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A *Solemys* Skull from the Late Cretaceous of Southern France

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Abstract: The first skull of *Solemys* (Testudines: Helochlydridae) is reported from the Late Cretaceous (Rognacian) Bastide Neuve locality, Fox Amphoux, Var, France. It is assigned to *Solemys gaudryi* (Matheron, 1869) on the basis of associated shell elements. Our study provides new insights regarding the skull morphology of the family Helochelydridae and suggests that *Helochelydra* from England and *Naomichelys* from North America appear to be closer to each other than to *Solemys*.

Keywords: Testudines; Helochelydridae; *Solemys gaudryi*; Late Cretaceous; Southern France; systematics

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1. Introduction

Helochelydridae Nopcsa, 1928, are a group of primitive turtles from the Cretaceous of Europe and North America. According to recent reviews, the family contains at least four well established genera in Europe and one in North America [1–3]. Although shell fragments are common in Cretaceous non-marine deposits, skull material is rare for this family. A complete skull of *Helochelydra nopcsai* Lapparent de Broin et Murelaga, 1999, has been reported from the Barremian of the Isle of Wight, England [4]. A nearly complete skeleton, including a damaged skull of *Naomichelys speciosa* Hay, 1908, from the Albian-Aptian of Texas, USA, has been described more recently [5,6]. Lastly, two complete skeletons of *Aragochersis lignitesta* Pérez-García, Espílez, Mampel, and Alcala, 2020, with poorly preserved skulls, have been reported from the Albian of Spain [3]. Here we describe a partial skull of the helochelydrid turtle *Solemys gaudryi* (Matheron, 1869), collected by two of us (P. and A. Méchin) from the Upper Cretaceous Rognacian of Bastide Neuve locality, Fox Amphoux, Var, Southern France. In order to justify the generic and specific assignment, some shell elements from the same locality are also included in the present study. The material studied herein is housed in the private collection of P. and A. Méchin (PAM), Bouches-du-Rhone, France, and at the Musée des Dinosaures (MDE), Espéraza, Aude, France.

2. Geological Setting

The Bastide Neuve locality is situated near the village of Fox Amphoux, in the northern part of the Var department (south-eastern France). The non-marine fossiliferous siltstones and sandstones, of Late Cretaceous age (Campanian) [7], have yielded a rich vertebrate fauna, including hybodont sharks, bony fishes, crocodiles, turtles (bothremydids, including the holotype of *Foxemys mechinorum* Tong et al., 1998, and helochelydrids), azhdarchid pterosaurs, birds, and various dinosaurs [7–16].

3. Systematic Palaeontology

Testudines Linnaeus, 1758

Helochelydridae Nopcsa, 1928

Emended diagnosis (for skull characters): skull roof sculpture matching that of the shell; skull roof well developed, temporal emargination very reduced or absent; medial process of squamosal present, reducing the parietal exposure on the temporal margin; foramen pro ramo nervi vidiani exposed on the ventral surface of the skull; two sets of tubercula basioccipitale, the anterior pair is formed at least partly by the pterygoid.

Solemydinae new subfamily

Solemys Lapparent de Broin et Murelaga, 1996

Solemys gaudryi (Matheron, 1869)

(Figures 1–4)

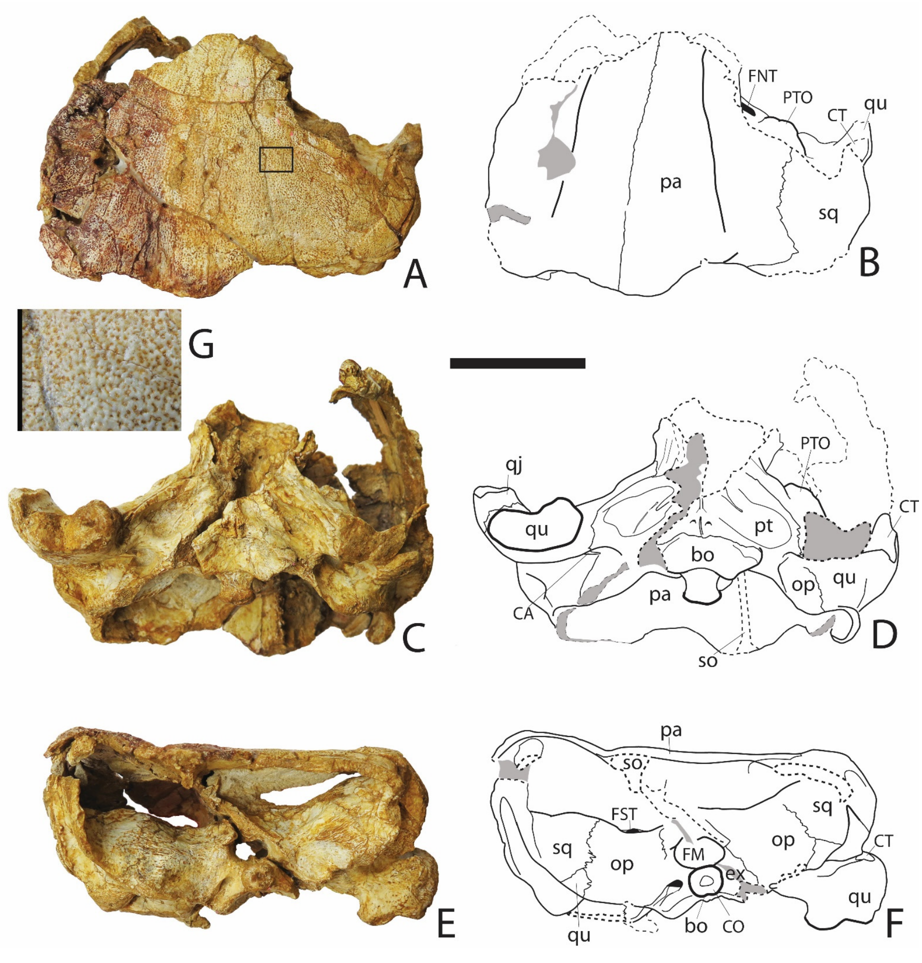

Figure 1. *Solemys gaudryi*, skull (PAM 485) in dorsal (**A**,**B**), ventral (**C**,**D**), and posterior (**E**,**F**) views and detail of the ornamentation on the skull roof (**G**). Scale bar = 5 cm (**A**–**F**) and 1 cm (**G**). Abbreviations: bo, basioccipital; BTB, basis tuberculi basalis; CA, columella auris; CM, condylus mandibularis; CO, condylus occipitalis; CT, cavum tympani; ep, epipterygoid; ex, exoccipital; FJA, foramen jugulare anterius; FM, foramen magnum; FNH, foramen nervi hypoglossi; FNT, foramen nervi trigemini; FPE, fenestra perilymphatica; FST, foramen stapedio-temporale; op, opisthotic; pa, parietal; pr, prootic; pt, pterygoid; PTO, processus trochlearis oticum; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal.

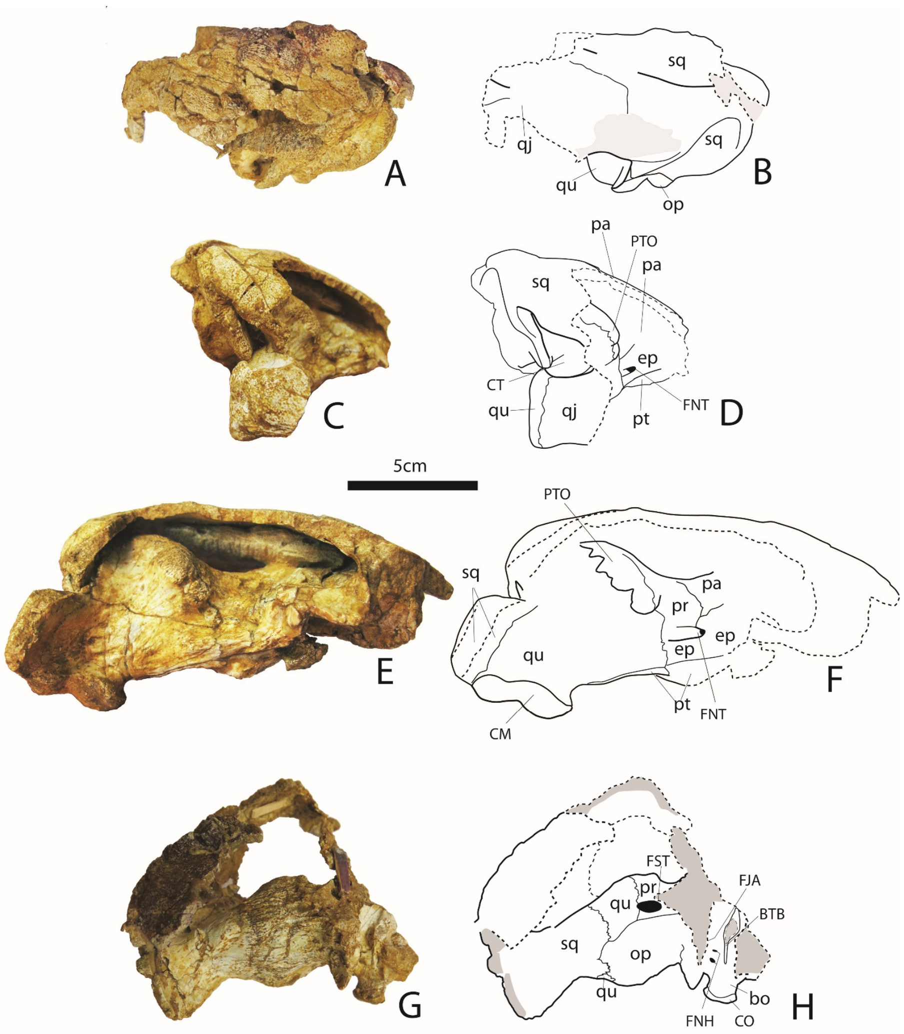

Figure 2. *Solemys gaudryi*, skull (PAM 485) in the left lateral (**A**,**B**), right lateral (**C**,**D**), right anterolateral (**E**,**F**) views and the dorsal view of the otic chamber and basioccipital with the skull roof removed (**G**,**H**). Scale bar = 5 cm. For abbreviations see Figure 1.

Emended diagnosis (skull features only): A member of Helochelydridae, different from *Helochelydra nopcsai*, *Aragochersis lignitesta,* and *Naomichelys speciose,* in having a small temporal emargination; a small medial process of the squamosal; the parietal contribution to the temporal margin greater than that from the squamosal (only seen for *Helochelydra nopcsai* and *Naomichelys speciosa*); the tubercula basioccipitale are less developed and not posteriorly directed, the anterior pair is larger than the posterior one and formed by the pterygoid and basioccipital; the osseous subdivision between the inner and middle ear cavities present.

Referred material: a partial skull (PAM 485), a fragment of plastron including complete left epiplastron and incomplete right epiplastron and entoplastron (MDE T54), an isolated xiphiplastron (MDE T55); Bastide Neuve locality, Fox Amphoux, Var, Southern France; Rognacian, Late Cretaceous.

3.1. Description and Comparisons

3.1.1. Skull (Figures 1–3)

Preservation: PAM 485 is the posterior portion of a skull, with the anterior part having been destroyed during the extraction. The skull has undergone post-mortem deformation, with the sagittal axis of the skull roof pushed leftward relative to the occipital condyle.

Measurements: The preserved part of the skull measures 8 cm along the midline of the skull roof and 12.5 cm at the level of the cavum tympani, which represents the greatest width of the skull. The preserved height of the skull at the midline of the posterior end of the skull is about 5.5 cm.

General aspect: The skull is robust and apparently wide, but as the specimen is crushed and its anterior part is missing, the general shape and the original height of the skull are uncertain. The skull roof is well developed as in *Helochelydra nopcsai*, *Aragochersis lignitesta,* and *Naomichelys speciosa*. The temporal emargination is very reduced, represented by a small notch on the posterior margin of the skull roof. In comparison, the temporal emargination of *Naomichelys speciosa* appears to be wider, while in *Helochelydra nopcsai*, the posterior border of the skull roof is almost straight. In ventral view, the skull is shortened posteriorly, the position of the condylus occipitalis is more anterior relative to the condylus mandibularis compared with that of *Helochelydra nopcsai* and *Aragochersis lignitesta*. In *Naomichelys speciosa,* these two structures are even more distant.

Skull roof ornamentation: the skull roof is covered with a distinct sculpture consisting of vermiculated low ridges that match the sculpture of the shell, but finer (about 1 mm wide), and the ridges are more coalesced (Figure 1G). This ornamentation is stronger than that of *Aragochersis lignitesta,* and different from the isolated low tubercles in *Helochelydra nopcsai* and *Naomichelys speciosa.*

Skull roof scales: A pair of anteroposteriorly directed scale sulci are clearly visible on the skull roof, located at about mid-width of each parietal, which indicates the presence of a single large parietal and a pair of temporal scales on the skull roof. In lateral view, a sulcus roughly parallel to the sulcus between the temporal and parietal scales is preserved on the left squamosal, separating the temporal scale above from the jugal scale below. In comparison, the scale sulci are absent (or not visible) on the skull surface of *Helochelydra nopcsai* and *Aragochersis lignitesta* [3,4]. In *Naomichelys speciosa*, some scale sulci are present on the posterior part of the dorsal skull roof, but a scale pattern cannot be traced [5].

Parietal: Both parietals lack the anterior portion, so its anterior extension and contacts are unknown. The parietals are large bones that extensively cover the skull roof. The only contact of the parietal clearly visible on the skull roof is with the squamosal laterally on the right side, whereas that on the left side is obscured by cracks. The main portion of the long parietal/squamosal suture runs anteroposteriorly, then turns medially when it gets close to the temporal margin. The contribution of the parietal to the temporal margin of the skull is nevertheless greater than that from the squamosal. In comparison, the posterior free margin of the parietal is narrower in *H. nopcsai* and *N. speciosa*, its contribution to the temporal margin is much smaller than that of the squamosal. The midline suture of the parietals extends posteriorly almost to the posterior end of the skull roof where the margin is a little damaged. The supraoccipital is possibly not exposed on the skull roof as in *Aragochersis lignitesta*, or has a small exposure on the skull roof posterior to the parietals as in *N. speciosa*. In *H. nopcsai*, the supraoccipital exposure on the skull roof is larger, and it lies between the parietals.

The descending process of the parietals is not complete on either side. It forms the lateral wall of the braincase and contacts the epipterygoid anteroventrally and the prootic ventrolaterally, but does not reach the foramen nervi trigemini. The contact with the supraoccipital ventrally is either damaged or obscured by cracks and matrix.

Quadratojugal: The left quadratojugal is damaged, while the right one is mostly missing, and only the posterior end of its ventral branch remains. As in *H. nopcsai*, *N. speciosa,* and *A. lignitesta*, the quadratojugal forms the anterior and lower edges of the cavum tympani and contacts the quadrate posteromedially and posteriorly. A clear quadratojugal/quadrate suture is visible within the cavum tympani, along its margin. The ventral branch of the quadratojugal extends posteriorly to almost fully cover the condylus mandibularis of the quadrate in lateral view, as in *H. nopcsai*, *N. speciosa,* and *A. lignitesta*. On the left side, a larger portion of the quadratojugal is preserved, but the contacts with the surrounding bones are much obscured by cracks, a contact with the jugal or postorbital is not discernible.

However, a quadratojugal/squamosal suture is visible anterodorsal to the cavum tympani, which runs posteriorly and then turns ventrally towards the cavum tympani.

Squamosal: Both squamosals are preserved but damaged. The squamosal forms the posterolateral corner of the skull roof and broadly contacts the parietal medially. As preserved on the right side, the squamosal sends a medial process along the temporal margin posterior to the parietal. The morphology of this bone on the left side is obscured by deformation and cracks. In comparison, the squamosals in both *H. nopcsai* and *N. speciosa* also have a medial process behind the parietal, as in our specimen. However, the process is more elongated anteroposteriorly and medially broader in *H. nopcsai* and *N. speciosa* than in *Solemys*, resulting in a much smaller exposure of the parietal on the temporal margin. The contact with the postorbital is not preserved on the right side, it is obscured by cracks on the left side. Ventrolaterally, the squamosal frames the cavum tympani dorsally and posteriorly, and contacts the quadrate ventrally. The contact with the quadratojugal anteroventrally above the cavum tympani is preserved on the left side. In posterior view, the squamosal forms a triangular fossa posterior to the cavum tympani that opens ventrally as in *H. nopcsai*, *N. speciosa,* and *A. lignitesta.*

Inside the upper temporal fossa, the squamosal contacts the quadrate and the opisthotic medially (Figure 2G,H).

Supraoccipital: The supraoccipital is damaged and has undergone a strong distortion. The supraoccipital is little or not exposed on the skull roof (see description of parietal). The posterior end of the crista supraoccipitalis is broken off, but it is apparent that the crista is short and would not extend beyond the posterior margin of the skull roof, as in *H. nopcsai* and *N. speciosa*. The supraoccipital forms the upper margin of the foramen magnum and contacts the exoccipital ventrally, the opisthotic laterally, and the parietal dorsally. The supraoccipital/prootic contact is obscured by cracks and matrix.

Figure 3. *Solemys gaudryi* (PAM 485), stereophotographs of the left otic region in the posterolateral view. For abbreviations see Figure 1.

Basioccipital and *exoccipital*: The basioccipital and exoccipitals are fused in *Solemys*, as in *H. nopcsai* and *N. speciosa*. Although the skull was damaged in the middle during the extraction, the basioccipital/exoccipital complex is almost complete, lacking only the right tubercula basioccipitale. In ventral view, the basioccipital is a roughly trapezoidal element; the main body of the bone is short anteroposteriorly with a clearly concave ventral surface. Anteriorly and anterolaterally, the basioccipital contacts the pterygoids along a curved suture. The middle portion of the pterygoids/basioccipital suture lies on a slope, while its lateral portion crosses a blunt ridge that ends at the anterior tuberculum basioccipitale. The condylus occipitalis is oval in posterior view and is likely formed by both basioccipital and exoccipitals, but the proportion of the contribution from each bone is unclear. Laterally, there are two sets of tubercula basioccipitale, the first pair (anterior), more prominent than the second, is formed by the pterygoids and basioccipital, the second pair (posterior) is formed by the basioccipital (Figure 1C,D). In comparison, *H. nopcsai*, *N. speciosa,* and *A. lignitesta* also have two sets of tubercula basioccipitale, but the first pair is formed by the pterygoids and the second by the basioccipital. In addition, they are more prominent and more posteriorly directed.

In posterior view, as the skull is crushed with the occipital condyle pushed to the right relative to the crista supraoccipitalis, the left otic region is better exposed. A foramen nervi hypoglossi lies on the dorsolateral surface of the neck of the condylus occipitalis on the left side, whereas it is not visible on the right side. Lateral to the condylus occipitalis on the left side, a dorsomedially–ventrolaterally directed, teardrop-shaped foramen is present on the posterior surface of the skull. Bordered by the basioccipital/exoccipital complex, it is partially open ventrally and extends in the direction of the foramen jugulare anterius. The latter is visible on the floor of the braincase, anterolateral to the dorsal opening of the foramina nervi hypoglossi. This foramen also houses a second foramen nervi hypoglossi, which lies under its dorsal edge and is slightly larger than the first one. Sterli and Joyce [17] termed a foramen in a similar position in *Kayentachelys aprix* the foramen jugulare intermedium, that is further split in the skull into the foramen jugulare anterius medially and into the fenestra perilymphatica laterally. The foramen in *Solemys* is apparently not fully homologuous to the foramen jugulare intermedium of *Kayentachelys*, but is more medially located. On the posterior surface of the skull, the exoccipital/basioocipital complex contacts the supraoccipital dorsally and the opisthotic laterally.

In dorsal view, the preserved part of the braincase floor is entirely formed by the basioccipital, the parabasisphenoid is apparently lacking, and no suture is visible on the floor of the braincase. The dorsal aspect of the basioccipital is characterized by a prominent sagittal ridge, the basis tuberculi basalis [18,19]. Starting at the level of the posterior foramen nervi hypoglossi, the ridge extends anteriorly and becomes higher and wider, and then ends at a point anterior to the foramen jugulare anterius. Posterolateral to this structure, two pairs of foramina nervi hypoglossi are visible on the braincase floor. Anterolateral to them lies the foramen jugulare anterius.

Prootic: The prootic forms a small medial portion of the processus trochlearis oticum, most of the process laterally is formed by the quadrate. The process is a huge protrusion directed anteriorly, with a rough surface and additional strong rugosities on its anterior end for the cartilago transiliens attachment. The composition of the processus trochlearis oticum of PAM 485 is more comparable to that of *H. nopcsai*; whereas in *N. speciosa*, the entire processus trochlearis oticum is formed by the prootic [5]. A large oval-shaped foramen stapedio-temporale is exposed on the left side (its long axis is perpendicular to the axis of the skull and measures about 5 mm); it lies anterior to the prootic/opisthotic suture and is almost entirely formed by the prootic, with a small contribution from the quadrate laterally. Anteroventrally and laterally, the prootic contacts the quadrate, whereas posteriorly it contacts the opisthotic. Medially, the prootic/parietal suture is preserved on the right side, located above the foramen nervi trigemini, and is distant from the processus trochlearis oticum. The prootic forms the upper rim of the foramen nervi trigemini. As in *H. nopcsai*, the prootic has a short contact with the epipterygoid dorsal to the foramen nervi trigemini, preventing the parietal from reaching that foramen.

Opisthotic: The opisthotic forms the posteromedial part of the floor of the fossa temporalis superior, where it contacts the supraoccipital/exoccipital complex medially, the prootic anteriorly, the quadrate anterolaterally and the squamosal laterally. On this floor, the opisthotic has an additional short lateral contact with the quadrate, posterior to the squamosal/opisthotic suture. Posteriorly, the short processus paraoccipitalis of the opisthotic extends to the level of the end of the condylus occipitalis.

The cavum acustico-jugulare is widely open posteriorly. On the posterior surface of the skull, the opisthotic sends a ventral process to meet the pterygoid, completely separating the foramen that leads to the foramen jugulare anterior (described above) from the fenestra postotica. The fenestra postotica is roofed by the opisthotic dorsally and is bordered by the quadrate laterally and ventrally, with a small contribution from the pterygoid ventromedially. Within the fenestra postotica, the processus interfenestralis is exposed and several structures can be recognized. The processus interfenestralis is a large process with a concave posterior surface that extends ventrally to meet a horizontal medial process of the pterygoid. It is located close to the posterior edge of the skull, so that a recessus scalae tympani enclosed by bone, as seen in modern turtles (e.g., *Chelonia mydas*), appears to be absent. The processus interfenestralis forms the posterior wall of the cavum labyrinthicum and defines medially the fenestra perilymphatica. Laterally, the process borders the fenestra ovalis that is oriented in the direction of the columella auris. The columella auris is preserved partly in situ on both sides. The aditus canalis stapedio-temporalis, located under the opisthotic shelf and the opening of the canalis cavernosus ventrolateral to the fenestra ovalis are distinguishable.

Pterygoid: In ventral view, the pterygoids extend medially to meet one another along the midline and reach the basioccipital posteriorly. The parabasisphenoid is not exposed on the ventral surface just anterior to the basioccipital, contrary to most turtles. The anterior part of the pterygoids is damaged. The remaining posterior part of the bone bears a sagittal ridge on its ventral surface, while a midline suture along the ridge is not clearly discernible. At the posterior end of the ridge, there is a pair of deep pits that are separated from one another by a fine sagittal groove. The right pit seems to be pierced by a small foramen, while there is no foramen within the left pit. Laterally, the pterygoids form a pair of large depressions on the ventral surface of the skull that are well defined laterally, medially, and posteriorly. The anterior end of both depressions is damaged, which allows the canalis cavernosus to be partially exposed. An anteromedially directed low ridge divides the anterior part of the depression and defines a groove-like structure medially. The anterior end of the groove is missing, so its extension or whether the groove ends at a foramen or not is unclear. In the right depression, a fine groove is preserved, extending anteromedially across the length of the depression to end at a small foramen, which likely transmitted the vidian nerve [18,20,21]. The foramen pro ramo nervi vidiani (foramen distalis nervi vidiani *sensu* Rollot et al. [22]) is visible at a similar position in *N. speciosa* and *H. nopcsai* [4,5].

Anterior to the pterygoid depressions described above, the pterygoids form a narrow waist and then enlarge again anteriorly. Whether a processus externus pterygoidei is developed or not cannot be determined because the relevant part of the bone is missing. An additional pair of elongate depressions is apparent at the level of the waist, along the lateral border of the pterygoids. In ventral view, the pterygoid contacts the basioccipital posteromedially and the quadrate laterally. Laterally on the side wall of the braincase, the pterygoid contacts the epipterygoid dorsally, ventral to the foramen nervi trigemini, but it does not contribute to that foramen.

In posterior view, the pterygoid sends a horizontal medial process between the processus interfenestralis of the opisthotic and the quadrate to form a small part of the ventromedial margin of the fenestra postotica and defines the ventral edge of the fenestra ovalis. Joyce et al. [4] tentatively identified a small foramen medioventrally to the cavum labyrinthicum as the foramen posterius canalis carotici interni in *H. nopcsai*. In *Solemys*, we were unable to locate this foramen in a similar position.

Epipterygoid and foramen nervi trigemini: The right epipterygoid is complete while the left one is damaged. The epipterygoid is a roughly C-shaped bone as seen in lateral view, which frames the foramen nervi trigemini from anterior and below. Dorsally, the epipterygoid is detached from the parietal along their suture by postmortem deformation. Ventrally, the epipterygoid sends a rod-like posterior process below the foramen nervi trigemini to contact the quadrate. The foramen is an oval opening. The prootic contributes to the dorsal and the quadrate to the posterior rim of that foramen. In addition to the contact with the parietal dorsally and the quadrate posteroventrally, the epipterygoid contacts the pterygoid ventrally and the prootic posterodorsally dorsal to the foramen nervi trigemini. The parietal is excluded from the margin of the foramen nervi trigemini by the epipterygoid/prootic contact.

Quadrate: The right quadrate is almost complete, but deformed; the left one lacks the condylus mandibularis. Laterally, the quadrate forms the small cavum tympani. Both cava are crushed so the original shape is unclear. The incisura columellae auris is open as a narrow fissure and the incomplete columella auris, a slender rod-like bone, is preserved in situ on both sides. The bottom of the cavum and the antrum postoticum are obscured by broken bones and matrix. The quadrate contacts the squamosal dorsal to the cavum tympani. The quadrate/quadratojugal contact is visible on the right side, within the cavum tympani along its ventral margin and on the lateral surface of the processus articularis of the quadrate.

Ventrally, the quadrate forms the processus articularis, which bears the condylus mandibularis. Well preserved on the right side, the condylus is a robust structure that is wider than long and is divided by an anteroposteriorly directed furrow into a larger medial portion and a smaller lateral portion. In ventral view, the quadrate/pterygoid suture extends from the base of the processus articularis anteromedially along a prominent ridge that defines the pterygoid depression laterally.

Within the fossa temporalis superior, the quadrate forms most of the processus trochlearis oticum and contacts the epipterygoid anteromedially, ventral to the foramen nervi trigemini; the prootic medially, dorsal to that foramen and the opisthotic posteromedially. In posterior view, the quadrate has a small exposure between the squamosal and the processus paroccipitalis of the opisthotic, ventral to the squamosal/opisthotic suture (Figure 1E,F). In *H. nopcsai*, a posteriorly directed process of the quadrate is also present between the squamosal and the processus paroccipitalis of the opisthotic, but it is dorsal to the squamosal/opisthotic suture in posterior view.

Parabasisphenoid: As in *H. nopcsai*, the parabasisphenoid is not visible on the ventral surface of the skull (see pterygoid), whereas this bone is well exposed ventrally in *N. speciosa* [5].

3.1.2. Shell (Figure 4)

Plastron: MDE T54 is a fragment of plastron consisting of both epiplastra and entoplastron (Figure 4A–C). The left epiplastron and entoplastron are complete, while the right epiplastron lacks its lateral portion (Figure 4A–C).

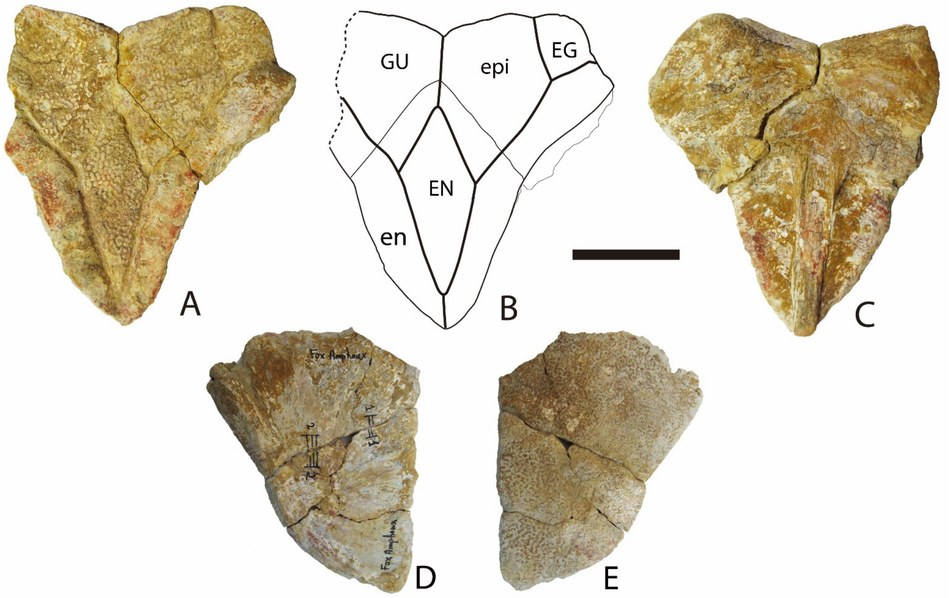

Figure 4. *Solemys gaudryi,* (**A**,**C**), anterior part of the plastron including both epiplastra and entoplastron (MDE T54) in ventral (**A**,**B**) and dorsal (**C**) views; (**D**,**E**), left xiphiplastron (MDE T55) in dorsal (**D**) and ventral (**E**) views. Scale bar = 5 cm. Abbreviations: EG, extragular scute; en, entoplastron; EN, entoplastral scute; epi, epiplastron; GU, gular scute.

The anterior edge of the plastron is clearly notched in the middle. The epiplastron is a five-sided plate that has a short contact with its counterpart. The contact with the entoplastron is long and straight, as long as the contact with the hyoplastron, and forms an acute angle with the latter. In comparison, the midline contact between the epiplastra is shorter in *N. speciosa* and *A. lignitesta*, and the epiplastron/entoplastron contact is shorter in *A. lignitesta.* The entoplastron is diamond-shaped and longer than wide, with the anterolateral borders being shorter than the posterolateral margins. The pair of gulars is large, longer than wide, extending onto the anterior part of the entoplastron. This differs from the wider and shorter entoplastron of *N. speciosa* and *A. lignitesta.* The extragular, complete on the left side, is a small, roughly square scute located on the anterolateral corner of the epiplastron. As in *N. speciosa* and *A. lignitesta*, there is a large diamond-shaped entoplastral scute. This scute is longer than wide, with the anterolateral edges clearly shorter than the posterolateral margins. The entire surface is covered with strong ornamentation consisting of raised vermiculated ridges and pustules that are more or less coalesced, but not dislocated.

On the visceral surface, there is a well-developed lip along the anterior border of the plastron that is covered by the sculpture. The lip is longer at the anterolateral corner than in the middle. A prominent arrow-shaped structure lies posterior to the lip, with a sagittal ridge extending along the midline of the entoplastron.

The isolated left xiphiplastron (MDE T55, Figure 4D,E) is nearly complete, lacking the anteromedial corner. The ornamentation matches that of the plastral fragment described above. The xiphiplastron has a long suture with its counterpart along its full length, and an anal notch is absent. The lateral rim is pinched at the lateral end of the femoroanal sulcus. The plate is thicker laterally than medially. MDE T55 is more elongated than the xiphiplastron of *N. speciosa* and *A. lignitesta*. On the inner surface, a lip is developed along the lateral border, which is wider anteriorly and becomes narrower posteriorly and then vanishes close to the posterior end. On the anterolateral part of the plate, a long and narrow groove with a pointed end lies along the lateral border to receive a process from the hypoplastron.

4. Phylogenetic Analyses

We performed phylogenetic analyses to estimate the position of *Solemys gaudryi* and the relationships of Helochelydridae with other turtle groups. The combined character/taxa matrices defined in Tong et al. [23] and Tong et al. [24] are used for our analyses. Nine new characters were appended to our matrix using characters described in Rollot et al. [25] that were not redundant with previous ones. As in previous analyses, only taxa with more than 30% of the characters scored were considered. Thanks to recent works on Paracryptodira and other basal turtles [3,25–27], we also scored relatively well documented taxa in our matrix, including *Arundelemys dardeni* Lipka et al., 2006; *Uluops uluops* Carpenter and Bakker, 1990; *Hayemys latifrons* (Hay, 1908); *Peckemys brinkmani* Lyson and Joyce, 2009; *Laurasichersis relicta* Pérez-García, 2020; and *Lakotemys australodakotensis* Joyce et al., 2020. Based on the revision of Tong and Li [26], we also scored *Nanhsiungchelys wuchingensis* Ye, 1966, in order to better document character evolution within pan-trionychoid turtles as our previous attempts failed to recover the monophyly of Trionychia with the supposed sister group (e.g., [23]). *Solemys vermiculata* and *Solemys gaudryi* were scored for 43% and 37% of total characters, respectively. A few characters were rescored after re-examination of the specimen anatomies and/or based on recent or ongoing studies (see Supplementary Materials S1). As a result, the matrix contained 122 taxa with 247 characters. A first, full analysis was run and later analyses were rerun in pruning selected key-taxa one by one to see their impact on the topology.

Parsimony analyses were performed under PAUP 4.0a169 [27] using random addition sequence and the tree bisection-reconnection branch swapping algorithm across 2500 replicas, setting the rearrangement limit to 10,000,000. Thirty five multistate characters were ordered as they represented morphoclines, and these multistate characters (three or four states) were scaled so they would count a maximum of one step between two taxa (see [23,24]). We used a molecular backbone based on the recent literature [28] to constrain the tree. The removal of *Kallokibotion bajazidi* from the analyses had a great impact, and the resulting topology is also presented here.

The general analysis yielded 97,012 equal trees of 1142.64 steps, but the number of new equal trees was still increasing after 2500 replicas of the heuristic search. However, several tree islands equal in length were hit multiple times and the consensus tree was stable well before to reach this limit. A second run was done to ensure repeatability. The Adams consensus showed that 23 nodes were not resolved, among which 11 were involved in the simplified phylogeny presented in Figure 5. The analysis without *Kallokibotion bajazidi* produced 150,196 equal trees of 1124.31 steps and was better resolved, the number of new islands of best trees (1124.31 steps) decreased after 2000 runs. Here, also, a second independent run was done to ensure repeatability. The Adams consensus showed that 13 nodes were not resolved, among which only three are involved in the simplified phylogeny presented in Figure 6.

All of the analyses recovered the monophyly of Helochelydridae, also a clade consisting of Macrobaenidae and Xinjiangchelyidae (as in [23,24]). Within Helochelydridae, three clades are constantly found: *Solemys* is monophyletic, *Aragochersis* is monotypic, and *Helochelydra* and *Naomichelys* form a monophyletic group. We suggest therefore naming the clade consisting of *Solemys vermiculata* and *S. gaudryi* Solemydinae as a new subfamily, and the clade consisting of *Helochelydra* and *Naomichelys* as Helochelydrinae Nopcsa, 1928. *Aragochersis lignitesta* is either a sister group of Helochelydrinae or a sister group of Helochelydrinae + Solemydinae. Although most clades remained stable in the analyses, changes occurred regarding the phylogenetic position and content of Compsemydidae, the content of Paracryptodira, the position of Cryptodira, and the position of *Aragochersis* within Helochelydridae when *Kallokibotion* was excluded from the analysis. In the general analysis, Pleurodira form a monophyletic group, and a monophyletic Eucryptodira group consisting of Cryptodira + Xinjiangchelyidae + Thalassochelydia + Macrobaenidae is found. Compsemydidae consists of at least six genera (*Calissounemys*, *Berruchelus*, *Compsemys*, *Peltochelys*, *Selenemys,* and *Kallokibotion*), but the relationships regarding the inclusion or exclusion of Compsemydidae relative to Paracryptodira are not resolved. Within Paracryptodira, the exact content of Pleurosternidae and Baenidae cannot be estimated even if most of them are clustered together, as evidenced by the comparison of Adams consensus and Strict consensus (see Supplementary Materials S2 and S3). Helochelydridae are the sister group of all other Paracryptodira, Panpleurodira, and Pancryptodira.

The exclusion of *Kallokibotion bajazidi* helps to resolve several nodes (Figure 6). The obtained phylogeny differs from the previous one in the position of the clade Pleurodira + Platychelyidae that becomes the sister group of Compsemydidae, and the clade Compsemydidae and Pleurodira + Platychelyidae is sister group of Paracryptodira. This arrangement allows for distinguishing three different types of carotid artery system configurations: primitive groups where the internal carotids split outside of the cranium, then penetrate into the skull via two distinct openings on the skull floor; compsemydids, pleurodirans, and paracryptodirans, where the internal carotids perforate the skull floor from the ventral side anterior to the basioccipital through a single foramen or opening; and eucryptodirans where the internal carotids perforate the skull more posteriorly. Based on CT scans, helochelydrids may fall in the second type [6]. Nevertheless, direct observations on the skulls were not able to locate the foramen posterior canalis carotici interni in this family with certainty ([4,5], this study). Although this topology is reminiscent of some previous topologies found in Tong et al. (2022) [24], we were not able to define autapomorphies uniting Compsemydidae and pleurodiran turtles. The second topology differs on other points: *Aragochersis* and *Riodevemys* are placed in the basalmost position of Helochelydridae and Compsemydidae, respectively.

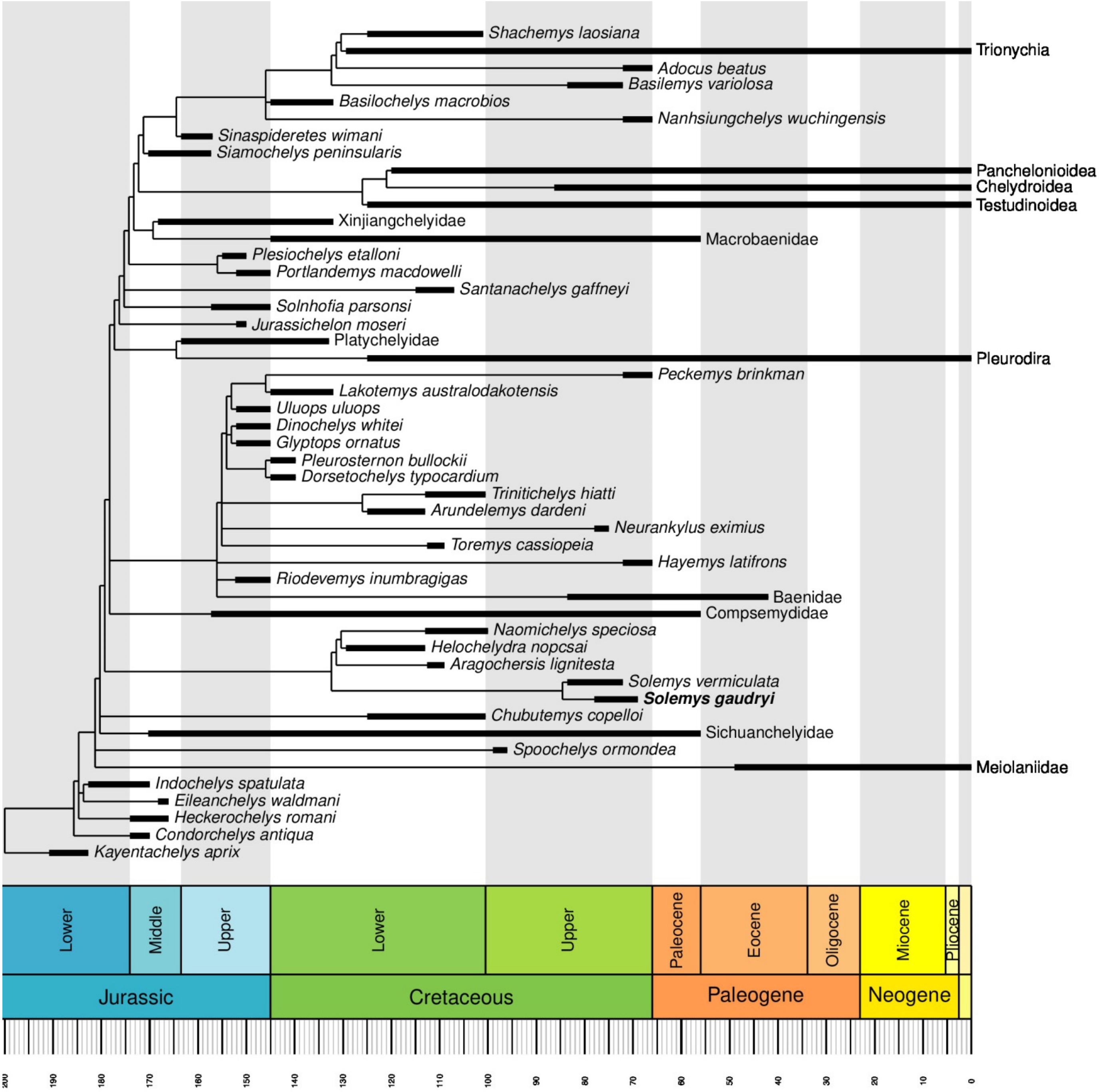

Figure 5. Simplified Adams consensus tree obtained for the constrained phylogenetic analyses (analysis 1, 1142.64 steps).

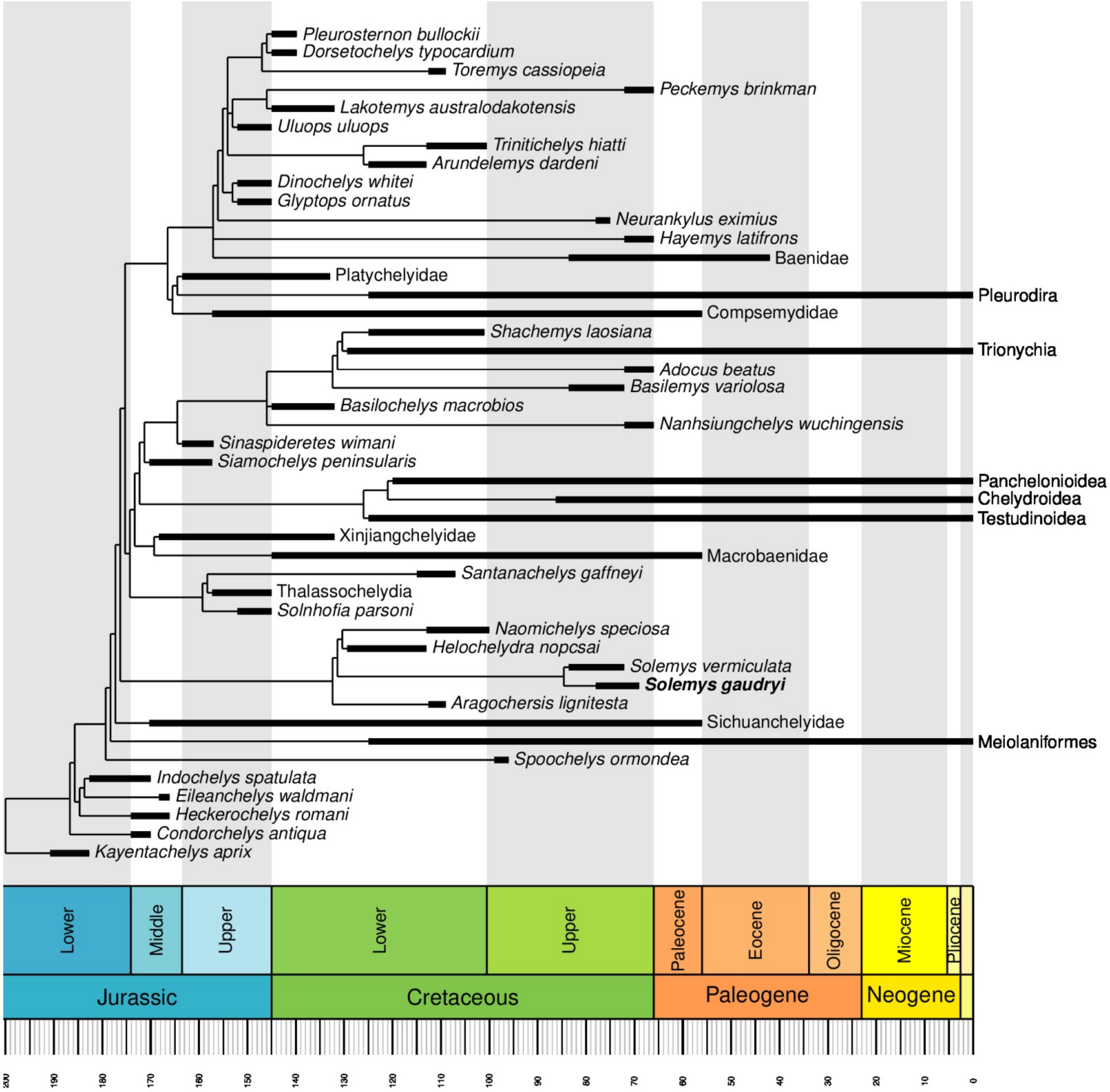

Figure 6. Simplified Adams consensus tree obtained excluding *Kallokibotion bajazidi* (analysis 2, 1124.31 steps).

5. Discussion

5.1. Systematic Assignment

On the basis of the morphology and ornamentation, the shell elements from Bastide Neuve are assigned to the helochelydrid *Solemys*. The family Helochelydridae is characterized by both shell and skull surface that are covered by a pronounced ornamentation and the sculpture on the skull surface matches that of the shell. However, the ornamentation of *Solemys* is distinct from that of *Helochelydra nopcsai*, *Naomichelys speciosa* and *Helochelys daubina* Meyer, 1855 [29]. The ornamentation of *Solemys*, as shown in the specimens from Bastide Neuve described above, consists of coalesced vermiculated ridges and tubercles; in contrast to the isolated pustules which are easily dislocated in *Helochelydra*, *Naomichelys* and *Helochelys*. In *Plastremys lata*, the shell sculpturing consists of broad and blunt tubercles that never coalesce and do not break from the shell [4].

The genus *Solemys*, endemic in the Late Cretaceous of southern Europe, contains two species based on shell morphology: *S. gaudryi* [30] and *S. vermiculata* Lapparent de Broin et Murelaga, 1996. On the basis of the morphology of the plastron, the shell elements from Bastide Neuve described above are assigned to *S. gaudryi* because the gular scutes are longer than wide, and extend greatly onto the entoplastron, and the entoplastral scute has the anterolateral edges much shorter than the posterolateral borders and is located at the center of the entoplastron [31,32]. In addition, the ornamentation of *S. vermiculata* is composed of rounded ridges that are finer (average 1.5 to 2 mm wide) than those of *S. gaudryi*. The ornamentation on the shell elements from Bastide Neuve agrees with that of *S. gaudryi*, which consists of sharper or rugose ridges, about 3 mm wide. Lapparent and Murelaga [32] reported *Solemys* aff. *gaudryi* from the Rognacian of Fox Amphoux.

The skull from Bastide Neuve described herein is assigned to Helochelydridae based on the sculptured skull roof and general morphology, which is comparable to that of *Helochelydra nopcsai* and *Naomichelys speciosa*. As the shell elements from the same locality are assigned to *S. gaudryi*, the skull in all likelihood belongs to the same species, although it is not directly associated with the shell elements.

5.2. Phylogenetic Relationships of *Solemys*

Although shell remains of *Solemys* are relatively common in the Upper Cretaceous non-marine deposits of southern Europe, PAM 485 is the first skull hitherto reported. In the family Helochelydridae, three taxa with skull material have been described (a complete skull of *Helochelydra nopcsai* from the Early Cretaceous (Barremian) of the Isle of Wight, England; a nearly complete skeleton of *Naomichelys speciosa*, including a damaged skull, from the Early Cretaceous Antlers Formation of Texas, USA; and two skeletons of *Aragochersis lignitesta* with poorly preserved skulls from the Early Cretaceous (Albian) of Spain to which the skull of *Solemys* is compared [3–5].

Joyce et al. [5] listed a series of skull characters shared by *Helochelydra* and *Naomichelys*, including (1) temporal emargination absent; (2) laterally set orbits; (3) anteriorly sloping snout; (4) relatively small prefrontals that do not meet one another along the midline; (5) elongate postorbital; (6) jugals retracted from the orbital margin; (7) absence of supratemporal; (8) posterior expansion of squamosal; (9) presence of triangular fossae behind the cavum tympani formed by squamosal; (10) two pairs of tubercula basioccipitale, the second one formed by the pterygoid; (11) foramen pro ramo nervi vidiani (VII) exposed on ventral surface; and (12) lack of osseous subdivision between the cavum acustico-jugulare and recessus scalae tympani. Among them, characters 4–7 are considered as derived stem turtle characters and characters 8–12 are unique synapomorphies shared by *Helochelydra* and *Naomichelys*.

The skull of *Solemys* is incomplete, lacking the anterior portion, so characters 2–6 are not preserved; characters 8–11 are present in the *Solemys* skull (PAM 485). Among these features, the posterior expansion of the squamosal by a medial process, two sets of tubercula basioccipitale and foramen pro ramo nervi vidiani (VII) exposed on ventral surface are synapomorphies of Helochelydridae, shared by *Helochelydra*, *Naomichelys*, and *Solemys*. The skulls of *Aragochersis*, although complete, are poorly preserved and lack many sutures and details of structures, only two sets of tubercula basioccipitale can be observed that are more comparable to those of *Helochelydra* and *Naomichelys* than to *Solemys*. The presence of triangular fossae behind the cavum tympani formed by the squamosal is not typical for helochelydrids, but is also present in other turtles (for example *Chelonia mydas*) for depressor mandibulae attachment [18].

As suggested by our phylogenetic hypotheses among Helochelydridae, *Helochelydra* and *Naomichelys* are apparently closer to one another than to *Solemys*. This is based not only on the shell and skull surface ornamentation, but also on the skull morphology. The medial process of the squamosal in *Helochelydra* and *Naomichelys* is longer anteroposteriorly and extends more medially when compared with that of *Solemys*. In consequence, the contribution of the parietal to the temporal margin is smaller than that of the squamosal in these two taxa, contrary to *Solemys* in which the temporal margin of the parietal is greater than that of the squamosal. The contribution of the parietal to the temporal margin is also greater than that of the squamosal in *Aragochersis*. Although two sets of tubercula basioccipitale are considered to be present in *Solemys*, the morphology of this structure is different from that of *Helochelydra*, *Naomichelys,* and *Aragochersis*. In these three taxa, two sets of tubercula basioccipitale are posteriorly directed and more prominent, the anterior pair and the posterior pair are similar in size, and the anterior pair is entirely formed by the pterygoid. In *Solemys*, the tubercula are weaker and not directed posteriorly, the anterior pair is more prominent than the posterior one and it is formed mainly by the pterygoid with a small contribution from the basioccipital posteriorly.

A notable difference between *Solemys* on the one hand, and *Helochelydra* and *Naomichelys* on the other hand appears to be the structure of the otic chamber. Joyce et al. [4,5] indicated that in both *Helochelydra* and *Naomichelys,* the osseous subdivision between the inner and middle ear cavities is lacking; the cavum labyrinthicum, cavum acustico-jugulare, and the recessus scalae tympani are conjoined to a single, large fossa and the processus interfenestralis of the opisthotic is also absent. *Solemys*, on the contrary, has a well-developed processus interfenestralis that walls the cavum labyrinthicum posteriorly and the foramen jugulare is separated from the fenestra postotica by bone. The structure of the otic chamber in *Solemys* is, however, relatively primitive as the recessus scalae tympani is not well defined by bone. The comparisons of the skull features between *Solemys*, *Helochelydra*, *Naomichelys,* and *Aragochersis* are summarized in Table 1. If *Helochelydra* is closer to *Naomichelys* than to *Solemys,* as mentioned above, the pterygoids completely covering the parabasisphenoid ventrally shared by *Helochelydra* and *Solemys* should be considered as independent acquisitions.

The structures related to the arterial system of helochelydrids are not well understood. Joyce et al. [4] tentatively identified a small foramen medioventrally to the cavum labyrhinticum as the foramen posterius canalis carotici interni in *H. nopcsai*. The position of this foramen in *Naomichelys* is unclear [5]. The study on the endocranial anatomy showed that there are two branches for the internal carotid artery that diverge just after entering the basicranium in the pterygoid/basisphenoid at the level of the basioccipital/basisphenoid suture, but the exact location where the cerebral and palatine arteries bifurcate cannot be reconstructed for this species due to the preservation of the specimen [6]. It is worth noting that in the original study of *Naomichelys,* the foramen posterior canalis carotici interni, the entrance of the carotid artery into the skull, was not clearly observed [5]. In *Solemys*, we are unable to locate this foramen in a similar position as in *Helochelydra*. A tiny foramen is present on the posterior end of the pterygoid, but it would be too small to be interpreted as the entrance of the internal carotid into the skull. Possible explanations might be as follows: an artefact of postmortem deformation that has concealed the foramen; the foramen is more anteriorly placed, thus not preserved in PAM 485; or the foramen is very reduced relative to the foramen stapedio-temporale.

Table 1. Comparison of the skulls of *Solemys gaudryi*, *Helochelydra nopcsai*, *Naomichelys speciosa,* and *Aragochersis lignitesta*.

Characters/Taxon	***Solemys gaudryi***	***Helochelydra nopcsai***	***Naomichelys speciosa***	***Aragochersis lignitesta***
Skull roof surface ornamentation	Present, fine tubercles and vermiculated ridges that are coalesced and not dislocated	Present, isolated pustules that are not coalesced but easily dislocated	Present, isolated pustules that are not coalesced but easily dislocated	Present, short, broad and blunt irregular tubercles, in contact with each other, generating a roughsurface
Skull surface sculpture matching that of the shell	Yes	Yes	Yes	No?
Skull roof scales	Present	Absent	Present	Absent
Temporal emargination	Small	Absent	Wider than in *Solemys*	Small

Table 1. *Cont.*

Characters/Taxon	*Solemys gaudryi*	*Helochelydra nopcsai*	*Naomichelys speciosa*	*Aragochersis lignitesta*
Supraoccipital exposure on skull roof	Very small or absent	Large, between the parietals	Small, posterior to the parietals	Very small or absent
Squamosal expanded medially behind the parietal	Yes	Yes	Yes	?
Contribution of the parietal to the temporal margin	Large, greater than that of squamosal	Smaller than that of squamosal	Smaller than that of squamosal	Large, greater than that of squamosal
Parietal excluded from foramen nervi trigemini edge by epipterygoid/prootic contact	Yes	Yes	?	?
Quadrate exposed between processus paroccipitalis of the opisthotic and squamosal dorsally	Yes, ventral to squamosal/opithotic suture	Yes, dorsal to squamosal/opithotic suture	No	?
Quadratojugal fully covers the processus articularis laterally	Yes	Yes	Yes	Yes
Pterygoids fully cover parabasisphenoid ventrally	Yes	Yes	No	Yes?
Tubercula basioccipitale	Two pairs Not posterior directed Posterior pair less developed than anterior	Two pairs Posteriorly directed Two pairs similar in size	Two pairs Posteriorly directed Two pairs similar in size	Two pairs Posteriorly directed Two pairs similar in size
Anterior pair of tubercula basioccipitale	Formed by pterygoids and basioccipital	Formed entirely by pterygoids	Formed entirely by pterygoids	Formed entirely by pterygoids
Position of condylus occipitalis relative to condylus mandibularis	Very close to one another	Close to one another	Distant from one another	Distant from one another
Foramen pro ramo vidiani exposed on ventral surface	Yes	Yes?	Yes	?
Osseous subdivision between the inner and middle ear cavities	Present	Absent	Absent	?
Processus interfenestralis of the opisthotic	Present	Absent	Absent	?

5.3. Relationships of Helochelydridae with Other Clades and Higher Relationships

Contrary to the recent papers of Rollot et al. [25,33], which placed Helochelydridae within Paracryptodira (or more exactly within Pleurosternidae), our analyses found Helochelydridae more basal relative to the so-called Paracryptodira. This would suggest that helochelydrids are potentially present from the Early Jurassic as a ghost lineage (or that related taxa have not yet been included in the phylogeny). The difference between our study and the studies of Rollot et al. [25,33] can be explained not only by the different characters selected, but also by the difference in included taxa that might impose different constraints on the analyses. The content of Paracryptodira and their phylogenetic relationships is still fluctuating. Within this clade or grade, as in Rollot et al. [25], we found a consistent Compsemydidae clade (with mostly European taxa except *Compsemys*) and we were able to define monophyletic Late Cretaceous Baenidae (American). Furthermore, among Jurassic and Early Cretaceous paracryptodiran taxa, relationships are more difficult to establish and no clear American or European clades can be identified, suggesting that geographical isolation generated the first vicariant evolution only since the midCretaceous with the opening of the Atlantic Ocean. It is, however, likely that migrations could still occur during the Late Cretaceous as one compsemydid is known in the Late Cretaceous of North America (which probably originated from a European stock) and one helochelydrid occurs in the Late Cretaceous of America. The relatively longtime span of *Naomichelys* during the Cretaceous in North America should, however, be considered with caution, and a review of the remains attributed to this genus from the Aptian to the Campanian could reveal a much more complicated history and interrelationships with other taxa.

Our study also showed that trionychoid turtles have deep origins in Asia and further constrain the first divergence within Cryptodira, as well as between Cryptodira and Pleurodira, to the Middle Jurassic rather than the Late Jurassic. It is worth noting that Early and Middle Jurassic turtles are still poorly documented and could represent some of the first important steps regarding the evolution of modern groups. Finally, as in Tong et al. [24], one of our phylogenetic hypotheses places Pleurodira as the sister group of Compsemydidae and this cluster as a sister group of Paracryptodira, resulting in a more inclusive crown group of Testudines. This new arrangement is in agreement with the position of the internal carotids relative to the skull floor, and this new homology hypothesis needs to be tested in future studies.

6. Conclusions

The first *Solemys* skull is reported from the Late Cretaceous (Rognacian) of Fox Amphoux, Var, Southern France. It is assigned to *S. gaudryi* (Matheron, 1869) on the basis of the associated shell elements. The detailed description and comparisons with other known skulls of Helochelydridae provide new insights on the skull morphology of the family. Based on the skull features, *Helochelydra* from England and *Naomichelys* from North America appear to be closer to one another than to *Solemys*.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15010058/s1, Supplementary Materials S1 Character List and Dataset; Supplementary Materials S2. Complete strict (above) and Adams (below) consensus cladograms; Supplementary Materials S3. Complete strict (above) and Adams (below) consensus cladograms excluding *Kallokibotion bajazidi*.

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References

1. Joyce, W.G. A Review of the Fossil Record of Basal Mesozoic Turtles. *Bull. Peabody Mus. Nat. Hist.* **2017**, *58*, 65–113. [CrossRef]
2. Joyce, W.G. A Review of Helochelydrid Shell Material from Late Albian to Early Cenomanian Greensands of Southern England, United Kingdom. *Anat. Rec.* **2022**, 1–13. [CrossRef] [PubMed]
3. Pérez-García, A.; Espílez, E.; Mampel, L.; Alcalá, L. A New Basal Turtle Represented by the Two Most Complete Skeletons of Helochelydridae in Europe. *Cretac. Res.* **2020**, *107*, 104291. [CrossRef]
4. Joyce, W.G.; Chapman, S.D.; Moody, R.T.; Walker, C.A. The Skull of the Solemydid Turtle *Helochelydra nopcsai* from the Early Cretaceous of the Isle of Wight (UK) and a Review of Solemydidae. *Spec. Pap. Palaeontol.* **2011**, *86*, 75–97.
5. Joyce, W.G.; Sterli, J.; Chapman, S.D. The Skeletal Morphology of the Solemydid Turtle *Naomichelys speciosa* from the Early Cretaceous of Texas. *J. Paleontol.* **2014**, *88*, 1257–1287. [CrossRef]
6. Paulina-Carabajal, A.; Sterli, J.; Werneburg, I. The Endocranial Anatomy of the Stem Turtle *Naomichelys speciosa* from the Early Cretaceous of North America. *Acta Palaeontol. Pol.* **2019**, *64*, 711–716. [CrossRef]

7. Tortosa, T. Vertébrés Continentaux Du Crétacé Supérieur de Provence (Sud-Est de La France). PhD Thesis, Paris 6, Paris, France, 2014.
8. Buffetaut, E.; Le Loeuff, J.; Mechin, P.; Mechin-Salessy, A. A Large French Cretaceous Bird. *Nature* **1995**, *377*, 110. [CrossRef]
9. Buffetaut, E.; Mechin, P.; Mechin-Salessy, A. An Archaic Bird (Enantiornithes) from the Upper Cretaceous of Provence (Southern France). *Comptes Rendus Académie Sci. Ser. IIA-Earth Planet. Sci.* **2000**, *331*, 557–561. [CrossRef]
10. Buffetaut, E.; Mechin, P.; Mechin-Salessy, A. An Azhdarchid Pterosaur from the Upper Cretaceous of Provence (Southern France). In *Mesozoic and Cenozoic vertebrates and paleoenvironments, tributes the career of Professor Dan Grigorescu*; Editura Ars Docendi: Bucharest, Romania, 2006; pp. 95–100.
11. Buffetaut, E.; Angst, D.; Mechin, P.; Mechin-Salessy, A. New Remains of the Giant Bird *Gargantuavis philoinos* from the Late Cretaceous of Provence (South-Eastern France). *Palaeovertebrata* **2015**, *39*, 1–6. [CrossRef]
12. Buffetaut, E.; Angst, D.; Mechin, P.; Mechin-Salessy, A. A Femur of the Giant Bird *Gargantuavis* from the Late Cretaceous of Var (South-Eastern France). *Carnets Nat.* **2019**, *6*, 47–52.
13. Le Loeuff, J.; Buffetaut, E. A New Dromaeosaurid Theropod from the Upper Cretaceous of Southern France. *Oryctos* **1998**, *1*, 105–112.
14. Tong, H.; Gaffney, E.S.; Buffetaut, E. *Foxemys*, a New Side-Necked Turtle (Bothremydidae, Pelomedusoides) from the Late Cretaceous of France. *Am. Mus. Novit.* **1998**, *3251*.
15. Martin, J.E. New Material of the Late Cretaceous Globidontan *Acynodon iberoccitanus* (Crocodylia) from Southern France. *J. Vertebr. Paleontol.* **2007**, *27*, 362–372. [CrossRef]
16. Cavin, L.; Buffetaut, E.; Dutour, Y.; Garcia, G.; Le Loeuff, J.; Méchin, A.; Méchin, P.; Tong, H.; Tortosa, T.; Turini, E. The Last Known Freshwater Coelacanths: New Late Cretaceous Mawsoniid Remains (Osteichthyes: Actinistia) from Southern France. *PLoS ONE* **2020**, *15*, e0234183. [CrossRef] [PubMed]
17. Sterli, J.; Joyce, W.G. The Cranial Anatomy of the Early Jurassic Turtle *Kayentachelys aprix*. *Acta Palaeontol. Pol.* **2007**, *52*, 675–694.
18. Gaffney, E.S. Comparative Cranial Morphology of Recent and Fossil Turtles. *Bull. Am. Mus. Nat. Hist.* **1979**, *164*, 65–376.
19. Gaffney, E.S. The Jurassic Turtles of North America. *Bull. Am. Mus. Nat. Hist.* **1979**, *162*, 91–136.
20. Albrecht, P.W. The Cranial Arteries and Cranial Arterial Foramina of the Turtle Genera *Chrysemys*, *Sternotherus*, and *Trionyx*: A Comparative Study with Analysis of Possible Evolutionary Implications. *Tulane Stud. Zool.* **1967**, *14*, 81–99.
21. Albrecht, P.W. The Cranial Arteries of Turtles and Their Evolutionary Significance. *J. Morphol.* **1976**, *149*, 159–182. [CrossRef]
22. Rollot, Y.; Lyson, T.R.; Joyce, W.G. A Description of the Skull of *Eubaena cephalica* (Hay, 1904) and New Insights into the Cranial Circulation and Innervation of Baenid Turtles. *J. Vertebr. Paleontol.* **2018**, *38*, e1474886. [CrossRef]
23. Tong, H.; Chanthasit, P.; Naksri, W.; Ditbanjong, P.; Suteethorn, S.; Buffetaut, E.; Suteethorn, V.; Wongko, K.; Deesri, U.; Claude, J. *Yakemys multiporcata* n. g. n. Sp., a Large Macrobaenid Turtle from the Basal Cretaceous of Thailand, with a Review of the Turtle Fauna from the Phu Kradung Formation and Its Stratigraphical Implications. *Diversity* **2021**, *13*, 630. [CrossRef]
24. Tong, H.; Tortosa, T.; Buffetaut, E.; Dutour, Y.; Turini, E.; Claude, J. A Compsemydid Turtle from the Upper Cretaceous of Var, Southern France. *Ann. Paléontologie* **2022**. [CrossRef]
25. Rollot, Y.; Evers, S.W.; Joyce, W.G. A Redescription of the Late Jurassic (Tithonian) Turtle *Uluops uluops* and a New Phylogenetic Hypothesis of Paracryptodira. *Swiss J. Palaeontol.* **2021**, *140*, 1–30. [CrossRef] [PubMed]
26. Tong, H.; Li, L. A Revision of the Holotype of *Nanhsiungchelys wuchingensis*, Ye, 1966 (Testudines: Cryptodira: Trionychoidae: Nanhsiungchelyidae). *Cretac. Res.* **2019**, *95*, 151–163. [CrossRef]
27. Swofford, D.L. *Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0*; Sinauer: Sunderland, MA, USA, 1998.
28. Thomson, R.C.; Spinks, P.Q.; Shaffer, H.B. A Global Phylogeny of Turtles Reveals a Burst of Climate-Associated Diversification on Continental Margins. *Proc. Natl. Acad. Sci. USA* **2021**, *118*, 1–10. [CrossRef]
29. Meyer, H.v. *Helochelys danubina*, Aus Dem Grünsande von Kelheim in Bayern. *Palaeontographica (1846–1933)*. 1855; 96–105.
30. Matheron, P. Mém. Acad. Imp. Sc. B.-L. Arts Marseille. 1869; 39.
31. Lapparent de Broin, F.d.; Murelaga, X. Une Nouvelle Faune de Chéloniens Dans Le Crétacé Supérieur Européen. *Comptes rendus de l'Académie des sciences. Série 2. Sci. De La Terre Et Des Planètes* **1996**, *323*, 729–735.
32. Lapparent de Broin, F.d.; Murelaga, X. Turtles from the Upper Cretaceous of Laño (Iberian Peninsula). *Estud. Del Mus. De Cienc. Nat. De Alava* **1999**, *14*, 135–211.
33. Rollot, Y.; Evers, S.W.; Pierce, S.E.; Joyce, W.G. Cranial Osteology, Taxonomic Reassessment, and Phylogenetic Relationships of the Early Cretaceous (Aptian-Albian) Turtle *Trinitichelys hiatti* (Paracryptodira). *PeerJ* **2022**, *10*, e14138. [CrossRef]