New insights on the anatomy and systematics of *Kallokibotion* Nopcsa, 1923, the enigmatic uppermost Cretaceous basal turtle (stem Testudines) from Transylvania

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Kallokibotion is a basal turtle (stem Testudines) described almost a century ago from generally poorly preserved specimens, from the Maastrichtian of the Haţeg Basin (Romania). A revision of these specimens, performed almost 25 years ago, allowed a better understanding of the taxon. *Kallokibotion* has remained an enigmatic form because of the limited number of available characters. However, it has frequently been included in general phylogenetic hypotheses of relationships among Testudinata or among basal forms. The information in these analyses has been based on the classic material because, until now, no new specimens had been figured and described in detail. Its phylogenetic position has been under discussion. Well-preserved new material is presented here. These specimens not only reveal detailed cranial and postcranial elements poorly known until now, refuting previous hypotheses about the anatomy of this taxon, but also allow us to identify numerous hitherto unknown characters. Thus, *Kallokibotion* is recognized as one of the best-characterized stem Testudines. A new diagnosis for its only known species, *Kallokibotion bajazidi*, is proposed. The incorporation of new information in several phylogenetic analyses shows *Kallokibotion* as the sister taxon of the crown Testudines.

ADDITIONAL KEYWORDS: cranial and postcranial skeleton – Haţeg Basin – *Kallokibotion bajazidi* – Maastrichtian – phylogenetic position – Sânpetru Formation – Testudinata.

INTRODUCTION

The information on the European continental vertebrate faunas of the last Stages of the Late Cretaceous is relatively good, thanks to the discovery of numerous sites, especially those corresponding to the Campanian and Maastrichtian (see, for example, Csiki-Sava *et al.*, 2015; Ortega *et al.*, 2015; Pereda Suberbiola *et al.*, 2015; Pérez-García *et al.*, 2016). Testudinata is one of the best-represented groups of reptiles in these sites (de Lapparent de Broin & Murelaga, 1999; Pereda Suberbiola, 2009). Two main groups of freshwater turtles are identified in both Western and Central-Eastern Europe: Dortokidae (stem Pleurodira) and Bothremydidae (Podocnemidoidea, Pleurodira) (de Lapparent de Broin & Murelaga, 1996, 1999; Gaffney, Tong & Meylan, 2006; Pérez-García, Ortega & Murelaga, 2012a; Pérez-García, Scheyer & Murelaga, 2012b). In contrast, the fauna of terrestrial turtles from the uppermost Cretaceous of both regions of the European archipelago is composed of different taxa, all of them corresponding to basal forms (stem Testudines). Several representatives of Solemydidae are identified in Western Europe. This clade is known from the Late Jurassic, being part of both the European and the North American records (de Lapparent de Broin & Murelaga, 1996, 1999; Joyce *et al.*, 2011; Scheyer, Pérez-García & Murelaga, 2015). Contrasting with

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this diverse clade, characterized by its relatively large biostratigraphic and paleobiogeographic distributions, the only currently recognized basal taxon in the other part of the European archipelago is *Kallokibotion* Nopcsa, 1923a (Nopcsa, 1923a, b; Gaffney & Meylan, 1992; Rabi, Vremir & Tong, 2013a; Csiki-Sava *et al.*, 2015). It corresponds to an enigmatic taxon, defined in the Haţeg Basin (Transylvania, Romania), and whose presence has not been confirmed outside Romania. Fragmentary material from Austria and Hungary, also from uppermost Cretaceous sites, could correspond to this form or to a closely related taxon (Rabi *et al.*, 2013a). Nopcsa (1923a, b) defined *Kallokibotion* from several specimens, generally poorly preserved. Gaffney & Meylan (1992) indicated that because of inconsistencies and ambiguities in the descriptions provided by Nopcsa (1923b), and considering the fragmentary nature of the known material, *Kallokibotion* was difficult to compare with other turtles. Thus, they revised in detail these classic specimens, performing a new study of the taxon. Contrary to the proposal of Nopcsa (1923b), Gaffney & Meylan (1992) recognized the presence of a probably single valid representative of this genus, *Kallokibotion bajazidi* Nopcsa, 1923a. However, Gaffney & Meylan (1992) indicated that the relatively poor preservation and the scarce availability of characters in the preserved remains restricted their ability to determine the osteology of *Kallokibotion*, their conclusions being hampered. Not only did Gaffney & Meylan (1992) place *Kallokibotion* in a cladistic framework of turtle relationships, but this taxon has subsequently been included in many of the main papers where general phylogenetic hypotheses about most clades of turtles were proposed, and in numerous analyses trying to establish a hypothesis about the relationships among basal forms (e.g. Gaffney, 1996; Gaffney *et al.*, 1998, 2007; Hirayama, Brinkman & Danilov, 2000; Joyce, 2007; Anquetin *et al.*, 2008; Sterli, 2008, 2010; Sterli & de la Fuente, 2010, 2011a, 2013; Anquetin, 2011; Joyce *et al.*, 2011; Pérez-García, 2012a, b; Pérez-García & Murelaga, 2012a, b, 2013; Rabi *et al.*, 2013b; Pérez-García, Gasulla & Ortega, 2014; Sterli, de la Fuente & Krause, 2015a; Sterli, de la Fuente & Umazano, 2015b; Joyce *et al.*, 2016; Szczygiellski & Sulej, 2016). However, the information generally included in these papers has not been increased since the study of Gaffney & Meylan (1992), because only very scarce material of this taxon has subsequently been presented (e.g. Csiki-Sava *et al.*, 2010; Rabi *et al.*, 2013a; Csiki-Sava *et al.*, 2015), and this has not been analysed. In fact, after the revision of this poorly known but relevant taxon performed by Gaffney & Meylan (1992) about 25 years ago, information on its anatomy has been barely increased. Many elements of the shell of this taxon are not known, nor

are many of the sutures of the skull or lower jaw. Due to the relatively limited information so far available on *Kallokibotion*, its phylogenetic position is now under discussion, having been recognized as both the sister taxon of Testudines (Joyce, 2007; Anquetin, 2011), or attributed to clades such as Meiolaniformes (Sterli & de la Fuente, 2013; Rabi *et al.*, 2013b; Sterli *et al.*, 2015a, b) or Paracryptodira (Szczygiellski & Sulej, 2016). Abundant and well-preserved new material attributable to *K. bajazidi*, from several locations in the Haţeg Basin, has recently been found (Fig. 1). Some of the most relevant specimens, which allow many characters hitherto unknown for this taxon to be described, are presented here (Figs 2–5). Their analysis provides us a better anatomical characterization for this basal turtle. Thus, some previous hypotheses about the anatomy of this taxon are confirmed, but others are refuted. The new specimens allow us to know, with great precision, its cranial anatomy, and also that of the shell, and to describe other poorly known or hitherto unknown bones, corresponding to both the axial and the appendicular skeletons. The new anatomical information is compared with that of other members of the stem group of Testudines, and a new diagnosis for *K. bajazidi* is provided. This new information significantly improves the coding of this taxon in previous data matrices so that its phylogenetic position is re-evaluated. In addition, the validity of a single species, *K. bajazidi*, is confirmed here thanks to the evidence provided by the new specimens as well as by the revision of the classic material.

INSTITUTIONAL ABBREVIATIONS

UBB, Universitatea Babeş-Bolyai, Paleotheriology Laboratory collection, Cluj-Napoca, Romania; NHMUK, Natural History Museum, London, UK.

ANATOMICAL ABBREVIATIONS

Ab, abdominal scute; An, anal scute; ang, angular; ar, accessory ridge; ax, axillary buttress; bo, basioccipital; bs, basisphenoid; c, costal; co, coracoid; cor, coronoid; den, dentary; dip, diapophysis; en, entoplastron; ep, epiplastron; ex, exoccipital; Fe, femoral scute; fem, femur; fic, foramen intermandibularis caudalis; fm, fossa meckelii; fna, foramen nervi auriculotemporalis; fr, frontal; fp, foramen praepalatinum; Gu, gular scute; hp, hypoplastron; Hu, humeral scute; hy, hyoplastron; ib, inguinal buttress; Ig, intergular scute; Inf, inframarginal scute; ju, jugal; M, marginal scute; me, mesoplastron; mx, maxilla; n, neural; na, nasal; ns, neural spine; nu, nuchal; op, opisthotic; p, peripheral; pa, parietal; Pc, pectoral scute; pf, prefrontal; Pl, pleural scute; pm, premaxilla; po, postorbital;
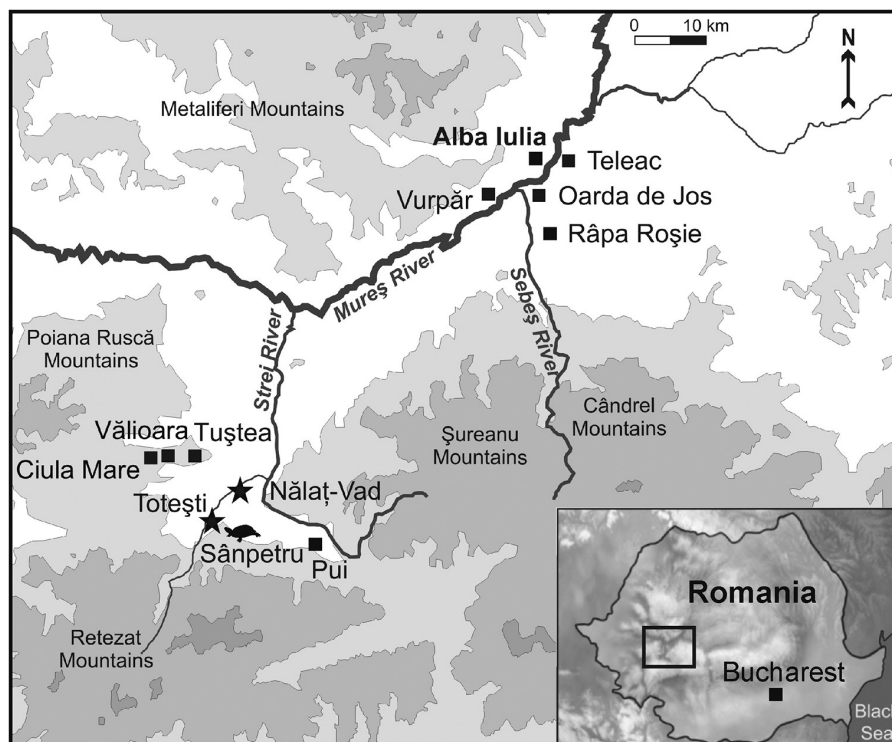
Figure 1. Geographic locations of the two areas from which the specimens of *Kallokibotion bajazidi* presented in this paper come, Toteşti and Nălaţ-Vad (Râul Mare, Hunedoara County, Transylvania, Romania), indicated by stars. The position of Sânpetru, the type locality of *Kallokibotion*, from which all the classic material of this taxon comes, is indicated by a drawing of a turtle.

pr, prootic; pra, prearticular; prz, prezygapophysis; pt, pterygoid; pz, postzygapophysis; q, quadrate; qj, quadratojugal; sca, scapula; so, supraoccipital; sp, suprapygal; sq, squamosal; sur, surangular; V, vertebral scute; vo, vomer; xi, xiphiplastron.

MATERIAL AND METHODS

A detailed anatomical study of several new specimens of *K. bajazidi*, from various locations of the Maastrichtian Sânpetru Formation, in the Haţeg Basin (Transylvania, Romania), is undertaken here. To perform this analysis, first hand comparisons with the classic material of this taxon [i.e. the specimens studied by Nopcsa (1923a, b) and revised by Gaffney & Meylan (1992), including the type material], also from the Haţeg Basin, have been made. These classic specimens are deposited in the Natural History Museum (London, UK), and the new specimens presented here are part of the Paleotheriology Laboratory collection of the Universitatea Babeş-Bolyai (Cluj-Napoca, Romania). A selection of specimens, which provide new anatomical information because elements hitherto unknown are preserved or which allow previous

anatomical hypotheses based on poorly preserved and scarce remains to be confirmed or refuted, are presented here. Thus, the description here is exclusively based on those elements that provide new information on this taxon. These new specimens come from two locations: Toteşti and Nălaţ-Vad. For the detailed description of other anatomical elements and characters, see Gaffney & Meylan (1992).

The new characters of *K. bajazidi* recognized for the first time in this paper, as well as all those that are here reinterpreted, are compared with those present in other proto-turtles and basal turtles (i.e. members of the stem group of Testudines). Thus, *K. bajazidi* is compared with *Odontochelys semitestacea* Li, Wu, Rieppel, Wang & Zhao, 2008, from the Carnian (Late Triassic) of China; three forms of the Norian (Late Triassic) of Germany: *Proganochelys quenstedti* Baur, 1887, *Keuperotesta limendorsa* Szczygiellski & Sulej, 2016 and *Proterochersis robusta* Fraas, 1913; *Proterochersis porebensis* Szczygiellski & Sulej, 2016, from the Norian of Poland; *Palaeochersis talampayensis* Rougier, de la Fuente & Arcucci, 1995, from the Norian-Rhaetian of Argentina; *Australochelys africanus* Gaffney & Kitching, 1994, from the Early Jurassic of South Africa; two Early Jurassic taxa: *Kayentachelys aprix* Gaffney,

Hutchison, Jenkins & Meeker, 1987, from Arizona, and *Indochelys spatulata* Datta, Manna, Ghosh & Das 2000, from India; the Early-Middle Jurassic form *Condorchelys antiqua* Sterli 2008, from Argentina; several Middle Jurassic taxa: *Heckerochelys romani* Sukhanov, 2006, from Russia, *Eileanchelys waldmani* Anquetin, Barrett, Jones, Moore-Fay & Evans 2008, from Scotland and *Siamochelys peninsularis* Tong, Buffetaut & Suteethorn 2006, from Thailand; the Early Cretaceous Australian form *Otwayemys cunicularius* Gaffney, Kool, Brinkman, Rich & Vickers-Rich, 1998; *Chubutemys copelloi* Gaffney, Rich, Vickers-Rich, Constantine, Vacca & Kool, 2007, from the Aptian-Albian (Early Cretaceous) of Argentina; *Patagoniaemys gasparinae* Sterli & de la Fuente, 2011a, from the Campanian-Maastrichtian (Late Cretaceous) of Argentina; *Mongolochelys efremovi* (Khozatsky, 1997) from the Maastrichtian of Mongolia; the Danian (early Palaeocene) *Peligrochelys walshae* Sterli & de la Fuente 2013, from Argentina; the solemydids *Helochelydra nopcsai* de Lapparent de Broin & Murelaga, 1999, from the Barremian (Early Cretaceous) of England and *Naomichelys speciosa* Hay, 1908, from the Aptian-Cenomanian of United States; and three meiolaniids: *Niolamia argentina* Ameghino, 1899, from the Late Cretaceous or Paleogene of Argentina, *Ninjemys oweni* (Woodward, 1888) from the Pleistocene of Australia and *Meiolania platyceps* Owen, 1886, from the Pleistocene of Australia (see Appendix 1). These comparisons are made through the direct observation of specimens corresponding to some of these taxa, and also by considering the information provided by several authors, especially: Owen (1886) and Gaffney (1983, 1985, 1996) for *Me. platyceps*; Baur (1887) and Gaffney (1990) for *Pro. quenstedti*; Woodward (1888) and Gaffney (1992) for *N. oweni*; Sterli & de la Fuente (2011b) for *Ni. argentina*; Hay (1908) and Joyce, Sterli & Chapman (2014) for *Na. speciosa*; Fraas (1913) and Szczygiellski & Sulej (2016) for *Pr. robusta*; Gaffney *et al.* (1987), Sterli & Joyce (2007) and Gaffney & Jenkins (2010) for *Ka. aprix*; Gaffney & Kitching (1994, 1995) for *A. africanus*; Rougier, de la Fuente & Arcucci (1995) and Sterli, de la Fuente & Rougier (2007) for *P. talampayensis*; Khozatsky (1997) for *Mo. efremovi*; Gaffney *et al.* (1998) for *O. cunicularius*; de Lapparent de Broin & Murelaga (1999) and Joyce *et al.* (2011) for *He. nopcsai*; Datta *et al.* (2000) for *I. spatulata*; Sukhanov (2006) for *H. romani*; Tong, Buffetaut & Suteethorn (2006) for *S. peninsularis*; Gaffney *et al.* (2007) and Sterli *et al.* (2015b) for *Ch. copelloi*; Anquetin *et al.* (2008) and Anquetin (2010) for *E. waldmani*; Li *et al.* (2008) for *Od. semitestacea*; Sterli (2008) and Sterli & de la Fuente (2010) for *C. antiqua*; Sterli & de la Fuente (2011a) for *Pa. gasparinae*; Sterli & de la Fuente (2013) for *Pe. walshae*; and Szczygiellski & Sulej (2016) for *Ke. limendorsa* and *Pr. porebensis*.

One of the most recent phylogenetic hypotheses in which the position of both *K. bajazidi* and most of the hitherto known members of the stem group of Testudines were analysed is that proposed by Sterli *et al.* (2015a). This hypothesis involves an update of that proposed by Sterli & de la Fuente (2011a), in which the states of several characters for *K. bajazidi* were amended (based on a revision of the classic specimens) in relation to those in previous phylogenetic hypotheses, such as those of Sterli (2008) and Joyce (2007). In order to evaluate the systematic position of *K. bajazidi*, based on the new information provided here, the encoding of this taxon in the data matrix of Sterli *et al.* (2015a) has been revised (see Appendix 2 and Supporting Information, Data 1). In addition, the encoding of *K. bajazidi* is also amended in another recently proposed data matrix, also based on that published by Joyce (2007): that performed by Joyce *et al.* (2016), in which the coding for some characters for this taxon had also been modified (see Appendix 2 and Supporting Information, Data 2). These two data matrices have been analysed using TNT 1.0 (Goloboff *et al.*, 2008) in order to find the most parsimonious trees (MPTs). A traditional search was used for each of these analyses, with 1000 replications of Wagner trees (using random addition sequences), followed by tree bisection recognition as a swapping algorithm, saving 100 trees per replication. To test the robustness of these phylogenetic hypotheses, Bremer support and bootstrap frequencies (based on 1000 replications) values were also obtained using TNT. One hundred and two taxa and 240 characters were considered in the analysis based on Sterli *et al.* (2015a) and 113 taxa and 244 characters in that based on Joyce *et al.* (2016). In order to identify wildcard taxa, a pruned strict tree was generated for both phylogenetic hypotheses obtained here (Trees → Comparisons → Pruned Trees, with the option 'listed as text' selected), with the removal of the most unstable operational taxonomic units *a posteriori*. Eight taxa act as wildcard taxa in the first analysis (i.e. *Macroclemys schmidti* Zangerl 1945, *Peligrochelys walshae*, *Gaffneylania auricularis* Sterli, de la Fuente & Krause 2015, *Siamochelys peninsularis*, *Dinochelys whitei* Gaffney 1979, *Chengyuchelys* Young & Chow 1953, *Hangaiemys hoburensis* Sukhanov & Narmandakh 1974 and *Indochelys spatulata*) and four in the second (i.e. *Xinjiangchelys junggarensis* Ye 1986, *Macroclemys schmidti*, *Shachemys laosiana* de Lapparent de Broin 2004 and *Indochelys spatulata*). Thus, reduced consensus trees are calculated.

SYSTEMATIC PALEONTOLOGY

Testudinata Klein, 1760

Kallokibotion Nopcsa, 1923a

Kallokibotion bajazidi Nopcsa, 1923a

([Figs 2–5](#))

Kallokibotium bajazidi Nopcsa, 1923b
Kallokibotium manificum Nopcsa, 1923b

New material: A selection composed of the most informative specimens belonging to the UBB collection. UBB ToK-2, a relatively complete skeleton, in which are preserved the skull (UBB ToK-2/1; [Fig. 2A–F](#)) and the lower jaws (UBB ToK-2/2 and UBB ToK-2/3; [Fig. 2G–L](#)); most elements of the carapace (UBB ToK-2/5 and UBB ToK-2/6; [Fig. 3A, B](#)); the almost complete plastron (UBB ToK-2/4; [Fig. 3C, D](#)); several cervical and dorsal vertebrae (UBB ToK-2/8, UBB ToK-2/7, UBB ToK-2/9; [Fig. 4A–P](#)); the left humerus (UBB ToK-2/13; [Fig. 4Q–V](#)); the left scapula (UBB ToK-2/5 + UBB ToK-2/7; [Fig. 4W](#)); an ungual phalanx (ToK-2/17; [Fig. 4X–AA](#)); the right ulna (ToK-2/18; [Fig. 4A B–AF](#)); the right radius (ToK-2/19; [Fig. 4A G–AK](#)); the proximal region of the left tibia (ToK-2/20; [Fig. 4A L–AO](#)); and other elements of the axial and appendicular skeletons including, among others, the almost complete right scapular girdle and the left femur, preserved in contact with the ventral region of the plastron ([Fig. 3D](#)). UBB ToK-1, a partial skeleton including the skull roof (UBB ToK-1/14; [Fig. 2M–N](#)); the right humerus (UBB ToK-1/5; [Fig. 4A P–AS](#)); the right scapula (UBB ToK-1/3; [Fig. 4A T–AU](#)); the left humerus (UBB ToK-1/6; [Fig. 4A V–AY](#)); the left scapula (UBB ToK-1/4; [Fig. 4A Z–BA](#)); and other elements of both the cranial skeleton and the shell. UBB NVK-7, a partial anterior region of a carapace of a juvenile specimen ([Fig. 5A, B](#)). UBB NVK-31, and almost complete shell, lacking the most posterior regions of both the carapace and the plastron ([Fig. 5C–H](#)).

Locality and horizon: The new specimens presented here come from two outcrops, Totești (the specimens whose collection number includes ToK) and Nălaț-Vad (the specimens whose collection number includes NVK), geographically located very close to Sânpetru, the locality where the classic material of *Kallokibotium* was found ([Fig. 1](#)). All these sites are located in the Hațeg Basin, a basin bounded by the Poiana Ruscă, Retezat, Țarcu and Șureanu mountains, in Râul Mare, Hunedoara County, Transylvania, Romania. The Sânpetru Formation is a Maastrichtian continental formation, of fluvial origin, exposed in the southern sector of the Hațeg Basin ([Codrea *et al.*, 2002](#); [Smith *et al.*, 2002](#); [Therrien *et al.*, 2002](#); [Van Itterbeeck *et al.*, 2004](#); [Therrien, 2005](#); [Van Itterbeeck, Markevich & Codrea, 2005](#)).

Emended diagnosis: A Testudinata belonging to the stem group of Testudines, with the following autapomorphies: nuchal plate composed of two elements, the most anterior being smaller and rectangular, and the other hexagonal and wider than long. It differs from the other stem Testudines by the following character combination: skull as wide as long; internarial process present, mainly formed by the premaxillae; interorbital space very wide, wider than the length of each orbit; orbits as high as long, laterally located; prefrontals in contact with the apertura narium externae; parietal–squamosal contact; absence of quadratojugal-squamosal contact; absence of supraoccipital exposure on the skull roof; processus trochlearis oticum present; in the ventral skull margin, larger exposure of the quadratojugal than that of the jugal; small cheek emargination, as high as long; very narrow triturating surfaces; presence of labial, lingual and accessory ridges on the maxillary; pterygoid-basioccipital contact present; foramen caroticum basisphenoidale entirely formed by the basisphenoid; canalis caroticus lateralis ventrally open at a foramen formed by the basisphenoid and pterygoids; well-developed cranial scutes, three pairs and a posterior odd scute being located on the sagittal plane; dentary reaching the articular, preventing the surangular-angular contact; high coronoid process; absence of retroarticular process; outer surface of the shell with an ornament pattern composed of tiny and low vermiculations and tubercles; absence of shell fontanelles; absence of a nuchal notch; eight neurals, the first one hexagonal with short latero-posterior margins, the second rectangular, and the others hexagonal with short latero-anterior margins or with subequal latero-anterior and latero-posterior margins; eight pairs of costals; 2 suprapygals; 11 pairs of peripherals; no cervical scute; sulcus between the third and fourth vertebrals on the fifth neural; no supramarginals; 12 pairs of marginals; marginals not reaching the costal series; osseous carapace-plastron connection; absence of cleithrum; axillary buttresses contacting the peripheral series and the first costal; inguinal buttresses contacting the eighth peripherals and the costal series; short and rounded anterior plastral lobe; a single pair of mesoplastra; posterior plastral lobe longer than the anterior, with substraight lateral margins; distinct anal notch; a pair of intergulars, overlapping the anterior region of the entoplastron; complete inframarginal series, composed by four scutes; amphicoelous cervical and caudal vertebrae; narrow cervical vertebrae; centrum of the seventh cervical longer than that of the eighth; high cervical postzygapophyses; low cervical ventral keel; first thoracic vertebra facing anteriorly directed; caudal vertebrae with tightly fitting zygapophyses concave anteriorly; triradiate pectoral girdle; well-developed and rod-shaped scapular and acromial processes, with a reduced lamina between them.
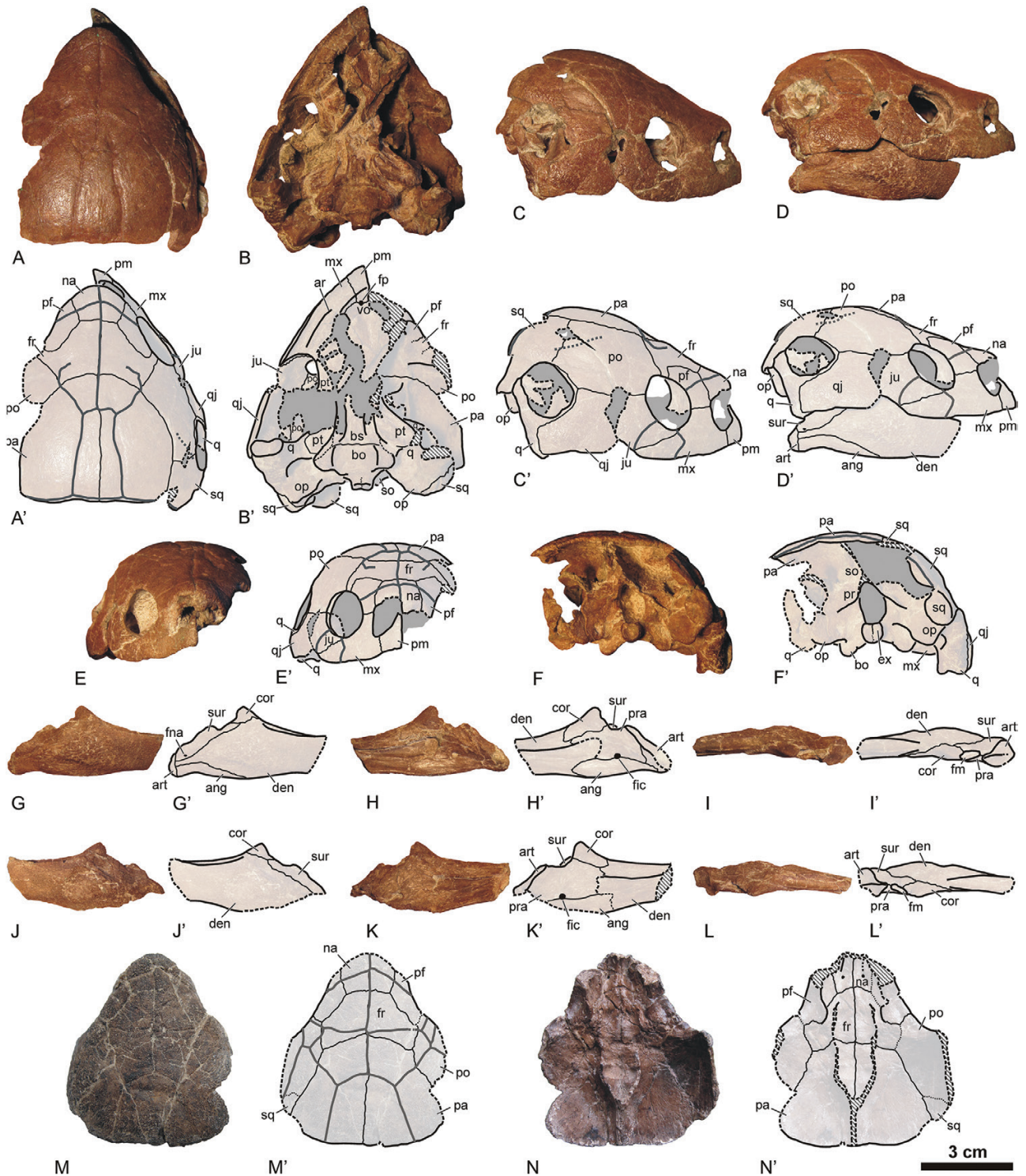
Figure 2. Cranial material of *Kallokibotion bajazidi*, from Toteşti (Râul Mare, Haţeg Basin, Romania), found in the Maastrichtian continental Sânpetru Formation. A–L, skull and lower jaw of the specimen of UBB ToK-2. A–F, UBB ToK-2/1, skull, in dorsal (A), ventral (B), right lateral (C, D), anterior (E) and posterior (F) views. G–I, UBB ToK-2/2, right branch of the lower jaw, in labial (G), lingual (H) and dorsal (I) views. J–L, UBB UBB ToK-2/3, left branch of the lower jaw, in labial (J), lingual (K) and dorsal (L) views. M, N, UBB ToK-1/14, skull roof of the specimen UBB ToK-1, in dorsal (M) and ventral (N) views.
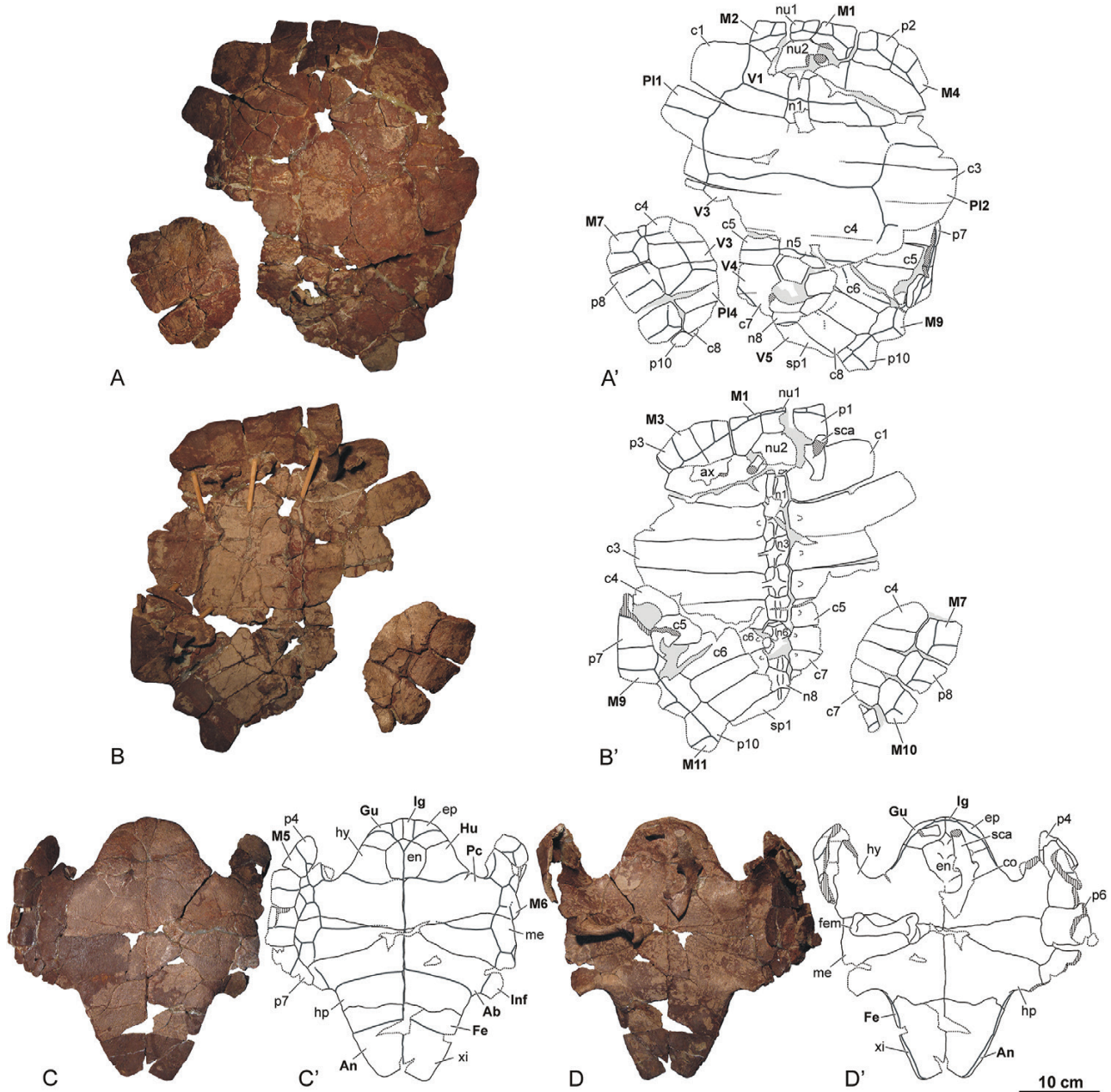
Figure 3. Shell of the specimen of *Kallokibotion bajazidi* UBB ToK-2, from Toteşti (Râul Mare, Haţeg Basin, Romania), found in the Maastrichtian continental Sânpetru Formation. A, B, UBB ToK-2/5 + UBB ToK-2/6, carapace, in dorsal (A) and ventral (B) views. C, D, UBB ToK-2/4, plastron, in ventral (C) and dorsal (D) views. Some elements of the shoulder girdle are preserved in contact with the visceral surfaces of both the carapace and the plastron (B–D). In addition, the left femur is located on the visceral surface of the plastron (D).

NEW INFORMATION ON THE ANATOMY OF *KALLOKIBOTION*

Skull and lower jaws

Several cranial remains are part of the classic collection of *K. bajazidi* (see Nopcsa, 1923a, b; Gaffney & Meylan, 1992). However, most of them correspond to partial skulls, and the only relatively complete skull,

NHMUK R4918, is deformed and poorly preserved (see Nopcsa, 1923b; Gaffney & Meylan, 1992). In fact, as was indicated by Gaffney & Meylan (1992), nearly the entire surface of this specimen was damaged during preparation, the visible sutures being mostly within the bone and not in the original surface position. In addition, most of its bones are broken and distorted. Moreover, several characters and elements
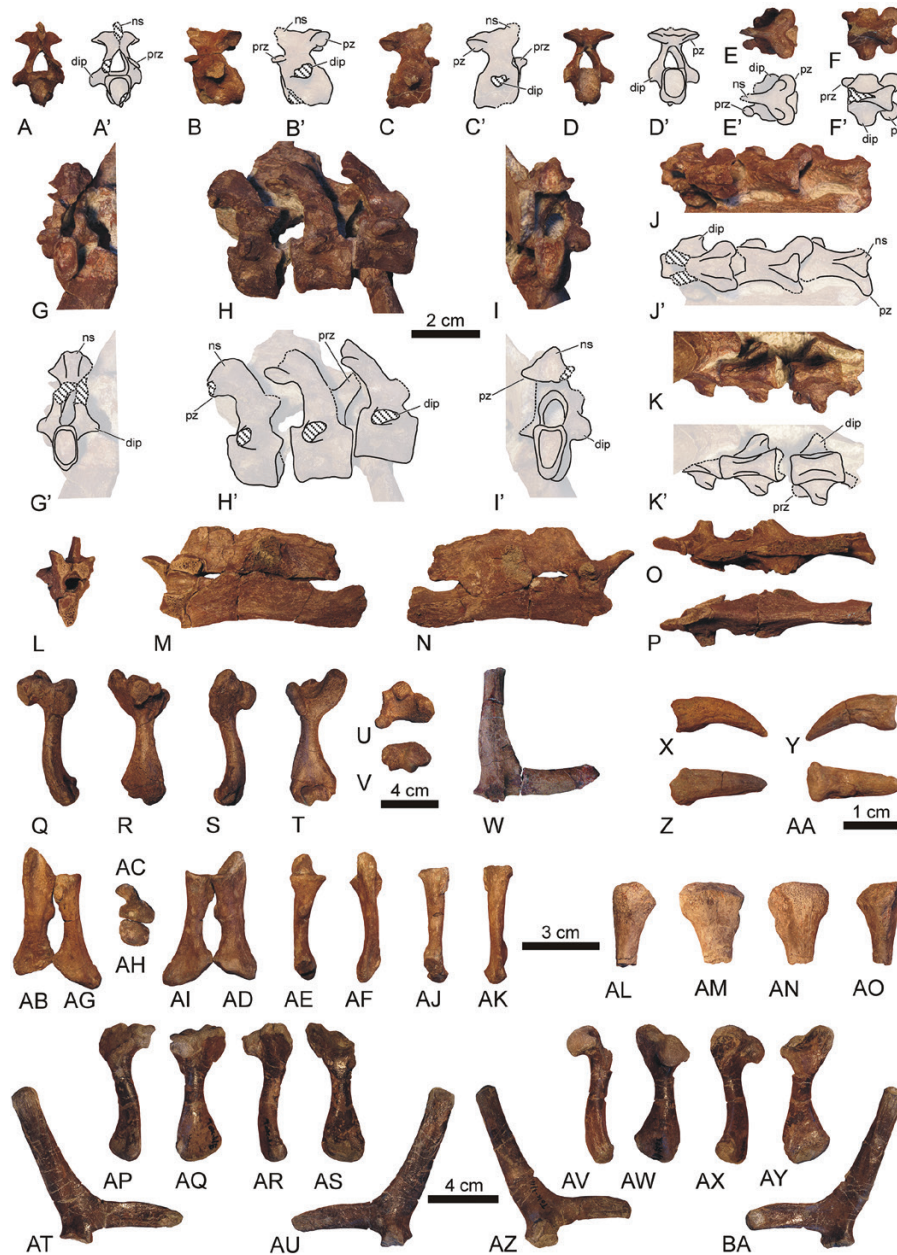
Figure 4. Axial and appendicular elements of two individuals of *Kallokibotion bajazidi*, from Totești (Râul Mare, Hațeg Basin, Romania), found in the Maastrichtian continental Sânpetru Formation. A–AO, bones of specimen UBB ToK-2. A–F, anterior cervical vertebra (axis), UBB ToK-2/8, in anterior (A), left lateral (B), right lateral (C), posterior (D), dorsal (E) and ventral (F) views. G–K, posterior cervical vertebrae (sixth to eighth vertebrae), UBB ToK-2/7, in anterior (G), right lateral (H), posterior (I), dorsal (J) and ventral (K) views. L–P, dorsal vertebrae, UBB ToK-2/9, in anterior (L), left lateral (M), right lateral (N), dorsal (O) and ventral (P) views. Q–V, left humerus, UBB ToK-2/13, in posterior (Q), dorsal (R), anterior (S), ventral (T), medial (U) and distal (V) views. W, left scapula, UBB ToK-2/5 + UBB ToK-2/7, in posterior view. X–AA, ungual phalanx, ToK-2/17, in lateral (X, Y), dorsal (Z) and ventral (AA) views. AB–AF, right ulna, ToK-2/18, in ventral (AB), proximal (AC), dorsal (AD), medial (AE) and lateral (AF) views. AG–AK, right radius, ToK-2/19, in ventral (AG), proximal (AH), dorsal (AI), lateral (AJ) and medial (AK) views. AL–AO, proximal region of the left tibia, ToK-2/20, in posterior (AL), dorsal (AM), ventral (AN) and anterior (AO) views. A–AO, bones of the specimen UBB ToK-1. AP–AS, right humerus, UBB ToK-1/5, in posterior (AP), dorsal (AQ), anterior (AR) and ventral (AS) views. AT–AU, right scapula, UBB ToK-1/3, in anterior (AT) and posterior (AU) views. AV–AY, left humerus, UBB ToK-1/6, in posterior (AV), dorsal (AW), anterior (AX) and ventral (AY) views. AZ–BA, left scapula, UBB ToK-1/4, in posterior (AZ) and anterior (BA) views.
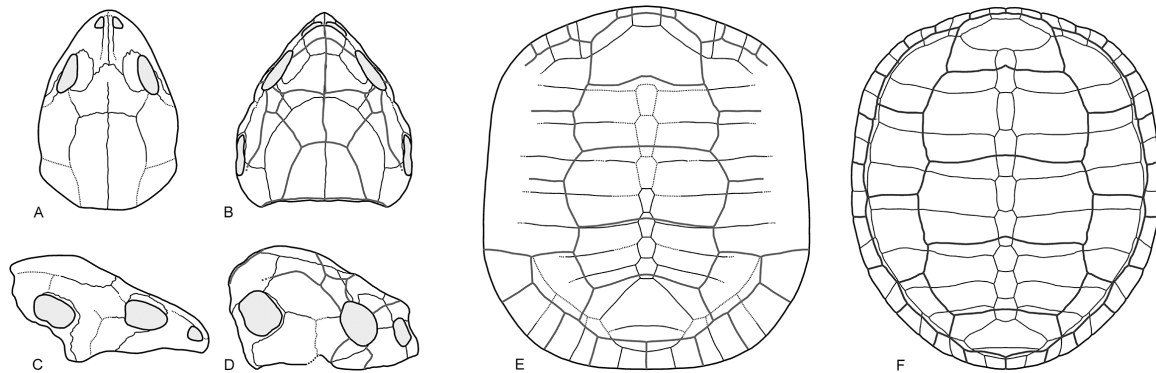
Figure 5. Elements of the shell of two specimens of *Kallokibotion bajazidi*, from Nălaț-Vad (Râul Mare, Haţeg Basin, Romania), found in the Maastrichtian continental Sânpetru Formation. A, B, UBB NVK-7, anterior region of the carapace in dorsal (A) and ventral (B) views. C–H, UBB NVK-31, shell in dorsal (C), ventral (D), right lateral (E), left lateral (F), anterior (G) and posterior (H) views.

were misinterpreted (e.g. the general morphology of the skull, as a result of the deformation of specimen NHMUK R4918, and the path and position of several sutures), are poorly known (e.g. the cranial scutes) or had not been hitherto preserved (see Fig. 6A, C). No new cranial remains have subsequently been referred.

Figure 6. Comparative reconstructions of the skull (A–D) and carapace (E, F) of *Kallokibotion bajazidi*, corresponding to those done by Gaffney & Meylan (1992) (A–C, E) and those proposed here based on the study of the new specimens and the revision of the classic collection of this taxon (B–D, F). A–C, modified from figure 1 of Gaffney & Meylan (1992). E, modified from figure 17 of Gaffney & Meylan (1992).

In dorsal view, the skull of *K. bajazidi* is here recognized as almost as wide as long, but not longer than wide as was previously proposed based for the deformed skull NHMUK R4918 (see Figs 2A–F, 6A–D). In lateral view, the height of the anterior end relative to the total height of the skull is much greater than that previously interpreted. The orbits are recognized as more laterally positioned than those previously interpreted by Gaffney & Meylan (1992), being as high as wide. The apertura narium externa is also identified as larger than previously considered.

Gaffney & Meylan (1992) indicated that the limits of the nasals were dubious. As they explained, the position of the premaxilla-nasal contact of NHMUK R4918 could be at any one of a number of breaks, the most likely position being recognized as one with a fairly short dorsal process on the premaxilla. Following this proposal, they indicated, in their amended diagnosis of this taxon, that the nasals form the internarial process. The new and well-preserved skull UBB ToK-2/1 (Fig. 2A–F) allows us to recognize that the premaxillae constitute most of the internarial process. Gaffney & Meylan (1992) indicated that, although the posterior area of the nasals is not well preserved, a nasal-prefrontal contact seems unlikely. This hypothesis is refuted here, since a relatively long contact between both bones is observed. Thus, the nasals are not recognized as long and narrow bones, as previously interpreted, but as relatively wide elements, the width of this pair of bones being greater than its length.

The prefrontals are identified here as part of the posterior margin of the apertura narium externae (Fig. 2C–E). Therefore, they do not contact the maxillae anteriorly or antero-dorsally, but ventrally. Although the frontal lies behind the prefrontal and prevents a prefrontal-postorbital contact in some specimens (Fig. 2A), this character is subject to variability, the prefrontal-postorbital contact being present in others (Fig. 2M). Gaffney & Meylan (1992) also recognized that the limits of the frontals were not entirely clear. Thus, they indicated that whether the maxilla reaches the frontal or if a nasal-prefrontal contact prevents this contact was not determinable. As has been indicated, a nasal-prefrontal contact is recognized here, preventing the contact between the frontals and the maxillae. The posterior contact of the frontals with the parietals is not always transverse, but it is subject to variability. Thus, it is oblique in UBB ToK-1/14 (Fig. 2M), but subrounded in UBB ToK-2/1 (Fig. 2A). The posterolateral contact of the frontals with the postorbitals, not entirely clear in any of the classic specimens, is recognized in the two skulls presented here. Thus, its oblique arrangement is confirmed.

A complete parietal is not preserved in any of the classic specimens. The latero-anterior contact of this bone with the postorbital and its latero-posterior contact with the squamosal are confirmed here. Although the parietal-squamosal contact is identified as relatively long, as was interpreted by Gaffney & Meylan (1992), it is markedly shorter than that between the parietals and the postorbitals. The morphology of the parietals is recognized as variable, their lateral margins being posteriorly identified as slightly convergent (Fig. 2A), slightly divergent (fig. 6 in Gaffney & Meylan, 1992) or markedly divergent (Fig. 2M). Thus, although Gaffney & Meylan (1992) included in their amended diagnosis of *K. bajazidi* the presence of relatively elongate parietals, the width of this pair of bones is recognized here as variable, being even greater than its length in some specimens (see Fig. 2A, M). Gaffney & Meylan (1992) indicated that an exposure of the supraoccipital on the dorsal surface of the skull roof does not appear to be present. This hypothesis is confirmed here. The crista occipitalis of both the classic

specimens and those presented here is posteriorly broken. It probably was very short.

Gaffney & Meylan (1992) noted that few of the postorbital contacts were identifiable. Thus, the so far available material does not allow us to recognize whether *K. bajazidi* had a relatively large and long postorbital, or if it were reduced. This bone is recognized here as large, contacting the squamosal by a relatively long suture, longer than that between the postorbital and the quadrate. The contact between the squamosal and the quadrate is identified here for the first time. This suture contacts the postero-dorsal margin of the cavum tympani. Although Gaffney & Meylan (1992) indicated that a suture appeared to be present between the squamosal and the quadratojugal, this hypothesis is refuted here. The exposure of the jugal along the ventral margin of the skull is confirmed. However, the new material allows us to interpret that the exposure of the quadratojugal along that margin is significantly greater than that of the jugal. A more developed cheek emargination than that hitherto proposed is observed. The deformation of the most complete skull so far known prevents good knowledge of this structure (see Fig. 6C–D). The cheek emargination is generated in both the jugal and the quadratojugal.

The contact of the quadratojugal with the postorbital is relatively subhorizontal. Due to the arrangement of the other bones in that region, the quadratojugal contacts neither the parietal nor the squamosal.

None of the margins of the premaxilla of *K. bajazidi* are so far known. Gaffney & Meylan (1992) indicated that, although the margin forming the ventral limit of the premaxilla of the known specimens was damaged, a strong premaxillary hook or notch did not appear to be present. The identification of an undeformed skull allows us to recognize the presence of a medial notch, developed throughout the ventral margin of the premaxilla, and the anterior region of the maxilla. As indicated, the premaxillae constitute most of the osseous separation between both apertura narium externae, the nasal-premaxillary contact being located at the dorsal margin of this structure. The suture between the premaxilla and the maxilla is recognized here for the first time. The margins of the maxilla of *K. bajazidi*, except that with the jugal, were so far unknown. The prefrontal-maxilla contact, recognized here for the first time, is subhorizontal, contacting the posterodorsal margin of the apertura narium externa. The palatal region of both the premaxillae and the maxillae were not well known because the lower jaws hid that region in the only specimen in which it was preserved (i.e. NHMUK R4918). This region is observed here for the first time. Thus, the triturating surface is identified as wider than that interpreted by Gaffney & Meylan (1992) (see fig. 8 in Gaffney & Meylan, 1992). A paired foramen praepalatinum is recognized, being

located on the suture between the premaxillae and the vomer. The vomer lacks a well-developed medial crest. An accessory ridge is recognized for the first time on each maxillary triturating surface of *K. bajazidi*. This accessory ridge is low, not being developed in the anterior region of the maxilla. The palatines do not contribute to the triturating surface. The analysis of the new material allows us to confirm that *K. bajazidi* lacks a processus trochlearis pterygoidei. The only processus articularis of the quadrates so far preserved were those of specimen NHMUK R4918. However, because they were articulated to the lower jaw, the morphology of this structure was not well known. The articular surface of this process can be observed in specimen UBB ToK-2/1 (Fig. 2B). It is approximately two times wider than long, and longer laterally than medially. The improved knowledge about the variability of *K. bajazidi* allows us to characterize the morphology of the basisphenoid as ranging from subrectangular to triangular.

Very limited information on the cranial scutes of *K. bajazidi* has so far been available. Gaffney & Meylan (1992) recognized, on specimen NHMUK R4921 (see fig. 6 in Gaffney & Meylan, 1992), two large paired scutes roughly overlying the frontals and parietals, and meeting on the midline. Thus, they interpreted that the antero-lateral margin of the most anterior of these pairs of scutes overlapped to the prefrontals, that margin being oblique to the sagittal axis. The posterior limit of that pair of scutes was recognized as perpendicular to the sagittal axis, being located on the posterior region of the frontals. Its latero-posterior margin was subparallel to the antero-lateral margin of the postorbitals. This pair of scutes is well preserved in specimen UBB ToK-1/14 (Fig. 2M), and partially preserved in UBB ToK-2/1 (Fig. 2A). Both specimens show that, anteriorly, that pair of scutes overlaps the posterior half of the nasals. The revision of NHMUK R4921 allows us to identify the most posterior pair of scutes recognized by Gaffney & Meylan (1992) as more complex than hitherto interpreted. In fact, *K. bajazidi* not only has the two pairs of cranial scutes recognized by these authors. The specimen that allows the better observation of the cranial scutes is UBB ToK-1/14 (Fig. 2M). Three pairs of scutes, and also a posterior odd scute, are recognized in the sagittal plane. Variability in some of them is identified. Thus, the rearmost pair of medial scutes overlaps the postorbitals in the specimen UBB ToK-1/14 (Fig. 2M), but are in contact with the medial margin of these bones in UBB ToK-2/1 (Fig. 2A). The odd scute is noticeably wider in UBB ToK-1/14 (Fig. 2M) than in UBB ToK-2/1 (Fig. 2A). Laterally, more pairs of scutes are identified on the parietals and the postorbitals (Fig. 2M), but also a relatively small pair is located on the region of contact between the maxillae and the jugals (Fig. 2C–E).

Despite the limited information available, Gaffney & Meylan (1992) indicated that the cranial scute pattern in *K. bajazidi* is not particularly close to any other known pattern. This pattern is here confirmed as different to that present in the other basal turtles.

The lower jaws of *K. bajazidi* were poorly known. As Gaffney & Meylan (1992) indicated, the lower jaws of two specimens, NHMUK R4918 and NHMUK R4921, had been identified. Those of NHMUK R4918 are complete, but attached to the skull. Therefore, their dorsal surfaces are not available. But, in addition, both lower jaws of that specimen, as the posterior half of the right ramus identified in NHMUK R4921, are poorly preserved. Therefore, Gaffney & Meylan (1992) indicated that only a few sutures were apparent, and described none of them. The posterior halves of the two rami are well preserved in specimen UBB ToK-2 (Fig. 2G–L). All the sutures corresponding to preserved bones are recognized. The rami are very narrow but relatively high. The lingual margin of the dentary is slightly higher than the labial margin. Both margins lack well-developed crenulations. The triturating surfaces are narrow. The presence of a low accessory ridge in the maxilla implies the presence of a shallow depression on the dorsal surface of the dentary for its reception. No pits are present in the posterior region of the triturating surface. The dentary is very long in lateral view. It is the largest bone of the mandible. It reaches the articular, preventing the contact between the surangular and the angular. The angular lateral exposure is larger than that on the medial surface. Although a splenial has not been preserved in any of the jaws, its presence in *K. bajazidi* cannot be ruled out. The coronoid process is high. This bone has a short exposure in lateral view, in relation to its medial exposure. The main body of this bone is situated posterior to the triturating surface. The coronoid (anteriorly), surangular (laterally and postero-laterally) and prearticular (medially and postero-medially) define the margins of the fossa meckelii. A well-developed foramen intermandibularis caudalis is recognized on the suture between the angular and the prearticular. The foramen nervi auriculotemporalis has a smaller size and is located on the postero-dorsal area of the surangular. The area articularis mandibularis is long but narrow and consists of two facets separated by a distinct anteroposterior ridge. Gaffney & Meylan (1992) indicated that a retroarticular process seems to be absent. This hypothesis can be confirmed here.

Shell

The classic material of *K. bajazidi* did not allow a good understanding of the shell, due to its poor preservation, as well as to the fragmentary nature of most of the remains (see Nopcsa, 1923b; Gaffney & Meylan, 1992). Although the plastron was relatively well known, the morphology and arrangement of several elements of the shell were dubious or unknown (see Fig. 6E). Thus, the interpreted morphology of the nuchal region of *K. bajazidi* was problematic. Gaffney & Meylan (1992) indicated, as part of their amended diagnosis for this taxon, the presence of a small and unusual rectangular nuchal, contrasting with the larger and posteriorly wider nuchals recognized in most turtles (Fig. 6E). de Lapparent de Broin & Murelaga (1999) indicated that the shape of the nuchal was unclear, probably not having been well interpreted by Gaffney & Meylan (1992). The presence of a short and rectangular plate, in contact with the anterior margin of the shell, is confirmed here (Figs 3A, 5A–D, 6F). That bony element was recognized as a peripheral plate by Nopcsa (1923b) and as a neural by Rabi *et al.* (2013a). However, the presence of a nuchal plate divided into two elements is recognized here, this rectangular plate being identified as the anterior element. Thus, the posterior and larger element is excluded from the anterior margin of the carapace. This posterior element is wider than long, its morphology being subhexagonal. The latero-anterior margins of the posterior element are substraight, while the latero-posterior margins are subrounded. The suture between both elements is perpendicular to the axial plane. Although a nuchal notch is not present in *K. bajazidi*, a small medial indentation is medially observed, due to the contact between two marginal scutes. First-hand review of some previously figured specimens, such as that corresponding to figure 19.9a in the paper of Rabi *et al.* (2013a), allows us to recognize the suture between both elements, which is compatible with the interpretations in figure 1 of Nopcsa (1923b) and in figure 17 of Gaffney & Meylan (1992) (see Fig. 6E). Gaffney & Meylan (1992) noted that the neural series were not well preserved in the known specimens of *K. bajazidi*. However, they interpret that eight neurals are probably present in this taxon. This hypothesis is confirmed here, and the morphology of all neurals can be described for the first time. Thus, the first neural, whose morphology had not so far been clearly delimited (Fig. 6E), is identified as hexagonal, its latero-posterior margins being significantly shorter than the latero-anterior ones (Figs 3A, 5C, 6F). This plate is anomalous in specimen UBB NVK-31 (Fig. 5C), being divided into two elements. The second neural has erroneously been interpreted as hexagonal (see Gaffney & Meylan, 1992). This plate is recognized here as rectangular. The other neurals are identified as hexagonal, with the latero-anterior margins being shorter than the latero-posterior in the case of the anterior plates, but both margins being subequal in the posterior neurals, these plates being approximately as wide as long. As was indicated by Nopcsa

(1923b) and Gaffney & Meylan (1992), *K. bajazidi* has two suprapygals. However, although the first one is generally wider than the second, this condition does not occur in all individuals (e.g. the juvenile specimen UBB SPK3, see fig. 3C in Csiki-Sava *et al.*, 2010 and fig. 19.9a, b in Rabi *et al.*, 2013a). The new specimens allow us to confirm the presence of eight pairs of costal plates. Therefore, as indicated by Gaffney & Meylan (1992), the interpretation of the presence of nine pairs made by Nopcsa (1923b) can be refuted. As Gaffney & Meylan (1992) indicated, the peripheral plates of the classic specimens of *K. bajazidi* are poorly preserved. Thus, they interpreted that this taxon could have 11 pairs of peripherals. This hypothesis is confirmed here. Guttering peripherals are not present in this taxon. Neither the distal margins of the anterior peripherals nor those of the posterior are curved upward.

Kallokibotion bajazidi had been generally characterized by the presence of cervical scutes. Nopcsa (1923b) interpreted this taxon to have a pair of wider than long cervicals. Gaffney & Meylan (1992) recognized the presence of a probable single wide cervical. These authors did not rule out that this scute could be divided into two by a sagittal sulcus. The new specimens allow us to recognize the presence of a sagittal sulcus on the anterior area of the anterior element of the nuchal region. However, that sulcus does not delimit two cervicals, but separates the two scutes corresponding to the first pair of marginals. Thus, *K. bajazidi* lacks cervical scutes. This taxon has twelve pairs of marginals, the number of these pairs of scutes having been considered by Gaffney & Meylan (1992) to not be determinable. Gaffney & Meylan (1992) also suggested some alternative hypotheses, such as the presence of fused first and second marginals, or of a very small cervical scute, entirely on the nuchal plate, but obscured by the poor preservation. Both hypotheses are refuted here. The width/length ratio of the first pair of marginals of the known specimens of *K. bajazidi* is recognized as variable. Thus, these scutes are proportionally wider in UBB NVK-31 (Fig. 5C) than in UBB NVK-7 (Fig. 5A), both ratios being part of the range of intraspecific variability previously recognized for the classic specimens (see Gaffney & Meylan, 1992). The sulcus between the third and fourth vertebral scutes, previously represented as located on the sixth neural plate (see Gaffney & Meylan, 1992 and Fig. 6E), is reidentified as located on the fifth neural (Figs 3A, 5C, 6F). The lateral margins of most of the pleurals were not recognized by the study of the classic specimens (see Gaffney & Meylan, 1992). The new fossils allow us to observe that the marginal series does not contact the costal plates, the pleuro-marginal sulcus being located close to the costo-peripheral suture. The absence of supramarginal scutes in *K. bajazidi* is observed here.

de Lapparent de Broin & Murelaga (1999) indicate that the contact between the plates of the carapace and those of the plastron was probably ligamentous. The new specimens allow us to refute this hypothesis, a sutured contact being recognized between the bridge peripherals and the plastral plates. The absence of cleithrum is confirmed. Although Gaffney & Meylan (1992) indicated that the axillary buttresses anteriorly reach the middle region of the second peripherals and extend onto the costal series, this hypothesis was subsequently questioned by other authors (e.g. Sterli & de la Fuente, 2013). The new fossils allow us to support the hypothesis proposed by Gaffney & Meylan (1992). Similarly, the inguinal buttresses are identified as in contact with both the peripheral series (reaching the eighth peripherals) and the fifth costals. The discovery of new specimens of *K. bajazidi* shows a greater range of intraspecific variability in the morphology of the entoplastron than that hitherto known, ranging from subrounded (Fig. 3C) to subrombic (Fig. 5D). The new material *K. bajazidi* also provides greater variability on the medial distance between both mesoplastra. Thus, the revision of NHMUK R4930 confirms that the mesoplastra contact medially in this specimen, the distance between these plates being variable compared with other known plastra. The presence of a distinct anal notch is reinterpreted for this taxon (see Joyce, 2007).

Variability in the arrangement of the humero-pectoral sulcus is identified here. Thus, it contacts the entoplastron in some specimens or slightly overlaps the rearmost edge of this plate (Fig. 3C), while it is placed posterior to the entoplastron in others (e.g. UBB ToK-1/1 and fig. 18 in Gaffney & Meylan, 1992). The new specimens allow us to characterize the inframarginal series. It is composed of four pairs of scutes (Fig. 3C). The second scute is the shortest. The two anterior inframarginals, and a part of the third, overlap the hypoplastra. The posterior half part of this scute, and the anterior region of the fourth, overlap the mesoplastra.

Other elements of the dorsal and appendicular skeletons

Scarce information on the cervical vertebrae of *K. bajazidi* has been available so far. That information comes from two specimens. As Gaffney & Meylan (1992) indicated, NHMUK R4916 has the sixth to eighth cervicals *in situ*, with the ventral areas free of matrix, but the dorsal surfaces are not accessible (see plate 1.18 in Nopcsa, 1923b). Therefore, a very limited number of characters are known. Nopcsa (1923b) identified six cervicals in the specimen NHMUK R4921, identified by him as the second, third and fifth to eighth cervicals. In all of them, except that recognized as the third

one, the centrum only was preserved. Considering the limited availability of characters, Gaffney & Meylan (1992) questioned the position of these elements, indicating that the vertebra identified by Nopcsa (1923b) as a third cervical could correspond to a most posterior cervical. This hypothesis is supported here by the study of several almost complete and well-preserved cervicals corresponding to the specimen UBB ToK-2 (Fig. 4A–K). These new vertebrae correspond to the axis, UBB ToK-2/8 (Fig. 4A–F), and to the three last cervicals (Fig. 4G–K). All preserved cervical centra exhibit an amphicoelous pattern, confirming the previous observations made by Gaffney & Meylan (1992). The centres are significantly higher than wide, especially those of the posterior cervical, being relatively narrow. The articulation between the axis and the vertebra with which it was in contact slopes strongly towards the anterior region. However, that with the posterior vertebra is subvertical. The anterior articulation of the axis is subtriangular, being noticeably wider dorsally than ventrally. Its posterior articulation is subrectangular, being slightly wider ventrally than dorsally. The posterior articulation of the eighth cervical is also triangular, and its width is slightly less than that of its anterior articulation. The length of the seventh cervical centrum is greater than that of both the sixth and the eighth. The presence of a low ventral keel is confirmed. It is present along the entire cervical series. The transverse processes are short, being located near the midline of the centra. They are laterally oriented in the second cervical, but slightly directed towards the posterior region in the last cervicals. In dorsal view, the neural arch of the axis forms a Y-shaped dorsal structure, slightly longer than wide. In ventral view, the cervical vertebrae are hourglass shaped. The neural arches of both the anterior and the posterior cervicals are very high, the height being greater than the length of the cervical centrum. Due to the height of the neural arches, especially those corresponding to the posterior cervicals, their prezygapophyses are very long. The articular surfaces of both the prezygapophyses and the postzygapophyses are well developed in all the vertebrae. Those of the postzygapophyses of the eighth cervical are subhorizontal. The inclination of these articular surfaces increases towards the anterior region of the cervical series. The prezygapophyses of all the vertebrae are widely separate from one another. However, the postzygapophyses of the eighth cervical are united in a single structure. The length of the neural spine, and also its height above the postzygapophysis, increases from the sixth to the eighth cervicals.

Two articulated thoracic vertebrae are recognized (Fig. 4M–P). These elements are very narrow. The neural spines are relatively high. A well-developed medial keel is present.

The shoulder girdle is a triradiate element (Figs 3D, 4W, AT–AU, AZ–BA). The scapula is sutured with the coracoid. The neck of the glenoid is relatively short. The scapula is a relatively robust bone. The scapular and acromial processes of the scapula are rod-shaped, both being elliptical in section. These elements are distally striated and are slightly curved. The scapular process is the longest, its length being about 1.5 times that of the acromial process. The angle between the two processes of the scapula is approximately 120°. A poorly developed bony surface connects both processes.

Both the ulna and the radius of *K. bajazidi* are identified here for the first time (Fig. 4AB–AK). The ulna is slightly longer than the radius. The olecranon process is well developed. The proximal articulation of the ulna constitutes a concave articular surface for the humerus. The morphology of this surface is symmetrical, with a long and elliptical expansion, ventrally directed. However, the proximal articulation of the radius corresponds to a subrounded surface, its width being slightly greater than its length. This articular surface is slightly concave. The articulation of the ulna is wider than that of the radius. The shaft of the ulna is triangular in cross section. The distal articular surface with the radius is very short. The distal surface for the articulation with the intermedium is shorter than that of the radius with this bone, being substraight. The lateral facet for the articulation with the ulnare is short and subrounded. In lateral view, the ulna is slightly curved. The radius is almost straight. This bone is more slender than the ulna. The shaft of the radius is almost circular in cross section. The distal part is very wide and has a relatively convex and long surface with the intermedium, and a short rounded surface with, at least, the medial centrale. Thus, these bones constitute a rounded surface for the articulation with the humerus, and a V-shaped distal surface for the articulation with the manus. When articulated, the radius and ulna are not at the same level. Thus, the proximal part is asymmetric, to articulate with the distal region of the humerus, but also the distal part is markedly asymmetric. The radius and the ulna delimit a relatively long fenestra between them, clearly divided into two parts by the presence of a well-developed medial process in the middle part of the diaphysis of the ulna (i.e. the bicipital tubercle), which corresponds to the region for the attachment of the bicipital tendon. Thus, an inverted teardrop shape is developed below this process. The fenestra is very narrow above this process.

Although a fragment of tibia of a classic specimen was known (NHMUK R4921), the preservation of the proximal region is better in specimen ToK-2/20 (Fig. 4A L–AO). It is a robust element. Its proximal articular surface is subelliptical.

Several well-preserved and complete humeri and femora were recognized among the classic specimens of *K. bajazidi*. These elements were figured and described in detail by Nopcsa (1923b) and Gaffney & Meylan (1992) (see plate III 1–11 in Nopcsa, 1923b and figs 30, 31 in Gaffney & Meylan, 1992). Therefore, the new specimens identified here (see Fig. 4Q–V, AP–AS, AV–AY) do not provide additional new characters nor refute the previous considerations.

Several disjointed unguals of specimen ToK-2 are preserved (Fig. 4X–AA). These bones were not hitherto identified in *K. bajazidi*. All of them are slightly recurved elements. These phalanges are narrow but relatively long. The proximal articular surface is concave. Distally, they form pointed tips. A claw was present on each of these elements.

DISCUSSION

IDENTIFICATION OF A SINGLE VALID SPECIES FOR *KALLOKIBOTION*

Nopcsa (1923b) distinguished two species from the same horizon and locality, *K. bajazidi* and '*Kallokibotium magnificum*'. However, Gaffney & Meylan (1992) indicated that the examination of the few characters proposed by Nopcsa (1923b) for the distinction between both species, in the broader context of variation within the turtle species, gives little support for the recognition of two taxa.

One of the characters recognized by Nopcsa (1923b) as different between both species was the morphology, number, width and disposition of the scutes located on the anterior margin of the carapace. Nopcsa (1923b) recognized a wide cervical scute in *K. bajazidi* (see fig. 1 in Nopcsa, 1923b), but the presence of a sagittal sulcus in '*K. magnificum*' (see fig. 3 in Nopcsa, 1923b). The first hand review of both specimens allows us to confirm that, as in the new carapaces of *K. bajazidi* presented here and in the other classic specimens, a cervical scute is absent, the sagittal sulcus between two marginal scutes being present. These marginals are always wider than long, but, as previously indicated, the ratio between these two dimensions is variable when different specimens are compared (see, for example, the specimens in Figs 3A, 5C).

As justified by Gaffney & Meylan (1992), the differences in the ratio between the width and length of the third vertebral scutes among specimens compared by Nopcsa (1923b) are very small, being compatible with the minor differences in shape that commonly vary intraspecifically in both extant and extinct species. The finding of new specimens allows us to further expand the range of variability known for this character in *K. bajazidi*.

Although Nopcsa (1923b) indicated in the diagnosis of '*K. magnificum*' that the posterior outline of the last vertebral scute was strongly convex, the revision of its holotype and only individual attributed to this species (see fig. 3 in Nopcsa, 1923b) allows us to recognize that the posterior margin of this scute was misinterpreted by Nopcsa (1923b). Thus, this sulcus is located in a rearmost position, in contact with the marginal series, and lacking that marked convexity. Its path is compatible with the known variability for this sulcus in *K. bajazidi*.

The presence of a medial contact between both mesoplastra of the holotype of '*K. magnificum*', proposed by Nopcsa (1923b), was considered as ambiguous by Gaffney & Meylan (1992). Although this contact was recognized here as present, it was shorter than that represented in figure 4 of Nopcsa (1923b). Variability in the distance between the mesoplastra is recognized comparing other specimens of *K. bajazidi*, that distance being significantly higher in NHMUK R11178 than in UBB ToK-2/4, in which both mesoplastra are very close to each other. Gaffney & Meylan (1992) indicated that individual variation in this character was probably present in this taxon, a hypothesis supported here. Thus, the revision of the type material of '*K. magnificum*', that of *K. bajazidi*, and all the classic material analysed by Nopcsa (1923a, b) and Gaffney & Meylan (1992), together with the study of the new specimens, allows us to confirm that they all belong to a single species, *K. bajazidi*, the validity of '*K. magnificum*' being refuted.

PHYLOGENETIC POSITION OF *KALLOKIBOTION BAJAZIDI*

The better understanding of the cranial and postcranial anatomy of *K. bajazidi* allows us to re-evaluate its phylogenetic position. As indicated, *K. bajazidi* was recognized as a member of Meiolaniformes in several recently published papers (see Rabi *et al.*, 2013b; Sterli & de la Fuente, 2013; Sterli *et al.*, 2015a, b). This clade was defined by Sterli & de la Fuente (2013) as the branch-based clade that includes all the taxa more closely related to *Me. platyceps* than to Cryptodira or Pleurodira. The new information about *K. bajazidi* presented here allows us to observe that it does not share several of the characters proposed by Sterli & de la Fuente (2013) for the diagnosis of this clade (e.g. the presence of a well-developed crista occipitalis, protruding significantly posterior to the foramen magnum). Sterli (2015) revised the diagnosis of the clade Meiolaniformes, including five new characters: presence of a ventral crest on the vomer, formed cervical vertebrae, opisthocoelous vertebrae in the anterior part of the tail, randomly distributed small pits on

the surface of the dermal bones of the skull and shell, and anteriorly inflected marginal scute sulci along the carapacial margin. The revision of *K. bajazidi* allows us to observe that none of these characters is shared with this taxon. Sterli (2015) indicated that the allocation of *K. bajazidi* and other Laurasiatic taxa to Meiolaniformes, a clade composed of unambiguous Gondwanan forms, should be revised in future works. None of the cladistic analyses performed here support its attribution to Meiolaniformes. The analyses performed considering the new encoding for *K. bajazidi* in the data matrix proposed by Sterli *et al.* (2015a) resulted in 13 000 most parsimonious trees, with a length of 898 steps (consistency index = 0.335; retention index = 0.766; rescaled consistency index = 0.257) (Fig. 7A, B). *Kallokibotion bajazidi* is not identified as a representative of Meiolaniformes, but as a member of its sister group. *Kallokibotion bajazidi* is obtained as part of a large polytomy in the analysis considering all taxa (Fig. 7A). However, it is recognized as the sister taxon of Testudines in the reduced consensus tree (Fig. 7B), *K. bajazidi* being defined by: external nares divided (character 32, state 0); labial, lingual and accessory ridges present (character 40, state 2); absence of vomer-pterygoid contact (character 43, state 1); processus pterygoideus externus like in testudinoids (character 70, state 1); tightly sutured prootic (character 78, state 1); neural formula 6 > 4 < 6 < 6 < 6 < 6 present (character 129, state 1); musk ducts absent (character 132, state 0); cervical scute absent (character 138, state 1); anal notch present (character 163, state 1); centrum of the seventh cervical longer than that of the eighth (character 185, state 1); and length of the humerus two times or less than the width of the proximal end (character 220, state 0).

The phylogenetic analyses performed with the new encoding for *K. bajazidi* in the data matrix proposed by Joyce *et al.* (2016) resulted in 4600 most parsimonious trees, with a length of 933 steps (consistency index = 0.319; retention index = 0.771; rescaled consistency index = 0.246) (Fig. 7C, D). *Kallokibotion bajazidi* is also obtained as the sister taxon of Testudines. In both trees, *K. bajazidi* is characterized by several of the characters recognized in the analyses based on the data matrix of Sterli *et al.* (2015a) [i.e. external nares divided (character 32, state 0); labial, lingual and accessory ridges present (character 39, state 2); neural formula 6 > 4 < 6 < 6 < 6 < 6 present (character 117, state 1); cervical scute absent (character 126, state 0); anal notch present (character 150, state 1); centrum of the seventh cervical longer than that of the eighth (character 172, state 1); and length of the humerus two times or less than the width of the proximal end (character 204, state 0)], as well as by a large prefrontal exposure (character 7, state 0) and the dorsal exposure

of the prootic reduced or absent (character 72, state 1). In addition, it is also recognized by the absence of vomer-pterygoid contact (character 42, state 1) when the wildcard taxa are excluded, as in the analyses based on the data matrix of Sterli *et al.* (2015a).

Therefore, *K. bajazidi* is obtained neither as a member of Meiolaniformes nor as a representative of Testudines (*sensu* Joyce, 2007) in any of these analyses. The consideration of two solemydids in the analyses based on the data matrix proposed by Joyce *et al.* (2016) confirms the position of Solemydidae as the sister group of the clade composed of *K. bajazidi* and Testudines. The detailed study of other forms probably closely related to *K. bajazidi* (i.e. a new taxon from the Paleocene of France currently under study, see Pérez-García, 2013), as well as the inclusion of other members of Solemydidae in these phylogenetic hypotheses (including well-preserved unpublished specimens, among them several skulls and relatively complete skeletons from the Lower and Upper Cretaceous of southwestern Europe, currently under study), will probably improve the understanding of the phylogenetic relationships among the most derived forms of the stem group of Testudines.

CONCLUSIONS

Kallokibotion is a relatively abundant basal turtle (stem Testudines) in the Maastrichtian continental deposits of the 'Haţeg Island' (Romania). It has not been recognized outside this region of the European uppermost Cretaceous archipelago. However, knowledge about this form was relatively limited, and several previous anatomical interpretations are recognized here as erroneous. *Kallokibotion* was described almost a century ago from several specimens, generally poorly preserved (Nopcsa, 1923a, b). Although the classic material was subsequently revised, especially by Gaffney & Meylan (1992), *Kallokibotion* remained as an enigmatic taxon, difficult to compare with other turtles because of the relatively limited number of characters available in these specimens. Although new material was subsequently found, these remains were not described in detail. Well-preserved new material from two sites near its type locality, Totești and Nălaţ-Vad, both in the Haţeg Basin, is presented here. The new specimens correspond to a relatively complete skeleton (including the skull; the lower jaws; most elements of the shell; cervical, dorsal and caudal vertebrae; elements of both girdles; and several appendicular bones), a partial skeleton (preserving the partial skull and shell, and bones of the scapular girdle and of the forelimbs) and almost complete shell of adult specimens, as well as a partial carapace of a juvenile specimen.
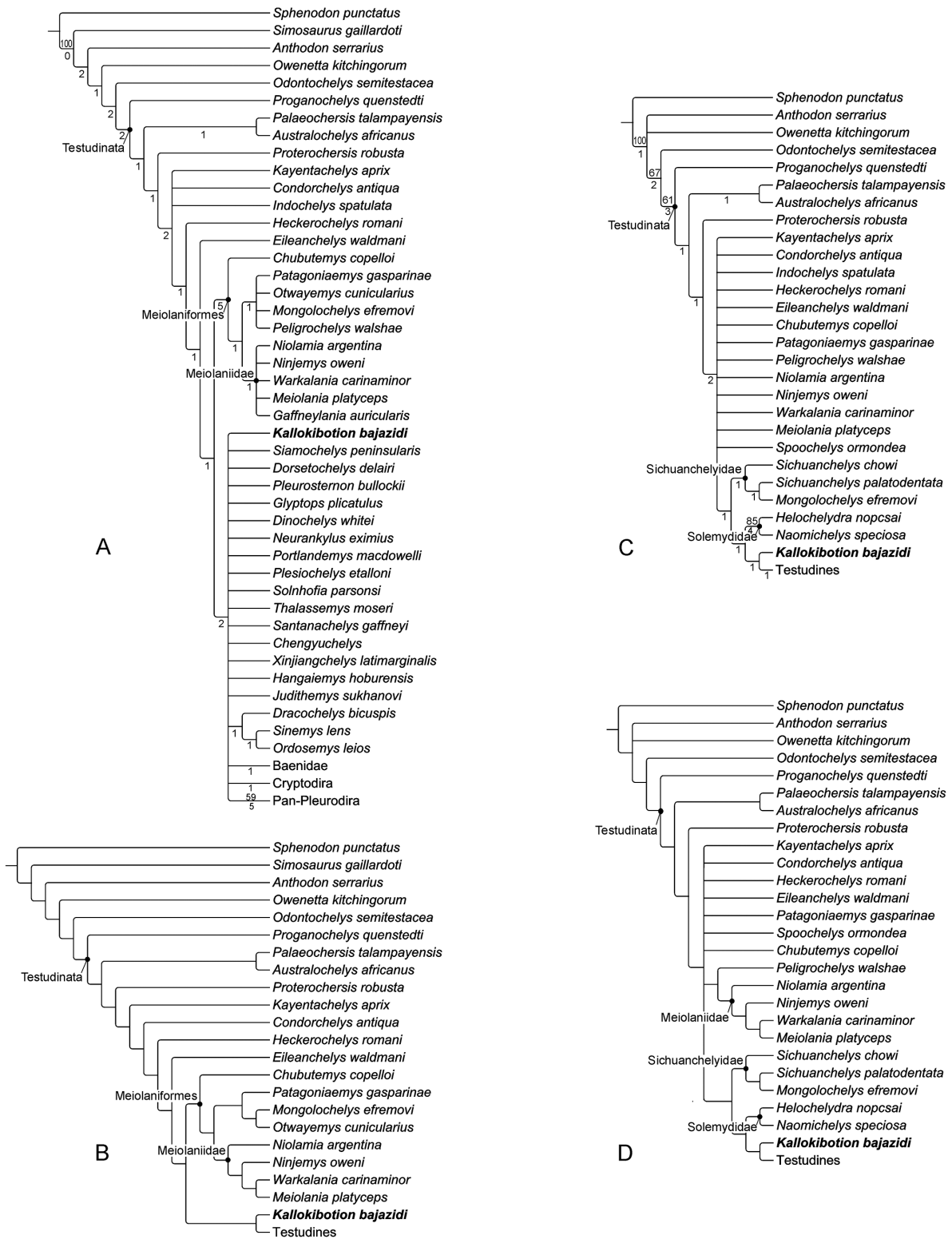
Figure 7. Phylogenetic position of *Kallokibotion bajazidi* obtained by the cladistic analyses performed here. A, strict consensus tree based on the data matrix of Sterli *et al.* (2015a). B, pruned strict consensus tree based on the data matrix of Sterli *et al.* (2015a). C, strict consensus tree based on the data matrix of Joyce *et al.* (2016). D, pruned strict consensus tree based on the data matrix of Joyce *et al.* (2016). Bootstrap frequencies that exceed 50% (top) and Bremer support values (bottom) are indicated.

The new specimens presented and studied in this paper allow us not only to know in detail numerous anatomical elements so far poorly known due to the preservation of the classic material but also to identify several unknown characters (Fig. 6). The study of a complete and undeformed skull, and that of a skull roof, allows us to observe sutures and sulci hitherto not preserved. The skull morphology of *Kallokibotion*, as well as that of many of the cranial bones, is reinterpreted. Furthermore, intraspecific variability in the morphology and arrangement of several cranial scutes and bones is recognized (e.g. absence or presence of a prefrontal-postorbital contact; oblique to subrounded frontal-parietal sutures; lateral margins of the parietals slightly convergent to markedly divergent towards the posterior region; subrectangular to triangular basisphenoid; rearmost pair of medial cranial scutes overlapping or not the postorbitals; posterior odd cranial scute more or less wide). The study of the relatively complete and well-preserved lower jaws of the new specimen in which the most complete skull is preserved allows us to recognize numerous previously unknown sutures in *Kallokibotion*. The classic material did not allow a good understanding of the shell of this taxon, especially of its carapace. The morphology of the shell, as well as the number, morphology and disposition of all plates and scutes of the carapace of *Kallokibotion*, is described here. Variability in several elements of the carapace is also recognized (e.g. that described for the first suprapygal and the first pair of marginals). In addition, poorly known characters for its plastron, the morphological variability of some bony elements (e.g. the entoplastron and the mesoplastra), knowledge of the arrangement and variability of some sulci (e.g. the arrangement of the inframarginal series, and the relationship between the humero-pectoral sulcus and the entoplastron), are also analysed. The recognized intraspecific variability cannot be justified by the ontogeny. It probably corresponds to individual variability. The identification of an almost complete axis and the study of the posterior cervical vertebrae (only observable in ventral view for the classic specimens) provide a better understanding of the cervical series. Appendicular elements hitherto unknown (e.g. the ulna and the radius) are also presented here.

Some of the new characters here identified for *Kallokibotion* in relation to those recognized by Gaffney & Meylan (1992) in their revision of this taxon are as follows: the presence of contact between the nasals and the prefrontals, preventing that between the frontals and the maxillae; identification of the postorbital as large, contacting the squamosal; cheek emargination, generated by both the jugal and the quadratojugal; absence of quadratojugal-parietal and quadratojugal-squamosal contacts; accessory ridge on the maxillary triturating surface; dentary-articular suture, preventing the surangular-angular contact; identification of an exclusive nuchal disposition, the nuchal area being composed of two elements, the most anterior being smaller and rectangular, and the other hexagonal and wider than long; 12 pairs of marginals; and absence of contact of the marginal series with the costal plates. Several previous hypotheses about the anatomy of this taxon are refuted. Thus, some of the new character states here recognized are as follows: the orbits are identified as more laterally positioned than previously interpreted; the apertura narium externae is recognized as larger; the premaxillae constitute most of the internarial process; the nasals are identified as relatively wide elements; the prefrontals are in contact with the apertura narium externae; the squamosals are not in contact with the quadratojugals; the morphology and disposition of the cranial scutes are reinterpreted, being recognized as exclusive for this taxon; cervical scutes are absent; the sulcus between the third and fourth vertebrals is located on the fifth neural; and a sutured contact is present between the carapace and the plastron. In addition, some previous hypotheses based on poorly known characters for *Kallokibotion* are here confirmed, such as the presence of a parietal-squamosal contact; the absence of an exposure of the supraoccipital on the dorsal surface of the skull roof; the absence of retroarticular process; the presence of eight plates composing the neural series (the morphology of these elements being reinterpreted here); and the presence of 11 pairs of peripherals.

Thus, the cranial and postcranial anatomy of *Kallokibotion* is now well known, and this taxon is recognized here as one of the best-characterized stem Testudines. The anatomical characters described for the first time in this paper for *Kallokibotion*, as well as those reinterpreted, have been compared to those of other representatives of the stem group of Testudines. As a result, a new diagnosis for *K. bajazidi* (a taxon justified here as the only valid species of this genus) has been proposed.

Kallokibotion bajazidi is a taxon frequently included in general phylogenetic hypotheses about the relationships among the members of Testudinata, and in analyses trying to establish a hypothesis about the phylogenetic relationships among the basal forms. As a result of these analyses, the phylogenetic position of *Kallokibotion* was under discussion, because it was obtained as being part of different clades (e.g. as a member of Meiolaniformes, as a representative of Paracryptodira and as the sister taxon of the crown Testudines). The study of this taxon performed here allows us to recode many of the previously considered characters, as well as encode other characters hitherto unknown. The phylogenetic analyses performed here show *K. bajazidi* as a member of the stem group of

Testudines, being recognized as closely related to the crown Testudines.

REFERENCES

Ameghino F. 1899. *Sinopsis geológica-paleontológica*. La Plata: Censo Nacional.

Anquetin J. 2010. The anatomy of the basal turtle *Eileanchelys waldmani* from the Middle Jurassic of the Isle of Skye, Scotland. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **101:** 67–96.

Anquetin J. 2011. Reassessment of the phylogenetic interrelationships of basal turtles (Testudinata). *Journal of Systematic Palaeontology* **10:** 3–45.

Anquetin J, Barrett PM, Jones MEH, Moore-Fay S, Evans SE. 2008. A new stem turtle from the Middle Jurassic of Scotland: new insights into the evolution and palaeoecology of basal turtles. *Proceedings of the Royal Society of London B: Biological Sciences* **278:** 879–886.

Baur G. 1887. Ueber den ursprung der extremitäten der ichthyopterygia. *Berichte Über de Versammlungen des Oberrheinischen Vereines* **20:** 17–20.

Codrea V, Smith T, Dica P, Folie A, Garcia G, Godefroit P, Van Itterbeeck J. 2002. Dinosaur egg nests, mammals and other vertebrates from a new Maastrichtian site of the Haţeg Basin (Romania). *Comptes Rendus Palevol* **1:** 173–180.

Csiki-Sava Z, Grigorescu D, Codrea V, Therrien F. 2010. Taphonomic modes in the Maastrichtian continental deposits of the Haţeg Basin, Romania–Palaeoecological and palaeobiological inferences. *Palaeogeography, Palaeoclimatology, Palaeoecology* **293:** 375–390.

Csiki-Sava Z, Vremir M, Vasile S, Brusatte SL, Dyke G, Naish D, Norell MA, Totoianu R. 2015. The East Side Story – the Transylvanian latest Cretaceous continental vertebrate record and its implications for understanding Cretaceous-Paleogene boundary events. *Cretaceous Research* **57:** 662–698.

Datta PM, Manna P, Ghosh SC, Das DP. 2000. The first Jurassic turtle from India. *Palaeontology* **43:** 99–109.

de Lapparent de Broin F. 2004. A new Shachemydinae (Chelonii, Cryptodira) from the Lower Cretaceous of Laos: preliminary data. *Comptes Rendus Palevol* **3:** 387–396.

de Lapparent de Broin F, Murelaga X. 1996. Une nouvelle faune de chéloniens dans le Crétacé supérieur européen. *Comptes Rendus de l'Academie des Sciences Paris* **323:** 729–735.

de Lapparent de Broin F, Murelaga, X. 1999. Turtles from Upper Cretaceous of Laño (Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Álava* **14:** 135–211.

Fraas E. 1913. *Proterochersis*, eine pleurodire Schildkröte aus dem Keuper. *Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg* **69:** 13–30.

Gaffney ES. 1979. The Jurassic turtles of North America. *Bulletin of the American Museum of Natural History* **162:** 93–135.

Gaffney ES. 1983. The cranial morphology of the extinct horned turtle, *Meiolania platyceps*, from the Pleistocene of Lord Howe Island, Australia. *Bulletin of the American Museum of Natural History* **175:** 361–480.

Gaffney ES. 1985. The cervical and caudal vertebrae of the cryptodiran turtle, *Melolania platyceps*, from the Pleistocene of Lord Howe Island, Australia. *American Museum Novitates* **2805:** 1–29.

Gaffney ES. 1992. *Ninjemys*, a new name for '*Melolania*' *oweni* (Woodward), a horned turtle from the Pleistocene of Queensland. *American Museum Novitates* **3049:** 1–10.

Gaffney ES. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History* **194:** 1–263.

Gaffney ES. 1996. The postcranial morphology of *Meiolania platyceps* and a review of the Meiolaniidae. *Bulletin of the American Museum of Natural History* **229:** 1–166.

Gaffney ES, Hutchison JH, Jenkins FA Jr, Meeker LJ. 1987. Modern turtle origins: the oldest known cryptodire. *Science* **237:** 289–291.

Gaffney ES, Jenkins FA. 2010. The cranial morphology of *Kayentachelys*, an Early Jurassic cryptodire, and the early history of turtles. *Acta Zoologica* **91:** 335–368.

Gaffney ES, Kitching JW. 1994. The most ancient African turtle. *Nature* **369:** 55–58.

Gaffney ES, Kitching JW. 1995. The morphology and relationships of *Australochelys*, an Early Jurassic turtle from South Africa. *American Museum Novitates* **3130:** 1–29.

Gaffney ES, Kool L, Brinkman DB, Rich TH, Vickers-Rich P. 1998. *Otwayemys*, a new cryptodiran turtle from the

Early Cretaceous of Australia. *American Museum Novitates* **3233:** 1–28.

Gaffney ES, Meylan PA. 1992. The Transylvanian turtle, *Kallokibotion*, a primitive Cryptodire of Cretaceous Age. *American Museum Novitates* **3040:** 1–37.

Gaffney ES, Rich TH, Vickers-Rich P, Constantine A, Vacca R, Kool L. 2007. *Chubutemys*, a new eucryptodiran turtle from the Early Cretaceous of Argentina, and the relationships of the Meiolaniidae. *American Museum Novitates* **3599:** 1–35.

Gaffney ES, Tong H, Meylan PA. 2006. Evolution of the side-necked turtles: the families Bothremydidae, Euraxemydidae, and Araripemydidae. *Bulletin of the American Museum of Natural History* **300:** 1–700.

Goloboff PA, Farris JS, Nixon KC. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* **24:** 774–786.

Hay OP. 1908. *The fossil turtles of North America*. Washington: Publications of the Carnegie Institution of Washington.

Hirayama R, Brinkman DB, Danilov IG. 2000. Distribution and biogeography of non-marine Cretaceous turtles. *Russian Journal of Herpetology* **7:** 181–198.

Klein IT. 1760. *Klassification und kurze Geschichte der vierfüßigen Thiere*. Lübeck: Jonas Schmidt.

Joyce WG. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History* **48:** 3–102.

Joyce WG, Chapman SD, Moody RTJ, Walker CA. 2011. The skull of the solemydid turtle *Helochelydra nopcsai* from the Early Cretaceous of the Isle of Wight (UK) and a review of Solemydidae. *Special Papers in Palaeontology* **86:** 75–97.

Joyce WG, Rabi M, Clark JM, Xu X. 2016. A toothed turtle from the Late Jurassic of China and the global biogeographic history of turtles. *BMC Evolutionary Biology* **16:** 236.

Joyce WG, Sterli J, Chapman SD. 2014. The skeletal morphology of the solemydid turtle *Naomichelys speciosa* from the Early Cretaceous of Texas. *Journal of Paleontology* **88:** 1257–1287.

Khozatsky LI. 1997. Large turtles from the Late Cretaceous of Mongolia. *Russian Journal of Herpetology* **4:** 148–154.

Li C, Wu XC, Rieppel O, Wang LT, Zhao LJ. 2008. An ancestral turtle from the Late Triassic of southwestern China. *Nature* **456:** 497–501.

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*). *Quarterly Journal of the Geological Society* **79:** 100–116.

Nopcsa F. 1923b. *Kallokibotium*, a primitive amphichelydean tortoise from the uppermost Cretaceous of Hungary. *Palaeontologia Hungarica* **1:** 1–34.

Ortega F, Bardet N, Barroso-Barcenilla F, Callapez PM, Cambra-Moo O, Daviero-Gómez V, Díez-Díaz V, Elvira A, Escaso F, García-Oliva M, Gómez B, Houssaye A, Knoll F, Marcos-Fernández F. Martín M, Narváez I, Pérez-García A, Serrano H, Torices A, Vidal D, Sanz JL. 2015. The biota of the Upper Cretaceous site of "Lo Hueco" (Cuenca, Spain). *Journal of Iberian Geology* **41:** 83–99.

Owen R. 1886. Description of some fossil remains of two species of a Megalanian genus (*Meiolania*) from "Lord Howe's Island". *Philosophical Transactions of the Royal Society of London B* **179:** 181–191.

Pereda Suberbiola X. 2009. Biogeographical affinities of Late Cretaceous continental tetrapods of Europe: a review. *Bulletin de la Société Géologique de France* **180:** 57–71.

Pereda Suberbiola X, Corral JC, Astibia H, Badiola A, Bardet N, Berreteaga A, Buffetaut E, Buscalioni AD, Cappetta H, Cavin, L, Díez Díaz V, Gheerbrant E, Murelaga X, Ortega F, Pérez-García A, Poyato F, Rage J-C, Sanz JL, Torices A. 2015. Late cretaceous continental and marine vertebrate assemblages from the Laño quarry (Basque-Cantabrian Region, Iberian Peninsula): an update. *Journal of Iberian Geology* **41:** 101–124.

Pérez-García A. 2012a. High diversity of pancryptodiran turtles in the Lower Cretaceous of Europe. *Cretaceous Research* **36:** 67–82.

Pérez-García A. 2012b. The European Lower Cretaceous *Chitracephalus dumonii* (Testudines: Cryptodira) and the diversity of a poorly known lineage of turtles. *Acta Palaeontologica Polonica* **57:** 575–588.

Pérez-García A. 2013. Did the Cretaceous-Paleocene extinction event cause the extinction of the lineages of primitive turtles (stem Testudines) from the Mesozoic of Europe? In: Torcida Fernández-Baldor F, Huerta P, eds. *Abstract book of the VI International Symposium about Dinosaurs Palaeontology and their Environment*. Salas de los Infantes: Colectivo Arqueológico y Paleontológico de Salas de los Infantes, 112–114.

Pérez-García A, Gasulla JM, Ortega F. 2014. A new species of *Brodiechelys* (Testudines, Pan-Cryptodira) from the Early Cretaceous of Spain: systematic and palaeobiogeographic implications. *Acta Palaeontologica Polonica* **59:** 333–342.

Pérez-García A, Murelaga X. 2012a. *Larachelus morla* gen. et sp. nov., a new member of the little-known European Early Cretaceous record of stem cryptodiran turtles. *Journal of Vertebrate Paleontology* **32:** 1293–1302.

Pérez-García A, Murelaga X. 2012b. *Galvechelone lopezmartinezae* gen. et sp. nov., a new cryptodiran turtle in the Lower Cretaceous of Europe. *Palaeontology* **55:** 937–944.

Pérez-García A, Murelaga X. 2013. *Camerochelys vilanovai* gen. et sp. nov., a new pan-cryptodiran turtle in the Early Cretaceous of the Iberian Range (Spain). *Cretaceous Research* **41:** 143–149.

Pérez-García A, Ortega F, Bolet A, Escaso F, Houssaye A, Martínez-Salanova J, de Miguel Chaves C, Mocho P, Narváez I, Segura M, Torices A, Vidal D, Sanz JL. 2016. A review of the upper Campanian vertebrate site of Armuña (Segovia Province, Spain). *Cretaceous Research* **57:** 591–623.

Pérez-García A, Ortega F, Murelaga X. 2012a. A new genus of Bothremydidae (Chelonii, Pleurodira) in the Cretaceous of Southwestern Europe. *Geobios* **45:** 219–229.

Pérez-García A, Scheyer TM, Murelaga X. 2012b. New interpretations of *Dortoka vasconica* Lapparent de Broin and Murelaga, a freshwater turtle with an unusual carapace. *Cretaceous Research* **36:** 151–161.

Rabi M, Vremir M, Tong H. 2013a. Preliminary overview of Late Cretaceous turtle diversity in Eastern Central Europe (Austria, Hungary, and Romania). In: Brinkman D, Holroyd P, Gardner J, eds. *Morphology and evolution of turtles*. The Nederland: Vertebrate Paleobiology and Paleoanthropology. Dordrecht: Springer, 251–259.

Rabi M, Zhou CF, Wings O, Ge S, Joyce WG. 2013b. A new xinjiangchelyid turtle from the Middle Jurassic of Xinjiang, China and the evolution of the basipterygoid process in Mesozoic turtles. *BMC Evolutionary Biology* **13:** 203.

Rougier GW, de la Fuente MS, Arcucci AB. 1995. Late Triassic turtles from South America. *Science* **268:** 855–858.

Scheyer T, Pérez-García A, Murelaga X. 2015. Shell bone histology of solemydid turtles (stem Testudines): palaeoecological implications. *Organisms Diversity and Evolution* **15:** 199–212.

Smith T, Codrea V, Săsăran E, Van Itterbeeck J, Bultynck P, Csiki Z, Dica P, Fărcaş C, Folie A, Garcia G, Godefroit P. 2002. A new exceptional vertebrate site from the Late Cretaceous of the Haţeg Basin (Romania). *Studia Universitatis Babeş-Bolyai, Geologia* **1:** 321–330.

Sterli J. 2008. A new, nearly complete stem turtle from the Jurassic of South America with implications for turtle evolution. *Biology Letters* **4:** 286–289.

Sterli J. 2010. Phylogenetic relationships among extinct and extant turtles: the position of Pleurodira and the effect of the fossil on rooting crown group turtles. *Contributions to Zoology* **79:** 93–106.

Sterli J. 2015. A review of the fossil record of Gondwanan turtles of the clade Meiolaniformes. *Bulletin of the Peabody Museum of Natural History* **56:** 21–45.

Sterli J, de la Fuente MS. 2010. Anatomy of *Condorchelys antiqua* Sterli, 2008, and the origin of the modern jaw closure mechanism in turtles. *Journal of Vertebrate Paleontology* **30:** 351–366.

Sterli J, de la Fuente MS. 2011a. A new turtle from the La Colonia Formation (Campanian–Maastrichtian), Patagonia, Argentina, with remarks on the evolution of the vertebral column in turtles. *Palaeontology* **54:** 63–78.

Sterli J, de la Fuente MS. 2011b. Re-description and evolutionary remarks on the Patagonian horned turtle *Niolamia argentina* Ameghino, 1899 (Testudinata; Meiolaniidae). *Journal of Vertebrate Paleontology* **31:** 1210–1229.

Sterli J, de la Fuente MS. 2013. New evidence from the Palaeocene of Patagonia (Argentina) on the evolution and palaeo-biogeography of Meiolaniformes (Testudinata, new taxon name). *Journal of Systematic Palaeontology* **11:** 835–852.

Sterli J, Joyce WG. 2007. The cranial anatomy of the Early Jurassic turtle. *Kayentachelys aprix. Acta Palaeonto–logica Polonica*. **52(4):** 675–694.

Sterli J, de la Fuente MS, Krause JM. 2015a. A new turtle from the Palaeogene of Patagonia (Argentina) sheds new light on the diversity and evolution of the bizarre clade of horned turtles (Meiolaniidae, Testudinata). *Zoological Journal of the Linnean Society* **174:** 519–548.

Sterli J, de la Fuente MS, Rougier GW. 2007. Anatomy and relationships of *Palaeochersis talampayensis*, a Late Triassic turtle from Argentina. *Palaeontographica Abteilung A* **281:** 1–61.

Sterli J, de la Fuente MS, Umazano AM. 2015b. New remains and new insights on the Gondwanan meiolaniform turtle *Chubutemys copelloi* from the Lower Cretaceous of Patagonia, Argentina. *Gondwana Research* **27:** 978–994.

Sukhanov VB. 2006. An archaic turtle, *Heckerochelys romani* gen. et sp. nov., from the Middle Jurassic of Moscow region, Russia. *Russian Journal of Herpetology* **13:** 112–18.

Sukhanov VB, Narmandakh P. 1974. A new early cretaceous turtle from the continental deposits of the Northern Gobi. *Trudy Sovmestnoi Sovetsko-Mongol'skoi Paleontologicheskoi Ekspeditsii* **1:** 192–220.

Szczygiellski T, Sulej T. 2016. Revision of the Triassic European turtles *Proterochersis* and *Murrhardtia* (Reptilia, Testudinata, Proterochersidae), with the description of new taxa from Poland and Germany. *Zoological Journal of the Linnean Society* **177:** 395–427.

Therrien F. 2005. Paleoenvironments of the Late Cretaceous (Maastrichtian) dinosaurs of Romania: insights from fluvial deposits and paleosols of the Transylvanian and Haţeg basins. *Palaeogeography, Palaeoclimatology, Palaeoecology* **218:** 15–56.

Therrien F, Jianu C-M., Bogdan S, Weishampel DB, King JW. 2002. Paleoenvironmental reconstruction of the Latest Cretaceous dinosaur-bearing formations of Romania: preliminary results. *Sargetia* **19:** 33–59.

Tong H, Buffetaut E, Suteethorn V. 2006. Middle Jurassic turtles from southern Thailand. *Geological Magazine* **139:** 687–697.

Van Itterbeeck J, Markevich VS, Codrea V. 2005. Palynostratigraphy of the Maastrichtian dinosaur and mammal sites of the Râul Mare and Bărbat Valleys (Haţeg Basin, Romania). *Geologica Carpathica* **56:** 137–147.

Van Itterbeeck J, Săsăran E, Codrea V, Săsăran L, Bultynck P. 2004. Sedimentology of the Upper Cretaceous mammal- and dinosaur-bearing sites along the Râul Mare and Bărbat rivers, Haţeg Basin, Romania. *Cretaceous Research* **25:** 517–530.

Woodward AS. 1888. Note on the extinct reptilian genera *Megalania*, Owen and Meiolania, Owen. *The Annals and Magazine of Natural History* **6:** 85–89.

Ye X-K. 1986. A Jurassic turtle from Junggar, Xinhjiang. *Vertebrata Palasiatica* **24:** 171–181.

Young C-C, Chow M-C. 1953. New fossil reptiles from Szechuan, China. *Acta Scientica Sinica* **2:** 216–243.

Zangerl R. 1945. Fossil specimens of Macro-chelys from the Tertiary of the plains. *Fieldiana: Geology* **10:** 5–12.

APPENDIX 1

Comparisons of the new anatomical characters of *Kallokibotion bajazidi* with those of other stem Testudines:

Skull and lower jaws: The presence of an almost as wide as long skull, in dorsal view, is shared with taxa such as *Pro. quenstedti* and *Meiolania platyceps*. It

is noticeably longer than wide in other members of stem group of Testudines such as *Od. semitestacea*, *Mongolochelys efremovi*, *Helochelydra nopcsai* and *Naomichelys speciosa*. However, taxa in which it is wider than long are also recognized (e.g. *Niolamia argentina*). As has been indicated, the orbits of *Kallokibotion bajazidi* are recognized as more laterally positioned than previously interpreted. The orbits are also laterally positioned in taxa such as *Pro. quenstedti*, *Palaeochersis talampayensis*, *Australochelys africanus*, *Kayentachelys aprix*, *Mo. efremovi*, *Ni. argentina* and *Me. platyceps*. However, they are located in a more dorsal position in other taxa such as *Eileanchelys waldmani* and *He. nopcsai*. The internarial process is absent in taxa such as *E. waldmani*, *Ch. copelloi*, *Mo. efremovi*, *He. nopcsai*, *Na. speciosa*, *Ni. argentina* and *Me. platyceps*. As in *K. bajazidi*, this process is present in other taxa such as *Od. semitestacea*, *Pro. quenstedti* and *P. talampayensis*. However, the premaxillae of these three taxa constitute the whole structure so that these bones extend beyond the apertura narium externae avoiding medial contact between the anterior region of both nasals.

The presence of a nasal-prefrontal contact is a widely distributed condition, being shared with forms such as *Od. semitestacea*, *Pro. quenstedti*, *P. talampayensis*, *Ka. aprix*, *E. waldmani*, *Ch. copelloi*, *He. nopcsai*, *Na. speciosa*, *Ni. argentina* and *Me. platyceps*. A relatively large dorsal exposure of the nasals is present in *P. talampayensis* and *Me. platyceps*, but not in *Ka. aprix*, *E. waldmani*, *Mo. efremovi*, *He. nopcsai* and *Na. speciosa*. The prefrontals make contact with the apertura narium externae in *K. bajazidi* as they do in *Od. semitestacea* and *He. nopcsai*. This contact is absent in other forms such as *Pro. quenstedti*, *P. talampayensis*, *Ka. aprix*, *E. waldmani* and *Me. platyceps*, taxa in which the nasals contact the maxillae. A frontal contribution to the orbit is present in *Ka. aprix*, *E. waldmani*, *He. nopcsai* and *Na. speciosa*, but not in *Od. semitestacea*, *Pro. quenstedti*, *P. talampayensis*, *Ch. copelloi*, *Mo. efremovi*, *Peligrochelys walshae*, *Ni. argentina* and *Me. platyceps*.

The absence of contact between the quadratojugal and the squamosal is shared with *Ka. aprix* and *Ch. copelloi*, but not with *Pro. quenstedti*, *P. talampayensis*, *E. waldmani* and *Na. speciosa*. In *Ch. copelloi*, *He. nopcsai* and *Me. Platyceps*, the supraoccipital is exposed on the dorsal surface of the skull roof. This condition differs not only from that observed in *K. bajazidi* but also in *Od. semitestacea*, *Pro. quenstedti*, *P. talampayensis*, *Ka. aprix* and *Mo. efremovi*. *Helochelydra nopcsai* lacks exposure of the jugal along the ventral margin of the skull, the maxilla being in contact with the quadratojugal in this area. However, the jugal is exposed in most taxa considered here, and this is also the case

in *K. bajazidi*. The exposure of the quadratojugal in that margin is significantly larger than that of the jugal in *Na. speciosa* and *Me. platyceps*, but not in *Pro. quenstedti*, *P. talampayensis*, *Ka. aprix* and *Ch. copelloi*. A cheek emargination is absent in *Pro. quenstedti*, *P. talampayensis*, *Ka. aprix*, *Ch. copelloi*, *Mo. efremovi*, *He. nopcsai*, *Ni. argentina* and *Me. platyceps*. This structure is present in *Na. speciosa*, but it is longer and, therefore, lower in relation to its length than that in *K. bajazidi*.

Kallokibotion bajazidi shares with *Pro. quenstedti*, *Ka. aprix*, *E. waldmani*, *Ch. copelloi*, *Mo. efremovi*, *Ni. argentina* and *Me. platyceps* the presence of contact between the vomer and the premaxillae. The absence of medial contact between both maxillae is also shared with all taxa here compared, as can be observed in forms such as *Pro. quenstedti*, *Ka. aprix*, *E. waldmani*, *Mo. efremovi*, *Ni. argentina* and *Me. platyceps*. The presence of labial, lingual and accessory ridges is shared with *Mo. efremovi* and *Me. platyceps*. *Proganochelys quenstedti*, *A. africanus*, *Ka. aprix*, *Pe. walshae*, *He. nopcsai* and *Ni. argentina* have both labial and lingual ridges. Only a well-developed labial ridge is present in the triturating surface of *P. talampayensis* and *Ch. copelloi*. All taxa compared here lack both contribution of the palatine to the triturating surface as development of a processus trochlearis pterygoidei. The presence of longer laterally than medially articular surface of the processes articularis of the quadrates is shared with *Ka. aprix*, *Condorchelys antiqua* and *He. nopcsai*, but not with *Od. semitestacea* and *Pro. quenstedti*. The morphology and distribution of the cranial scutes of *K. bajazidi* is recognized as unique to this taxon.

The presence of a narrow ramus of the lower jaw is shared with taxa such as *Mo. efremovi* and *Me. platyceps*. Other taxa, such as *Na. speciosa*, have a wide ramus. In lateral view, the length of the dentary experiences a relative high degree of interspecific variability when comparing the taxa considered here. As indicated, the dentary of *K. bajazidi* reaches the articular, preventing contact between the surangular and the angular. The posterior margin of the dentary of *Mo. efremovi* is located near the articular, but these bones do not contact each other. Therefore, a short contact between the surangular and the angular is present. This suture is markedly longer in *Pro. quenstedti*, due to the greater distance between the dentary and the articular. *Meiolania platyceps* also lacks lateral contact between the dentary and the articular, but the contact between the surangular and the angular is not present in lateral view, because the surangular reaches the bottom of the jaw. Taxa such as *Pro. quenstedti*, *Mo. efremovi* and *Me. platyceps* have a coronoid process lower than that in *K. bajazidi*. This process is also high in *He. nopcsai*, but significantly longer than that in *K. bajazidi*.

Proganochelys quenstedti and *P. talampayensis* have a well-developed retroarticular process. This structure is poorly developed in *Mo. efremovi*, being absent in *He. nopcsai* and *Me. platyceps*, as in *K. bajazidi*.

Postcranial skeleton: The presence of a nuchal plate divided into two elements is not shared with any other form of the stem group of Testudines. All compared taxa, except *Od. semitestacea*, have a carapace. The absence of a nuchal notch is shared with *Proterochersis robusta*, *Keuperotesta limendorsa*, *P. talampayensis*, *Heckerochelys romani* and *Me. platyceps*, but not with *Pro. quenstedti*, *Pr. porebensis*, *Ka. aprix*, *Indochelys spatulata*, *E. waldmani*, *Siamochelys peninsularis*, *Pa. gasparinae*, *Mo. efremovi* and *Na. speciosa*. *Kallokibotion bajazidi* shares the presence of eight neurals with taxa such as *C. antiqua*, *S. peninsularis* and *Na. speciosa*. The number of these plates is greater in forms such as *Ka. aprix*, *I. spatulata* and *Mo. efremovi*. The morphology of the neural series observed in *K. bajazidi*, with the first neural being hexagonal, its latero-posterior margins being significantly shorter than the latero-anterior, the second one being rectangular, and the others hexagonal, is shared with *Ka. aprix* and *S. peninsularis*. The morphology of the first neural of *I. spatulata* is different, the shorter margins being the latero-anterior. However, the morphology of the other neurals of this taxon is shared with *K. bajazidi*. Only the first and third neurals of *H. romani* are known. They are hexagonal, their latero-posterior margins being shorter. *Kayentachelys aprix* has a single suprapygal. The second suprapygal is wider than the first in taxa such as *I. spatulata*, *C. antiqua* and *S. peninsularis*. However, the opposite condition is recognized in *E. waldmani*. *Kallokibotion bajazidi* shares with taxa such as *I. spatulata*, *E. waldmani*, *S. peninsularis*, *Ch. copelloi* and *Na. speciosa* the presence of eight pairs of costal plates. The number of costals is larger in forms such as *Pro. quenstedti*, *Ka. aprix* and *C. antiqua*. The presence of 11 pairs of peripherals is shared with taxa such as *C. antiqua*, *Ch. copelloi*, *Mo. efremovi* and *Na. speciosa*, but not with *Pro. quenstedti*, a taxon with a greater number of peripherals.

The absence of a cervical scute contrasts with the condition seen in forms such as *Pro. quenstedti*, *Pr. robusta*, *Pr. porebensis*, *Ke. limendorsa*, *H. romani*, *E. waldmani*, *S. peninsularis*, *Pa. gasparinae*, *Mo. efremovi* and *Na. speciosa*. Twelve pairs of marginals are also present in taxa such as *C. antiqua*, *E. waldmani*, *S. peninsularis*, *Ch. copelloi* and *Na. speciosa*. The number of these scutes is greater in *Pro. quenstedti*, *Pr. robusta* and *Pr. porebensis*. The sulcus between the third and fourth vertebral scutes is also located on the fifth neural in *S. peninsularis*, *Mo. efremovi* and *Na. speciosa*. It is located on the sixth neural in *Ka. aprix*, *I. spatulata*, *C. antiqua* and *E. waldmani*.

Kayentachelys aprix, *I. spatulata*, *C. antiqua*, *H. romani*, *S. peninsularis*, *Ch. copelloi*, *Mo. efremovi*, *Na. speciosa* and *Me. platyceps* lack supramarginal scutes. A partial row of supramarginals is present in *Ke. limendorsa*, *Pr. robusta* and *Pr. porebensis*. *Proganochelys quenstedti* has a complete row.

Kallokibotion bajazidi shares with *Pro. quenstedti*, *Ke. limendorsa*, *Pr. robusta*, *Pr. porebensis*, *P. talampayensis* and *E. waldmani* the presence of an osseous connection between the carapace and the plastron. By contrast, a ligamentous connection is present in *Ka. aprix*, *H. romani*, *S. peninsularis*, *O. cunicularius*, *Ch. copelloi*, *Pa. gasparinae*, *Mo. efremovi* and *Me. platyceps*. Although the axillary buttresses of *K. bajazidi* contact the peripheral series and the first pair of costals, they are exclusively in contact with the peripherals in forms such as *Pro. quenstedti*, *Pr. robusta*, *Pr. porebensis*, *Ke. limendorsa*, *P. talampayensis*, *Ka. aprix*, *H. romani*, *S. peninsularis*, *Ch. copelloi*, *Pa. gasparinae*, *Mo. efremovi*, *Na. speciosa* and *Me. platyceps*. Similarly, the inguinal buttresses do not contact both the peripherals and the costal series, but only the peripheral series, in these taxa. The inguinal buttresses also reach the eighth peripherals in *Ch. copelloi*, *Mo. efremovi*, *Na. speciosa* and *Me. platyceps*. However, they terminate on the seventh peripherals in *S. peninsularis* and on the sixth peripherals in *O. cunicularius*. Two pairs of mesoplastra are present in *Od. semitestacea*, *K. limendorsa*, *Pr. robusta* and *Pr. porebensis*. A single pair, making medial contact, is also recognized in *Pro. quenstedti*, *Ka. aprix* and *S. peninsularis*. *Otwayemys cunicularius*, *Ch. copelloi* and *Me. platyceps* lack mesoplastra. The presence of a distinct anal notch is shared with *Pr. robusta*, *Pr. porebensis* and *I. spatulata*, but not with *Od. semitestacea*, *Pro. quenstedti*, *P. talampayensis*, *Ka. aprix*, *S. peninsularis*, *Na. speciosa* and *Me. platyceps*. The humero-pectoral sulcus of *He. nopcsai* and *Na. speciosa* overlaps the posterior region of the entoplastron. This sulcus is placed posterior to the entoplastron in other taxa such as *Pro. quenstedti*, *Ka. aprix*, *S. peninsularis*, *O. cunicularius* and *Mo. efremovi*.

Kallokibotion bajazidi shares with *Od. semitestacea*, *Pro. quenstedti* and *P. talampayensis* the presence of amphicoelous cervical vertebrae. This condition is not shared with forms such as *O. cunicularius*, *Pa. gasparinae*, *Na. speciosa* and *Me. platyceps*. The centra of the cervicals are wider than high, or as wide as high, in *Pro. quenstedti*, *P. talampayensis* and *Na. speciosa*. *Patagoniaemys gasparinae* shows an intermediate situation between those described for these taxa and for *K. bajazidi*. The cervical centra of *O. cunicularius*, *Pa. gasparinae* and *Na. speciosa* are distinctly keeled ventrally. The keel is absent or poorly developed in *Pro. quenstedti*, *P. talampayensis* and *Me. platyceps*.

Although the prezygapophyses of the cervical vertebrae of *Pro. quenstedti* and *Na. speciosa* are lower than those of *K. bajazidi*, those of *P. talampayensis* and *Pa. gasparinae* are also very high. The postzygapophyses of the eighth cervical vertebra of *Pro. quenstedti* are well separated from each other. Those of *Na. speciosa* are close to each other, but not united in a single structure such as that present in *K. bajazidi*.

The scapular dorsal blade of *Od. semitestacea* is rod like, lacking an acromial process. *Proganochelys quenstedti* and *Pr. porebensis* lack a tubular scapular and acromial processes. These processes are well developed in forms such as *Ch. copelloi*, *He. nopcsai*, *Na. speciosa* and *Me. platyceps*. The angle between both processes in *K. bajazidi* is similar to that in *Pr. porebensis*, but lower than that in *Pro. quenstedti* and *Ke. limendorsa*. The marked proximal and distal asymmetries between the radius and the ulna of *K. bajazidi* are much higher than those observed for *Od. semitestacea*. The asymmetries between both bones are slightly higher than those in *Pro. quenstedti* (especially in the proximal region), but similar to those in *P. talampayensis* and *Na. speciosa*.

APPENDIX 2

Recoded characters for *Kallokibotion bajazidi* in the two data matrices used for the phylogenetic analyses performed in this paper:

Changes for *K. bajazidi* in the data matrix of Sterli *et al.* (2015a). 3 (Nasal C): ?→1 (greatly reduced relative to that of all other elements); 10 (Frontal A): ?→0,1 (0 corresponding to the absence of frontal contribution to the orbit and 1 to the presence of this contribution); 14 (Parietal C): 0 (short anterior extension of the lateral braincase wall)→?; 15 (Parietal D): ?→0 (overhanging process of the skull roof absent); 34 (Premaxilla C): ?→0 (foramen praepalatinum present); 37 (Maxilla A): ?→0 (do not contact each other in ventral view); 38 (Maxilla B): ?→0 (triturating surface not involving palatine or its contribution is minor); 40 (Maxilla D): ?→2 (labial, lingual and accessory ridges present); 41 (Maxilla E): ?→1 (accessory ridge only in some sectors of the triturating surface); 45 (Vomer D): ?→0 (vomer-premaxilla contact present); 46 (Vomer E): 1 (narrow and tall ventral crest on vomer present all along the vomer)→0 (absent); 47 (Vomer F): ?→0 (domed palate absent); 53 (Quadrate F): 3 (incisura columella auris present and closed, enclosing stapes and the Eustachian tube)→?; 63 (Pterygoid E): ?→0 (processus trochlearis pterygoidei absent); 72 (Supraoccipital A): 1 (crista occipitalis protruding significantly posterior to the foramen magnum)→?; 75 (Exoccipital A): ?→0

(medial contact of exoccipitals dorsal to foramen magnum absent); 86 (Basisphenoid D): 2→1,2 (1 being triangular and 2 rectangular); 129 (Neural A): 0 (neural formula 6 > 4 < 6 < 6 < 6 < 6 absent)→1 (present); 131 (Peripheral A): ?→1 (11 pairs); 138 (Cervical A): ?→1 (cervical absent, carapacial scutes otherwise present); 139 (Supramarginal A): ?→2 (absent); 142 (Vertebral C): 0 (sulcus between vertebral 3 and 4 on neural VI)→1 (on neural V); 143 (Marginal A): ?→0 (marginal scutes overlap onto costals absent); 144 (Plastron A): ?→0 (connection between carapace and plastron osseous); 157 (Hyoplastron A): ?→1 (axillary buttresses contact peripherals and first costal); 160 (Mesoplastron A): 1→0,1 (0 corresponding to one or two pairs with medial contact and 1 to one reduced pair); 161 (Hypoplastron A): ?→1 (inguinal buttresses contact peripherals and costal V); 162 (Hypoplastron B): 2 (inguinal buttress terminates on peripheral 6)→0 (inguinal buttress terminates on peripheral 8); 163 (Xiphiplastron A): 0 (distinct anal notch absent)→1 (present); 174 (Humeral B): ?→0,1 (0 corresponding to humero-pectoral sulcus only in the hyoplastra and 1 to humero-pectoral sulcus crossing the entoplastron); 185 (Cervical vertebra C): 0 (cervical centrum 8 < 7 absent)→1 (present); 201 (Dorsal rib B): ?→0 (contact dorsal rib 9-10 with costals present); 202 (Dorsal rib C): ?→1 (dorsal rib X short); 214 (Cleithrum A): 1 (present, osseous contact with carapace absent)→2 (absent).

Changes for *K. bajazidi* in the data matrix of Joyce *et al.* (2016): 3 (Nasal C): ?→1 (greatly reduced relative to that of all other elements); 10 (Frontal A): ?→0,1 (0 corresponding to the absence of frontal contribution to the orbit and 1 to the presence of this contribution); 14 (Parietal C): 0 (length of anterior extension of the lateral braincase wall inter)→?; 15 (Parietal D): ?→0 (overhanging process of the skull roof absent); 34 (Premaxilla C): ?→0 (foramen praepalatinum present); 37 (Maxilla A): ?→0 (do not contact each other in ventral view); 39 (Maxilla D): ?→2 (labial, lingual and accessory ridges present); 40 (Maxilla E): ?→1 (accessory ridge only in some sectors of the triturating surface); 44 (Vomer D): ?→0 (vomer-premaxilla contact present); 45 (Vomer E): ?→0 (narrow and tall ventral crest on vomer absent); 60 (Pterygoid E): ?→0 (processus trochlearis pterygoidei absent); 70 (Exoccipital A): ?→0 (medial contact of exoccipitals dorsal to foramen magnum absent); 78 (Basisphenoid B): ?→0 (paired pits on ventral surface absent); 117 (Neural A): 0 (neural formula 6 > 4 < 6 < 6 < 6 < 6 absent)→1 (present); 119 (Peripheral A): ?→1 (11 pairs); 126 (Cervical A): 1 (one)→0 (none); 127 (Supramarginal A): ?→2 (absent); 130 (Vertebral C): 0 (sulcus between vertebral 3 and 4 on neural VI)→1 (on neural V); 131 (Marginal A): ?→0 (marginal scales overlap onto costals absent); 132 (Plastron A): ?→0 (connection between carapace and plastron osseous);

144 (Hyoplastron A): ?→1 (axillary buttresses contact peripherals and first costal); 147 (Mesoplastron A): 1→0,1 (0 corresponding to one or two pairs with medial contact and 1 to one reduced pair); 148 (Hypoplastron A): ?→1 (inguinal buttresses contact peripherals and costal V); 149 (Hypoplastron B): ?→0 (inguinal buttress terminates on peripheral 8); 150 (Xiphiplastron A): 0 (distinct anal notch absent)→1 (present); 156 (Extragular B): 1 (medial contact present, contacting one another anterior to the intergulars)→0 (medial contact absent); 161 (Humeral B): ?→0,1 (0 corresponding to humero-pectoral sulcus only in the hyoplastra and 1 to humero-pectoral sulcus crossing the entoplastron); 172 (Cervical vertebra C): 0 (cervical centrum 8 < 7 absent)→1 (present); 186 (Dorsal rib B): ?→0 (contact dorsal rib 9-10 with costals present); 187 (Dorsal rib C): ?→1 (dorsal rib X short).

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Data 1. Data matrix used here for the analyses based on that proposed by Sterli *et al.* (2015a).
Data 2. Data matrix used here for the analyses based on that proposed by Joyce *et al.* (2016).