RESEARCH ARTICLE

The last surviving Thalassochelydia—A new turtle cranium from the Early Cretaceous of the Purbeck Group (Dorset, UK)

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Abstract

Background. The mostly Berriasian (Early Cretaceous) Purbeck Group of southern England has produced a rich turtle fauna dominated by the freshwater paracryptodires *Pleurosternon bullockii* and *Dorsetochelys typocardium*. Each of these species is known by numerous relatively complete shells and by a single cranium. The two other turtles found in the Purbeck Group (*Hylaeochelys belli*, a species of uncertain affinities, and the terrestrial helochelydrid "*Helochelydra*" *anglica*) are known only from shell remains.

Methods. In the present contribution, we describe a new turtle cranium from the Purbeck Group of Swanage, Dorset (southern England). We also explore the phylogenetic relationships of this new cranium and of *Hylaeochelys belli* in the context of a recently published global turtle matrix.

Results. Before complete preparation, the new Purbeck cranium was provisionally referred to *Dorsetochelys typocardium*, but our analysis clearly contradicts a referral to this species in particular and to paracryptodires in general. In contrast, the new cranium shares a number of features with the Late Jurassic, coastal marine Thalassochelydia, including a posterolaterally open foramen posterius palatinum, a strong ridge on the posterior surface of the processus articularis of the quadrate, a strong posterior orientation of the processus articularis in ventral view, and a processus trochlearis oticum limited to the medial part of the otic chamber and bordered by a deep recess laterally. Our phylogenetic analysis confirms a placement of the new Purbeck cranium within the clade Thalassochelydia.

Discussion. In terms of morphology, the new Purbeck cranium does not correspond to any known taxon. However, we refrain from naming a new species based on it because there is a good chance that this cranium actually belongs to the shell-based species *Hylaeochelys belli* (also recovered as a thalassochelydian in our phylogenetic analysis). Unfortunately, we lack any objective evidence to support this conclusion for the moment. In any case, the new Purbeck cranium confirms what others have previously suggested based on *Hylaeochelys belli*: thalassochelydian turtles survived the Jurassic-Cretaceous transition.

Keywords: Paracryptodira; Thalassochelydia; Late Jurassic; Early Cretaceous; Morphology; Phylogeny

Introduction

The Purbeck Group of Dorset (southern England) has been extensively exploited since the nineteenth century, both for building stones and more directly for fossil material. Turtles are among the most common vertebrate remains found in these layers and are mostly represented by relatively complete shells. The comprehensive revision of this material long remained overdue, but the recent works of Milner (2004) and Pérez-García (2012) and Pérez-García (2014) greatly clarified the situation. Four turtle species are now recognized in the Purbeck Group: *Pleurosternon bullockii* (Owen, 1842), *Dorsetochelys typocardium* (Seeley, 1869), "*Helochelydra*" *anglica* (Lydekker, 1889), and *Hylaeochelys belli* (Mantell, 1844).

Pleurosternon bullockii and *Dorsetochelys typocardium* are representatives of Paracryptodira (sensu Lyson and Joyce, 2011). Each of these species is primarily known based on rich shell material (Milner, 2004). The cranium is also known based on two referred specimens from the Purbeck Group. The cranium of *Pleurosternon bullockii* was initially described as the new species *Mesochelys durlstonensis* by Evans and Kemp (1975), but following Gaffney and Meylan (1988) the two species were considered as synonyms. However, Milner (2004) was the first to really assess this synonymy (Joyce and Anquetin, 2019). The cranium of *Dorsetochelys typocardium* was initially described as the new species *Dorsetochelys delairi* by Evans and Kemp (1976) and was recently synonymized with the shell-based "*Glyptops*" *typocardium* (Pérez-García, 2014).

No cranium of "*Helochelydra*" *anglica* or *Hylaeochelys belli* has ever been described in the literature. "*Helochelydra*" *anglica* is a representative of Helochelydridae (sensu Joyce et al., 2016), a group of terrestrial stem turtles characterized notably by a typical shell ornamentation consisting of distinct tubercules (Joyce, 2017). As far as we know, the cranium of helochelydrids is quite distinctive in terms of morphology and bears the same bone surface sculpturing as the shell (Joyce et al., 2011, 2014). Although there is no strong morphological argument to support or discredit this hypothesis, *Hylaeochelys belli* has been repeatedly suggested to have affinities with Plesiochelyidae (Lydekker, 1889; Nopcsa, 1928; Hirayama et al., 2000; Lapparent de Broin, 2001; Milner, 2004; Karl et al., 2007; Pérez-García, 2012). However, plesiochelyids are usually found in more frankly marine deposits and are believed to go extinct at the Jurassic-Cretaceous transition due to the disappearance of their coastal marine habitat in Europe (e.g., Bardet, 1994; Lapparent de Broin et al., 1996; Anquetin et al., 2017). Therefore, *Hylaeochelys belli* is usually left out of consideration in studies dealing with plesiochelyids or more generally with Thalassochelydia, the clade uniting plesiochelyids and other Late Jurassic coastal marine turtles (Anquetin et al., 2017; Evers and Benson, 2019).

In the present contribution, we describe a new turtle cranium from the Purbeck Group of Dorset, representing only the third turtle cranium known from this geological unit. This skull (DORCM G.10715) was first mentioned by Milner (2004) and provisionally referred to *Dorsetochelys delairi* (now *Dorsetochelys typocardium*). The specimen was fully extracted from the matrix for the present study. A preliminary version of this work was provided by André and Anquetin (2018). We herein provide a detailed description of this new material and extend comparisons not only with other Purbeck turtles, but also with Late Jurassic thalassochelydians. The phylogenetic relationships of DORCM G.10715 are also explored by including it in a recently published global analysis of turtles (Evers and Benson, 2019).

Material and methods

Material

DORCM G.10715 consists in a fairly complete but severely dorsoventrally flattened turtle cranium. It was found in 1985 by David Costain, a professional collector, and presented to the Dorset County Museum in Dorchester (United Kingdom) the following year. According to the label, the specimen was subsequently prepared in the Department of Zoology of the University of Oxford, but this preparation was only superficial. The skull remained embedded in the matrix and only observable in palatal view (Fig. 1). Apart from a mention in Milner (2004), this skull was never described or figured in the literature.

The specimen was borrowed from the DORCM by JA in 2010 and fully prepared in 2016 by Renaud Roch (Jurassica Museum, Porrentruy, Switzerland) using standard techniques. Two scales and three teeth referable to *Scheenstia* sp. (Lepisosteiformes, Ginglymodi, Actinopterygii) were found in the block of matrix during preparation.

Figure 1. The cranium DORCM G.10715 before full extraction from the matrix. Only the palatal aspect is visible. Note the presence of a lepisosteiform tooth (see Material) just anterior to the cranium.

Geological setting

DORCM G.10715 was collected in Durlston Bay (near Swanage, Dorset, UK) from fallen blocks immediately south of the Zigzag path on the shore (British National Grid reference: SZ 0342 7790; Fig. 2). Therefore, the exact stratigraphical position of the specimen is ambiguous. However, the strata forming the cliff where the specimen was found correspond to the 'Middle Purbeck Beds' and beginning of the 'Upper Purbeck Beds', following the informal denomination (see below). According to the label accompanying the specimen, the block was tentatively assigned to the Chief Beef Beds based on the lithology of the matrix and knowledge of the sections. The Chief Beef Beds consist of alternating dark shales and bands of hard shell-limestones deposited under brackish conditions (Batten, 2002). DORCM G.10715 was indeed found in a hard limestone rich in shell fragments.

Durlston Bay represents one of the largest exposures of the Purbeck Group along the Dorset coast. The Purbeck Group consists of a succession of limestones and calcareous shales and marls with occasional evaporites that were deposited in a marginal setting (Allen and Wimbledon, 1991; Clements, 1993). The climate during this period is interpreted to have been semi-arid and becoming wetter toward the top of the sequence (Allen, 1998; Batten, 2002). The Purbeck Group represents a transition between the marine succession of the underlying Portland Limestone Group and the non-marine sediments of the overlying Wealden Group, reflecting a major regression occurring at the end of the Jurassic and onset of the Cretaceous (e.g., Rawson, 2006).

For long, the Purbeck Group was subdivided into Lower, Middle and Upper Purbeck. This is the only stratigraphical data we have for most of the fossils collected in the nineteenth century (e.g., Milner, 2004). The Purbeck Group is now divided into two formations: the oldest Lulworth Formation and the youngest Durlston Formation (Townson, 1975). Ensom (1985) at Worbarrow Tout and Clements (1993) at Durlston Bay formalized the nineteenth century tradition to finely separate the Purbeck Group into 15 or so

Figure 2. **Map of the south Dorset coast showing the place where DORCM G.10715 was found (red star).**

members, each of them consisting of several beds (**Fig. 3**). Later, **Westhead and Mather (1996)** argued 75
that these so-called members were difficult to follow at the regional scale. Therefore, these authors pro- 76
posed to divise the Purbeck Group into five members and to relegate the traditional members to the bed 77
status, but the latter continue to be used at least locally for the level of stratigraphical detail they provide 78
(**Ensom, 2002**). There is an agreement among specialists that most of the Purbeck Group is Berriasian 79
(Early Cretaceous) in age, but the exact position of the Jurassic-Cretaceous boundary has been debated. 80
Several studies place the boundary at the base of the '*Cypris*' Freestones (e.g., **Allen and Wimbledon,** 81
1991; **Feist et al., 1995**), but others have argued that the limit is higher in the Lulworth Formation (see 82
Ensom, 2002). In any case, DORCM G.10715 can be confidently assigned to the Berriasian. 83

Anatomical comparisons 84

Since DORCM G.10715 was tentatively referred to *Dorsetochelys typocardium* by **Milner (2004)**, it was 85
primarily compared with this taxon based on the original description (**Evans and Kemp, 1976**) and first 86
hand observation of the holotype and only-known cranium, DORCM G.23. By extension, the new Purbeck 87
cranium was also compared with other pleurosternids, notably *Glyptops ornatus* and *Pleurosternon bul-* 88
lockii, based on the primary literature (**Gaffney, 1979b**; **Evans and Kemp, 1975**) and first hand observa- 89
tion of the relevant material. For a recent reassessment of non-baenid paracryptodire taxonomy, the 90
reader is referred to **Joyce and Anquetin (2019)**. However, it became clear early on that the cranium 91
DORCM G.10715 shared similarities with other European turtles, notably Thalassochelydia (see **Anquetin** 92
et al., 2017). Comparisons were therefore extended to that group as well based on published literature 93
(**Gaffney, 1975, 1976**; **Rieppel, 1980**; **Anquetin et al., 2015**; **Püntener et al., 2017**), as well as first hand 94
observation of the available material. Anatomical descriptions in the present study follow the nomen- 95
clature formalized by **Gaffney (1972, 1979a)** as updated by **Rabi et al. (2013)** for the carotid system and 96
Rollot et al. (2018) for the vidian nerve system. 97

3D model 98

In order to complement the photographs and line drawings provided herein and to facilitate future com- 99
parisons, we produced a textured 3D mesh of DORCM G.10715 with a structured-light surface scanner 100
(Artec Space Spider, Artec Group). The 3D model was computed with the dedicated software Artec Studio 101
13 Professional, and can be freely accessed on OSF (see **Supplementary information**). 102

Stage	Group	Forma-tion	Informal division	Member	Beds	DB#	
Berriasian	PURBECK GROUP	DURLSTON FM.	UPPER PURBECK	PEVERIL POINT MEMBER	Upper '*Cypris*' Clays and Shales		
					Unio Beds	221	🐢
					Broken Shell Limestone	220	🐢 (this study)
				STAIR HOLE MEMBER	Chief Beef Beds	219	
			MIDDLE PURBECK		*Corbula* Beds		
					Scallop Beds	145	
					Intermarine Beds		🐢
						112	
					Cinder Bed	111	🐢
		LULWORTH FM.		WORBARROW TOUT MEMBER	Cherty Freshwater Beds	110	
					Marly Freshwater Beds	83	🐢
					Soft Cockle Beds		
			LOWER PURBECK		Hard Cockle Beds	34	
				RIDGEWAY MBR	'*Cypris*' Freestones	33 17	
-?-				MUPE MEMBER	Broken Beds, Caps, and Basal Beds	16	
Tithonian	PORTLAND LIMESTONE GROUP						

Figure 3. Stratigraphy of the Purbeck Group in Durlston Bay, Dorset, UK. The old informal subdivision into Lower, Middle and Upper Purbeck is conserved since many fossils lack more precise stratigraphical information. The horizons that are known to have produced substantial turtle material (see Milner, 2004) are indicated by a turtle shell icon on the right. Beds and bed numbers (DB) follow Clements (1993). Members follow Westhead and Mather (1996). See also Ensom (2002).

Phylogenetic analysis

In order to infer the phylogenetic relationships of the new cranium DORCM G.10715, we used one of the most recent global morphological matrix for turtles (Evers and Benson, 2019). In addition to DORCM G.10715, we also scored *Hylaeochelys belli* and a merged 'DORCM G.10715 + *Hylaeochelys belli*' because we think they may represent the same species (see Alpha taxonomy). The matrix is provided as Supplementary information. At first, DORCM G.10715 and *Hylaeochelys belli* (an exclusively shell-based species) were treated as distinct terminal taxa. A second analysis was performed in which both were merged into a single terminal taxon.

We followed the general analytical procedure detailed by Evers and Benson (2019). Analyses were performed in TNT 1.5 for Windows (Goloboff et al., 2008; Goloboff and Catalano, 2016). The relationships of extant taxa were constrained using a molecular backbone following the topology of Pereira et al. (2017). Characters were treated as unordered and equally weighted. Branches were set to collapse if branch length is zero. *Proganochelys quenstedti* was used as outgroup. Tree searches were performed using New Technology algorithms in TNT with default settings, tree drifting (Goloboff, 1999), parsimony ratchet (Nixon, 1999), and constraints enforced. The initial level of the driven search and the number of times the minimum tree length should be found were both set to 30. The most parsimonious trees (MPTs) were subjected to an additional round of tree bisection and reconnection (TBR). The resulting MPTs were used to compute a strict consensus tree. Consistency index (CI) and retention index (RI) were

calculated using the STATS script bundled with TNT. Absolute Bremer support values were calculated in TNT using TBR branch swapping to generate suboptimal trees up to 20 steps longer than the MPTs.

It should be noted that a slightly updated version of Evers and Benson's (2019) matrix was published more recently (Evers et al., 2019). This update is focussed mostly on chelonioid sea turtles with an increased taxon sampling for that group and a revision of postcranial characters related to their marine lifestyle. These modifications would not affect the phylogenetic position of DORCM G.10715. In addition, they resulted in a less resolved consensus among Mesozoic turtles (notably Xinjiangchelyidae, Sinemydidae, and Macrobaenidae) and a poorly supported sister-group relationship between Angolachelonia (i.e., Thalassochelydia + Sandownidae) and pleurodires (Evers et al., 2019). Therefore, we preferred to use the original matrix of Evers and Benson (2019) in the present study.

Institutional abbreviations

DORCM, Dorset County Museum, Dorchester, UK.
NHMUK, Natural History Museum, London, UK.

Systematic paleontology

TESTUDINATA Klein, 1760 (sensu Joyce et al., 2004)
THALASSOCHELYDIA Anquetin et al., 2017

Remark. Thalassochelydians are traditionally considered to be basal pan-cryptodiran turtles (Gaffney and Meylan, 1988; Lapparent de Broin et al., 1996; Joyce, 2007; Anquetin et al., 2015; Zhou and Rabi, 2015). However, some recent phylogenetic analyses have placed them along the stem of crown-group turtles (Sterli, 2010; Sterli et al., 2013; Cadena and Parham, 2015; Evers and Benson, 2019). This is in part the result of the instable position of the clade Pan-Pleurodira from one analysis to the next. According to Evers and Benson (2019), whose matrix we herein use to investigate the phylogenetic relationships of DORCM G.10715, Thalassochelydia are sister group to Sandownidae Tong and Meylan, 2013 forming the clade Angolachelonia Mateus et al., 2009, which is placed as the most crownward clade of stem turtles. However, forcing Thalassochelydia or Sandownidae as stem-group cryptodires or even as stem-group chelonioids only requires two to four additional steps, and forcing one group drags its sister group along maintaining the clade Angolachelonia (Evers and Benson, 2019). Two updated versions of the Evers and Benson's (2019) matrix place Angolachelonia as sister group to Pleurodira (Evers et al., 2019) and as stem chelonioids (Gentry et al., 2019). Therefore, the position of Thalassochelydia must be considered uncertain and prone to change for the time being. Finally, it should also be noted that a recent study suggested that sandownids more likely derived from thalassochelydian ancestors (Evers and Joyce, 2020).

Thalassochelydia indet.
Figure 4

Referred material. DORCM G.10715, a relatively complete, but dorsoventrally crushed cranium.
Locality. Durlston Bay, Swanage, Dorset, UK. Probably Chief Beef Beds, Stair Hole Member, Durlston Formation, Purbeck Group (Berriasian, Early Cretaceous). See Geological setting above.
Remark. DORCM G.10715 cannot be referred to any known species at the moment and could potentially represent a new taxon. However, there is a reasonably good chance (see Alpha taxonomy) that this material actually belongs to the shell-based species *Hylaeochelys belli* (Mantell, 1844) known from the Purbeck and Wealden of England, as recently revised by Pérez-García (2012). Therefore, we refrain from establishing a new taxon based on this new skull and wait for more material to conclude on this matter.
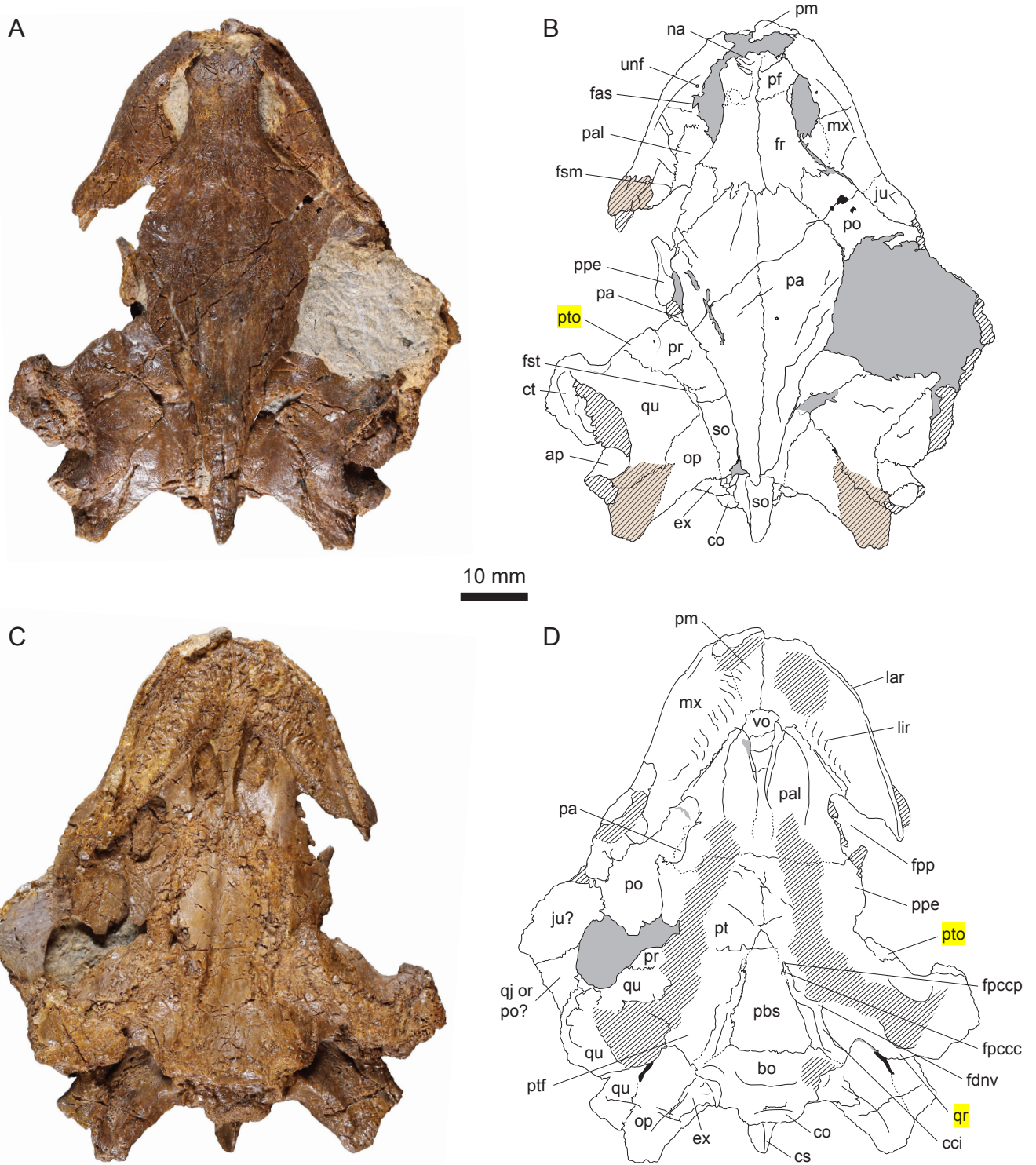
Figure 4. DORCM G.10715, Purbeck Group (Berriasian), Swanage, Dorset, UK. (A) Photograph of the specimen in dorsal view; (B) Interpretative drawing in dorsal view; (C) Photograph of the specimen in ventral view; (D) Interpretative drawing in ventral view. Matrix is figured in gray. Hatchings represent heavily eroded areas. Sutural surfaces are indicated in light brown and hatchings. The shade difference between the dorsal and ventral sides is natural. Abbreviations: ap, antrum postoticum; bo, basioccipital; cci, canalis caroticus internus; co, condylus occipitalis; cs, crista supraoccipitalis; ct, cavum tympani; ex, exoccipital; fas, foramen alveolare superius; fdnv, foramen distalis nervi vidiani; fpccc, foramen posterius canalis carotici cerebralis; fpccp, foramen posterius canalis carotici palatinum; fpp, foramen palatinum posterius; fr, frontal; fsm, foramen supramaxillare; fst, foramen stapedio-temporale; ju, jugal; lar, labial ridge; lir, lingual ridge; mx, maxilla; na, nasal; op, opisthotic; pa, parietal; pal, palatine; pbs, parabasisphenoid; pf, prefrontal; pm, premaxilla; po, postorbital; ppe, processus pterygoideus externus; pr, prootic; pt, pterygoid; ptf, pterygoid fossa; pto, processus trochlearis oticum; qj, quadratojugal; qr, quadrate ridge; qu, quadrate; so, supraoccipital; unf, unnamed foramen; vo, vomer.

Description

General description

DORCM G.10715 consists of a relatively complete, isolated cranium that was severely crushed dorsoventrally during fossilization (see 3D mesh available as Supplementary information). As preserved, the cranial roof contacts the palate, and the entire internal anatomy is unfortunately lost to us. The squamosals as well as most of the jugals and quadratojugals are missing (Fig. 4). The ventral aspect of the skull was exposed when discovered and subjected to weathering (Fig. 1), notably the pterygoids and the triturating surface. The dorsal surface of the cranium is better preserved. The skull roof is smooth and lacks any sign of the ornamentation typically found in all non-baenid paracryptodires for which the skull is known, including the pleurosternids *Glyptops ornatus*, *Pleurosternon bullockii*, and *Dorsetochelys typocardium* (Evans and Kemp, 1975, 1976; Gaffney, 1979b; Pérez-García, 2012; Joyce and Anquetin, 2019). As preserved, the skull dimensions are as follows: length (midline) = 76.37 mm; length (max) = 78.12 mm; width (at the level of the processus articularis of the quadrates) = 60.34 mm.

Dermal roofing elements

Nasal

The complete skull roof was pushed down during the dorsoventral compression of the skull and now rests on the dorsal surface of the palatal region. Similarly, the roof of the nasal cavity got separated from the dorsal processes of the maxillae and now lies on the floor of the cavity (Fig. 4A–B). The dorsal margin of the apertura narium externa, seemingly formed by the nasal bones, was greatly damaged in the process. Only fragments of the posterior part of the nasals are visible anterior to the prefrontals, but the exact limit between these elements is elusive. It is unknown whether the nasals contacted the maxillae laterally, but this is highly probable. There is evidence for a nasal-frontal contact beneath the prefrontal (see Frontal below).

Prefrontal

As a result of the dorsoventral crushing that occurred during fossilization, the anterior and anterolateral contacts of the prefrontals with the nasals and the maxillae are poorly preserved. Laterally, the prefrontals form the anterodorsal margin of the orbits. Posteriorly, the prefrontals have a mostly transverse suture with the frontals. As seen from the right prefrontal, these bones meet one another on the midline along their entire length and are somewhat quadrangular in shape (Fig. 4A–B). This is clearly different from the condition in the pleurosternids *Glyptops ornatus*, *Pleurosternon bullockii* and *Dorsetochelys typocardium* in which the prefrontals have limited dorsal exposure along the orbit margin and never meet in the midline (Evans and Kemp, 1975, 1976; Gaffney, 1979b). The medial part of the left prefrontal is damaged and reveals that the frontals extend anteriorly beneath the prefrontals to meet the nasals (see Frontal below). This morphology where the medial part of the prefrontal consists in a thin sheet of bone that covers the anterior medial process of the frontal dorsally without preventing a frontal-nasal contact underneath recalls the condition in the thalassochelydian plesiochelyid turtles *Plesiochelys etalloni*, *Plesiochelys planiceps* and *Portlandemys mcdowelli* (Gaffney, 1976), although not all thalassochelydians show this morphology (Rieppel, 1980; Anquetin et al., 2015).

Frontal

The frontals are complete and well preserved in DORCM G.10715 (Fig. 4A–B). In dorsal view, they contact the prefrontals anteriorly, the postorbitals posterolaterally, and the parietals posteromedially. The anterior suture with the prefrontal is mostly transverse. The posterior sutures with the postorbital and parietal are strongly interdigitating. The frontals meet one another medially along their entire length.

Laterally, they form the dorsal margin of the orbits. The damage of the medial part of the left prefrontal   208
reveals that the frontals extend anteriorly beneath the prefrontals to meet the nasals. As noted above, a   209
similar morphology was described in some, but not all, thalassochelydians (**Gaffney, 1976**; **Anquetin et**   210
al., 2015). Detecting this condition is not always easy and it cannot be excluded that it is present in other   211
basal pan-cryptodires as well. However, it is never present in pleurosternids where a broad anterior   212
process of the frontals clearly separates the relatively small prefrontals in dorsal view.   213

Parietal   214

Only the anterior and medial parts of the parietals are preserved in DORCM G.10715 (**Fig. 4A–B**). As pre-   215
served, the parietals contact the frontals anteriorly along a transverse, strongly interdigitating suture,   216
and the postorbital anterolaterally. Posteroventrally, the parietals also have an overlapping contact with   217
the crista supraoccipitalis formed by the supraoccipital. The other usual contacts of the parietals in the   218
ethmoid region and in the roof of the cavum cranii are not preserved due to the dorsoventral crushing of   219
the specimen. The medial margin of the upper temporal emargination is partly preserved on both sides.   220
On the right side, the margin reaches the level of the foramen stapedio-temporale. On the left side, the   221
medial margin of the upper temporal emargination can be followed as far anteriorly as the processus   222
trochlearis oticum. DORCM G.10715 is therefore characterized by an extensive upper temporal emargina-   223
tion that probably revealed much of the dorsal surface of the otic chamber in dorsal view. However, the   224
exact shape of the emargination is unknown. In pleurosternids, the upper temporal emargination is at   225
best poorly developed (**Evans and Kemp, 1975, 1976**; **Gaffney, 1979b**; **Joyce and Anquetin, 2019**).   226

Jugal   227

The jugal is badly preserved in DORCM G.10715. The left jugal is completely missing, only a sutural scar   228
on the dorsal surface of the maxilla shows where the jugal articulated (**Fig. 4A**). Of the right jugal, only   229
the anteroventral part in the floor of the orbit is preserved in anatomical position, still sutured to the   230
maxilla. There is apparently no developed medial process on the jugal. The contribution of the jugal to   231
the orbit is unknown. The temporal bar is broken on each side of the cranium, but a flat piece of bone   232
lies where the right temporal bar should have been (**Fig. 4C–D**). This piece possibly corresponds to the   233
ventral part of the jugal and quadratojugal, although it is now oriented horizontally rather than vertically.   234
If this interpretation is correct, the slightly concave medial margin of this piece would indicate a modest   235
lower temporal emargination. Another possibility is that this piece of bone corresponds to the jugal   236
and postorbital. If this second interpretation is correct, then the slightly concave medial margin would   237
correspond to the posteroventral margin of the orbit. The first interpretation may appear more likely at   238
first as it requires less rotation of the flat piece of bone during dorsoventral compression, but the second   239
interpretation is supported by the shiny aspect of the visible bone surface which would indicate that this   240
is the internal face of the bones that now faces ventrally.   241

Quadratojugal   242

Little can be said about this bone. A small portion of the right quadratojugal may be preserved, but this   243
remains uncertain (see **Jugal** above).   244

Postorbital   245

Most of the postorbital is missing in DORCM G.10715 (**Fig. 4A–B**). On the left side, only the anteriormost   246
part of the bone is preserved. On the right side, a slightly larger portion of the postorbital is preserved   247
and forms the posterodorsal margin of the orbit. A large area of matrix in the right temporal region   248
could not be removed during preparation without compromising the stability of the fossil. The posterior   249
part of the right postorbital is hidden beneath this matrix, but can be seen in ventral view posterolateral   250

to the foramen palatinum posterius (Fig. 4C–D). The postorbital contacts the frontal anteromedially and the parietal medially. The other contacts of the bone are obscure. It is unknown if and how much the postorbital contributes to the margin of the upper temporal emargination.

Palatal elements

Premaxilla

The premaxillae are poorly preserved in DORCM G.10715. Only the midline suture between the two premaxillae can be seen clearly (Fig. 4C–D). However, it is apparent that the premaxillae contact the maxillae laterally and the vomer posteriorly. Foramina praepalatinum were likely present, but this cannot be confirmed due to poor preservation. Dorsally, the premaxillae form the ventral margin of the apertura narium externa (Fig. 4A–B).

Maxilla

The ventral aspect of the maxillae is broken and eroded in several places (Fig. 4C–D). The maxilla contacts the premaxilla and vomer anteromedially, the palatine medially, and the jugal posterodorsally. The upper jaw is relatively short compared to the length of the skull. It is U-shaped with moderately diverging rami and a broad, well-rounded anterior part. The triturating surface is broad and its width increases anteriorly. The labial ridge is thin and damaged, which makes it impossible to infer its height. The lingual ridge is broad and serrated, although we do not know whether these serrations were also apparent on the rhamphotheca. It is widest and highest at the level of the anteriormost ventral exposure of the vomer. It is vaguely sinusoidal in outline: concave anterolaterally for most of its length, the ridge curvature shifts to concave posteromedially on the premaxilla (Fig. 4C–D). The lingual ridge is apparently lowest on the premaxilla. The trough between the labial and lingual ridges is shallow. Its width varies with the curvature of the lingual ridge. *Glyptops ornatus* and *Pleurosternon bullockii* have relatively narrow triturating surface with a low, simple lingual ridge (Evans and Kemp, 1975; Gaffney, 1979b). Compared to these two taxa, the triturating surface of *Dorsetochelys typocardium* is broader and widens slightly posteriorly. *Dorsetochelys typocardium* is further characterized by a relatively poor development of the lingual ridge and an unusually extensive contribution of the palatine to the triturating surface (Evans and Kemp, 1976). Thalassochelydians generally have high labial and lingual ridges separated by a deep trough (Gaffney, 1976; Rieppel, 1980; Anquetin et al., 2015). DORCM G.10715 is clearly different from any of the aforementioned taxa.

In dorsal view, the maxilla forms a large portion of the floor of the fossa orbitalis (Fig. 4A–B). Only the base of the ascending process is preserved and the contacts this process probably had with the nasal and prefrontal dorsally cannot be confirmed. The anterior border of each maxilla is broken, but there is no doubt that the bone formed the lateral margin of the apertura narium externa. The lateral part of the foramen alveolaris superior can be seen medially at the base of the ascending process of the maxilla. This foramen faces dorsomedially and probably opened in the foramen orbito-nasale (not visible here). On the left side, a smaller, but well defined foramen opens slightly anterior to the foramen alveolaris anterior on the floor of the orbit (Fig. 4A–B). The same foramen was probably also present on the right side, but the area is damaged. The nature of this foramen remains uncertain, but a similar foramen was described in several thalassochelydians as well as in the stem-group chelonioid *Toxochelys*, although the distribution and homology of this feature remains to be investigated (Gaffney, 1976; Anquetin et al., 2015).

Vomer

As usual the vomer forms the medial septum of the apertura narium interna (Fig. 4C–D). The sutures of the vomer with other elements are poorly preserved, with exception of the dorsal suture with the

palatines that can be seen relatively easily in some areas. Anteroventrally, the vomer widens and contacts the premaxillae and maxillae, but this area is poorly preserved (e.g., the foramina praepalatinum cannot be seen). Posterodorsally, the vomer flattens and widens to form part of the palatal roof. There, the vomer appears to contact the pterygoids as well as the palatines.

Palatine

In ventral view, the palatines contact the vomer medially, the maxillae anterolaterally, and the pterygoids posteriorly (Fig. 4C–D). The suture with the pterygoids is poorly preserved but visible by intermittence. Although this area is not very well preserved, it appears that the palatines are fully separated from one another in ventral view as a result of a contact between the vomer and the pterygoids. This is also the condition observed in most thalassochelydians, except *Jurassichelon oleronensis* (Rieppel, 1980) and perhaps *Plesiochelys planiceps* (Gaffney, 1975, 1976). Anteromedially, the palatines form the arched roof of the nasal canals and apertura narium interna. Laterally, the palatines form an anterolateral process that braces the medial margin of the triturating surface. In contrast to the assertion of Milner (2004), the palatine does not contribute to the triturating surface in DORCM G.10715, which clearly differentiates this specimen from the remarkable condition observed in *Dorsetochelys typocardium* (Evans and Kemp, 1976). Posterolaterally, the palatine forms the anterior and medial margins of a large and kidney-shaped foramen palatinum posterius that remains open posterolaterally due to the absence of a contact between the pterygoid and maxilla/jugal. Paracryptodires in general have a relatively small foramen palatinum posterius that is closed posterolaterally by a broad bar of bone (Evans and Kemp, 1975, 1976; Gaffney, 1979b; Joyce and Lyson, 2015). In contrast, an open foramen palatinum posterius is relatively rare among turtles. It is known only in some thalassochelydians (*Plesiochelys* spp. and *Jurassichelon oleronensis*) and some protostegids (e.g., Gaffney, 1976; Hirayama, 1998; Kear and Lee, 2006; Joyce, 2007; Cadena and Parham, 2015; Anquetin et al., 2017; Evers et al., 2019). Protostegids are generally considered to be early pan-chelonioids, but they have been repeatedly hypothesized to be closely related to thalassochelydians (e.g., Joyce, 2007). Modern sea turtles lack a foramen palatinum posterius altogether.

Palatoquadrate elements

Quadrate

The severe dorsoventral compression of DORCM G.10715 strongly affected the quadrate, notably the middle ear, ethmoid region, and processus articularis (see 3D mesh available as Supplementary information). On the dorsal surface of the otic chamber, the quadrate contacts the prootic anteromedially, the supraoccipital medially, and the opisthotic posteromedially (Fig. 4A–B). The brief contact between the quadrate and supraoccipital prevents the prootic and opisthotic to meet in dorsal view. Posterolaterally, the quadrate also had a large contact with the squamosal. This element is now lost and the position of the suture with quadrate is difficult to place. In this area, the squamosal simply lies above the quadrate and leaves little marks on the surface of the latter when disarticulated. The quadrate forms the lateral half of the foramen stapedio-temporale and processus trochlearis oticum. The latter structure is modest in development and remarkable in being quite oblique in orientation. Evers and Benson (2019) noted that some turtles, including most thalassochelydians, have a processus trochlearis oticum limited to the medial part of the otic chamber and framed laterally by a deep recess. This condition is apparently also present in DORCM G.10715 (Fig. 4A–B). The cavum tympani and antrum postoticum were both apparently well developed. The incisura columellae auris probably remained open posteroventrally. The ventral part of the quadrate is poorly preserved, being both crushed dorsoventrally and much eroded (Fig. 4C–D). However, it should be noted that a strong ridge is present on the posterior surface of the processus articularis of the quadrate. This ridge prolongates the posterior margin of the pterygoid laterally on the posterior surface of the processus articularis and appears to bend ventrally on the more lateral

parts of the processus articularis. This ridge strongly reminds the well-developed, ventrally-infolding ridge present in thalassochelydians (Gaffney, 1976; Anquetin et al., 2015). A similar, though less pronounced ridge is also present in sandownids (Evers and Benson, 2019; Evers and Joyce, 2020). As noted by Evers and Benson (2019) for thalassochelydians and sandownids, the processus articularis of the quadrate is oriented strongly posteriorly relative to the sagittal plane.

Pterygoid

The ventral aspect of the pterygoids is much eroded. The pterygoid contacts the vomer (probably) and palatine anteriorly, the quadrate posterolaterally (suture not preserved), the basioccipital posteromedially, the parabasisphenoid medially, and the other pterygoid anteromedially (Fig. 4C–D). It was reported that *Pleurosternon bullockii* and *Glyptops ornatus* lack a midline contact of the pterygoids due to a long ventral exposure of the parabasisphenoid that would reach the vomer anteriorly (Evans and Kemp, 1975; Gaffney, 1979b), but this may be a preservational artifact (Joyce and Anquetin, 2019. Anterolaterally, the pterygoid forms a well-developed processus pterygoideus externus. The vertical plate of the processus pterygoideus externus is triangular in outline with a low anterior part and a high posterior part (Fig. 4A–B). In ventral view, the anterior part of the processus pterygoideus externus forms an anterolaterally oriented process that defines the posterolateral margin of the foramen palatinum posterius (Fig. 4C–D). As noted above, there is no contact between the pterygoid and the maxilla and/or jugal in this area, and the foramen palatinum posterius remains open posterolaterally.

As preserved, the canalis caroticus internus runs in an open gutter on the ventral surface of the cranium (Fig. 4C–D). It is unknown whether the canal was at least partly floored in life, or if it remained open. In any case, the canalis caroticus internus was superficial (i.e., running close to or on the bone surface). This is clearly reminiscent of the condition in some thalassochelydians, such as *Plesiochelys etalloni*, *Plesiochelys bigleri*, and *Jurassichelon oleronensis* (Gaffney, 1976; Rieppel, 1980; Anquetin et al., 2015; Püntener et al., 2017). It should be noted that the canalis caroticus internus is fully floored posteriorly in some thalassochelydians such as *Portlandemys* spp. and *Neusticemys neuquina* (Gaffney, 1976; Anquetin et al., 2015; González Ruiz et al., 2020). Anquetin et al. (2015) and Raselli and Anquetin (2019) provided a thorough survey of this feature in thalassochelydians. Posteriorly, the canalis caroticus internus is located only on the pterygoid a short distance lateral to the suture with the parabasisphenoid. At about mid-length, the canalis caroticus internus bends medially and then runs along the parabasisphenoid-pterygoid suture up to the split between the two branches of the internal carotid artery (see Parabasisphenoid). The foramen distalis nervi vidiani seems to open in the pterygoid just lateral to the mid-length bending of the canalis caroticus internus. The pterygoid fossa is relatively shallow and triangular in outline, contrasting with the much narrowed pterygoid fossa observed in *Dorsetochelys typocardium*.

Braincase elements

Supraoccipital

The supraoccipital contacts the prootic anteroventrally, the quadrate laterally (short contact), and the opisthotic posterolaterally (Fig. 4A–B). The contacts with the parietal anterodorsally and the exoccipital posteroventrally are not directly observable due to the strong dorsoventral compression of the cranium. Only the posterodorsal part of the crista supraoccipitalis can be observed. The crista does not extend much posteriorly, reaching only as far as the opisthotics (it can be surmised that the squamosals reached further posteriorly). The part of the crista supraoccipitalis that is not covered dorsally by the parietals forms a narrow, triangular horizontal plate that prolongates the skull roof posteriorly.

Exoccipital

The exoccipitals are severely affected by the dorsoventral compression of the cranium that resulted in a contact between the crista supraoccipitalis and condylus occipitalis. The exoccipital apparently contacted the supraoccipital mediodorsally, the opisthotic dorsolaterally, and the basioccipital ventromedially (**Fig. 4**). The only preserved suture is the one with the opisthotic in the roof of the cavum acustico-jugulare. Two foramina nervi hypoglossi are visible on the left side, but only one is preserved on the right side. Below this point, the preservation of the exoccipitals is extremely poor. Therefore, it is unknown whether the exoccipital contacted the pterygoid as in many cryptodires (**Gaffney, 1979a**). The extent to which the exoccipitals contribute to the condylus occipitalis is also uncertain.

Basioccipital

The basioccipital contacts the parabasisphenoid anteriorly along a seemingly transverse suture (poorly preserved), the pterygoid anterolaterally along a broad and oblique suture, and the exoccipital dorsally (**Fig. 4C–D**). The tubercula basioccipitale are poorly preserved. Compared to *Dorsetochelys typocardium*, the basioccipital has a shorter ventral exposure and a broader contact with the pterygoid.

Prootic

In DORCM G.10715, the prootic can only be observed on the dorsal surface of the otic chamber (**Fig. 4A–B**). The rest of the bone, notably in the ethmoid region, is not accessible. As preserved, the prootic contacts the parietal anteromedially, the quadrate laterally and anteroventrally, and the supraoccipital posteriorly. As noted above, a brief contact of the quadrate and supraoccipital posterior to the foramen stapedio-temporale prevents the prootic and opithotic to meet on the dorsal surface of the otic chamber. As usual, the prootic forms the medial half of the foramen stapedio-temporale and processus trochlearis oticum. The latter structure is modest in development, remarkable in being oriented quite obliquely relative to the transverse axis, and limited to the medial part of the otic chamber (see **Quadrate**).

Opisthotic

The opisthotic contacts the supraoccipital medially, the quadrate anterolaterally, and the exoccipital posteriorly (suture not preserved dorsally). At first it may appear that the opisthotic as an extensive dorsal exposure, but this is due to the disarticulation and loss of the squamosal on both sides (**Fig. 4A–B**). As noted above, there is no anterior contact with the prootic on the dorsal surface of the otic chamber. Due to the postmortem dorsoventral crushing of the cranium, the processus interfenestralis of the opisthotic is not preserved. The processus paroccipitalis is dorsoventrally flattened (seemingly the natural condition) and forms an acute posterior ridge. A similar morphology is found in a wide array of turtles including Sandownidae, Trionychia, Pleurodira, Pleurosternidae, and several stem-group turtles (**Evers and Benson, 2019**).

Parabasisphenoid

In ventral aspect, the parabasisphenoid contacts the pterygoid laterally and the basioccipital posteriorly (**Fig. 4C–D**). The bone is triangular in outline with a concave ventral surface. This concavity is more pronounced posteriorly along the suture with the basioccipital. The anterior part of the superficial canalis caroticus internus runs on the parabasisphenoid-pterygoid suture and is formed by both elements (see **Pterygoid**). The preservation is not perfect, but the split between the cerebral and palatine branches of the internal carotid artery can still be observed in the anteriormost part of the canalis caroticus internus. The foramen posterius canalis carotici cerebralis opens mediodorsally in the canalis caroticus internus and is formed by the parabasisphenoid. The palatine branch continues anteriorly for a short distance and enters the foramen posterius canalis carotici palatinum formed mostly (if not exclusively) by the

pterygoid. As noted above, the morphology of the internal carotid sytem in DORCM G.10715 clearly re- 425
minds the condition observed in some thalassochelydians, such as *Plesiochelys etalloni*, *Plesiochelys bigleri*, 426
and *Jurassichelon oleronensis* (Gaffney, 1976; Rieppel, 1980; Anquetin et al., 2015; Püntener et al., 2017). 427
This point is developed further in the Discussion below. Unfortunately, the morphology of the paraba- 428
sisphenoid inside the cranium is not accessible. 429

Phylogenetic relationships 430

In our first analysis, the cranium DORCM G.10715 and the shell-based species *Hylaeochelys belli* were 431
treated as separate terminal taxa. This analysis resulted in four most parsimonious trees (MPTs; Tree 432
Length = 1540 steps; Consistency Index = 0.260; Retention Index = 0.653). The strict consensus tree (TL = 433
1546 steps; CI = 0.259; RI = 0.651) corresponds fairly well to the topology obtained by Evers and Benson 434
(2019) for their analysis with unordered characters (Fig. 5A). The differences are: the support of the clade 435
Paracryptodira, the resolution of the relationships among Xinjianchelyidae, and the improve resolution 436
of the relationships among the clades Sinemydidae + Macrobaenidae and Thalassochelydia. DORCM 437
G.10715 and *Hylaeochelys belli* both fall within Thalassochelydia. *Hylaeochelys belli* is resolved as the most 438
basal thalassochelydian, whereas DORCM G.10715 is recovered as the sister-group of the Late Jurassic 439
Jurassichelon oleronensis. The inclusion of DORCM G.10715 and *Hylaeochelys belli* in the matrix tends to 440
have a negative effect on Bremer support values in the central portions of the consensus tree (i.e., from 441
Xinjiangchelyidae to Trionychia) compared to the reference analysis of Evers and Benson (2019). 442

In our second analysis, the cranium DORCM G.10715 and the shell-based species *Hylaeochelys belli* 443
were merged into a single terminal taxon, reflecting our suggestion that they may indeed represent the 444
same species (see Alpha taxonomy). This second analysis also resulted in four MPTs (TL = 1541 steps; 445
CI = 0.260; RI = 0.653). The topology of the strict consensus tree (TL = 1547 steps; CI = 0.259; RI = 0.651) 446
is exactly the same as the one obtained during our first analysis (Fig. 5B). The merged DORCM G.10715 + 447
Hylaeochelys belli is recovered at the same position as the isolated cranium DORCM G.10715 before, that 448
is as the sister-group of *Jurassichelon oleronensis*. Merging *Hylaeochelys belli* with DORCM G.10715 has a 449
positive effect on Bremer support values compared to our first analysis. Most of the Bremer values are 450
the same as the one obtained by the reference analysis of Evers and Benson (2019). Notable discrep- 451
ancies include the slightly lower support for the clade Sinemydidae + Macrobaenidae and the clade that 452
unites them to other turtles, and the slightly increased support for the clade Thalassochelydia. 453

In our two analyses, the clade Angolachelonia is supported by the same eight unambiguous synapo- 454
morphies as in the reference analysis (Evers and Benson, 2019): the foramen stapedio-temporale is 455
concealed in dorsal view (ch. 18.0); the posterior surface of the quadrate bears a strong ridge ventral 456
to the incisura columellae auris (ch. 83.1); the articular process of the quadrate is directed strongly pos- 457
teriorly (ch. 84.1); the medial contact of the pterygoids is longer than the parabasisphenoid at midline 458
(ch. 94.0); the pterygoid contacts the medial edge of the mandibular condyle when seen in ventral view 459
(ch. 103.1); the posterior margin of the coronoid has a deep notch (ch. 181.1); the anterior part of the 460
coronoid bears a foramen leading to the fossa meckelii (ch. 182.1); the coronoid process is relatively high 461
and dorsally or posterodorsally pointed (ch. 184.1). In our second analysis, the clade Thalassochelydia is 462
supported by the same eight unambiguous synapomorphies as the one obtained by Evers and Benson 463
(2019): the processus trochlearis oticum is limited to the medial part of the otic chamber and a deep 464
recess is present lateral to it (ch. 81.1); presence of a fossa on the posterodorsal surface of the floor of 465
the supratemporal fossa (ch. 113.1); the foramina anterius canalis carotici cerebralis are located close 466
together (ch. 142.1); the splenial is present (ch. 185.0); costals lack lateral ossification (ch. 210.2); rib-free 467
peripherals are present (ch. 211.1); vertebrals 2–4 are significantly broader than pleurals (ch. 224.0); cen- 468
tral cervical articulations are not formed (ch. 278.0). In our first analysis, the presence of the shell-based 469
Hylaeochelys belli renders most of these characters ambiguous and the clade Thalassochelydia is only sup- 470
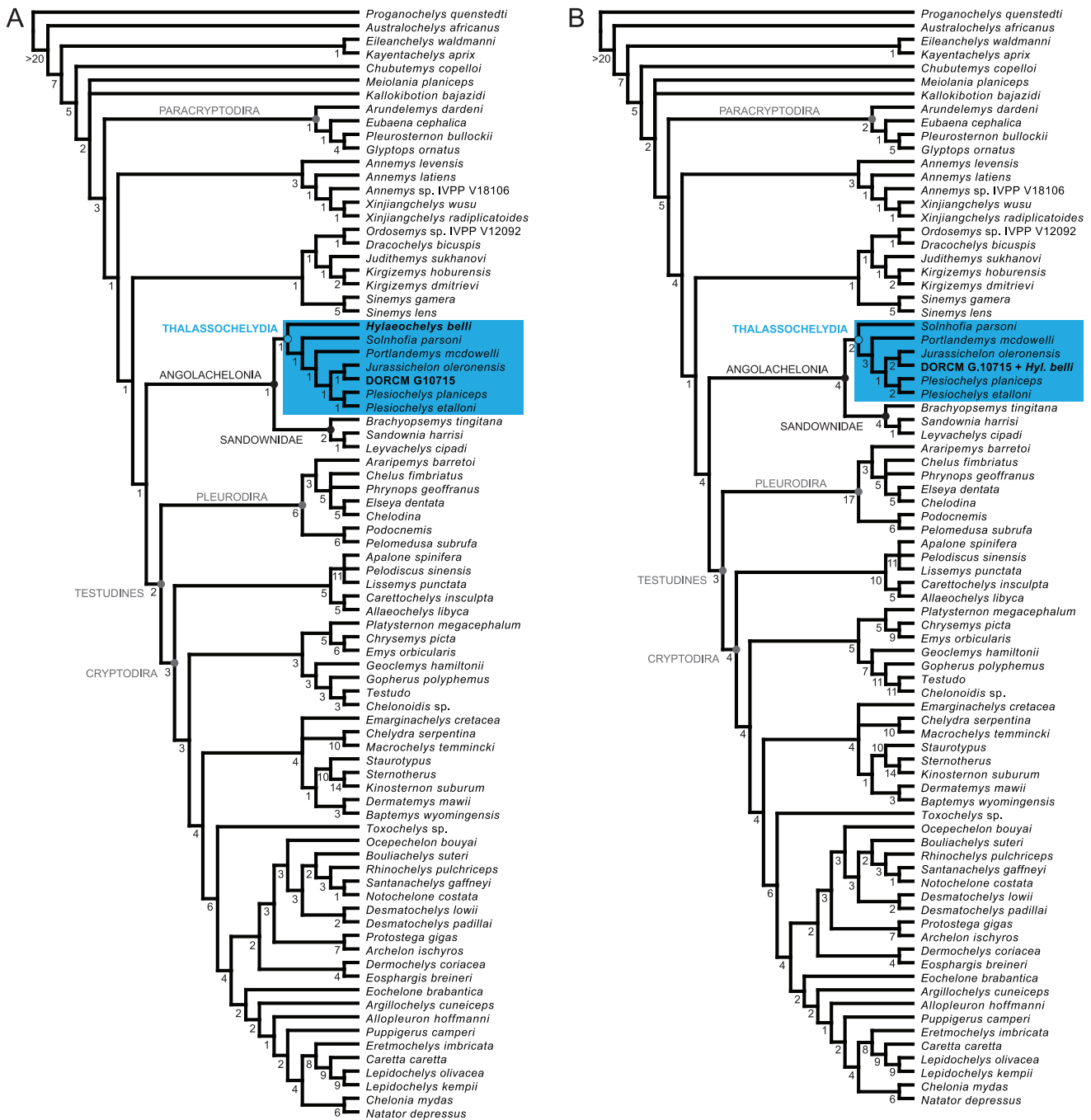
Figure 5. Phylogenetic relationships of DORCM G.10715 and *Hylaeochelys belli*. (A) Strict consensus tree (TL = 1546 steps; CI = 0.259; RI = 0.651) of four MPTs with DORCM G.10715 and *Hylaeochelys belli* treated as distinct terminal taxa; (B) Strict consensus tree (TL = 1547 steps; CI = 0.259; RI = 0.651) of four MPTs with DORCM G.10715 and *Hylaeochelys belli* merged into a single terminal taxon. Numbers below nodes correspond to Bremer support values.

ported by the presence of rib-free peripherals (ch. 211.1) and the vertebrals 2–4 broader than pleurals (ch. 224.0), explaining the reduced support for the clade in this analysis. Finally, in both of our analyses, the clade formed by *Jurassichelon oleronensis* and DORCM G.10715 (or DORCM G.10715 + *Hylaeochelys belli*) is supported by the following unambiguous synapomorphies: the medial contact of the pterygoids is equal to or shorter than the parabasisphenoid at midline (ch. 94.1); the presence of a poorly developed crista supraoccipitalis (ch. 110.0); the internal carotid arterial system is partially embedded, a foramen posterius canalis carotici interni is present, and the split into palatine and cerebral arteries happens at

the fenestra caroticus and is thus ventrally exposed (ch. 147.1). It should be noted for the record that ⁴⁷⁸ thalassochelydians are particularly difficult to score for the latter character due to intraspecific variability ⁴⁷⁹ and preservation bias (**Anquetin et al., 2015**). ⁴⁸⁰

Discussion ⁴⁸¹

Beta taxonomy ⁴⁸²

When it was still partly embedded in matrix (**Fig. 1**), DORCM G.10715 was provisionally referred to *Dorse-* ⁴⁸³ *tochelys delairi* (now *Dorsetochelys typocardium*) based on a short list of tentative observations: palate ⁴⁸⁴ of similar size and shape, "the palatines contribute to the triturating surface, the pterygoids meet an- ⁴⁸⁵ teriorly ahead of the foreshortened basisphenoid and there is an abbreviated pterygoid-basisphenoid ⁴⁸⁶ contact" (**Milner, 2004**). The description above disagrees with this first assignment. The triturating sur- ⁴⁸⁷ face of DORCM G.10715 is relatively short and U-shaped, and the palatines do not contribute much to it. ⁴⁸⁸ The large, kidney-shaped, and posterolaterally open foramen palatinum posterius of the new cranium is ⁴⁸⁹ also clearly different from the relatively small, rounded, and closed foramen observed in *Dorsetochelys* ⁴⁹⁰ *typocardium* (**Evans and Kemp, 1976**. The fact that the pterygoids meet anteriorly to the parabasisphe- ⁴⁹¹ noid, therefore reducing the length of the contact between these elements, is actually only remarkable ⁴⁹² within the context of non-baenid paracryptodires by comparison with *Pleurosternon bullockii* and *Glyptops* ⁴⁹³ *ornatus* (but see **Joyce and Anquetin, 2019**), but not when turtles are considered more globally. ⁴⁹⁴

Furthermore, DORCM G.10715 exhibits several characteristics that clearly exclude it from Paracryp- ⁴⁹⁵ todira. The skull roof surface is smooth and lacks any indication of the ornamentation typically found in ⁴⁹⁶ non-baenid paracryptodires and basal baenids (see **Joyce and Lyson, 2015**; **Joyce and Anquetin, 2019**). ⁴⁹⁷ The prefrontals of DORCM G.10715 have a relatively large exposure on the skull roof and they meet on ⁴⁹⁸ the midline, whereas they are reduced to small lappets in most paracryptodires and even absent from the ⁴⁹⁹ skull roof in derived forms. The upper temporal emargination is relatively extensive in DORCM G.10715, ⁵⁰⁰ contrasting with the at-most modest emargination seen in non-baenid paracryptodires. ⁵⁰¹

DORCM G.10715 actually shows a number of features that support a close relationships with Thalas- ⁵⁰² sochelydia. The most obvious of these features is the presence of a relatively large and posterolater- ⁵⁰³ ally open foramen palatinum posterius. This is found only in some thalassochelydians and some early ⁵⁰⁴ pan-chelonioids (e.g., **Gaffney, 1976**; **Joyce, 2007**; **Evers and Benson, 2019**). The presence of a well- ⁵⁰⁵ developed ridge on the posterior surface of the processus articularis of the quadrate is also a strong ⁵⁰⁶ argument. This prominent ridge on the quadrate below the incisura columallae auris was first noted by ⁵⁰⁷ **Parsons and Williams (1961)** in *Solnhofia* and **Gaffney (1976)** in *Plesiochelys* and *Portlandemys*, but it is ⁵⁰⁸ more generally present in all thalassochelydians for which this particular area of the cranium is known ⁵⁰⁹ (**Anquetin et al., 2015**). More recently, it was noted that a somewhat similar, albeit less pronounced, ⁵¹⁰ ridge was also present in sandownids and possibly also a couple of additional taxa (**Evers and Benson,** ⁵¹¹ **2019**). The ridge present in DORCM G.10715 is incompletely preserved but clearly reminds the condition ⁵¹² and development observed in thalassochelydians. Other similarities between DORCM G.10715 and tha- ⁵¹³ lassochelydians include the presence of a small foramen in the maxilla along the anteroventral margin ⁵¹⁴ of the orbit, a nasal-frontal contact below the prefrontals, and possibly the configuration of the canalis ⁵¹⁵ caroticus internus (but see below). In addition to the previous, new characters supporting Angolachelonia ⁵¹⁶ (Thalassochelydia + Sandownidae) or Thalassochelydia more specifically were recently proposed by **Ev-** ⁵¹⁷ **ers and Benson (2019)**. As in angolachelonians, the articular process of the quadrate is directed strongly ⁵¹⁸ posteriorly in DORCM G.10715, and as in thalassochelydians (not exclusive), the processus trochlearis ⁵¹⁹ oticum is limited to the medial part of the otic chamber and bordered laterally by a deep recess. The ⁵²⁰ presence of all of these features in DORCM G.10715 is enough to firmly place this specimen within Tha- ⁵²¹ lassochelydia, as unsurprinsignly confirmed by the phylogenetic analysis (see above; **Fig. 5**). ⁵²²

We believe the interrelationships of Thalassochelydia to be poorly understood for the moment. In our phylogenetic analysis, the sister group relationships between DORCM G.10715 (or DORCM G.10715 + *Hylaeochelys belli*) and *Jurassichelon oleronensis* is only supported by three "reversals" to plesiomorphic conditions, namely a midline contact of the pterygoids that is equal or shorter than the length of the parabasisphenoid, a poorly developed crista supraoccipitalis, and a partly embedded internal carotid system with the split into cerebral and palatine branches still exposed ventrally (see above). Therefore, we will refrain from any comment on these relationships herein and only retain the clear placement of DORCM G.10715 within Thalassochelydia.

Alpha taxonomy

Although DORCM G.10715 shares many features with thalassochelydians, it is also distinct from any known species in that group. The peculiar morphology of the upper triturating surface (see **Maxilla** above) and the kidney-shaped foramen palatinum posterius clearly set DORCM G.10715 apart from the rest (**Fig. 4**). However, we intentionally refrain from naming a new species based on this specimen because we believe there is a great chance that it actually represents the cranium of the shell-based species *Hylaeochelys belli*, which is found in the same layers. This is why DORCM G.10715 is left in open nomenclature herein (Thalassochelydia indet.).

Thanks to intensive fossil collection since the nineteenth century, we can consider the Purbeck turtle fauna to be relatively well known. Following **Milner (2004)** and **Pérez-García (2012) and Pérez-García (2014)**, four distinct species can be recognized in this assemblage. *Pleurosternon bullockii* and *Dorsetochelys typocardium*, both known by a cranium and numerous shells, are paracryptodires. "*Helochelydra*" *anglica* is known only by fragmentary shell remains and is a representative of Helochelydridae, a group of terrestrial stem turtles characterized by a distinctive cranial anatomy (see **Joyce, 2017**). DORCM G.10715 does not belong to any of these three species. The fourth Purbeck turtle, *Hylaeochelys belli*, is known by numerous well-preserved shells from the Purbeck and Wealden Groups of southern England (**Milner, 2004**; **Pérez-García, 2012**). Unfortunately, none is associated with cranial material. Distinguished by a smooth shell with very wide vertebral scales and the absence of mesoplastra, *Hylaeochelys belli* was repeatedly proposed to be a representative, or at least a close relative, of the Late Jurassic Plesiochelyidae (**Lydekker, 1889**; **Nopcsa, 1928**; **Hirayama et al., 2000**; **Lapparent de Broin, 2001**; **Milner, 2004**; **Karl et al., 2007**; **Pérez-García, 2012**), a conclusion supported by the phylogenetic analysis proposed herein since *Hylaeochelys belli* is recovered as a basal Thalassochelydia when scored as a distinct terminal taxon (see above; **Fig. 5**).

Since both DORCM G.10715 and the shell-based *Hylaeochelys belli* co-occur in the Purbeck Group and appear to be representatives of Thalassochelydia, a group usually considered to disappear at the end of the Jurassic (e.g., **Bardet, 1994**; **Anquetin et al., 2017**), we believe that there is a reasonably good chance that they actually represent the same species. Although we lack more definitive evidence for the moment, it should be noted that the shell corresponding to the cranium DORCM G.10715 can be estimated to be around 38–40 cm in length (supposing the cranium represents about 20% of the carapace length as common in these turtles), which matches fairly well with the size range of *Hylaeochelys belli* (**Milner, 2004**; **Pérez-García, 2012**). Furthermore, when DORCM G.10715 and *Hylaeochelys belli* are merged into a single terminal taxon (see our second phylogenetic analysis) they fit snugly into the phylogenetic hypothesis of **Evers and Benson (2019)** without causing much disruption in terms of topology and character distribution. This should definitely not be taken as hard evidence, but it somewhat suggests that this association makes sense.

Finally, it should be reminded that two undescribed turtle mandibles from the Purbeck Group in Swanage are housed in the Natural History Museum in London: NHMUK OR21974x and NHMUK OR44815 (**Lydekker, 1889**; **Milner, 2004**). Unfortunately, we saw these mandibles before conducting the present study. However, based on our observations at the time and photographs of the specimens, we believe we
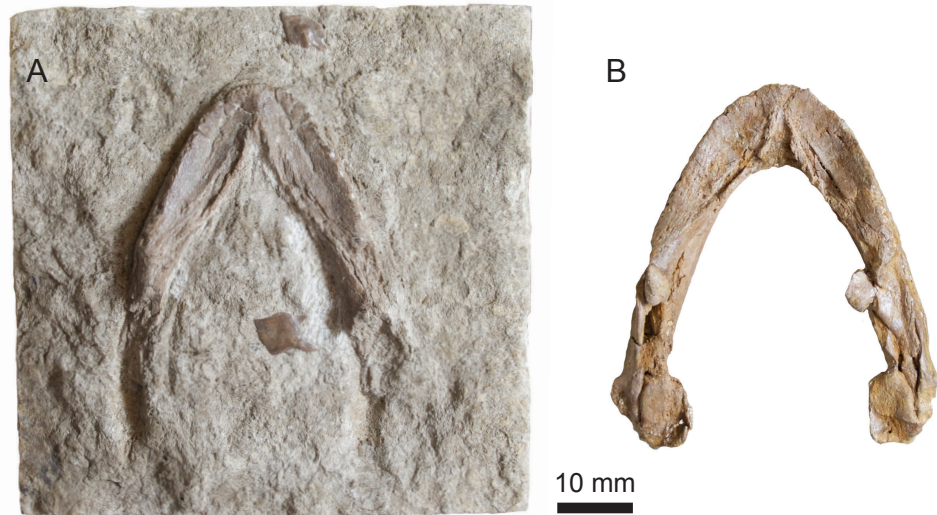
Figure 6. **Two undescribed mandibles, Purbeck Group (Berriasian), Swanage, Dorset, UK.** (A) NHMUK OR21974x in dorsal view; (B) NHMUK OR44815 in dorsal view. The mandibles are lit mainly from the right to accentuate relief. Mentioned by Lydekker (1889) and Milner (2004).

can make a few pertinent comments here. The morphology of the triturating surface is remarkable and indicates that the two mandibles belong to the same taxon (Fig. 6). The anterior outline of the mandibles is rather rounded. The triturating surface is relatively short and broad, with low lingual and labial ridges. The lingual ridges become more pronounced anteriorly and do not meet one another on the symphysis, rather bordering a narrow sagittal gutter. This morphology matches fairly well that of DORCM G.10715 (Fig. 4) and we are relatively confident that they can all be assigned to the same taxon, which is possibly *Hylaeochelys belli*. Interestingly, the more complete of these two mandibles (NHMUK OR44815) possesses a well-developed processus coronoideus projecting posteriorly, an angolachelonian feature (non-exclusive) according to Evers and Benson (2019).

Notes on the internal carotid arterial system in Paracryptodira

The configuration of the internal carotid arterial system and more specifically the position of the foramen posterius canalis carotici interni has been given a great significance in terms of turtle systematics (Albrecht, 1976; Gaffney, 1979a). Paracryptodires are usually depicted as having a foramen posterius canalis carotici interni located halfway along the parabasisphenoid-pterygoid suture and facing ventrally. The split between the two branches of the internal carotid artery (that is when the palatine branch is present; see Rollot et al., 2018) occurs within the bones and is therefore not visible in ventral view (Gaffney, 1979a; Joyce and Lyson, 2015; Joyce and Anquetin, 2019).

The previous description applies fairly well to baenids, but less so to non-baenid paracryptodires. This became plainly apparent to us when we revised the latter while describing DORCM G.10715. In *Pleurosternon bullockii* and *Glyptops ornatus*, the internal carotid artery penetrates the cranium at the level of the fused and still visible basipterygoid process, which lies in a shallow depression along the parabasisphenoid-pterygoid suture. In both of these species, the authors describe and illustrate a short sinus that extends posterolaterally from the foramen posterius canalis carotici cerebralis and crosses the medial part of the basipterygoid process (Evans and Kemp, 1975; Gaffney, 1979b). Just lateral to the foramen posterius canalis carotici cerebralis and anterolateral to the previously described sinus lies the small foramen posterius canalis carotici palatinum (not readily observable in *Pleurosternon bullockii*). In other words, it would seem that the internal carotid artery runs for a short length in a sinus (equivalent to a ventrally open canalis caroticus internus) along the parabasisphenoid-pteryoid suture, then splits

into a palatine and cerebral branches before really entering the cranium through the two corresponding foramina. The split of the internal carotid artery is therefore exposed in ventral view in these two species and there is no proper foramen posterius canalis carotici interni, because the internal carotid artery does not travels through a canal before splitting into its cerebral and palatine branches, only through a short, ventrally open sinus.

In *Dorsetochelys typocardium*, the internal carotid artery runs in a ventrally open groove extending from the posterior margin of the pterygoid to the anterior half of the parabasisphenoid-pterygoid suture and there is no visible basipterygoid process (Evans and Kemp, 1976). This groove corresponds to a ventrally open canalis caroticus internus. For most of its length, the groove follows the suture between the parabasisphenoid and pterygoid, but the posteriormost part of the groove bends laterally and lies only on the pterygoid. In the most anterior part of the groove the cerebral branch of the internal carotid artery enters the basisphenoid through the foramen posterius canalis carotici cerebralis (Evans and Kemp, 1976). Although the original description only mentions this foramen, our personal observations confirm that a small foramen posterius canalis carotici palatinum formed mostly by the pterygoid can be seen just anterolateral to the foramen for the cerebral branch. Therefore, here again, there is no proper foramen posterius canalis carotici interni and the split between cerebral and palatine branches is exposed in ventral view. More importantly, the condition in *Dorsetochelys typocardium* is strikingly reminiscent of what was described in a number of thalassochelydians, including DORCM G.10715 (this study), *Plesiochelys etalloni*, *Plesiochelys bigleri*, and *Jurassichelon oleronensis* (Gaffney, 1976; Rieppel, 1980; Anquetin et al., 2015; Püntener et al., 2017). Ironically, Hirayama et al. (2000) used this similitude to suggest that the cranium of *Dorsetochelys typocardium* (their *Dorsetochelys delairi*) could be the cranium of *Hylaeochelys belli*, a form they considered to have plesiochelyid affinities.

The cranium is known in only two other non-baenid paracryptodires (Joyce and Anquetin, 2019). In the Late Jurassic *Uluops uluops*, the internal carotid artery also travels in a ventrally open groove running along the parabasisphenoid-pterygoid suture (Carpenter and Bakker, 1990). The authors clearly compared this condition to that of *Plesiochelys etalloni* and *Jurassichelon oleronensis*, as discussed by Rieppel (1980). The material of *Uluops uluops* is currently being properly described by Yann Rollot and colleagues, but we can already expect the arrangement of the internal carotid arterial system to be more similar to what we have in *Dorsetochelys typocardium* than in baenids. The Late Cretaceous *Compsemys victa* is characterized by a highly derived cranial anatomy (Lyson and Joyce, 2011). It appears that a proper and relatively large foramen posterius canalis carotici interni is formed halfway along the suture between the much reduced parabasisphenoid and the pterygoid. So the condition in *Compsemys victa* is probably more similar to baenids, although it should be noted that the foramen posterius canalis carotici interni faces posteriorly instead of ventrally in this species.

The above discussion highlights that the morphology of the internal carotid arterial system in non-baenid paracryptodires is much more variable than usually considered. We do not believe that the similitude between the condition in the paracryptodire *Dorsetochelys typocardium* (possibly also *Uluops uluops*) and some thalassochelydians indicates close relationships. It more probably represents either a more generalized ancestral state or a similar transitional step toward more derived arrangements of the internal carotid arterial systems in both groups. For simplicity, we omitted to mention xinjianchelyids, sinemydids and macrobaenids here, but they also represent transitional forms with their own specific arrangement of the internal carotid arterial system (Rabi et al., 2013). A more comprehensive revision of the existing variation in these early turtles is needed and will probably greatly impact the way characters of the internal carotid arterial system are interpreted for systematic purposes and coded in phylogenetic analyses. A possible outcome of such a revision is that future phylogenetic analyses may fail to retrieve a monophyletic Paracryptodira.

Conclusion

The Late Jurassic deposits of western and central Europe have a predominantly marine origin. Turtles from these deposits are mostly referred to the clade Thalassochelydia, a diversified group of coastal marine turtles known almost exclusively from that part of the world (Anquetin et al., 2017). Thalassochelydians are generally believed to go extinct at the end of the Jurassic following the drastic reduction of their preferred habitats (Bardet, 1994). Until now, no fossil turtle has been unambiguously assigned to the Thalassochelydia after the Jurassic (Anquetin et al., 2017).

The onset of the Early Cretaceous in western and central Europe is marked by a transition to more proximal and then fully continental depositional settings, as illustrated by the succession of the Purbeck and Wealden facies. Turtle faunas from these deposits are dominated by freshwater and terrestrial forms, notably paracryptodires and helochelydrids (Milner, 2004). As exemplified by *Hylaeochelys belli* (see above), some Cretaceous turtles have been proposed to be close relatives of thalassochelydians based on a general resemblance of the shell, but these tentative conclusions were never supported by unequivocal morphological arguments (notably based on the cranial anatomy).

In the present contribution, we show that the cranium DORCM G.10715 from the Purbeck of Swanage (Dorset, England) can be confidently referred to Thalassochelydia. This is the first conclusive evidence that thalassochelydians survived the Jurassic-Cretaceous boundary and associated environmental changes in Europe. We also suggest that DORCM G.10715 is probably the skull of *Hylaeochelys belli*, although we lack conclusive evidence on that point. The fact that the Purbeck material is associated with marginal deposits and that the species *Hylaeochelys belli* persists into the more frankly continental Wealden Group could suggest that thalassochelydians became adapted to new environmental conditions after the Jurassic. But we cannot exclude that this may be a preservational artefact due to the lack of continental deposits in the Late Jurassic.

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Competing interests

The authors declare they have no personal or financial conflict of interest relating to the content of this study.

Author contributions

JA conceived the study, completed the description, analyzed and interpreted the data, prepared figures, and wrote the manuscript. CA performed the initial description, prepared figures, wrote an initial draft, and revised the manuscript.

Data availability

The 3D data, the updated phylogenetic matrix, and the individual figure files have been deposited and made public on OSF (doi: 10.17605/OSF.IO/95P78).

Supplementary information

- Textured 3D surface mesh of DORCM G.10715. doi: 10.17605/OSF.IO/95P78

- Updated character-taxon morphological matrix derived from Evers and Benson (2019). doi: 10.17605/OSF.IO/95P78

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