 103–121.
- Groessens-Van Dyck, M.-Cl.
1983. Etude des Cheloniens du Montien Continental de Hainin (Hainaut, Belgique). Bulletin de la Société belge de Géologie 92(2): 67–76.
1984. Les tortues du Paléocène continental de Hainin et Vinalmont (Belgique). Stvdia Palaeocheloniologica I: 133–139.
- Hutchison, J. H., and D. M. Bramble
1981. Homology of the plastral scales of the Kinosternidae and related turtles. Herpetologica 37(2): 73–85.
- Mlynarski, M.
1966. Die fossilen Schildkröten in den ungarischen Sammlungen. Acta Zoologica Cracoviensia XI(8): 224–288.
- Nopcsa, F.
1923a. On the geological importance of the primitive reptilian fauna of the Uppermost Cretaceous of Hungary; with a description of a new tortoise (*Kallokibotion*). Quart. Jour. Geol. Soc. 79(1): 100–116.
- 1923b. *Kallokibotium*, a primitive amphicheylean tortoise from the uppermost Cretaceous of Hungary. Palaeont. Hungarica 1: 1–34.
- Weishampel, D., D. Grigorescu, and D. Norman
1991. The dinosaurs of Transylvania: island biogeography in the Late Cretaceous. National Geographic Research & Exploration 7(2): 196–215.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates*, *Bulletin*, and *Anthropological Papers* published during the last five years are available free of charge. Address orders to: American Museum of Natural History Library, Department D, Central Park West at 79th St., New York, N.Y. 10024.

THIS PUBLICATION IS PRINTED ON ACID-FREE PAPER.