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A review of helochelydrid shell material from late Albian to early Cenomanian greensands of Southern England, United Kingdom

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Abstract

A number of helochelydrid turtle shell remains were recovered over the course of the 19th century from mid-Cretaceous sediments throughout Southern England, including the poorly figured and described types of *Trachydermochelys phlyctaenus* from the Cambridge Greensand of Cambridgeshire, *Plastremys lata* from the Upper Greensand of the Isle of Wight, and "*Trachydermochelys*" *rutteri* from the Melbury Sandstone of Dorset. A review of stratigraphic provenience suggests that all material originates from late Late Aptian portions of the Upper Greensand or early Early Cenomanian portions of the West Melbury Marly Chalk Formation, a relatively narrow time window geologically speaking. As described, *Trachydermochelys phlyctaenus* is a problematic taxon, because the most plausible type series is a chimera that includes two helochelydrid morphotypes in addition to protostegid remains. This conundrum is resolved through the designation of a lectotype. A review of all historic material confirms the presence of three English taxa distinct from *Helochelydra danubina*, a coeval taxon named from Germany. At least four helochelydrid taxa, therefore, occurred in western Europe during the Early to Late Cretaceous transition.

KEYWORDS

Cambridge Greensand, Early Cretaceous, *Helochelydridae*, Late Cretaceous, *Testudinata*, Upper Greensand Formation, West Melbury Marly Chalk Formation

1 | INTRODUCTION

A narrow band of glauconitic nearshore greensands crops out across Southern England, United Kingdom, which, broadly speaking, separates classically Early Cretaceous from classically Late Cretaceous strata (Rawson, 2006). These sediments were historically classified under a plethora of regional names that included the term "greensand," but more recent stratigraphic work suggests that they were deposited within two separate transgressive events that occurred near the Albian-Cenomanian boundary (Rawson, 2006).

The glauconitic sands of the lower (late Albian) transgressive event dominate towards the southwest of Southern England, where they are referred to as the Upper Greensand Formation (a.k.a. Upper Greensand), while coeval marine clays, which dominate towards the northeast of Southern England, are termed the Gault Clay Formation (Rawson, 2006). These sediments yielded a small number of terrestrial helochelydrid fossil turtle remains, either directly, or indirectly reworked into the base of the above lying West Melbury Marly Chalk Formation of the upper (early Cenomanian) transgressive event (Unwin, 2001; Joyce et al., 2014; see Section 2.1). These reworked fossils had historically been collected in the form of phosphatized nodules from the "Cambridge Greensand" around Cambridge, Cambridgeshire, during the "Coprolite Mining Rush" of the mid nineteenth century (Grove, 1976). Even though the turtle fauna from this greensand is dominated by marine turtles (see Evers et al., 2019 for recent review), Seeley (1869) and Lydekker (1889) also reported a small collection of helochelydrid shell remains under the name *Trachydermochelys phlyctaenus*, but did not provide any figures, making it difficult for the broader community to assess the validity and relationships of this taxon, in particular the surface texture that purportedly diagnosed it. Owen (1881) reported a partial helochelydrid shell from the Upper Greensand Formation of the Isle of Wight, Hampshire, under the name *Plastremys lata*, but the description is minimal and figures lacking, making it once again impossible to assess the validity of this taxon.

At the beginning of the twentieth century, Andrews (1920) describes a partial shell from Melbury Down near Shaftesbury, Dorset, under the name *Trachydermochelys rutteri*. Although the fossil was reported as originating from the "Upper Greensand," which implies a late Albian age, the outcrop is now placed at the base of the West Melbury Marly Chalk Formation (Mortimore et al., 2001; Hopson, 2005; see Section 2.3). This fossil is, therefore, the only helochelydrid from England that originates directly from the upper transgressive event. In contrast to previous authors, Andrews (1920) figured the new specimen to which he had access, but the drawing conceals the exact nature of the helochelydrid shell sculpturing that decorates its shell. Andrews (1920) noted similarities in the surface sculpturing of all three named shell taxa from the mid-Cretaceous English greensands, but suggested that differences in surface sculpturing combined with differences in stratigraphic age support the recognition of three separate species within the genus *Trachydermochelys*.

Nopcsa (1928) attributed *Trachydermochelys* to *Helochelydridae* (his Helochelydrinae) and confirmed the distinctness of its surface sculpturing among representatives of that clade. Lapparent de Broin and Murelaga (1999) reaffirmed the close relationships among English *Plastremys*/*Trachydermochelys* material from the mid-Cretaceous greensands, but remained uncommitted in regards to their possible synonymy. Joyce et al. (2014) and Joyce (2017) soon after concluded that all English greensand turtles originate from roughly coeval deposits and that the apparent range of variability in the sculpturing among named taxa from these sediments only represented interspecific variability. However, as they concluded the name *Trachydermochelys phlyctaenus* to be a nomen dubium, they recognized *Plastremys lata* as the oldest available name. Joyce et al. (2014) and Joyce (2017) otherwise inferred that the historic material from the Cambridge Greensand includes a previously unrecognized helochelydrid taxon, which they attributed to the earliest Cenomanian taxa *Helochelys danubina* von Meyer, 1855 based on similarities in sculpturing and temporal considerations, a conclusion contradicted by Pérez-García, Bardet, et al. (2020) by reference to the same material.

The more recent literature addressing the taxonomy of English helochelydrids is centered on turtles from other regions or stratigraphic intervals (i.e., Joyce, 2017; Joyce et al., 2014; Lapparent de Broin & Murelaga, 1999; Pérez-García, Bardet, et al., 2020). It is, therefore, not surprising that all specimens relevant to resolving the taxonomy of the greensand helochelydrids remain unfigured to date and their taxonomy remains intractable to the broader scientific community. In addition, subsequent work suggests that the identification of *Trachydermochelys phlyctaenus* as a nomen dubium may not have been justified (Joyce & Anquetin, 2019). The purpose of this contribution is to rectify this situation by providing figures and descriptions of the most relevant specimens from the mid-Cretaceous English greensands and by clarifying the taxonomic status of *Trachydermochelys phlyctaenus* through the designation of a lectotype.

2 | GEOLOGICAL SETTINGS

All material described herein was collected from three distinct localities in England: the "Cambridge Greensand" in the vicinity of the city of Cambridge, Cambridgeshire, the "Melbury Sandstone" near Melbury Down, Dorset, and the "Upper Greensand" on the Isle of Wight, Hampshire. The most important comparative material, the holotype of *Helochelys danubina*, was collected from near Regensburg, Bavaria, Germany (Figure 1). The age of the fossils recovered from all four localities is summarized below.

2.1 | Cambridge greensand

The systematic mining of phosphatic nodules during the nineteenth century near the city of Cambridge, Cambridgeshire yielded a diverse fossil fauna consisting of marine and terrestrial invertebrates and vertebrates (Grove, 1976). The nodules are found at the very base of the West Melbury Marly Chalk Formation, a unit that was historically referred to as the Cambridge Greensand. The

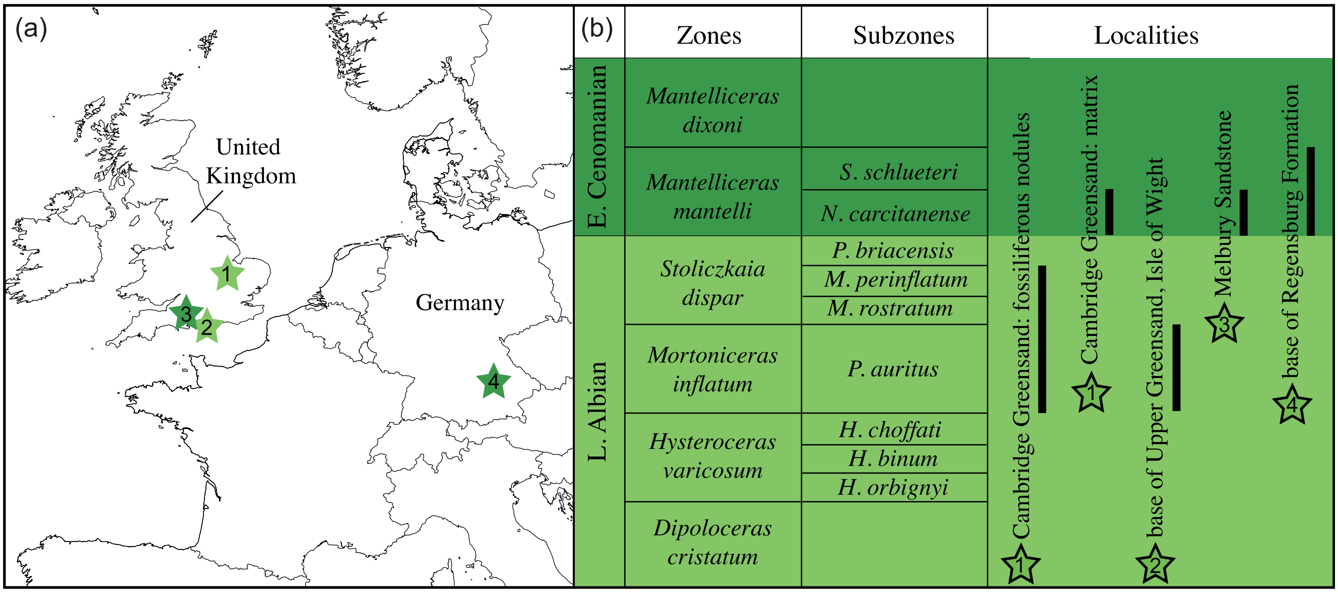

FIGURE 1 The stratigraphic framework of European localities discussed in the text that yielded mid-Cretaceous (late Albian to early Cenomanian) helochelydrid turtle remains. The late Albian ammonite zonation follows Owen (2012), that of the early Cenomanian follows Gale (1995). (1) Cambridge Greensand, Cambridgeshire, United Kingdom; (2) Upper Greensand, Isle of Wight, Dorset, United Kingdom; (3) Melbury Sandstone, Dorset, United Kingdom; (4) base of Regensburg formation, Bavaria, Germany

age of the unit had historically confounded researchers, as the fossiliferous nodules include phosphatized Ammonites originated from the *auritus* to *perinflatum* Subzones (Gallois et al., 2016), which corresponds to the late portions of the late Albian (Owen, 2012), but the matrix contains foraminifera from the *carcitanensis* Subzone, which is located at the very base of the Cenomanian (Hart, 1973). However, as the nodules occur at the base of a transgressive sequence, they are now interpreted as been late Albian fossils from the underlying Gault Clay Formation that had been reworked into Cenomanian sediments at the base of the West Melbury Marly Chalk Formation (Hart & Lyndsey, 2020; Unwin, 2001), an interpretation already hinted at in much earlier work (Jukes-Browne & Hill, 1900). The helochelydrid remains from the Cambridge Greensand, therefore, are late late Albian in age (Figure 1). A recent review of non-shell turtle remains from the Cambridge Greensand yielded three distinct skull morphotypes, three mandibular morphology, and three humeral morphotypes (Evers et al., 2019). The most common skull morphotype is referable to the protostegid *Rhinochelys pulchriceps* (Evers et al., 2019).

2.2 | Upper Greensand, Isle of Wight

The helochelydrid described by Owen (1881), *Plastremys lata*, appears to be the only vertebrate fossil to ever have been described from the Upper Greensand of the Isle of Wight, at least as suggested by a search of the Paleobiology Database (https://paleobiodb.org; accessed January 7th, 2022). Parkinson (1881), the lead author of the study that includes Owen's (1881) description, reported that the turtle had been collected from the base of the Upper Greensand along St. Lawrence beach, but a geological map of Britain suggests that the Gault Clay is exposed at this location (https://mapapps.bgs.ac.uk; accessed January 7th, 2022). However, Parkinson (1881) was well aware of the stratigraphy of the Isle of Wight and his description of a layer of nodules at the base of the Upper Greensand overlaps with that of more recent accounts (Gale et al., 1996; Hopson & Farrant, 2015), I conclude this conflict to be related to limitations associated with displaying three-dimensional stratigraphic information onto a two-dimensional map. The base of the Upper Greensand was recently dated to the *auritus* Subzone at a section near Sandown, about 10 km to the northeast of the type locality, which corresponds to the middle of the late Albian (Gale et al., 1996). The type locality of *Plastremys lata*, therefore, appears to correlate tightly with the age of the nodules retrieved from the Cambridge Greensand (Figure 1).

2.3 | Melbury Sandstone

The holotype of *Plastremys* (formerly *Trachydermochelys*) *rutteri* originates from Melbury Down (Andrews, 1920), a downland (chalk land) located southeast of the city of

Shaftesbury. A number of quarries north of the down historically yielded building stones referred to as the Melbury Sandstone from which this turtle very likely originated. As the Melbury Sandstone resembles the underlying Shaftesbury sandstone, it was historically grouped with the underlying sediments into the Upper Greensand, even though it yielded a rich marine invertebrate fauna referable to the *carcitanense* Subzone (Bristow et al., 1995), which corresponds to the very base of the Cenomanian (Gale, 1995). However, the Melbury Sandstone appears to represent transgressional sedimentation at the base of the West Melbury Marly Chalk Formation, much like the Cambridge Greensand, so the unit is now classified as a member at the base of that formation (Hopson, 2005; Mortimore et al., 2001). The holotype of *Plastremys rutteri* is therefore likely early early Cenomanian in age (contra Joyce et al., 2014; Joyce, 2017) and slightly younger than the fossiliferous nodules from the Cambridge Greensand, even if the Cambridge Greensand itself correlates tightly in age (Figure 1).

2.4 | Regensburg formation

The holotype of *Helochelys danubina* was salvaged from a construction site near Kelheim, Bavaria, Germany (von Meyer, 1855), so its exact provenance is not known. A number of greenstones were quarried under different names for construction over the course of the last centuries in the broader vicinity of the city of Regensburg, just northeast of Kelheim. Lithostratigraphic work suggests that all such stones were quarried from the base of the Saale Member of the Regensburg Formation (https://litholex.bgr.de). The base of this member is referable to the *mantelli* Zone (Niebuhr et al., 2009), which corresponds to the early early Cenomanian (Gale, 1995). The holotype of *Helochelys danubina* is therefore about equal in age to the holotype of *Plastremys rutteri* but marginally younger than the types of *Plastremys lata* and *Trachydermochelys phlyctaenus* (Figure 1).

3 | RESULTS

3.1 | Systematic paleontology

Testudinata Klein, 1760

Helochelydridae Chkhikvadze, 1970

Trachydermochelys phlyctaenus Seeley, 1869

Lectotype—CAMSM 56424, an entoplastron (Figure 2a,b), previously referred to *Helochelydra nopcsai* (Joyce et al., 2011).

Type locality—Cambridgeshire, UK; Cambridge Greensand (Seeley, 1869), West Melbury Marly Chalk Formation, late Albian fossils reworked into early Cenomanian sediments (Figure 1a, locality 1; also see Section 2.1).

Diagnosis—*Trachydermochelys phlyctaenus* can be diagnosed as a representative of *Helochelydridae* by the presence of a shell surface texture consisting of raised tubercles, a thickened epiplastral lip, and an enlarged entoplastron with raised interclavicular ossification on its dorsal surface. *Trachydermochelys phlyctaenus* resembles the roughly coeval *Helochelys danubina* and the somewhat older *Helochelydra nopcsai* by having a tubercle density of approximately 8–10 per linear centimeter, but the tubercles differ by being lower, less circular, and distinct. The surface texture of the roughly coeval *Plastremys lata* consists of low welts only while that *Plastremys rutteri* is similarly distinct, but significantly coarser (see Figure 2).

Referred material—CAMSM B56326, B56330, B56332, B56340–B56343, B56345, B56347–48, 10 shell fragment; CAMSM B56425–42, B56444–45, 20 shell fragments (paralectotypes of *Trachydermochelys phlyctaenus*); CAMSM B56446, a partial right epiplastron (a paralectotype of *Trachydermochelys phlyctaenus*, Figure 2c,d); NHMUK 43981, a shell fragment; NHMUK 46375, a peripheral fragment. All referred specimens originate from the Cambridge Greensand and were previously referred to *Trachydermochelys phlyctaenus* by Seeley (1869) and Lydekker (1889), but not figured. A number of additional specimens previously referred to this taxon by these authors are here recognized as belong to *Plastremys rutteri* (see below).

Description—The vast majority of historic finds housed at CAMSM, including what is identified as the original syntype series (see Section 4), was mounted onto heavy card stock over the course of the last century and can therefore not be viewed from all sides. Until all material has been removed from said card stock, I find it prudent to not further identify each element, but note that the material certainly includes costals, peripherals, and plastral bones.

All fragments from the Cambridge Greensand herein referred to *Trachydermochelys phlyctaenus* are characterized by a surface texture consisting of densely set, raised protuberances (Figure 2a–d). Approximately 8–10 protuberances cover each linear centimeter of the shell. The protuberances are typically isolated from one other, but sometimes coalesce into groups of twos. Although some variation is apparent in regards to the exact height and size of these protuberances, the texture is relatively consistent across the shell, as in *Helochelys danubina* (von Meyer, 1855), but not *Plastremys lata* and *Plastremys rutteri* (see below). In contrast to *Helochelys danubina* (von Meyer, 1855), however, the protuberances are low and do not dislocate easily.

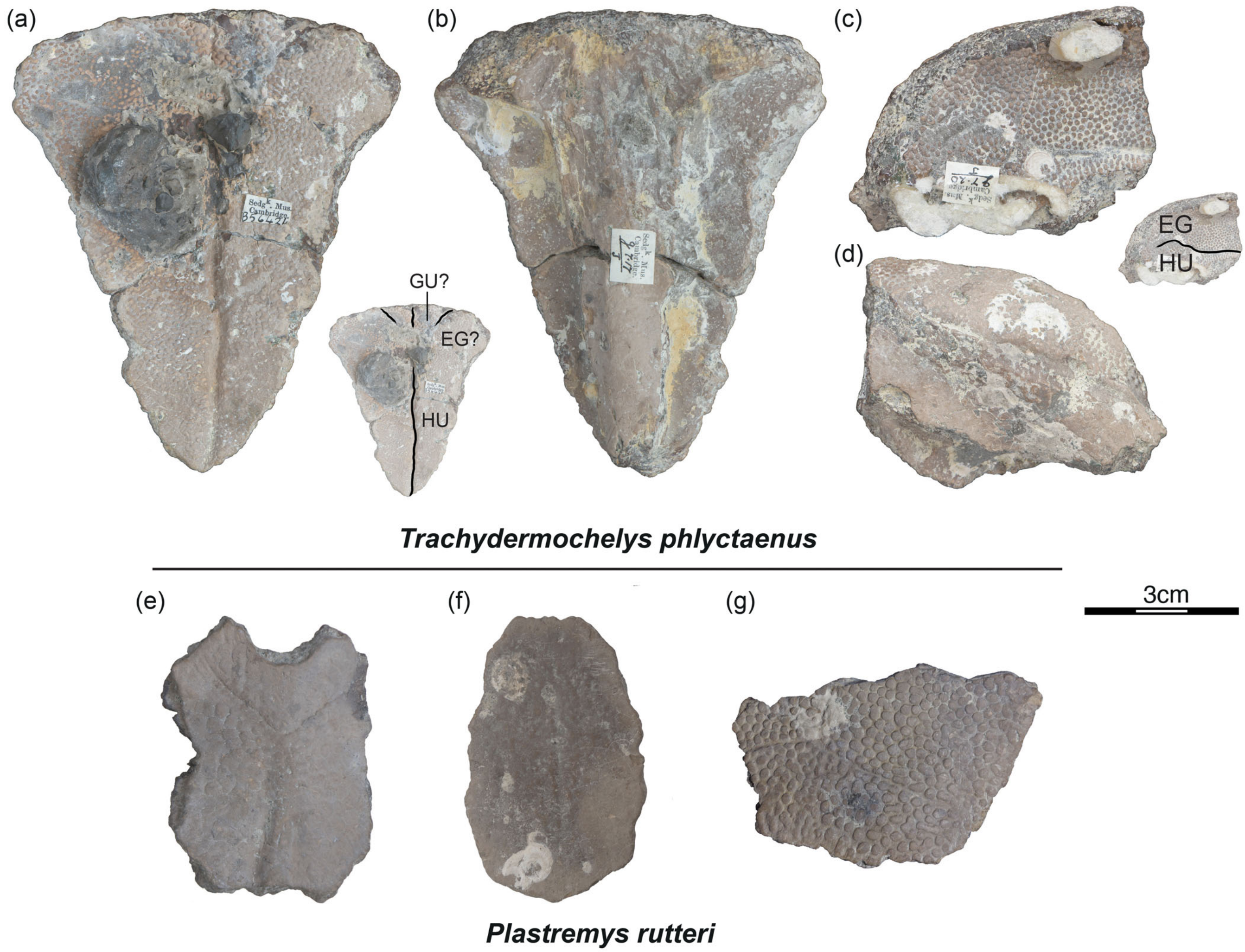

FIGURE 2 Early Cretaceous (late Albian) helochelydrid turtle material from the Late Cretaceous (early Cenomanian) Cambridge Greensand of Cambridgeshire, United Kingdom. *Trachydermochelys phlyctaenus* Seeley, 1869: CAMSM 56424, an entoplastron, lectotype in (a) ventral and (b) dorsal view, the inset highlights scute sulci; CAMSM B56446, a partial right epiplastron, one of many paralectotypes, in (c) ventral and (d) dorsal view, the inset highlights scute sulci. *Plastremys rutteri* (Andrews, 1920): (e) CAMSM B56349, a neural; (f) NHMUK R2251, a neural; (f) CAMSM B56029, a shell fragment. All material is figured to scale to allow direct comparison of their surface texture. EG, extragular scute; GU, gular scute; HU, humeral scute

Two elements are highlighted herein because they have already been removed from the card stock and cleaned and because their morphology is particularly telling, in particular an entoplastron (Figure 2a,b), which I here select as the lectotype, and a partial right epiplastron, one of the resulting paralectotypes (Figure 2c,d). As preserved, the large entoplastron is a triangular element (Figure 2a,b). Comparison with the lozenge to kite-shaped entoplastra of published helochelydrids (Hay, 1908; Joyce et al., 2014; Lapparent de Broin & Murelaga, 1999) suggests that the anterior half to third of the bone, which originally articulated with the epiplastra, eroded completely, but that the remainder, which originally articulated with the hyoplastron, is relatively intact. On the visceral side, a pronounced, T-shaped ridge is apparent that represents the raised remnants of the interclavicle, typical also for other helochelydrids (Hay, 1908; Joyce et al., 2014; Lapparent de Broin & Murelaga, 1999). A median sulcus crosses the entoplastron, but phosphatic nodules that cover the broadest parts of this bone make it difficult to clarify if this sulcus is continuous. Faint, diagonal sulci seem to converge upon the midline on both sides of the bone, but the place where they would meet with the median sulcus is covered by said nodules as well. These diagonal sulci are best interpreted as the contact of the gulars with the humerals (Hay, 1908; Joyce et al., 2014; Lapparent de Broin & Murelaga, 1999). If correct, this would imply that the phosphatic concretions hide an extremely small entoplastral scute, or that an entoplastral scute is absent altogether. It is unclear how complete the available epiplastron is (Figure 2c,d). The posteromedial contact with the entoplastron is preserved as a deep grove that suggests that the epiplastra clasped the entoplastron from dorsal and ventral. The anterior margin of the element looks to be rounded, but this may be an artifact of erosion. The skin-scute sulcus encroaches significantly onto the dorsal side of the element. A single sinuous sulcus crosses the epiplastron transversely, which is interpreted as the contact between the extragular and humeral scutes. If correct, the part of the bone that would document the sulcus between the gular and extragular appears to be missing.

Comments—The rationale why CAMSM B56424–B56453 represents the syntype series of *Trachydermochelys phlyctaenus*, not CAMSM 56340–6 (contra Joyce, 2017), for the designation of CAMSM 56424 as the lectotype, and for the validity of *Trachydermochelys phlyctaenus* (contra Joyce et al., 2014; Joyce, 2017) is outlined below (see Section 4).

Plastremys lata Owen in Parkinson, 1881.

Holotype—NHMUK R48, a partial, disarticulated shell (Figure 3).

Type locality—St. Lawrence, Isle of Wight, Hampshire, UK (Parkinson, 1881); Upper Greensand (Owen in Parkinson, 1881), middle late Albian, Early Cretaceous (Figure 1a, locality 2; also see Section 2.2).

Diagnosis— *Plastremys lata* can be diagnosed as a representative of *Helochelydridae* by the presence of a large plastron with rounded lobes, enlarged mesoplastra with a full midline contact, and an osseous bridge. A shell surface texture consisting of raised tubercles is only indistinctly developed as low welts in the bridge region. The central portion of the plastron lacks a distinct surface texture. All other known helochelydrids have a more distinct shell surface texture consisting of raised tubercles.

Referred material—None.

Description—The holotype and only known specimen of *Plastremys lata*, NHMUK R48, consists of the articulated right hyo-, meso-, hyo-, and xiphiplastron, right peripherals IV–VIII, and at least four disarticulated costals (Figure 3). The back side of the specimen displays no bones and is therefore not figured here. Less than half of the original surface of the available bones is preserved

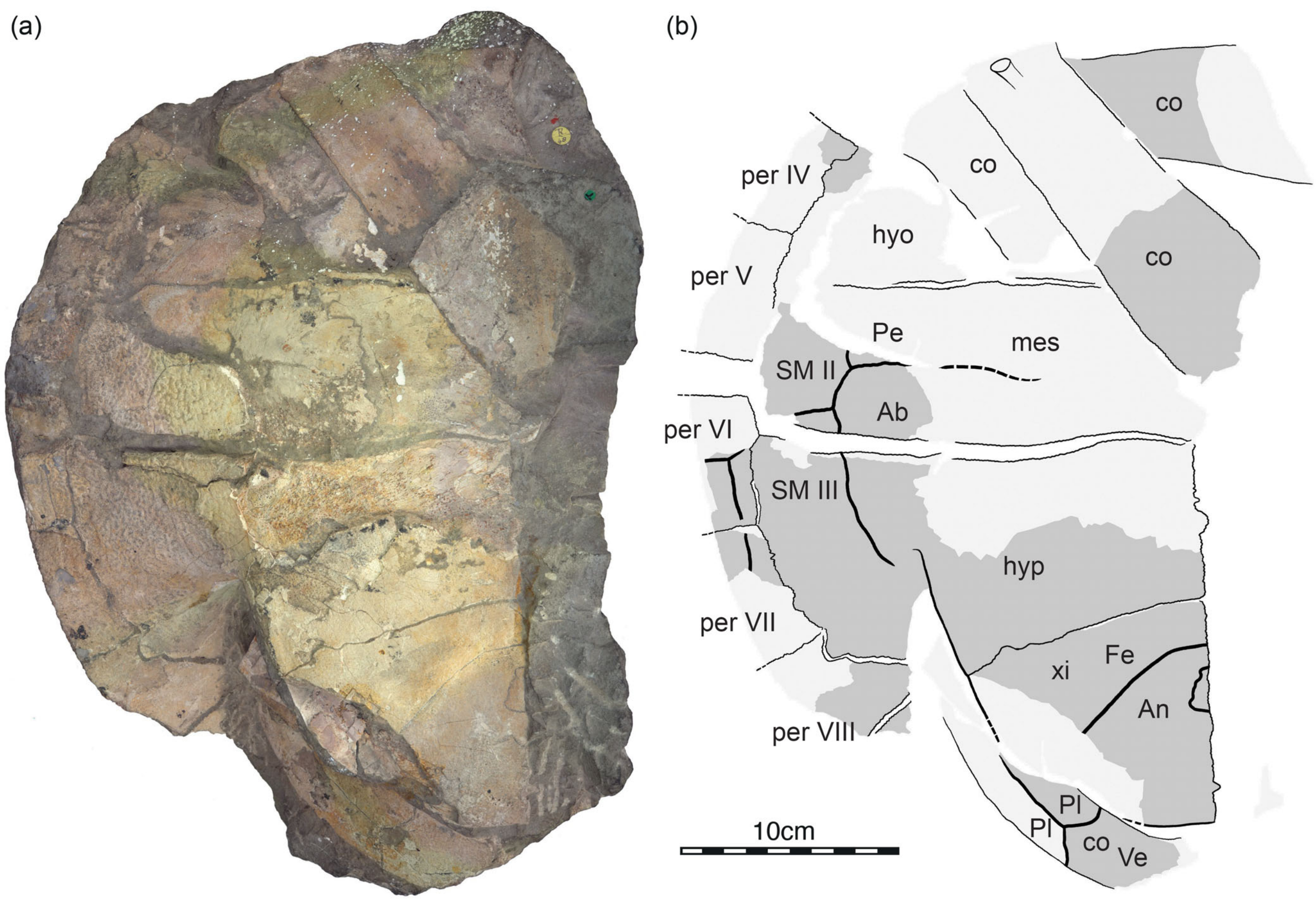

FIGURE 3 Helochelydrid turtle material from the Early Cretaceous (late Albian) Upper Greensand of the Isle of Wight, Hampshire, United Kingdom. *Plastremys lata* Owen, 1881, NHMUK R48, holotype, (a) photograph and (b) line drawing in ventral view. Ab, abdominal scute; An, anal scute; co, costal; Fe, femoral scute; hyo, hyoplastron; hyp, hypoplastron; mes, mesoplastron; Pe, pectoral scute; per, peripheral; Pl, pleural scute; SM, supramarginal scute; Ve, vertebral scute; xi, xiphiplastron

(dark shaded areas in Figure 3b), the remainders having been abraded (light shaded areas in Figure 3b). The original surface texture of the shell can therefore only be gleaned for parts of the posterior plastral lobe, the bridge region, the underside of the bridge peripherals, and the costals. The bridge region and the lower side of the peripherals are covered by low, poorly defined protuberances that crowd the surface. About four such protuberances can be found for each linear centimeter. The surface of the posterior plastral lobe and the costals, by contrast, appears to be completely smooth. This smoothness appears to be authentic, not taphonomic, as there are no signs of abrasion and as scute sulci are well preserved. The sculpturing therefore differs starkly from that of *Trachydermochelys phlyctaenus* (see above) and *Plastremys rutteri* (see below).

The plastron has broad lobes that liked covered much of the carapace from below. Owen (in Parkinson, 1881) reported the mesoplastron to be absent, but Andrews (1920) clarified it to be present after all. The mesoplastron is large and once contacted its counterpart along its full anteroposterior length. The hyoplastron laterally contacts peripherals IV and V. It is likely anterior contact with peripheral III is hidden from view. The mesoplastron laterally contacts peripherals V and VI, and the hyoplastron peripherals VI through VIII. The pectoral-abdominal sulcus crosses the mesoplastron at midlength. The abdominal-femoral sulcus is not preserved, but likely was positioned on the damaged, anterior half of the hypoplastron. The anal scute is restricted to the xiphiplastron. The available sulci on the bridge are identified as the remnants of inframarginal II and III by reference to *Aragochersis lignitesta* (Pérez-García, Espílez, et al., 2020) and *Naomichelys speciosa* (Joyce et al., 2014). This implies that inframarginal II had a relatively broad anteromedial contact with the pectoral and a broad posteromedial contact with the abdominal. A costal located behind the plastron shows remnants of a vertebral and two pleurals.

Comments—Please see Section 4 regarding the taxonomic distinctness of *Plastremys lata* relative to *Plastremys rutteri* (contra Joyce et al., 2014; Joyce, 2017).

Plastremys rutteri (Andrews, 1920).

Holotype—NHMUK R4214, a steinkern with most of the plastron, but only portions of the carapace (Andrews, 1920, fig. 1; Figure 4).

Type locality—Melbury Abbas, Dorset, United Kingdom (Andrews, 1920); Melbury Sandstone, early early Cenomanian (Figure 1a, locality 3; also see Section 2.3).

Diagnosis— *Plastremys rutteri* can be diagnosed as a representative of *Helochelydridae* by the presence of a shell surface texture consisting of raised tubercles, a neural series that includes octagonal elements, three suprapygals of which the second is V-shaped and the third lenticular, and a well-developed plastron consisting of a large entoplastron, large mesoplastra with a midline contact, an osseous bridge, and a thickened epiplastral lip. The surface texture is much coarser than that of any other named helochelydrid by consisting of about four distinct tubercles per linear centimeter, which, however, fade towards oblivion over the neurals.

Referred material: CAMSM B56029, a shell fragment (Figure 2g); CAMSM B56045, B56046, B56070, B56328, B56329, B56331, B56336, B56070, B56339, B56344, B56346, 11 shell fragments; CAMSM B56349, a neural (Figure 2e); CAMSM B56350–B56352, three partial neurals; CAMSM B56353–B56355, B56357–B56365, 12 shell fragments; CAMSM B56443, B56604, B56605, three plastral notch fragments; NHMUK R2251, 24 shell fragments, including one large neural (Figure 2f); NHMUK 35188, 35188a, 35188b, three shell fragments. All listed specimens originate from the Cambridge Greensand and were previously referred by Seeley (1869) and Lydekker (1889) to *Trachydermochelys phlyctaenus*, but not figured.

Description of holotype—The shell of NHMUK R4214 was likely deposited intact, but significant erosion of the carapace exposes much of its steinkern. At present, only remnants of the left peripherals, left costals VII–IX, suprapygals, and pygal remain (Figure 4). The entire shell is decorated by distinct protuberances. In general, about four such protuberances can be found for each linear centimeter, but in some regions as few as three are found (lateral portions of the femoral scute), while in others five or six are developed (e.g., inguinal notch). In the central parts of the plastron, the pustules are lower and more densely packed but remain distinct nevertheless. Though little is preserved, the available parts of the carapace suggest that the pustules are distinct along the margins of the carapace, but quickly flatten out towards near oblivion along the neural series.

Three left costals are preserved in the posterior parts of the shell, but the six pairs of rib-head preserved as imprints in the steinkern suggest that these are not costals VI–VIII, but rather costals VII–IX, which posterolaterally inserts between peripheral IX and X, X and XI, and XI, respectively (Figure 4c–e). Although incipiently developed costals IX have been reported for the helochelydrid *Naomichelys speciosa* (Joyce et al., 2014), fully developed costals IX are an anomaly among helochelydrids.

In contrast to Andrews (1920), I do not find evidence of a neural followed by two suprapygals, but rather of three suprapygals (Figure 4d–e). Suprapygal I is incompletely preserved, but appears to have been an irregular element with convexly rounded anterior contacts with the costals and neurals and a concavely rounded posterior contact with suprapygal II. Suprapygal II is an

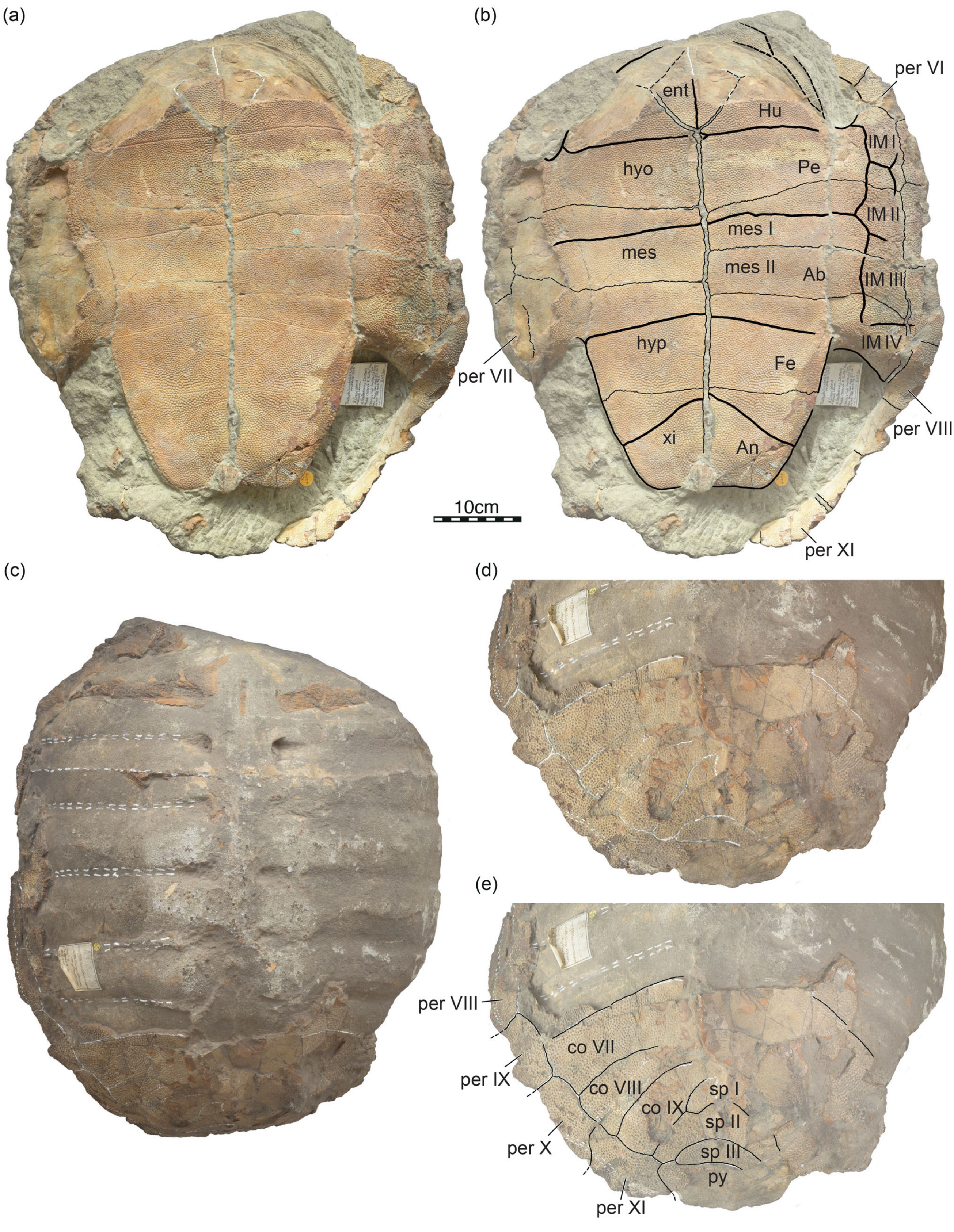

FIGURE 4 Helochelydrid turtle material from the Late Cretaceous (early Cenomanian) Melbury Sandstone of Melbury Abbas, Dorset, United Kingdom. *Plastremys rutteri* (Andrews, 1920), NHMUK R4214, holotype, (a) photograph and (b) line drawing in ventral view; (c) photograph in dorsal view; (d) photograph and (e) line drawing of posterodorsal view. An, anal scute; Ab, abdominal scute; co, costal; ent, entoplastron; Fe, femoral scute; Hu, humeral scute; hyo, hyoplastron; hyp, hypoplastron; IM, inframarginal scute; mes, mesoplastron; Pe, pectoral scute; per, peripheral; py, pygal; sp, suprapygal; xi, xiphiplastron

enlarged element that anteriorly contacts suprapygal I along a convexly rounded anterior contact, costal IX anterolaterally, and peripheral XI and the pygal posteriorly. Suprapygal III is a small, semi-lunar element that is located between suprapygal II and the pygal, but is only inserted into suprapygal II. As a result, suprapygal II has the shape of a reverted V. The arrangement of the suprapygals closely mirrors that of other helochelydrids (Joyce et al., 2014; Pérez-García, Espílez, et al., 2020).

Only remnants of the peripherals are preserved along the left margin of the shell (Figure 4). The apparent contacts with the costals are described above, those with the plastron below. It is unclear if peripherals with a V-shape in cross section are developed anteriorly or posteriorly to the bridge region.

Although much of the posterior part of the carapace is preserved in good condition, I am not able to trace carapacial sulci with confidence.

In contrast to the carapace, the plastron only shows minor damage, particularly along portions of the right bridge and the anterior margin of the anterior plastral lobe (Figure 4a,b). As in other helochelydrids, the plastron consists of an entoplastron and paired epi-, hyo-, meso-, hypo-, and xiphiplastra. As an anomaly, already noted by Andrews (1920), the left mesoplastron is doubled. There is no evidence of fontanelles.

The epiplastra are not preserved anymore, but their extent can be estimated by reference to the imprint they left behind in the steinkern and faint traces here interpreted as their sutures with the entoplastron and hyoplastron (Figure 4a,b). The imprints suggest that the anterior plastral lobe was short, but rounded and that the epiplastron and hyoplastron jointly formed a distinct lip on the dorsal side of the plastron that was decorated with pustules. The entoplastron is only partially preserved, but the faint outlines preserved on the steinkern suggest that it was a diamond shaped element with equilateral sides. The hyo-, meso-, and hypoplastral jointly form the main body of the plastron. No plastral concavity is apparent that might indicate the sex of the animal. The full length of the bridge is suturally connected with the carapace. As an anomaly, as noted above, the left mesoplastron is doubled. This is somewhat unfortunate, as the left bridge is better preserved as the right bridge, therefore obscuring more natural bridge contacts. The sutures of the right bridge mirrored onto the left, nevertheless, suggest that the hyoplastron contacted the posterior two thirds of peripheral VI, all of peripheral V, and the anterior region of peripheral VI, the single mesoplastron the central portions of peripheral VI, and the hypoplastron the posterior region of peripheral VI, all of peripheral VII, and the anterior two thirds of peripheral VIII. The xiphiplastra are large, blocky elements that contact the hypoplastra along a transverse suture. The posterior plastral lobe is more elongate, but longer than the anterior plastral lobe, has a trapezoidal outline, and lacks a notable anal notch.

The plastron preserves parts of a pair of humeral, pectoral, abdominal, femoral, and anal scutes in addition to four pairs of inframarginals (Figure 4a,b). The parts of the plastron that would preserve the gulars, extragulars, and a potential entoplastral scute are missing. If present, however, the entoplastral scute must have been relatively small and placed along the anterior half of the entoplastron. The humeral-pectoral sulcus is oriented transverse and aligns laterally with the axillary notch. The pectoral-abdominal sulcus is developed asymmetrically, likely as a result of the anomalous presence of two mesoplastra on the left side. The abdominal-femoral sulcus is mostly oriented transverse and aligns with the inguinal notch laterally. The femoral-anal sulcus is restricted to the xiphiplastron, but is oriented diagonally. Four, not two (Andrews, 1920) pairs of inframarginals can be traced on the left bridge. However, given the anomalous presence of two mesoplastra on the left side of the shell, I have low confidence in the preserved contacts between the inframarginals and the remaining plastral scutes being representative of this taxon.

The above description broadly matches that of Andrews (1920). The main differences pertain to the arrangement of the suprapygals, better resolution of the costals, and a different inframarginal count.

Description of material from Cambridge Greensand—A few dozen shell fragments from the Cambridge Greensand are united by a shell sculpturing consisting of low protuberances that cover the surface of the shell at a density of about 4 per linear centimeter (Figure 2e–g). In the majority of fragments, the protuberances are distinct (Figure 2g), but in some, including all element identified as neurals, the protuberances flatten (Figure 2e) or almost indistinct (Figure 2f). In all regards, the sculpturing closely resembles that of the holotype of *Plastremys rutteri* (see above). The only elements that can be identified with confidence are the neurals. The best-preserved elements have an "octagonal" (Figure 2e) or "square" (Figure 2f) outline (i.e., have a shape allowing for eight or four contacts with the surrounding elements, respectively). In additional to hexagonal element, octagonal and square neurals have previously been reported for the helochelydrid *Naomichelys speciosa* (Joyce et al., 2014).

Comments—Please see Section 4 for the rationale recognizing *Plastremys rutteri* as a valid species of helochelydrid turtle and the referral of isolated shell material from the Cambridge Greensand to this taxon.

4 | DISCUSSION

4.1 | Trachydermochelys phlyctaenus

Availability of name—The name *Trachydermochelys phlyctaenus* was proposed long before international codes established firm rules for the creation of taxonomic names. In the introductory remarks to his catalog of the fossils held at CAMSM, Seeley (1869, p. XV) stated in a footnote that the "provisional names" he provided "[...] are only intended for the convenience of students using the Museum, and not necessarily to take rank as names of described species." As the International Commission on Zoological Nomenclature (ICZN, 1999, Art. 11.5) demands that newly proposed names be deemed valid when proposed to be considered available, Joyce et al. (2014) concluded *Trachydermochelys phlyctaenus* to be a nomen dubium, also as no subsequent author had made the name available. However, subsequent consultation with a member of the International Commission of Zoological Nomenclature lead Joyce and Anquetin (2019) to conclude that Seeley's names should not be disregarded on this ground alone. The taxonomic status of *Trachydermochelys phlyctaenus* must therefore be reassessed.

To be considered available for nomenclatural purposes, historic names, among others, need to be associated with a description, definition, or indication (ICZN, 1999, Art 12.1). In contrast to many other names simply listed by Seeley (1869), the name *Trachydermochelys* is associated with the brief statement that serves as a description or definition: "*a new [...] genus, which had an exterior pustulous ornamentation not unlike* Trionyx, *and was covered with scutes*." The species epithet *phlyctaenus* is only mentioned once in the preface, but is it clearly associated with the newly established genus *Trachydermochelys*. I, therefore, conclude that *Trachydermochelys phlyctaenus* is available for nomenclatural purposes, contrary to my original opinion (Joyce et al., 2014).

Type material—It is difficult to establish the type material of *Trachydermochelys phlyctaenus*, as three separate series of specimens serve as candidates.

Seeley (1869) typically listed material for each new taxon in the index to his catalog of material housed at CAMSM. Here, the named *Trachydermochelys phlyctaenus* is associated with the listing "[J] g7. 11, p.35" (Seeley, 1869, p. XIX), which is short hand for the location of the specimens in the collections, in particular case J, drawer g7, tablet 11, as listed on page 35. These specimens, all of which are peripherals, are now cataloged as CAMSM B56412–14 (not figured). Somewhat confusingly, these specimens are listed on page 34, not 35, lack helochelydrid sculpturing, and, in my opinion, likely belong to the protostegid *Rhinochelys pulchriceps*, which dominates the chelonian fauna of the Cambridge Greensand (Evers et al., 2019). This material is therefore inconsistent with Seeley's (1869) description of *Trachydermochelys*.

The second set of specimens is associated with the short description Seeley provided for the name *Trachydermochelys*. It consists of 20 specimens that collectively form Seeley's (1869) Series 6, which was stored in case J, drawer 5, tablets 1–9, specimens now cataloged under the numbers CAMSM B56318–56337 (unfigured). Although most of these specimens remain glued to heavy card stock, it is apparent that they form a chimera consisting of vertebrae and long bones of *Rhinochelys pulchriceps* (see Evers et al., 2019) intermixed with particularly untelling remains of a finely textured and coarsely texture helochelydrid. This is partially inconsistent with Seeley's description of this taxon.

As noted above, Seeley's (1869) listed "[J] g7. 11, p.35" as the location of specimens referred to *Trachydermochelys phlyctaenus*. This may be a typographic error referring to his "Series 11," not "tablet 11," 30 specimens which indeed are listed on page 35 under the heading *Trachydermochelys*. These specimens are now cataloged as CAMSM B56424–53. This series, too, is a chimera, which consists of helochelydrid and protostegid material, but the first 23 specimens (i.e., CAMSM B56424–46) include unusually complete fragments with a consistent shell sculpture, including a relatively complete entoplastron (CAMSM B56424, Figure 2a,b) and an epiplastron (CAMSM B56446, Figure 2c,d). Indeed, the shell material may well originate from the same, poorly preserved individual. I find it likely that this series of individuals is what Seeley (1869) intended to list, because much of the material nicely exhibits the surface sculpturing he lists for this taxon, because it includes the most complete listed material with said surface sculpturing, and because a typographic error is plausible.

Seeley (1869) did not explicitly list any specimens as being types, but the specimens he listed in the index to his work typically point towards the material now thought to be types. Following the ICZN (1999, Art 72.1.1.), the type series of *Trachydermochelys phlyctaenus* either includes all specimens listed under that name (i.e., all three series listed above), or just the specimens listed in the index (i.e., plausibly his "Series 11"). In either case, the listed specimens represent a chimera, which calls for the designation of a lectotype. The nomenclatural implications are significant, as the listed specimens include at least one protostegid and two helochelydrid taxa. As Seeley (1869) explicitly listed helochelydrid surface texturing as diagnostic, it is prudent to select one of the two helochelydrid taxa. And as the material representing the coarse textured helochelydrid (herein referred to *Plastremys rutteri*) is too fragmentary to allow rigorously diagnosing a taxon, it is prudent to choose a plausibly diagnostic specimens among the fine-textured material. For these reasons, I here select CAMSM B56424, a near complete entoplastron (Figure 2a,b), as the lectotype, as this element exhibits the greatest amount of diagnostic characters among the available material.

Validity—Finely textured helochelydrid shell remains with a sculpture resembling the lectotype of *Trachydermochelys phlyctaenus* (i.e., a texture consisting of relatively fine, needle-like protrusions) have been reported from across the Late Jurassic (Tithonian) to Late Cretaceous (Cenomanian) of Europe, but most fossils are fragmentary and do not provide useful anatomical details beyond their surface texture (Joyce, 2017; Joyce et al., 2014; Pérez-García, 2017; Pérez-García, Bardet, et al., 2020). To avoid a taxonomic impasse, I here follow the approach of Joyce et al. (2014) by only grouping fragmentary turtle remains with the same surface texture if they approximately originate from the same time and place, in this case the late Albian to early Cenomanian of Europe. Only two finely textured helochelydrids have been named from this time period to date: *Helochelys danubina* and *Trachydermochelys phlyctaenus*.

Helochelys danubina is based on a partial shell from an early Cenomanian Saale Member of the Regensburg Formation exposed near the city of Regensburg, Bavaria, southern Germany (von Meyer, 1855; see Section 2.4). The holotype was figured and described in good detail by von Meyer (1855), but its anatomy cannot be reproduced anymore, as it was destroyed during the second World War (Joyce, 2017). The most notable characteristic of *Helochelys danubina* is the surface texture consisting of raised protuberances. The lithograph that accompanies von Meyer's (1855) description suggests that the protuberances are evenly spaced across the shell and do not coalesce. Some protuberances are illustrated as three-dimensional objects, others as round circles, but it is unclear if the circles represented dislocated protrusions, or if the artist was exasperated by the task of illustration hundreds of protrusions. The former seems more plausible. Despite all uncertainties, the illustrations are striking in that the figured surface texture closely resembles that of the early Cretaceous (Barremian) *Helochelydra nopcsai* from the Isle Wight, United Kingdom, a surface texture that had not been figured previously.

As the surface texture of the lectotype of *Trachydermochelys phlyctaenus* had not been figured before, I previously concluded that it is referable to *Helochelydra nopcsai* (Joyce, 2017; Joyce et al., 2014). I note here, however, that the surface texture of *Trachydermochelys phlyctaenus* is lower, more tightly packed, and more break-resistant than that of *Helochelys danubina* or *Helochelydra nopcsai*. I, therefore, revise my opinion and recognize *Trachydermochelys phlyctaenus* as a valid helochelydrid taxon after all.

4.2 | *Plastremys lata* and *Plastremys rutteri*

At present, two names are available from the mid-Cretaceous of England that refer to helochelydrids with a coarse surface texture: *Plastremys lata* from the late late Albian of the Isle of Wight, Hampshire (Owen in Parkinson, 1881) and *Plastremys* (orig. *Trachydermochelys*) *rutteri* from the early early Cenomanian of Melbury Abbas, Dorset (Andrews, 1920). The two types had never been properly figured before and were previously difficult to observe casually in the collections of the NHMUK because they are difficult to lift and turn. I previously noted during a cursory visit to NHMUK that both shells are covered by a coarse surface texture and synonymized the two, with *Plastremys lata* being the senior synonym. This study, however, clearly suggests that the two specimens are covered by a texture quite different from one another. While the shell of *Plastremys lata* is only decorated by extremely low welts in the bridge region, that of *Plastremys rutteri* is systematically covered by large, discrete protrusions that only fade towards the midline of the shell. It therefore reverse my position and regard the two taxa as valid.

A number of fragmentary helochelydrid remains from the mid-Cretaceous of Europe display a course texture as well, including late Albian fragments from the early Cenomanian Cambridge Greensand (Figure 2e–g), fragments from the early Cenomanian of France (Vullo et al., 2010), and the holotype of the late Aptian to early Albian *Trachyaspis turbulensis* Bergounioux, 1957 from Spain (recently refigured in Pérez-García, 2017). Additional Spanish fragments were recently reported from the mid to late Cenomanian of Algora, Spain (Pérez-García, Bardet, et al., 2020). In all cases, the dense surface texture that covers these fossils closely approximates *Plastremys rutteri*, not *Plastremys lata*. Using temporal and spatial considerations, the English and French specimens are certainly referable to *Plastremys rutteri*. The greater temporal or spatial distance to the Spanish material, however, renders synonymy of *Plastremys rutteri* with *Trachyaspis turbulensis* highly plausible, but less certain.

5 | CONCLUSIONS

The results of this study can be summarized by the following conclusions:

1. All historically described English helochelydrid remains to originate from a relatively narrow time window at the Early to Late Cretaceous transition. In particular, material from the Cambridge Greensand of Cambridgeshire, including the type material of *Trachydermochelys phlyctaenus*, and the Upper Greensand of the Isle of Wight, including the type of *Plastremys lata*, have a late late Albian age, while specimens from the Melbury Sandstone of Melbury Abbas, Dorset have an early early Cenomanian age. The English material therefore has a similar age to helochelydrids from France and Germany, including the early early Cenomanian type material of *Helochelys danubina*.
2. Historic material collected from the Cambridge Greensand highlights the presence of two distinct helochelydrids from that deposit, one with a fine shell texture the other with a coarse shell texture. Although it is unclear what exact list of specimens comprise the type series of *Trachydermochelys phlyctaenus*, it certainly is a chimera that includes a near-complete entoplastron with fine surface texture (CAMSM 56424), which is herein designated as the lectotype. The newly selected lectotype, together with referred specimens, suggests that *Trachydermochelys phlyctaenus* was evenly covered by a fine texture that can readily be distinguished from *Helochelys danubina*.
3. Two valid helochelydrids are known from the mid-Cretaceous of England with a coarse texture. The coarse texture of *Plastremys lata* is only developed in the bridge region in the form of low welts. The shell of *Plastremys* (orig. *Trachydermochelys*) *rutteri*, on the other hand, is systematically covered by a coarse texture consisting of distinct tubercles. Temporal and geographic considerations suggest that fragmentary remains with a similar texture from the Cambridge Greensand and France are referable to *Plastremys rutteri*. The coeval Spanish taxon *Trachyaspis turbulensis* exhibits the same sculpturing as well, but geographic considerations questions render a synonymy less certain.

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