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Original article

A compsemydid turtle from the Upper Cretaceous of Var, southern France

Une tortue comsemydidée du Crétacé supérieur du Var, sud de la France

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ABSTRACT

Calissounemys matheroni gen. et sp. nov. (Testudines) is described on the basis of a skull and shell elements from the Upper Cretaceous of Var, southern France. This new taxon is assigned to the family Compsemydidae and characterized by a thick-boned, robust skull, a shallow temporal emargination, a crista supraoccipitalis not extending beyond the posterior edge of the skull roof, large nasals meeting along the midline for their full length; frontals retracted from the orbital margin, absence of a cheek emargination, a large jugal forming a substantial part of the orbital margin, absence of a secondary palate and an uneven upper triturating surface; and the shell with vertebral 1 clearly wider than vertebrals 2-3, with the lateral margins strongly divergent towards the anterior border and wider than long vertebrals 2-3. This find increases the diversity of the Late Cretaceous turtle fauna from southern France, and fills a stratigraphical gap in the fossil record of Compsemydidae between the Early Cretaceous and the Paleocene in Europe.

Calissounemys matheroni gen. et sp. nov. (Testudines) est décrit à partir d'un crâne et d'éléments de la carapace provenant du Crétacé supérieur du Var, sud de la France. Le nouveau taxon est attribué à la famille des Compsemydidae et caractérisé par un crâne robuste aux os épais, une échancrure temporale faible, une crista supraoccipitalis ne dépassant pas le rebord postérieur du toit crânien, de grands nasaux se rejoignant sur la ligne médiane sur toute leur longueur, le frontal rétracté du rebord de l'orbite, l'absence d'une échancrure jugale, un grand jugal formant une part substantielle du rebord de l'orbite, l'absence d'un palais secondaire, et la surface triturante supérieure inégale ; la carapace avec l'écaille vertébrale 1 plus large que les vertébrales 2-3, aux rebords latéraux divergents vers l'avant, et les vertébrales 2-3 plus larges que longues. Cette découverte augmente la diversité de la faune de tortues du Crétacé supérieur du sud de la France et comble une lacune stratigraphique dans le registre fossile de Compsemydidae entre le Crétacé inférieur et le Paléocene en Europe.

1. Introduction

Evolutionary relationships of basal turtles and their palaeobiogeographical interpretation are regularly improved by the inclusion of new fossils, especially when these document important morphological transitions. The recent discovery of two basal groups of turtles in the Paleocene of Europe has challenged previous hypotheses and provided a better image of palaeobiogeographical relationships within the Asian and North American landmasses during that period (Pérez-García, 2012, 2020). These discoveries have improved our knowledge of two small and poorly known families: Sichuanchelyidae and Compsemydidae. The first may have originated from Asia during the Jurassic and dispersed to Europe at some point, while the latter, mostly known in Europe from the Jurassic to the Paleocene, may have later dispersed to North America by the Late Cretaceous or before (cf. phylogenetic interpretation of Joyce and Rollot, 2020). These two groups are part of, or close to a larger group of turtles, the Paracryptodira, which were restricted to North America and Europe (Joyce et al., 2016; Joyce and Anquetin, 2019). However, major gaps in the fossil record remain to be filled to test these palaeobiogeographical hypotheses.

The Late Cretaceous turtle faunas of Western Europe are particularly promising for refining and challenging these scenarios. The Upper Cre-

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taceous deposits in this part of the world are rich in fossil turtle remains, but so far, neither sichuanchelyids nor compsemydids had been described. Two major groups are recognized: Bothremydidae, more precisely Foxemydina, which are endemic to Europe and share a common ancestry with Bothremydina (known from North America, North Africa and Europe in the Cretaceous) and Helochelydridae (known from North America and Europe in the Cretaceous). Other groups of turtles are present but known from only one or a few localities: the enigmatic *Kallokibotion bajazidi* (a primitive turtle of uncertain affinities) and rare turtles of the pleurodiran family Dortokidae (endemic to Europe). While Sichuanchelyidae might have reached Europe during the Paleocene from their place of origin (Asia), the absence of Compsemydidae would be more difficult to explain because European and North American faunas share several similarities until the Paleocene.

In this paper, we describe a new compsemydid turtle from the Campanian of Var, southern France that fills part of the gap. The material, consisting of a skull and isolated shell elements, is housed in the Muséum d'Histoire Naturelle d'Aix-en-Provence (MHNAix), Bouches-du-Rhône, France.

2. Geological setting

The Pourrières-Jas Neuf Autoroute 1 locality (PJNA1, also known as 'Jas Neuf Sud') is situated along the A8 motorway near the village of Pourrières, Var, France (Fig. 1). The site consists of a thick sandstone formation corresponding to braided or meandering river deposits. These fossiliferous sandstones are located in the Lower Argiles Rutilantes Formation (lower Rognacian facies, upper Campanian) (Fig. 2; Cojan and Moreau, 2006). Besides stratigraphical positioning based on local continental facies, the only available biomarkers are isolated dinosaur eggshell fragments discovered in red clays overlying the studied sandstone formation. These fragments have been identified as *Megaloolithus aureliensis* (Vianey-Liaud, pers. com.), confirming the late Campanian age (~C33) of the site.

The fossil-bearing horizons, consisting of a series of deposit sequences in different channelized structures, have yielded hundreds of macrofossils, including freshwater and terrestrial taxa such as hybodont sharks, turtles (*Foxemys* sp., *Solemys* sp.), crocodiles (cf. *Allodaposuchus*), pterosaurs (azhdarchids) and dinosaurs (titanosaurs, the abelisaurid *Arcovenator escotae*, the ornithopod *Rhabdodon* sp. and nodosaurids) (Tortosa et al., 2014).

The material described in the present paper comes from different sedimentary units of channelized deposits: Unit 2, Unit 3, Unit 7 and Unit 8 (Fig. 3). For each channelized unit, a succession of deposit sequences is visible, corresponding to the lateral migration of the channels through time (for example the channelized unit 2 consists of 14 deposit sequences, Units 2A to 2M). These sequences are recognized from the study of the typical grain size distribution taking place during the channel filling. In the framework of this work, the deposit sequences 2I, 3C, 7B and 8I are worth mentioning because they yielded the remains of four turtle individuals identified as 'individual A' (MHNAix-PV.2020.4.1), 'individual B' (MHNAix-PV.2014.3.19 and MHNAix-PV.2020.4.2), 'individual C' (MHNAix-PV.2018.22.4 and .5) and 'individual D' (MHNAix-PV.2020.4.3), respectively. Among deposit sequences 3C and 7B, the matching of individuals (respectively 'B' and 'C') was made possible on the basis of the similarities of the shell elements proportions, their preservation state and differences with other clearly identified turtles (bothremydids or helochelydrids).

3. Systematic palaeontology

Testudines Linnaeus, 1758
Compsemydidae Pérez-García, Royo-Torres and Cobos, 2015
Type genus: *Compsemys* Leidy, 1856

Emended diagnosis (for skull characters): A basal group of Testudines with a robust thick-boned skull that is oblong as seen from above, reduced temporal emargination, cheek emargination absent or shallow, laterally facing orbits, external narial opening facing anteriorly, large nasals, large prefrontals not meeting along the midline, frontals excluded from the orbital margin, orbit as large as or larger than cavum tympani, postorbital contributing to the cavum tympani margin, and expanded and sub-rectangular quadratojugal.

Included species: *Compsemys victa* Leidy, 1856; *Berruchelus russelli* Pérez-García, 2012; *Selenemys lusitanica* Pérez-García and Ortega, 2011; *Peltochelys duchastelii* Dollo, 1884, *Calissounemys matheroni* gen. et sp. nov., and possibly, *Riodevemys inumbragigas* Pérez-García, Royo-Torres and Cobos, 2015 and *K*[illegible]*zidi* Nopcsa, 1923.

Distribution: Late Jurassic to Paleocene of Europe and Late Cretaceous to Paleocene of North America.

Calissounemys matheroni gen. et sp. nov.
(Figs. 4–6)

Etymology: The genus name derives from Calissoun, Provençal dialect for Calisson, a traditional rhombic candy from Aix-en-Provence, in the vicinity of which the new turtle has been discovered. The species name is in honour of the 19th century French palaeontologist Philippe Matheron who studied the first Late Cretaceous fossil turtle remains from southern France.

Holotype: MHNAix-PV.2014.3.19, an almost complete skull.

Hypodigm: MHNAix-PV.2018.22.4 and MHNAix-PV.2020.4.2; two nearly complete right costals 1; MHNAix-PV.2018.22.5, a right costal 3

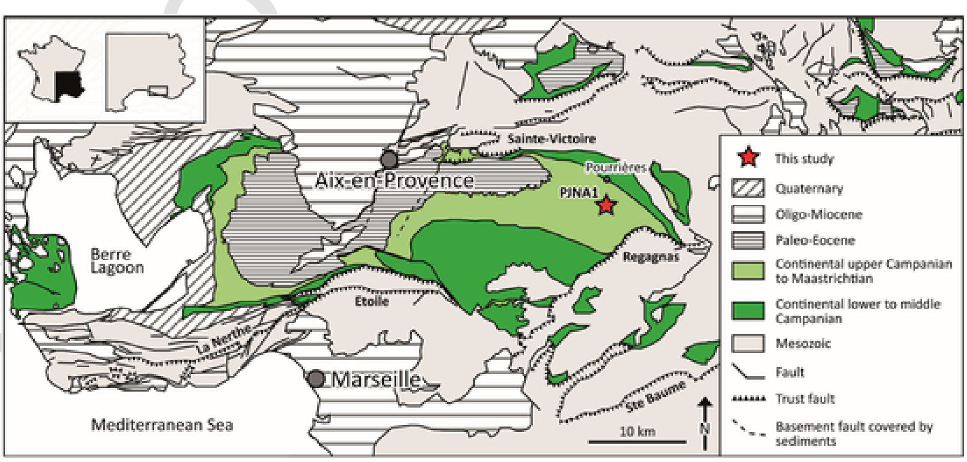

Fig. 1. Geographical location of Pourrières-Jas Neuf Autoroute 1 (PJNA1) in the continental Upper Cretaceous of Aix-en-Provence Basin (after Tortosa et al., 2014).
Localisation géographique de Pourrières-Jas Neuf Autoroute 1 (PJNA1) dans le Crétacé supérieur continental du bassin d'Aix-en-Provence (D'après Tortosa et al., 2014).

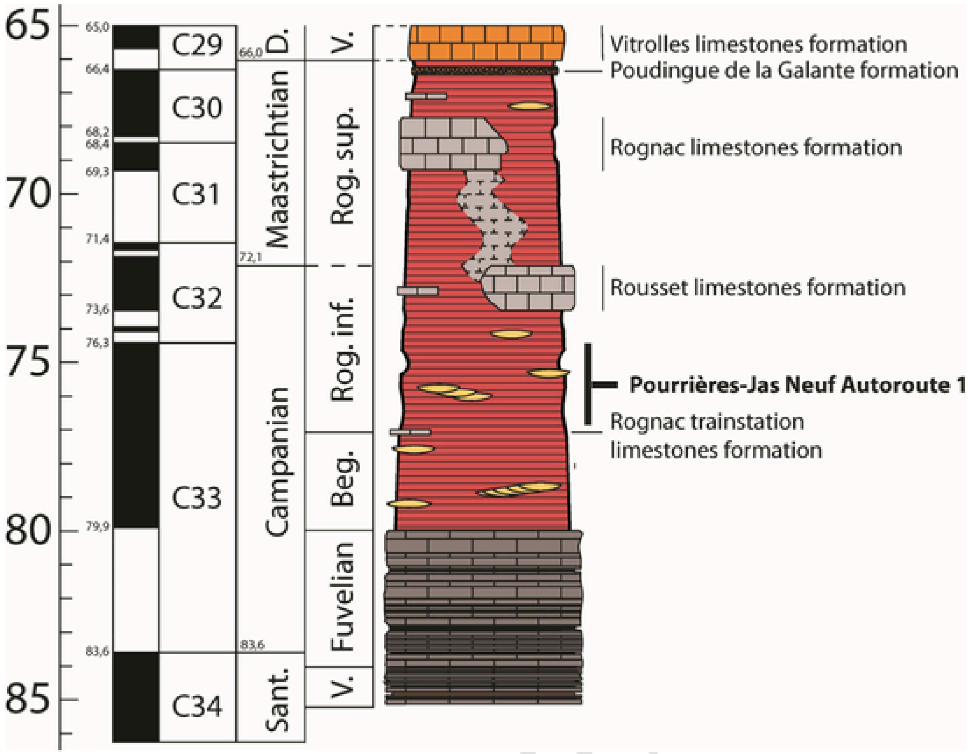

Fig. 2. Stratigraphical position of Pourrières-Jas Neuf Autoroute 1 (PJNA1) in a synthetic log of the continental Upper Cretaceous of Provence. Time scale with standard ages, geomagnetic polarity, chronozones, marine stratigraphy and local continental facies after Cojan and Moreau (2006), Gradstein et al. (2020) and Tortosa et al. (2014).

Position stratigraphique de Pourrières-Jas Neuf Autoroute 1 (PJNA1) dans le log synthétique du Crétacé supérieur continental de Provence. Échelle chronologique avec l'âge standard, la polarité géomagnétique, les chronozones, la stratigraphie marine et les faciès continentaux d'après Cojan et Moreau (2006), Gradstein et al. (2020) et Tortosa et al. (2014).

lacking the medial end; MHNAix-PV.2020.4.1, an almost complete right hyoplastron and incomplete entoplastron, and MHNAix-PV.2020.4.3, an almost complete right hypoplastron and incomplete xiphiplastron, all from the type locality and horizon.

Type locality and horizon: Pourrières-Jas Neuf Autoroute 1 (PJNA1), Pourrière, Var, France; upper Campanian (lower Rognacian), Upper Cretaceous (Tortosa, 2014).

Diagnosis: A compsemydid turtle with a unique combination of characters as follows: skull robust with well-developed thick-boned skull roof and very shallow temporal emargination; skull surface covered with sculpture that matches that of the shell; crista supraoccipitalis covered by the parietal dorsally and not extending beyond the posterior edge of the skull roof; large nasals meeting along the midline for their full length; frontals retracted from the orbital margin; squamosal/parietal contact present; pterygoid midline contact present; cheek emargination absent and large jugal forming substantial part of orbital margin; and the shell with vertebral 1 clearly wider than vertebrals 2-3, with the lateral margins strongly divergent towards the anterior border and vertebrals 2-3 wider than long. The skull differs from that of *C. victa* in having a more reduced frontal, absence of a hook on the upper jaw, absence of secondary palate, uneven upper triturating surface and a larger and more elongate basisphenoid. The shell is similar to that of *C. russelli* but different from those of *C. victa*, *Selenemys lusitanica*, *Riodevemys inumbragigas* in having vertebral 1 wider than vertebral 2, with the lateral margins strongly divergent anteriorly and from those of *C. victa* and *Peltochelys duchastelii* in having wider than long vertebrals 2-3.

Measurements: see Table 1.

Description:

Skull. The skull is almost complete and has not undergone much deformation. The posterior part of the skull roof is damaged. The surface of the bones is eroded, and some sutures are not clearly visible.

General aspect. The skull is robust and thick-boned, the parietal being about 3 mm thick. It has an oblong shape as seen from above. The snout region is relatively wide. The external narial opening faces anteriorly and is not visible in dorsal view. Separated from one another by a wide interorbital space, the orbits are of moderate size, located far forward and facing laterally, so that they are not visible in dorsal view, as in *C. victa*, but unlike pleurosternids and baenids (Lyson and Joyce, 2011; Joyce and Lyson, 2015; Joyce and Anquetin, 2019). The skull roof is well-developed, the temporal margin, complete on the right side and nearly so on the left side, is only slightly emarginated. The short crista supraoccipitalis is covered by the parietal and does not extend beyond the posterior edge of the skull roof. In lateral view, the skull is tall in its posterior half and slopes downward from about its midlength toward the snout. The cheek margin is straight without emargination as in *C. victa*. The cavum tympani is clearly smaller than the orbit, as in *C. victa*. The skull roof surface is covered with fine sculpture consisting of irregular low ridges and tubercles that are coalescent and pierced by numerous pores which resembles but does not fully match the finely beaded and ridged texturing described in *C. victa* (Lyson and Joyce, 2011). The dorsal surface of the skull also bears well-defined sulci showing that a complex arrangement of scales was present on the skull. The skull belongs to an adult individual, consequently the sutures are sometimes obliterated.

Nasal. The nasal is a large elements forming the upper edge of the external narial opening. In dorsal view, the nasals taper posteriorly and meet one another along the midline for their full length as in *C. victa*. Also as in *C. victa*, the nasal extends anteriorly as far as the underlying premaxilla, but unlike pleurosternids and baenids, in

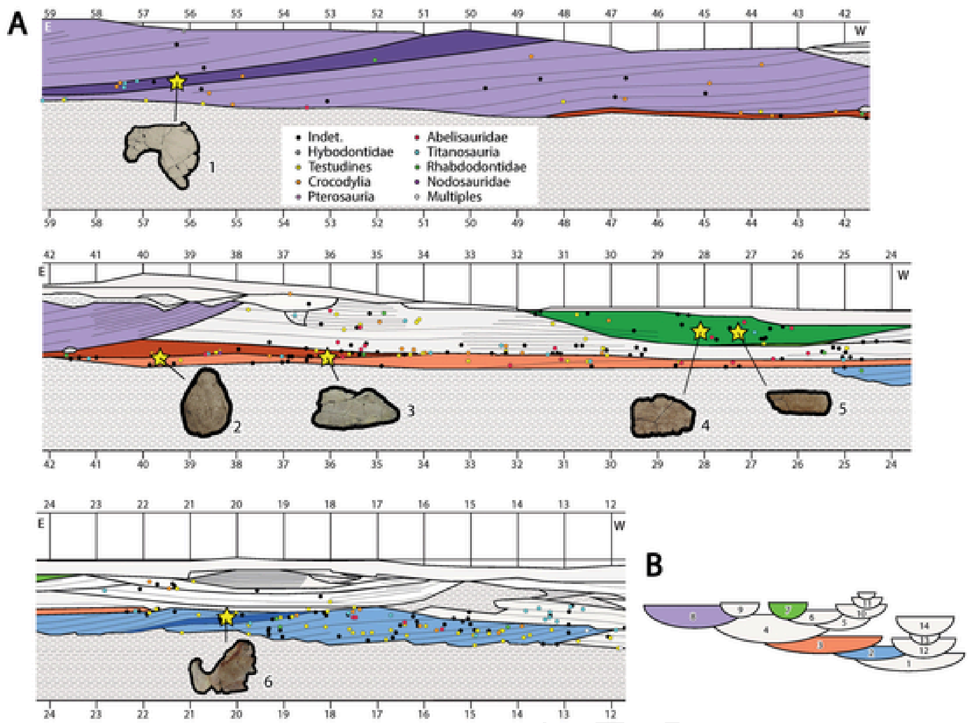

Fig. 3. Pourrières-Jas Neuf Autoroute 1 (PJNA1) with the outcrop segment '59-12′ with the position of material of *Calissounemys matheroni* gen. et sp. nov. in their respective channel deposits (A) and synthetic organisation of channelized structures (B) (after Tortosa, 2014). Channelized structures indicated by colours with units (light) and sequences (dark): Unit 2I (blue), Unit 3C (brown), Unit 7B (green) and Unit 8I (purple). Material of *Calissounemys matheroni* gen. et sp. nov.: 1, right hypoplastron and xiphiplastron (MHNAix-PV.2020.4.3, 'individual D'); 2, skull (MHNAix-PV.2014.3.19, 'individual B'); 3, right costal 1 (MHNAix-PV.2020.4.2, 'individual B'); 4, right costal 1 (MHNAix-PV.2018.22.4, 'individual C'); 5, costal 3 (MHNAix-PV.2018.22.5, 'individual C'); 6, right hyoplastron and entoplastron (MHNAix-PV.2020.4.1, 'individual A'). Scale in me[...]
Pourrières-Jas Neuf Autoroute 1 (PJNA1) avec le segment d'affleureme[...]59-12 » avec la position des spécimens de *Calissounemys matheroni* gen. et sp. nov. dans leurs dépôts de chenaux respectifs (A) et l'organisation synthétique de structures chenalisées (B) (d'après Tortosa, 2014). Structures chenalisées indiquées par des couleurs avec des unités (clair) et des séquences (foncé) : Unité 2I (bleu), Unité 3C (marron), Unité 7B (vert) et Unité 8I (violet). Matériel de *Calissounemys matheroni* gen. et sp. nov. : 1, hypoplastron et xiphiplastron droits (MHNAix-PV.2020.4.3, « individu D ») ; 2, crâne (MHNAix-PV.2014.3.19, « individu B ») ; 3, costale 1 droite (MHNAix-PV.2020.4.2, « individu B ») ; 4, costale 1 droite (MHNAix-PV.2018.22.4, « individu C ») ; 5, costale 3 (MHNAix-PV.2018.22.5, « individu C ») ; 6, hyoplastron et entoplastron droits (MHNAix-PV.2020.4.1, « individu A »). Échelle en mètres.

which the premaxilla extends more anteriorly than the nasal. Anteroventrally, the nasal has a short contact with the maxilla. Laterally, the nasal contacts the prefrontal and posteriorly, the frontal.

Prefrontal. The prefrontal is an anteroposteriorly elongate strip-shaped element that forms the anterior half of the upper rim of the orbit. It is more reduced than that of *C. victa*. The prefrontal is located lateral to the nasal instead of posterior to it as seen in pleurosternids, this position is more comparable to that of *C. victa*. Widely separated by a broad nasal/frontal contact, the left and right prefrontals do not meet one another medially as in Paracryptodira. In addition to the contact with the nasal anteriorly, the prefrontal contacts the maxilla anteroventrally and the frontal medially. Posteriorly, the prefrontal has a short contact with the postorbital along the orbital margin, separating the frontal from the orbital margin.

Frontal. The frontal is a relatively large element that forms most of the skull roof between the orbits, but does not contribute to the orbital margin, separated from it by a short prefrontal/postorbital contact. The frontal is not markedly narrowed anteriorly, in contrast to *C. victa* in which the two frontals form a pentagonal dorsal surface (Lyson and Joyce, 2011). Anteriorly, the frontal has a broad contact with the nasal, which is greater than that of *C. victa*. In addition to a long contact with its counterpart along the midline, the frontal contacts the prefrontal anterolaterally and the postorbital posterolaterally. The suture with the parietals posteriorly is curved forward.

Parietal. The parietal is the largest bone on the skull roof and forms the medial portion of the temporal margin. The surface of the bones is damaged, the lateral sutures with the postorbital can be partly traced, whereas the contact with the squamosal is discernible on the right side. The midline contact between the parietals runs posteriorly to the temporal margin, the supraoccipital is apparently not exposed on the skull roof. The descending process of the parietals is not visible, obscured by the extensive skull roof and matrix.

Postorbital. The postorbital is an anteroposteriorly elongate bone that forms the posterodorsal portion of the orbital margin. Anteriorly, anteromedially and medially, the postorbital contacts the prefrontal, the frontal and the parietal respectively. Anteroventrally, it has a straight contact with the jugal. Posteroventrally, the postorbital/quadratojugal suture runs posteriorly then seems to turn downward, a small ventral process of the postorbital is apparently present anterodorsal to the cavum tympani. As the bone surface in this region is damaged, this interpretation remains tentative. If our interpretation is correct, the postorbital reaches the cavum tympani margin as in *C. victa*.

Jugal. The jugal is a large and roughly sub-triangular element that forms the posterior margin of the orbit and part of the cheek margin between the maxilla and the quadratojugal. Similar to *C. victa*, the contribution of the jugal to the orbital margin is substantial, greater than in baenids and pleurosternids in which this contribution is reduced to absent. In addition to the contact with the postorbital dorsally, the jugal has a straight vertical contact with the quadratojugal posteriorly and an oblique contact with the maxilla anteroventrally. In ventral view, the jugal does not contribute to the triturating surface. The contacts with the pterygoid and palatine are not visible.

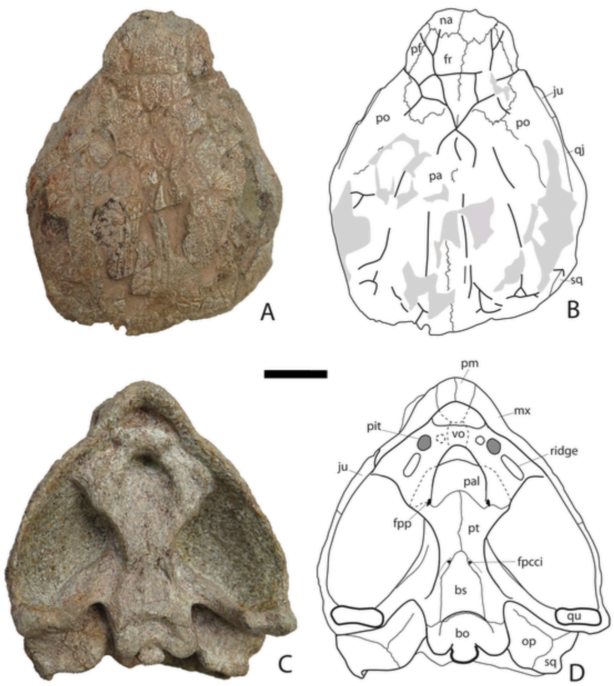

Fig. 4. *Calissounemys matheroni* gen. et sp. nov. (Testudines: Compsemydidae) from the Upper Cretaceous of Var, southern France. Holotype (MHNAix-PV.2014.3.19), an isolated skull in dorsal (A–B) and ventral (C–D) views. Scale bar = 2 cm. Abbreviations: bo: basioccipital; bs: basisphenoid; ex: exoccipital; fpcci: foramen posterius canalis carotici interni; fpp: foramen palatinum posterius; fr: frontal; ju: jugal; mx: maxilla; na: nasal; op: opisthotic; pa: parietal; pal: palatine; pf: prefrontal; pm: premaxilla; po: postorbital; pt: pterygoid; qj: quadratojugal; qu: quadrate; so: supraoccipital; sq: squamosal; vo: vomer.
Calissounemys matheroni gen. et sp. nov. (Testudines : Compsemydidae) du Crétacé supérieur du Var, sud de la France. Holotype (MHNAix-PV.2014.3.19), crâne isolé en vues dorsale (A–B) et ventrale (C–D). Barre d'échelle = 2 cm. Abréviations : bo : basioccipital ; bs : basisphénoïde ; ex : exoccipital ; fpcci : foramen posterius canalis carotici interni ; fpp : foramen palatinum posterius ; fr : frontal ; ju : jugal ; mx : maxillaire ; na : nasal ; op : opisthotique ; pa : pariétal ; pal : palatin ; pf : préfrontal ; pm : prémaxillaire ; po : postorbital ; pt : ptérygoïde ; qj : quadratojugal ; qu : carré ; so : supraoccipital ; sq : squamosal ; vo : vomer.

Quadratojugal. The right quadratojugal is almost complete whereas the left one is damaged, lacking its posterodorsal portion. Ventrally, the quadratojugal forms the straight cheek margin together with the jugal and maxilla. Anteriorly, the quadratojugal has a broad vertical contact with the jugal and dorsally with the postorbital. Posteriorly, the quadratojugal frames the cavum tympani anteriorly and ventrally, but does not form the rim of the cavum, in contrast to *C. victa*. The quadratojugal extends far posteriorly under the cavum tympani to cover part of the condylus mandibularis of the quadrate laterally.

Squamosal. The left squamosal is almost entirely missing; the right one is damaged. The squamosal is short and forms the lateral portion of the temporal margin and frames the cavum tympani posterodorsally. A shallow triangular fossa that opens ventrally is preserved on the posterolateral surface of the left squamosal, as in the helochelydrids *Helochelydra nopcsai* and *Naomichelys speciosa* (Joyce et al., 2011, 2014). As preserved on the right side, the squamosal contacts the parietal medially, preventing the postorbital from being exposed along the temporal margin. The contact with the postorbital anteriorly is not clearly visible because of the damaged surface. Within the temporal fossa, the squamosal contacts the quadrate anteromedially and the opisthotic medially.

The palate is well preserved, but the sutures between the individual bones are not all discernible.

Premaxilla. Dorsally, the paired premaxillae form the ventral edge of the external narial opening and ventrally the anterior portion of the triturating surface and its labial ridge. The sub-nasal portion of the premaxilla is low. The apertura narium externa is a single opening that is much wider than high and faces anteriorly. It appears also larger than that seen in *C. victa*. The labial ridge of the triturating surface is blunt and smooth, a hook-like structure as seen in *C. victa* is absent. On the skull and palatal surfaces, the premaxilla contacts the maxilla posterolaterally and its counterpart along the midline. In ventral view, there is a deep depression on the midline of the triturating surface, just posterior to the labial ridge, as in *C. victa*, presumably to receive a tooth-like structure on the lower jaw. The premaxilla apparently contacts the vomer posterior to the depression, but the suture is not clearly visible.

Maxilla. Dorsally, the maxilla forms the anterior and lower rim of the orbit. The suborbital portion of the maxilla is low and has a nearly straight ventral edge. In lateral view, the maxilla contacts the nasal and the prefrontal anterodorsally. The contact with the jugal posteriorly appears to follow an oblique sulcus that extends from the posteroventral corner of the orbit to the cheek margin. In ventral view, the maxillae form most of the triturating surface, which is relatively broad; but a secondary palate is not developed, in contrast to *C. victa*. The labial ridge is moderate in height with a blunt edge while the lingual ridge is not distinct. The triturating surface is uneven, a tooth-like structure lies posterior to the premaxilla/maxilla suture. An additional blunt ridge extending parallel to the labial ridge lies on the posterior part of the triturating surface. Between these two structures lies a small pit (see Fig. 4). The contacts of the maxilla with the surrounding bones on the palate are not clearly visible. On the triturating surface the maxilla apparently contacts the premaxilla and vomer anteromedially and the palatine medially.

Vomer. The shape of the vomer is unclear since the contacts with the surrounding bones are not discernible. Anteriorly, the vomer appears to contribute to the triturating surface posterior to the premaxillae. The apertura narium interna faces posteroventrally and is located more anteriorly than in *C. victa* (Hutchison and Holroyd, 2003; Lyson and Joyce, 2011).

Palatine. The palatines form the central portion of the palate and part of the edge of the apertura narium interna, and contribute to the posteromedial portion of the triturating surface. The contact with the pterygoids posteriorly is curved forward and located more anteriorly than that of *C. victa*. The contact with the vomer is not clearly visible. The foramen palatinum posterius is a small and anteroposteriorly elongate opening that lies medial to the posteromedial corner of the triturating surface. It is surrounded mostly by the palatine, with a small contribution from the pterygoid posteriorly.

Pterygoid. The pterygoids form part of the palate posterior to the palatines. Anteriorly, the pterygoids have a curved contact with the palatines (and probably the vomer). Anterolaterally, the pterygoid likely has a short contact with the maxilla, lateral to the foramen palatinum posterius, but the suture is not clearly discernible. The lateral border of the pterygoids is almost straight, the processus externus pterygoidei is not distinct, however a faint swelling is present on the lateral margin of the palate, lateral to the foramen palatinum posterius. The pterygoids are markedly constricted about half way of their length then widen again posteriorly. Medially the pterygoid has a broad contact with its counterpart along the midline as in *C. victa*, unlike *Glyptops ornatus* and *Pleurosternon bullockii* in which this contact is absent, prevented by a long ventral exposure of the basisphenoid and unlike *Helochelydra nopcsai* in which the contact extends posteriorly and covers the basisphenoid in ventral view. The pterygoid extends far posteriorly between the quadrates and the basisphenoid to reach the basioccipital. The pterygoid/basioccipital contact is broad and almost transverse. Posterolaterally and medial to the pterygoid/quadrate suture, the pterygoid forms an almost anteroposteriorly directed shallow groove

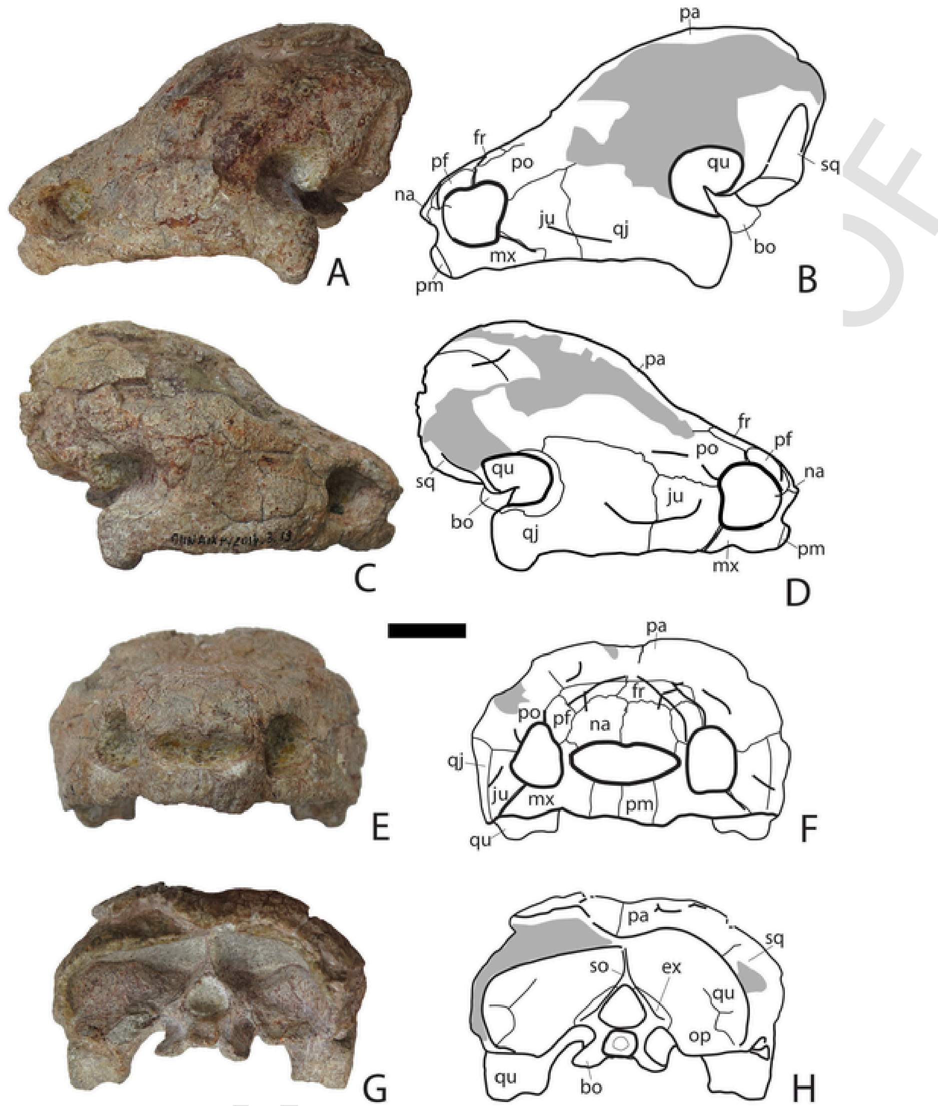

Fig. 5. *Calissounemys matheroni* gen. et sp. nov. (Testudines: Compsemydidae) from the Upper Cretaceous of Var, southern France. Holotype (MHNAix-PV.2014.3.19), an isolated skull in left lateral (A–B), right lateral (C–D), anterior (E–F) and posterior (G–H) views. Scale bar = 2 cm. Abbreviations see Fig. 4.
Calissounemys matheroni gen. et sp. nov. (Testudines : Compsemydidae) du Crétacé supérieur du Var, sud de la France. Holotype (MHNAix-PV.2014.3.19), crâne isolé en vues latérale gauche (A–B) ; latérale droite (C–D) ; antérieure (E–F) et postérieure (G–H). Barre d'échelle = 2 cm. Abréviations voir Fig. 4.

that slopes anterodorsally and is open at both anterior and posterior ends.

Epipterygoid. The epipterygoid and the foramen nervi trigemini on both sides are obscured by the skull roof and the matrix.

Quadrate. Both quadrates are complete. In lateral view, the quadrate forms the roughly circular cavum tympani. The cavum is notably reduced in size, being clearly smaller than the orbit as in *C. victa*, in contrast to pleurosternids and baenids. The contacts with the squamosal dorsally and posteriorly, and with the quadratojugal anteriorly and ventrally are visible along the margin of the cavum. The cavum is entirely formed by the quadrate, without contribution from the quadratojugal. The incisura columellae auris is widely open posteroventrally. The antrum postoticum is obscured by matrix.

In ventral view, the quadrate terminates in a relatively slender condylus mandibularis. The articular facet is concave and short anteroposteriorly. The quadrate contacts the pterygoid medially and the squamosal and the opisthotic posteriorly. Within the fossa temporalis superior, the quadrate contacts the opisthotic medially and the squamosal posteriorly.

Supraoccipital. The supraoccipital is not exposed on the skull roof. The crista supraoccipitalis is a little damaged, but its posterior end is intact, which shows that the crista is short and does not extend beyond the temporal margin of the skull roof. The posterior end of the lower part of the crista even does not extend beyond the edge of the foramen magnum. Ventrally, the supraoccipital forms the upper edge of the foramen magnum. The foramen magnum is located far anterior relative to the edge of the skull roof. On the floor of the upper temporal fossa, the contacts with the exoccipital ventrally and the opisthotic laterally are visible while the contacts with the parietal and prootic are obscured by the extensive skull roof and matrix.

Basioccipital and exoccipital. The basioccipital and the exoccipitals are fused into a single complex as in *Helochelydra nopcsai* and *Naomichelys speciosa*. In ventral view, the basioccipital is a roughly rectangular element, wider than long, with a deeply concave surface. A pair of large and flat tubercula basioccipitale with a rounded outline is developed on the posterolateral corner of the basioccipital. Anteriorly, the basioccipital contacts the basisphenoid. Anterolaterally, it has a broad contact with the pterygoid. Together with the exoccipitals, the basioccipital forms the condylus occipitalis, but the contribution from each bone cannot be determined. The condyle has a short neck, the concave articular surface slanting toward the front. In posterior view, the basioccipital/exoccipital complex forms the

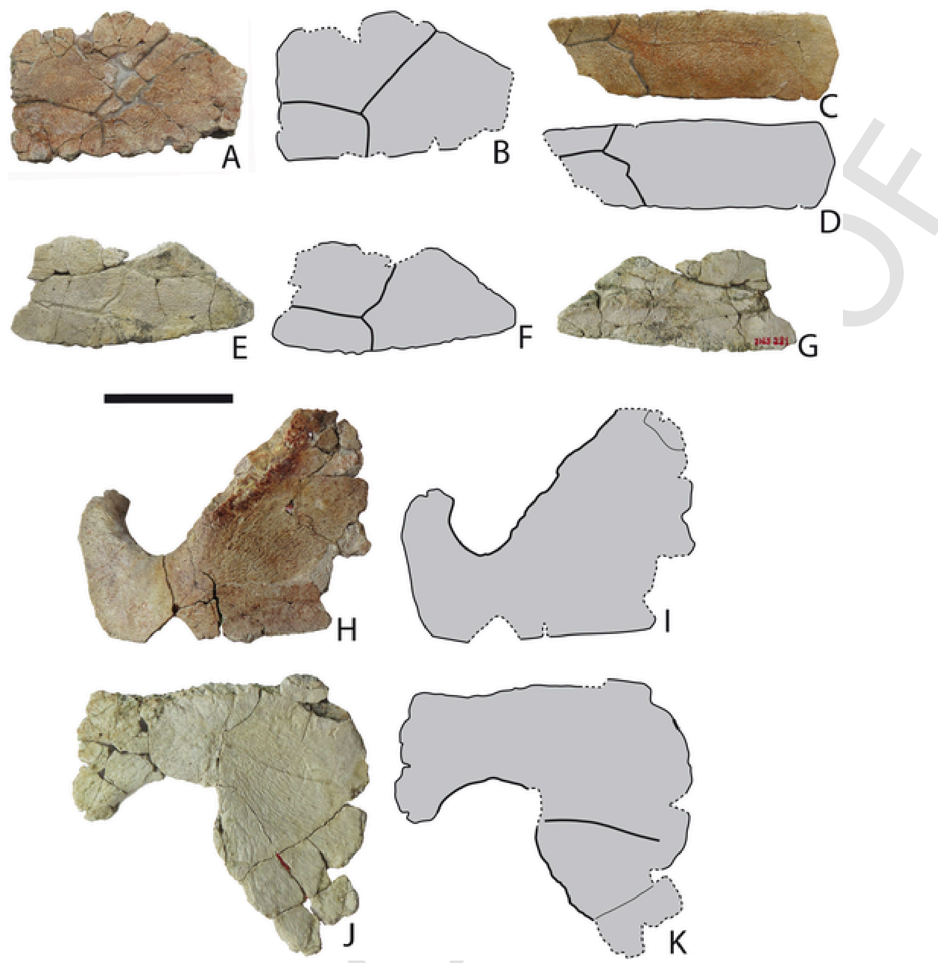

Fig. 6. Shell of *Calissounemys matheroni* gen. et sp. nov. (Testudines: Compsemydidae) from the Upper Cretaceous of Var, southern France. A–B, right costal 1 (MHNAix-PV.2018.22.4) and C-D, right costal 3 (MHNAix-PV.2018.22.5) in dorsal view; E–G, right costal 1 (MHNAix-PV.2020.4.2) in dorsal (E–F) and ventral (G) views; H–I, right hyoplastron and entoplastron (MHNAix-PV.2020.4.1) and J–K, right hypoplastron and xiphiplastron (MHNAix-PV.2020.4.3) in ventral view. Scale bar = 5 cm.

Éléments de carapace de *Calissounemys matheroni* gen. et sp. nov. (Testudines : Compsemydidae) du Crétacé supérieur du Var, sud de la France. A–B, costale 1 droite (MHNAix-PV.2018.22.4) et C–D, costale 3 droite (MHNAix-PV.2018.22.5) en vue dorsale ; E–G, costale 1 droite (MHNAix-PV.2020.4.2) en vues dorsale (E–F) et ventrale (G) ; H–I, hyoplastron et entoplastron droits (MHNAix-PV.2020.4.1) et J–K, hypoplastron et xiphiplastron droits (MHNAix-PV.2020.4.3) en vue ventrale. Barre d'échelle = 5 cm.

Table 1

Measurements of *Calissounemys matheroni* gen. et sp. nov. (Testudines: Compsemydidae) from the Upper Cretaceous of Var, southern France (in mm. Incomplete value in parentheses).

Mesures de *Calissounemys matheroni* gen. et sp. nov. (Testudines : Compsemydidae) du Crétacé supérieur du Var, sud de la France (en mm. Valeurs incomplètes entre parenthèses).

	Length	Width	Height
Skull (MHNAix-PV.2014.3.19)	98	94	56
Shell			
Right costal 1 (MHNAix-PV.2020.4.2)	(41)	95	–
Right costal 1 (MHNAix-PV.2018.22.4)	55	(93)	–
Costal 3 (MHNAix-PV.2018.22.5)	31	(115)	–
Right hyoplastron (MHNAix-PV.2020.4.1)	70	105	–
Right hypoplastron (MHNAix-PV.2020.4.3)	83	109	–

lower and lateral rim of the foramen magnum, frames the foramen jugulare posterius medially, and contacts the supraoccipital dorsally and the opisthotic laterally. The foramina nervi hypoglossi are not apparent.

Prootic. The prootics are obscured by matrix. The foramen stapedio-temporale is not visible.

Opisthotic. The opisthotic is an anteroposteriorly elongate element. Posteriorly, it forms a shelf above the fenestra postotica that slopes gently downward, extending to the level of the posterior end of the condylus occipitalis. In the fossa temporalis superior, the opisthotic contacts the quadrate and the squamosal laterally, and the exoccipital and the supraoccipital medially. The contact with the prootic is obscured by the extensive skull roof and matrix. There is no descending process from the opisthotic, so that the fenestra postotica and the foramen jugulare posterius are confluent into a large opening. Within this opening, the processus interfenestralis of the opisthotic is exposed, extending downward to the pterygoid.

Basisphenoid. In ventral view, the basisphenoid is an elongate pentagonal bone, with a narrow groove along the anterolateral portion of the suture with the pterygoid. The groove starts about at half-length of the basisphenoid and extends anteromedially to end 5 mm from the tip of the basisphenoid. The groove is deeper at its anterior end, where the foramen posterius canalis carotici interni is located. Posteriorly, the basisphenoid/basioccipital suture lies under a steep step.

Shell. The carapace surface is covered with shallow irregular grooves that match those of the skull, and the striations perpendicular to the sutures are present close to the anterior and posterior borders of each plate. This sculpture seems to be finer than that of *B. russelli*

(Pérez-García, 2012). Costal 1 (MHNAix-PV.2018.22.4 and MHNAix-PV.2020.4.2) is roughly triangular in shape. The medial portion of the anterior border (the contact with the nuchal) is nearly parallel to the posterior rim; laterally the anterior border slopes posteriorly to join the posterior margin. In MHNAix-PV.2018.22.4, the width is about twice the length, whereas MHNAix-PV.2020.4.2 is shorter, with its width about 2.5 times its length. The inner surface of costal 1 bears a long swelling, extending transversely from the rib head to the lateral end, but not reaching the posterior border of the plate. Costal 1 is shorter than that of *C. victa*, but more resembles that of *B. russelli* (Gaffney, 1972; Pérez-García et al., 2015a). The contact with the nuchal is less oblique than in *C. victa* and *B. russelli.* Costal 3 lacks its medial end, its anterior and posterior margins are parallel. The inner surface bears a low blunt swelling extending along the full width of the plate.

The scute sulci are well imprinted. Vertebral 1 is clearly wider than vertebral 2, with the lateral borders divergent anteriorly. Vertebrals 2 and 3, when reconstructed, are apparently wider than long as in *B. russelli*, whereas *C. victa* has square vertebrals 2-3.

The outer surface of the plastron is sculptured with fine plications. The anterior and posterior lobes are relatively short and wide with strongly convergent lateral borders. The axillary and inguinal buttresses are moderately developed, similar to *C. victa* and *B. russelli*. The entoplastron is incomplete, when reconstructed, it would appear to be wide. The bridge length of the hyoplastron is shorter than the hypoplastron. The hypoplastron has a short free margin along the midline, located about 1 cm from its anterior rim, indicating the presence of a small central fontanelle. The scute sulci are barely visible on the plastron. The only sulcus discernible is the abdominofemoral on the posterior lobe.

4. Comparisons and discussion

The skull described above is characterized by a well-developed, thick-boned skull roof, a squamosal/parietal contact, a sculptured skull surface, large nasals meeting along the midline and large prefrontals separated from one another by the frontals that contact the nasals. A prominent feature of the skull is that the foramen posterius canalis carotici interni lies midway along the pterygoid/basisphenoid suture, as found in basal turtles, in particular the group Paracryptodira (Pleurosternidae and Baenidae) (Gaffney, 1975; Joyce, 2007) and the recently erected family Compsemydidae (Pérez-García et al., 2015b).

Erected by Gaffney in 1975, Paracryptodira was originally composed of two main clades referred to distinct families: Pleurosternidae Cope, 1868 (Glyptopsidae Marsh, 1890) and Baenidae Cope, 1873 (Gaffney, 1975). The group was later expanded to include a third family, Compsemydidae that consists of *C. victa* and *B. russelli* (Pérez-García et al., 2015b). Our knowledge about the diversity and phylogenetic relationships of Paracryptodira has been greatly improved during the last decade, Baenidae and non-baenid Paracryptodira have been thoroughly revised recently (Joyce and Lyson, 2015; Joyce and Anquetin, 2019). Currently, Pleurosternidae are known from the Jurassic to the Paleocene in Europe and North America; and Baenidae, endemic to North America, are known from the mid-Cretaceous to the Eocene. Compsemydidae, the third family of Paracryptodira for some authors (Pérez-García et al., 2015b; Joyce and Rollot, 2020) includes originally *C. victa* Leidy, 1856 from the Late Cretaceous to Paleocene of North America and *B. russelli* Pérez-García, 2012 from the Paleocene of France (Pérez-García et al., 2015b). In their recent review of non-baenid Paracryptodira, Joyce and Anquetin (2019) gave up Compsemydidae and synonymized *Berruchelus* with *Compsemys*. More recently, in a review of *Peltochelys duchastelii*, Joyce and Rollot (2020) resurrected Compsemydidae and assigned *Selenemys lusitanica* and *Riodevemys inumbragigas* from the Late Jurassic of Portugal and Spain respectively, and the enigmatic *Peltochelys duchastelii* from the Early Cretaceous of Belgium to that family. Previous phylogenetic analyses placed Compsemydidae in the basalmost (Pérez-García et al., 2015a, 2015b), or basal position among Paracryptodira (Joyce and Rollot, 2020). The recent analysis of Rollot et al. (2021) also suggests that Helochelydridae could be part of the Paracryptodira, but the low sampling of basal groups in this study might partially explain that attraction. Our phylogenetic analyses provide a new hypothesis suggesting that Compsemydidae could possibly be the sister group of Pleurodira rather than part of the Paracryptodira (see phylogenetic analyses), it also shows that Compsemydidae and Helochelydridae are monophyletic and well distinct from one another. Skull material is in general well represented in Pleurosternidae and Baenidae, with which the skull from Var is compared. Unfortunately, among Compsemydidae, only one skull of *C. victa* has been described (Lyson and Joyce, 2011), and the family is based mainly on shell features (Pérez-García et al., 2015b; Joyce and Anquetin, 2019; Joyce and Rollot, 2020). Although the skull of *C. matheroni* provides valuable information about the characteristics of the family Compsemydidae, it does not allow to define synapomorphic features that could clearly unite Compsemydidae with Paracryptodira (Pleurosternidae and Baenidae).

As in Paracryptodira, the interpterygoid vacuity is completely closed in *C. matheroni* (MHNAix-PV.2014.3.19) and the internal carotid artery enters the skull via the foramen posterius canalis carotici interni which is located midway along the pterygoid/basisphenoid suture. This character has been used to erect Paracryptodira and to refer compsemydids to that group (Gaffney, 1975; Pérez-García et al., 2015b). Among this group, MHNAix-PV.2014.3.19 most resembles the compsemydid *C. victa*, but is distinct from pleurosternids and baenids (Lyson and Joyce, 2011). Our specimen shares with *C. victa* a series of features: (**1**) a thick-boned robust skull that is oblong as seen from above, (**2**) laterally facing orbits that are not visible in dorsal view, (**3**) large nasals, (**4**) large prefrontals, (**5**) frontals excluded from the orbital margin, (**6**) cheek emargination absent, (**7**) orbit larger than cavum tympani, (**8**) postorbital contributing to the cavum tympani margin, (**9**) large jugal that contributes to a substantial portion of the orbital rim and (**10**) enlarged, sub-quadrate quadratojugal. Characters 3 and 4 are primitive features also found in pleurosternids such as *Glyptops ornatus*, *Pleurosternon bullockii*, *Uluops uluops* and *Dorsetochelys typocardium* (Evans and Kemp, 1976, 1975; Evers et al., 2020; Gaffney, 1979; Rollot et al., 2021), and the basal baenid *Arundelemys dardeni* (Evers et al., 2021; Lipka et al., 2006), whereas characters 5-9 seem to be apomorphies uniting *C. matheroni* and *C. victa*. Characters 1-2 are shared by *C. matheroni* and *Comspemys victa*, and also present in *Uluops uluops* and *Arundelemys dardeni*. In addition, a well-developed skull roof without temporal emargination and the presence of a parietal/squamosal contact, preventing the postorbital from being exposed along the temporal margin seen in our specimen are also primitive characters among Paracryptodira, although these characters are not preserved in *C. victa*. In comparison, pleurosternids (*Pleurosternon bullockii*, *Dorsetochelys typocardium*, *Glyptops ornatus*, and *Dinochelys whitei*) and baenids have a more slender skull with thinner bones, the orbits face dorsolaterally, the temporal and cheek emarginations are more developed, the frontals form part of the orbital rim, the contribution from the jugal to the orbital rim is generally small or even absent (the jugal is retracted from the orbital margin in *Pleurosternon bullockii* and some baenids such as *Plesiobaena antiqua* and *Eubaena cephalica*) (Gaffney, 1972; Brinkman, 2003; Rollot et al., 2018), a slender and more elongate quadratojugal and a quadratojugal/squamosal contact is present, excluding the postorbital from the anterodorsal rim of the cavum tympani. The cavum tympani and orbit are similar in size in pleurosternids, whereas some baenids, such as *Cedrobaena putorius* and *Peckemys brinkman*, have a cavum tympani that is clearly larger than the orbits (Lyson and Joyce, 2009; Joyce and Lyson, 2015).

C. matheroni (MHNAix-PV.2014.3.19) differs from *C. victa* notably in the structure of the upper jaw. Although a depression is present on the midline contact of the premaxillae in both *C. victa* and *C. matheroni*, which suggests that a hook-like structure is present on the lower jaw, a hook is absent on the upper jaw in our specimen, whereas a hook formed by the premaxilla and maxilla is well-developed in *C. victa*. Although the triturating surface in both *C. matheroni* and *C. victa* is uneven with a blunt ridge lateral to the maxilla/palatine suture, an additional tooth-like structure and pits are developed on the triturating surface of the skull from Var, whereas such structures are apparently absent in *C. victa*. In *C. matheroni*, the triturating surface is less developed than that of *C. victa*, a secondary palate is absent, whereas in *C. victa*, a secondary palate is developed, with a clearly longer midline length. The morphological differences of the triturating surface likely correspond to different feeding strategies. Other differences on the skull can be observed. Although the nasals are narrowed posteriorly in both taxa, with the lateral margins convergent backward, the nasal of *C. victa* is triangular as seen from above whereas in our specimen it is sub-rectangular. The prefrontal of *C. victa* is less reduced, with a longer prefrontal/nasal suture when compared with the skull of *C. matheroni*. The basisphenoid of *C. matheroni* is pentagonal in shape and elongate, being clearly longer than the triangular basisphenoid of *C. victa*. In lateral view, the suborbital bar is low in our specimen, whereas it is more developed in *C. victa*.

Three incomplete costals and two plastral fragments from the same locality as the skull can be confidently assigned to *C. matheroni* on the basis of the fine ornamentation on the shell surface which matches that of the skull. Although these shell elements are fragmentary, they provide some distinctive features relative to other Compsemydidae. The morphology of costal 1 of *C. matheroni* more resembles that of *B. russelli*, *Selenemys lusitanica* and *Riodevemys inumbragigas*, being short and narrowed laterally, different from the longer costal 1 of *C. victa* that lacks a lateral narrowing (Gilmore, 1919; Gaffney, 1972; Pérez-García and Ortega, 2011; Pérez-García, 2012; Pérez-García et al., 2015b). In *Peltochelys duchastelii*, costal 1 has a longer contact with the nuchal. Vertebral 1 of *C. matheroni* is clearly wider than vertebrals 2-3, with the lateral margins strongly divergent towards the anterior border, similar to *B. russelli* (Pérez-García, 2012, Fig. 3D–F), whereas in *C. victa*, vertebral 1 is only slightly wider than vertebral 2 with slightly divergent lateral margins. In *Selenemys lusitanica* and *Riodevemys inumbragigas*, vertebral 1 is narrower than vertebrals 2-3. Vertebrals 2-3 of *C. matheroni* are similar to those of *B. russelli*, *Selenemys lusitanica* and *Riodevemys inumbragigas*, being wider than long, whereas these scutes are square in *C. victa* and *Peltochelys duchastelii*. In summary, the shell morphology of *C. matheroni* seems to be more similar to that of *B. russelli* than to that of other compsemydids.

C. matheroni is distinct from Helochelydridae, a basal group of turtle known from the Cretaceous of Europe and North America, remains of which are common in the Campanian-Maastrichtian beds of southern Europe (France and Spain) (Lapparent de Broin and Murelaga, 1996, 1999; Joyce et al., 2014; Joyce, 2017; Pérez-García et al., 2020). *C. matheroni* lacks an important synapomorphy of Helochelydridae, a well-developed second tuberculum basioccipitale formed by the pterygoid (Joyce, 2017). It has been recently suggested that the second pair of tubercula basioccipitale was present in some pleurosternids (*Dorsetochelys tipocardium*, *Glyptops ornatus*, *Pleurosternon bullockii*) (Rollot et al., 2021); but in these taxa, the structure is not as strong as in *Helochelydra nopcsai* and *Naomichelys speciosa*, and the tubercula are anteroposteriorly developed and not coalesced medially to form a nearly continuous bulge on the skull floor at the posterior border of the pterygoids. Our phylogenetic hypotheses show that the reported structure in pleurosternids are not homologous with that of the helochelydrids as they are acquired independently. In addition, the skulls of helochelydrids (e.g. *Helochelydra nopcsai* and *Naomichelys speciosa*) differ from that of *C. matheroni* in having more reduced nasals, frontals contributing to the orbital margin, a small cheek emargination, the orbit smaller than the cavum tympani, the postorbital excluded from the cavum tympani margin, the jugal with a small contribution to the orbital margin or retracted from it, and the unexpanded and C-shaped quadratojugal. Our phylogenetic analyses recovered the clade Helochelydridae in a more basal position relative to Paracryptodira, including Compsemydidae.

5. Phylogenetic analyses

In order to estimate the phylogenetic relationships of *C. matheroni* with other turtles, we performed the phylogenetic analyses using the character/taxa matrix of Joyce et al. (2016), which was later modified by Pérez-García and Codrea (2018) and Pérez-García (2020). We discarded the characters relative to skull scute pattern [character 91 to 105 of Joyce et al. (2016)] since the position and the homology of cranial scutes are difficult to define among groups. Characters relative to plastral kinesis [134 to 136 of Joyce et al. (2016)] have been recoded to better differentiate hinge in terms of position and homology. Original characters 112, 113 and 244 of Joyce et al. (2016) regarding carapace sculpturing which are redundant were recoded as a single character. Character 131 of Joyce et al. (2016) regarding the position of marginals relative to costals was recoded as three new characters in order to better take into account the primary homology. Two additional characters described in Joyce and Rollot (2020) were added and seven new characters relative to the first vertebral scute, the fifth vertebral scute, the first peripheral, and the first costal plate were added to the matrix. The resulting matrix totalizes 238 characters (see Appendix 1 for complete list of characters and character state definition).

In addition to *C. matheroni* and the taxa scored in the analyses of Joyce et al. (2016), we scored the characters for other recently described or re-described Paracryptodira including *Riodevemys inumbragigas*, *Selenemys lusitanica*, *Peltochelys duchastelii*, *Toremys cassiopeia*, *B. russelli* and *C. victa* (Lyson and Joyce, 2011; Pérez-García and Ortega, 2011; Pérez-García, 2012; Pérez-García et al., 2015a, 2015b; Joyce and Rollot, 2020). We added *Aragochersis lignitesta*, a recently described helochelydrid from the Lower Cretaceous of Spain (Pérez-García et al., 2020) to our analyses in order to better assess potential relationships between *C. matheroni* and this clade. Several character states were rescored from our observations or based on recently published revisions (Tong et al., 2012, 2014; Pérez-García and Codrea, 2018; Evers et al., 2020; Joyce and Rollot, 2020; Pérez-García, 2020; Li et al., 2021). In order to reduce bias of branch attractions due to weak character sampling within taxa and to win some time during the heuristic search, we deleted taxa for which states were scored for less than 30 percent of the characters from the matrix, as well as the terminal units "*Ordosemys* sp" and *Macrochelys schmidti*. The analysis was therefore run on 112 taxa and 238 characters. The matrix is given in Appendix 1.

Parsimony analyses were performed under PAUP 4.0.169 (Swofford, 1998) using random addition sequence, and the tree bisection-reconnection branch swapping algorithm setting the rearrangement limit to 10,000,000. Two thousand and five hundred replicates were run in order to reach good convergence in terms of total equally parsimonious tree obtained. Thirty-three multistate characters were ordered because they represented morphological clines. All ordered multistate characters (three or four states) were scaled so they would count a maximum of one step between two taxa (in other terms, in doing so those characters would not have a disproportionate effect above binary and unordered characters on phylogeny estimation).

We used a molecular backbone based on the recent literature (Guillon et al., 2012; Lourenço et al., 2012; Crawford et al., 2015; Thomson et al., 2021) to constrain the tree. Two sets of analyses were performed. Analysis 1 is based on the 112 taxa and 238 characters. In the second set (analysis 2), we first estimated the phylogeny without *C. matheroni* and grafted it later onto the obtained consensus tree in keeping resolved constraints imposed by the backbone. For both analyses, we estimated how many supplementary steps were necessary to force *C. matheroni* within Helochelydridae.

The first analysis resulted in 93079 equal trees of 964.31 steps. The simplified Adams consensus tree is shown in Fig. 7. The second analysis resulted in 50544 equal trees of 964.81 steps, the Adams consensus tree is shown in Fig. 8. The complete strict consensus and Adams consensus trees are shown in Appendix 2. Both analyses recovered *C. matheroni* within Compsemydidae and that clade well distinct from Helochelydri-

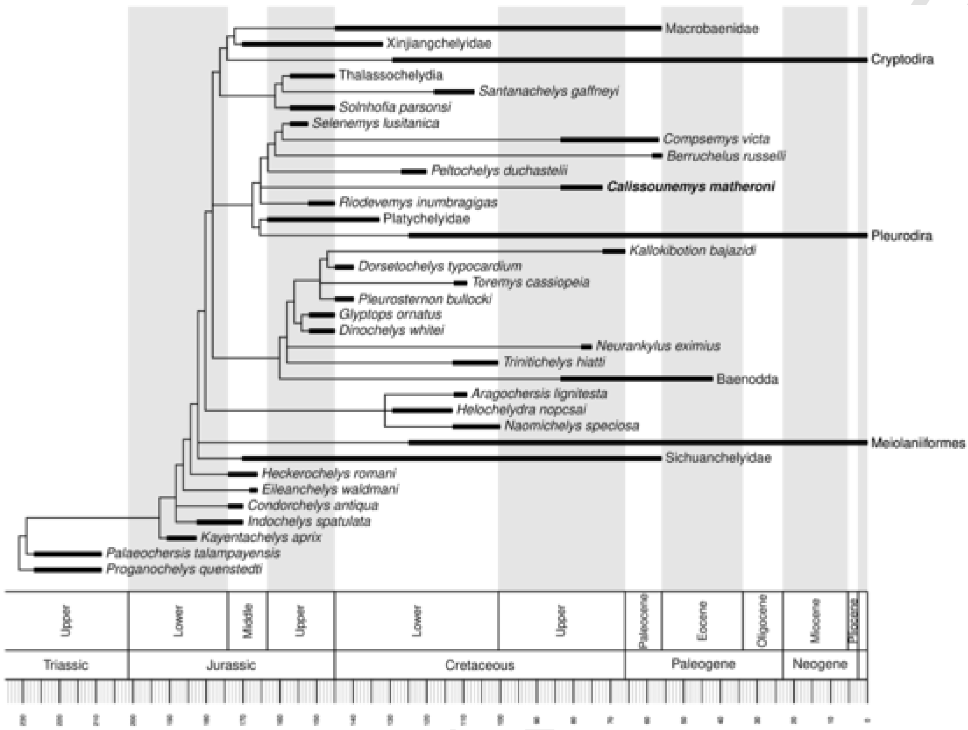

Fig. 7. Simplified Adams consensus tree obtained for the constrained phylogenetic analyses (analysis 1, 964.31 steps).
Adams consensus cladogramme simplifié obtenu pour les analyses phylogénétiques contraintes (analyse 1, 964.31 pas).

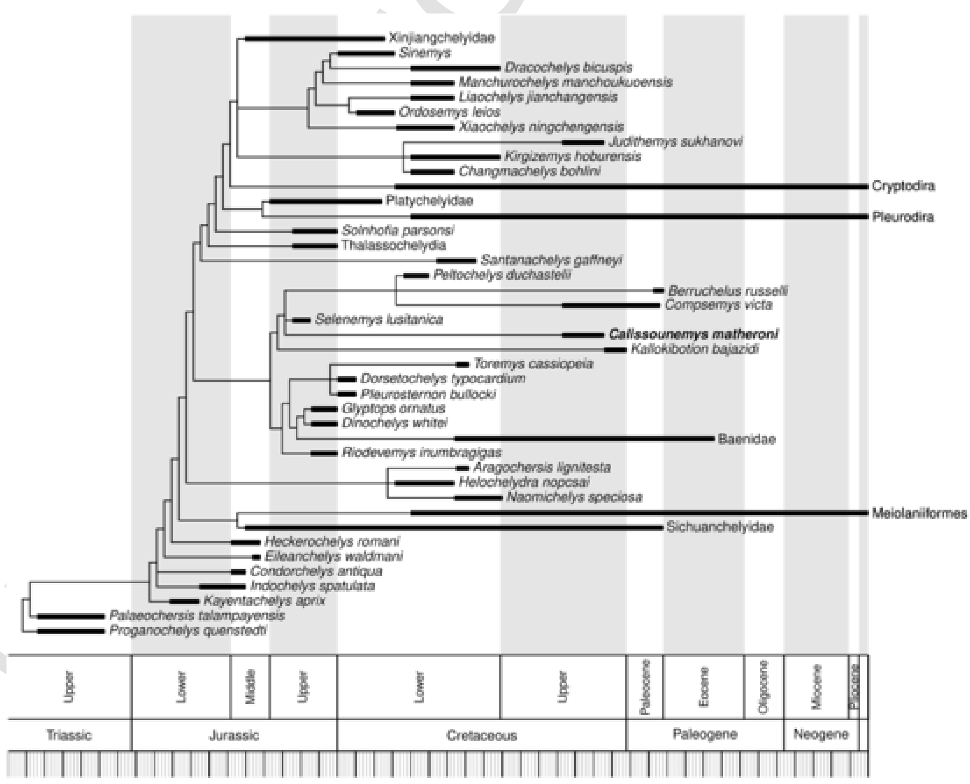

Fig. 8. Simplified Adams consensus tree obtained excluding first *Calissounemys* and subsequently regrafting it to the obtained topology (analysis 2, 964.81 steps).
Adams consensus cladogramme simplifié obtenu en excluant d'abord Calissounemys et en le regreffant à la suite à la topologie obtenue (analyse 2, 964.81 pas).

dae. It costed respectively 6 and 4.5 more steps in terms of parsimony to force *C. matheroni* to be a helochelydrid rather than a compsemydid when using resulting topologies based on analyses 1 and 2 and keeping resolved constraints imposed by the backbone. Although close in terms of parsimony steps, the two analyses differed in several points: the position of Compsemydidae at the base of Pan-Pleurodira or Paracryptodira, the inclusion of *Trinitichelys hiatti* and *Neurankylus eximius* either in Baenidae or in Pleurosternidae, the position of *K. bajazidi* as sister group of *Dorsetochelys typocardium* or as a Compsemydidae, the position of *Riodevemys inumbragigas* as a compsemydid outside of Paracryptodira or at the base of Paracryptodira, and the monophyly or not of 'Macrobaenidae'. Other relationships were similarly resolved between analyses.

The first analysis (the shortest of two) recovers Compsemydidae as a clade with *C. matheroni*, *Peltochelys duchastelii*, *C. victa*, *Riodevemys inumbragigas*, *Selenemys lusitanica* and *B. russelli*. Compsemydidae is the sister group of pan-Pleurodira. As *Peltochelys duchastelii* is considered as a compsemydid, this phylogenetic relationship resurrects the original idea of Dollo (1884) who noticed similarities of neck motion between juvenile *Peltochelys duchastelii* and Pleurodira. It is, however, unlikely that cervical morphology used alone would clearly help to prefer one or another hypothesis as it has been demonstrated elsewhere that evolution of neck motion in basal Pleurodira is more complex than originally thought (Anquetin et al., 2017). Under the phylogenetic scenario suggested by this analysis, *Trinitichelys hiatti*, *Neurankylus eximius* and *K. bajazidi* are recognized as Pleurosternidae.

The compsemydid group recovered here is in agreement with the definition of Compsemydidae in Joyce and Rollot (2020) and includes *Peltochelys duchastelii*, *Riodevemys inumbragigas* and *Selenemys lusitanica*, while Pérez-García et al. (2015b) assigned *R. inumbragigas* and *S. lusitanica* to Baenoidea. We consider therefore that the characters used by Joyce and Rollot (2020) for Compsemydidae are diagnostic but the position of *Riodevemys inumbragigas* within Compsemyidae needs to be confirmed since this species does not show any synapomorphy of the group except the sinuous midline sulcus of the plastron (Joyce and Rollot, 2020). In the Adams consensus *Selenemys lusitanica* forms a clade with *C. victa*, and *B. russelli* and *Peltochelys duchastelii* are successive sister groups of this clade. Other relationships within the group are not resolved (position of *C. matheroni* and *Riodevemys inumbragigas*) and need to be clarified in the future by new discoveries, which, in terms of carapace morphology, may help to understand evolutionary patterns in the group regarding the mesoplastron reduction and nuchal exclusion from the carapacial rim. The discovery of more shell material of *C. matheroni* would certainly be important to establish whether the nuchal is excluded from the anterior carapacial rim. Further material of *Peltochelys duchastelii* (skull, vertebrae) is needed to understand whether the loss of mesoplastron in this taxon is an independent synapomorphy or not. Although we followed most character changes suggested by Pérez-García and Codrea (2018) and Pérez-García (2020), we were not able to reproduce the results of Pérez-García (2020) regarding the position of *K. bajazidi*, instead this taxon is defined in our first set of analyses as a Pleurosternidae. It should be reminded that correcting several other character states and rescaling ordered multistate characters to avoid over-weighting in our analyses might partially explain this disagreement.

In analysis 1, Paracryptodira do not include Compsemydidae anymore. While previous authors (as well as our study) have not found clear synapomorphic characters uniting all Paracryptodira, our analysis does not show clear synapomorphies uniting Pleurodira and Compsemydidae, nor any clear synapomorphies for Baenoidea. These relationships might therefore be challenged by the inclusion/exclusion of characters or by the inclusion of other taxa. Nevertheless, five more steps are necessary to exclude Pleurodira from Baenoidea and to place Compsemydidae as sister group of Baenoidea if other phylogenetic relationships are not modified. Compsemydidae seems to be bettter defined: the skulls of compsemydids so far known show many differences from those of Pleurosternidae and Baenidae, in particular their nasal and prefrontal configuration and the relative size of their cavum tympani (see description and discussion). In addition compsemydids have a special morphology of the anterior part of the carapace (nuchal partly or completely excluded from the anterior margin of the carapace).

Although not the most parsimonious but differing just by 0.5 steps, the second analysis shows an interesting alternative hypothesis. In this analysis, clade compositions and relationships are more classical (the analysis shows several similarities with the work of Joyce et al., 2016). The result of this analysis is in better agreement with the palaeobiogeographical and stratigraphical records (cf. Pleurosternidae and Baenidae and the more reduced gap regarding the record of basal forms leading to Baenodda). For this analysis, if no other relationships are modified, 15.6 more steps would be required to prune Compsemydidae as they are recovered and graft it as sister group of Pleurodira. This is in part explained because Compsemydidae differs in terms of taxonomic composition. In particular, this second analysis considers *K. bajazidi* as a compsemydid, a hypothesis that was independently found with another set of characters and taxa in Rollot et al. (2021). This suggests that, in this taxon, the nuchal plate is not divided in two plates as suggested by Pérez-García and Codrea (2018), as serial homology is unlikely, but instead that the anterior element is a neoformed peripheral element and the posterior one a true nuchal plate following the initial hypothesis of Nopcsa (1923). *K. bajazidi* has also a sculptured shell surface and its skull morphology shows more similarities with compsemydids than with helochelydrids. Compsemydidae (defined here by the exclusion of the nuchal plate from the anterior margin of the carapace) also differ from analysis 1 regarding *Riodevemys inumbragigas,* which is moved to a basal position respective to Baenoidea. The relationships within Compsemydidae differ from the previous hypotheses: while *Peltochelys duchastelii*, *B. russelli* and *C. victa* form a clade, the positions of *Selenemys lusitanica* and *C. matheroni* relative to this clade vary but they are always less basal than *K. bajazidi* within the family. Finally, the second analysis does not recover 'Macrobaenidae' as monophyletic. As in the first analysis, *Basilochelys macrobios*, *Sinaspideretes wimani,* and *Siamochelys peninsularis* are Xinjiangchelyidae, but not basal Trionychoidae (see Appendix 2). Contrary to Rollot et al. (2021), none of our analyses recovered helochelydrids within Paracryptodira; but helochelydrids were found in each scenario more basal than pleurosternids, baenids or compsemydids; even with modification on the codings of the anterior turbercula basioccipitale following Rollot et al. (2021) (results not shown).

6. Other compsemydids from the Late Cretaceous of Southern France

Tong and Claude (2017) reported turtle remains from the Campanian (Late Cretaceous) of the Bellevue locality, Campagne-sur-Aude, southern France, which they referred to Paracryptodira. The material includes a skull and an isolated costal plate. The skull is close to *C. matheroni* (MHNAix-PV.2014.3.19) in many aspects, including the thick-boned oblong-shaped skull, shallow temporal emargination, anteriorly facing external narial opening, laterally facing orbits and the postorbital reaching the cavum tympani margin; but also distinct from MHNAix-PV.2014.3.19 in a series of features (e.g. a shallow cheek emargination, a flat triturating surface, the presence of a pair of large processi pterygoidei externi and the jugal retracted from the orbital margin). The material from Bellevue represents a different taxon of Compsemydidae and will be described in a separate paper.

7. Conclusions

Over 200 years of research on vertebrate fossils from the Upper Cretaceous (Campanian-Maastrichtian) of southern France have resulted in the discovery of a rich turtle fauna. This fauna, consisting of pleurodiran bothremydids and dortokids, and the basal turtle group helochelydrids, is dominated by the bothremydids, followed by the helochelydrid *Solemys*. The recent discoveries of compsemydid turtle remains, including *C. matheroni* gen. et sp. nov. described in the present work, increase the diversity of this rich turtle fauna and fill a gap in the record of this primitive turtle lineage between the Early Cretaceous and the Paleocene in Europe. This find provides information to amend the diagnosis of the family on the skull features. From a palaeobiogeographical point of view, the discovery of compsemydids in the Upper Cretaceous deposits of southern France provides additional evidence to support the hypothesis that this lineage originated in Europe and dispersed to North America prior to the Campanian.

Disclosure of interest

The authors have not supplied their declaration of competing interest.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.annpal.2022.102536.

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