

The helochelydrid turtle *Helochelydra nopcsai* from the Early Cretaceous (late Barremian – early Aptian) fissure fills of Balve, North Rhine-Westphalia, Germany, including a large sample of granicones

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Abstract

Early Cretaceous (late Barremian – early Aptian) fissure fill deposits near Balve, North Rhine Westphalia, Germany, have yielded a rich continental vertebrate fauna over the course of the last two decades. More than 250 fragmentary specimens, including more than 150 osteoderms (i.e., granicones), represent the late Early Cretaceous helochelydrid *Helochelydra nopcsai*, which had previously been reported from the UK, France, and Spain. The new material mostly differs from that from the type section by exhibiting a reduced to absent entoplastral scute and by displaying distinct cranial scute sulci, both of which are interpreted as intraspecific variation. Although morphological insights are limited, the new material reveals that the visceral cavity extends anteriorly and posteriorly to the bridge, a relatively novel feature previously reported for an eclectic mix of compsemeydids, pleurosternids, and other helochelydrids. The available sample of granicones reveals great shape diversity, but a morphometric analysis concludes that no distinct morphotypes exist.

Key Words

granicones, *Helochelydridae*, *Testudinata*

Introduction

Helochelydra nopcsai is a helochelydrid turtle from the Lower Cretaceous of Europe (Joyce, 2017). The type specimen, NHMUK R171, a fragmented shell and associated girdles from the Early Cretaceous (Barremian) Wessex Formation of the Isle of Wight, England, was originally described by Nopcsa (1928) as a new taxon, but only given the genus name *Helochelydra*. Nopcsa (1928) realized that rare turtles from the Cretaceous of Europe and North America, including the German *Helochelys danubina* Meyer, 1855 and the North American *Naomichelys speciosa*, are unified by a highly unusual shell surface texture consisting of pin-like tubercles, a grouping for which he proposed the name Helochelydrinae. Nopcsa (1928) provided a relatively detailed description of

NHMUK R171, but the associated figures insufficiently document the apparent morphology. As the ICZN (1999) demands that all valid genera include at least one named species, Lapparent de Broin and Murelaga (1999) many decades later named the new species *Helochelydra nopcsai*, which is based on NHMUK R171 as well and now serves as the type species of *Helochelydra*.

Joyce et al. (2011) more recently provided description of IWCMS 1998.21, a nearly complete cranium and associated postcranial fragments from the Wessex Formation of the Isle of Wight, England, which they referred to as *Helochelydra nopcsai* based on apparent similarities in shell surface texture and its provenience from the type formation. As fragmentary helochelydrids had been reported from numerous localities across Europe in the previous decades, Joyce et al. (2011) also provided a taxonomic review of

the group that focused on shell surface texture, as this is the only characteristic that can be studied in fragmentary shell material. This review concluded that many specimens are known from across the Cretaceous of Europe that show a surface texture similar to that of *Helochelydra nopcsai*, but also that it is prudent to restrict this taxon to the Early Cretaceous (Barremian) Wessex Formation and its correlates. Following this recommendation, Joyce (2017) attributed fragmentary material from the Early Cretaceous (Hauterivian/Barremian) of France (Néraudeau et al. 2012) and the Early Cretaceous (Barremian) of Spain (Pérez García 2009; Pérez-García et al. 2012, 2013; Scheyer et al. 2015) to *Helochelydra nopcsai*, thereby extending the range of this taxon across western Europe.

The evolutionary relationships of helochelydrids with other turtles are not fully understood. Although early phylogenetic assessments of the group differed with regard to placing helochelydrids as stem-cryptodires (Hirayama et al. 2000) or stem-turtles (Joyce et al. 2011), this was largely due to the variable interpretation of multiple relatively closely related turtle clades with a Mesozoic origination as either crown or stem turtles. Since then, most studies interpret these clades (e.g., meiolaniforms, paracryptodires) as perichelydian stem turtles (e.g., Joyce 2017). Latest studies agree that helochelydrids are placed more crownwardly than meiolaniforms or sichuanheliids (e.g., Joyce et al. 2016; Rollot et al. 2021, 2022a, b; Tong et al. 2022, 2023), although it is not clear if they represent an evolutionary lineage distinct from other clades (Joyce et al. 2016; Tong et al. 2022, 2023), or if they constitute a subclade of paracryptodires (Rollot et al. 2021, 2022a, b).

In addition to the unusual shell surface texture and several cranial and postcranial characteristics (e.g., Rollot et al. 2022b), at least some helochelydrids are characterized by the presence of textured osteoderms called granicones (Owen, 1878). These elements had initially been collected in isolation from Early Cretaceous (Berriasian) sediments of the English Purbeck Limestone Formation, but their identity as helochelydrid osteoderms had not been established until they were found associated with the near complete skeleton of the North American helochelydrid *Naomichelys speciosa* (Barret et al. 2002; Joyce et al. 2014). A single granicone had previously been reported from the Wessex Formation of the Isle of Wight (Sweetman, 2007), which likely represent *Helochelydra nopcsai* (Joyce et al. 2011; Joyce 2017), but as the turtle fauna from this formation remains poorly known, this association remains tentative for the moment.

In the Busche quarry near Balve-Beckum, North Rhine Westphalia, Germany, mining operations have cut into a cave system whose origin can be traced back to deep hydrothermal karst. The cavities are completely filled with late Early Cretaceous (late Barremian–early Aptian) sediments, which have yielded a rich vertebrate fauna, including turtles, still being excavated and evaluated at present (Schwermann et al. 2018). Only a few larger objects (up to a maximum of 30 cm) have been found to date. Work so far has mainly focused on isolated theropod teeth (Lanser and Heimhofer 2015), salamanders

(Skutschas et al. 2020), sauropods (Hornung et al. 2023), and mammals (Martin et al. 2021, 2022). A preliminary analysis of several hundred turtle fragments from this quarry highlights the presence of more than 200 isolated specimens, including more than 150 granicones, that can be attributed to *Helochelydra nopcsai*. The primary goal of this contribution is to describe this material and to discuss its attribution to *Helochelydra nopcsai*. The remainder of the turtle fauna, which preliminarily is thought to include *Chitracephalus dumonii*, *Peltochelys duchastelii*, and a new species of pleurosternid, will be provided elsewhere.

Institutional abbreviations: **IWCMS**, Dinosaur Isle Museum, Sandown, United Kingdom; **NHMUK**, Natural History Museum, London, United Kingdom; **WMNM**, LWL-Museum of Natural History, Münster, Germany.

Materials and methods

Geological settings

The Busche Quarry is located just to the northeast of the village of Beckum within the commune of Balve, North Rhine-Westphalia, Germany (Fig. 1). The rock being quarried there is a Devonian limestone, which is punctured by fissures filled with sand rich clays (Lanser and Heimhofer 2015). Palynological evidence suggests that the fissures were filled during the late Barremian to early Aptian (Lanser and Heimhofer 2015). Most of the *Helochelydra nopcsai* remains presented herein were collected over the course of the last 20 years from two distinct fissures, of which the smaller one is a relatively narrow passage no more than 4 m wide, while the large one represents a large cavern that may reach 35 m in diameter. All specimens can therefore be traced back to a spatially confined area. As the turtle fauna appears homogenous across the fossiliferous deposits and as systematic collecting failed to find plausible associations among elements, we here treat the fauna as being homogeneous, while acknowledging that it may be affected by time averaging. Specimens range from black to tan in color, reflecting variation in mineral overgrowth and weathering (Fig. 2).

Visualization

A fragment of a left parietal and a selection of the best-preserved carapace and shell fragments and granicones were subjected to scanning at the CT Image Core Facility of the Department of Geosciences, University of Fribourg, using a microcomputed tomography (μ CT) scanner Bruker Skyscan 2211. Three scanning sessions were performed for the granicones. The first scan was performed with a voltage of 110 kV, a current of 475 μ A, an exposure of 120 ms, and a titanium filter, resulting in 4279 coronal slices with a voxel size of 12 μ m. The second scan was performed with a voltage of 110 kV, a current of 450 μ A, an exposure of 120 ms, and a titanium filter, resulting in 4743 coronal slices with a voxel size of 12 μ m. The third granicone scan was performed with

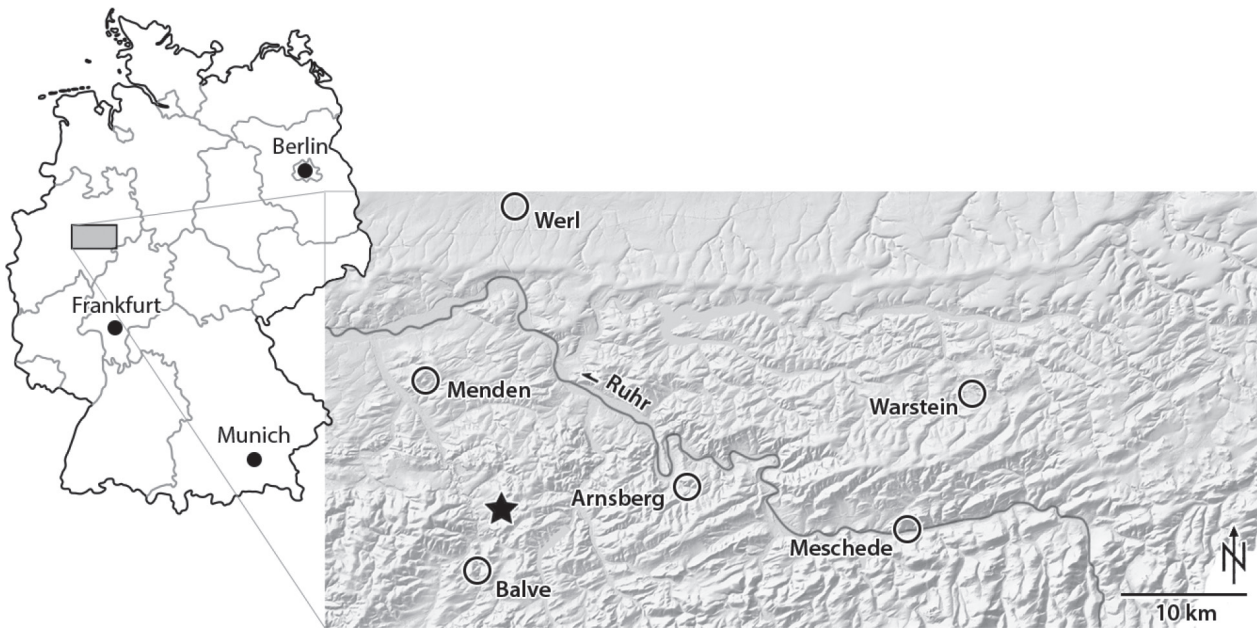


Figure 1. A simplified map of Germany highlighting location of the Busche quarry (black star) near Balve, North Rhine Westphalia, Germany.

a voltage of 110 kV, a current of 450 μA , an exposure of 50 ms, and a titanium filter, resulting in 3750 coronal slices with a voxel size of 12 μm . The scanning of the carapace and shell fragments required 4 scanning sessions. The first scan was performed with a voltage of 190 kV, a current of 210 μA , an exposure of 200 ms, and a molybdenum filter. The second scan was performed with a voltage of 190 kV, a current of 95 μA , an exposure of 180 ms, and a molybdenum filter. The third scan was performed with a voltage of 189 kV, a current of 600 μA , an exposure of 220 ms, and a molybdenum filter. The fourth scan was performed with a voltage of 190 kV, a current of 95 μA , an exposure of 220 ms, and a molybdenum filter. A total of 1997, 2230, 2079, and 3150 coronal slices were obtained, respectively, all with a voxel size of 45 μm . The left parietal fragment was scanned separately, with a voltage of 110 kV, a current of 450 μA , an exposure of 37 ms, and a titanium filter, resulting in 2110 coronal slices with a voxel size of 31 μm .

All specimens were segmented in Amira 3D (2021.2; <https://www.fei.com/software>) using the magic wand tool. The 3D models were exported as .ply files and visualized in Meshlab (2022.02; <https://www.meshlab.net>). All models are available at MorphoSource (<https://www.morphosource.org/projects/000497160>).

Morphometric analysis

A qualitative assessment of all available granicones suggested that three informal morphotypes can be recognized: cone-shaped granicones, hook-shaped granicones with offset apices, and flat, plate-like granicones (see Description below). We used Principal Components Analysis (PCA) to investigate if the pre-assigned morphotypes form separate clusters in morphospace. For this purpose, we took four basic measurements from the 136 best preserved

granicones: the maximum length of the base, the minimum width of the base, height of the apex, and offset of the apex relative to the center of the base. All measurements were taken in right angles relative to another using digital calipers with an accuracy to 1/100 of a millimeter (see Suppl. material 1 for data). We conducted a PCA using the `prcomp` function in R 4.2.2 (R Core Team 2022). Specimens were scaled to have unit variance before analysis. We calculated re-scaled proportions of variance explained for PC2–4 to the exclusion of PC1, as the latter was associated with size.

Systematic paleontology

Testudinata Klein, 1760

Helochelyridae Chkhikvadze, 1970

Helochelydra nopcsai Lapparent de Broin & Murelaga, 1999

Type material. NHMUK R171 (holotype), a fragmentary shell associated with limb and girdle elements (Nopcsa 1928).

Type locality. Isle of Wight, United Kingdom (Nopcsa, 1928).

Type stratum. Wessex Formation, Wealden Group, Barremian, Early Cretaceous (Joyce et al. 2011).

Diagnosis. *Helochelydra nopcsai* can most easily be diagnosed as a helochelydrid by the presence of a secondary pair of occipital tubercles that are formed by the pterygoids, a triangular fossa that is formed by the squamosal at the posterior margin of the skull, a shell covered by a surface texture consisting of distinct tubercles, expansion of the visceral cavity to the front and back of the peripheral series (also present in some compsemeydids and pleurosternids), and presence of an entoplastral scute.

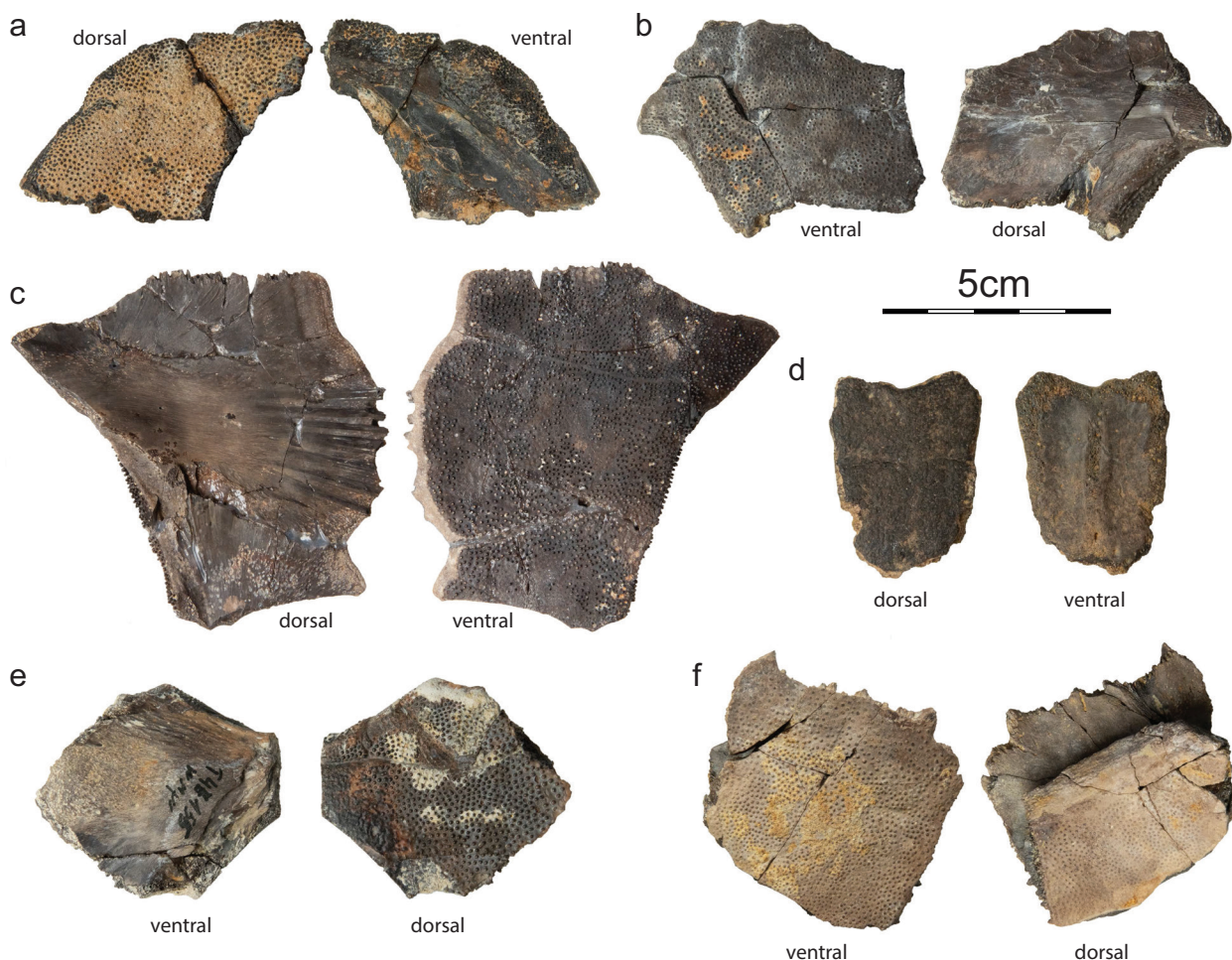


Figure 2. Shell remains of *Helochelydra nopcsai* from the Early Cretaceous (late Barremian – early Aptian) of Balve, North Rhine-Westphalia, Germany. Photographs of select specimens highlighting variation in preservation. (a) WMNM P88818, a right epiplastron (also see Fig. 5b); (b) WMNM P88824, a right partial hypoplastron (also see Fig. 5k); (c) WMNM P88823, a partial left hypo- and xiphiplastron (also see Fig. 5i); (d) WMNM P88808, a partial, anterior neural (also see Fig. 3a); (e) WMNM P88813, a partial nuchal (also see Fig. 4b); (f) WMNM P88816, a partial left peripheral XI (also see Fig. 4h). All specimens are to scale.

Helochelydra nopcsai can be distinguished from other helochelydrids by a shell surface texture consisting of evenly spaced tubercles that easily dislocate (also present in *Helochelys danubina*), cone-, hook-, and plate-shaped osteoderms (also present in *Naomichelys speciosa*), and pterygoids that fully cover the parabasisphenoid ventrally. No other helochelydrid is known to possess compound granicones. *Helochelydra nopcsai* currently cannot be distinguished from *Helochelys danubina* using morphological features, because the latter is poorly known and its holotype lost. Stratigraphic criteria (i.e., an age difference of more than 20 Ma) nevertheless suggest that they represent distinct taxa.

Referred material. Early Cretaceous (Barremian), Wessex Formation, Isle of Wight, United Kingdom (material referred by Lapparent de Broin and Murelaga 1999 and Joyce et al. 2011; Pleurosternidae of Sweetman and Insole 2010); Early Cretaceous (Hauterivian–Barremian), Nouvelle-Aquitaine, France (Solemydidae of Néraudeau et al. 2012); Early Cretaceous (Barremian), Aragon, Castile and León, La Rioja, and Valencia, Spain (Solemydidae of Pérez García 2009; Pérez-García et al.

2012, 2013; Scheyer et al. 2015); Early Cretaceous (late Barremian – early Aptian), Balve, Germany (all material described herein).

Description. Although the available sample consists of more than 250 specimens, including more than 150 granicones, only a small number of specimens provide useful anatomical information. This description is therefore focused on the most informative specimens.

Surface texture. The surface of all available shell material and granicones is evenly covered by distinct tubercles (Figs 2–5). Each tubercle is columnar and clearly separated from neighboring tubercles. The tubercles of the shell easily dislocate at their base, where they leave behind a circular scar, which can easily be recognized under the microscope. Although some variation is apparent across the shell (e.g., tubercles are less densely spaced over the neurals), most are about 0.5 to 1 mm wide, about 0.5 to 1.5 mm tall, and separated from neighboring tubercles by about 1.5 to 2 mm. The tubercles are less distinct on the available cranial fragment and all granicones, but similar in dimensions. In all regards, the surface texture closely approximates to that of *Helochelydra nopcsai* material

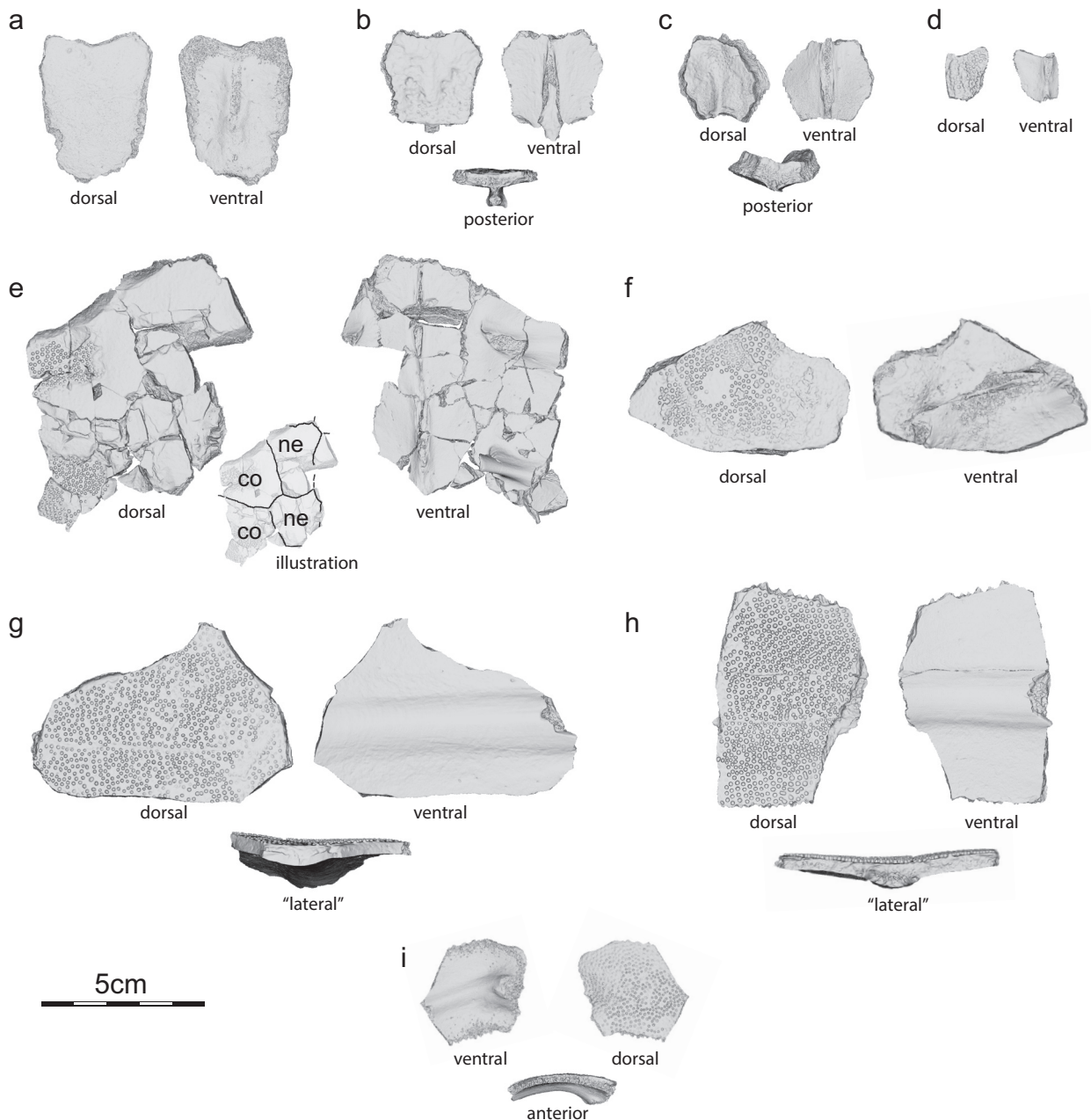


Figure 3. Neural and costal remains of *Helochehydra nopcsai* from the Early Cretaceous (late Barremian – early Aptian) of Balve, North Rhine-Westphalia, Germany. All images were obtained from CT generated 3D models. (a) WMNM P88808, a partial, anterior neural; (b) WMNM P49476, a partial, posterior neural; (c) WMNM P49351, a partial, posterior neural; (d) WMNM P88809, a partial, posterior neural; (e) WMNM P88807, a carapacial fragment consisting of two neurals and remnants of three adjacent costals; (f) WMNM P88810, a partial left costal I; (g) WMNM P88812, a partial costal; (h) WMNM P88811, a partial costal; (i) WMNM P49470, a partial right costal. Anatomical direction are placed in quotes for elements with uncertain orientation. With the exception of the illustrations, all specimens are to scale. *Abbreviations:* co = costal; ne = neural.

from the Wessex Formation of England (NHMUK R171, R5195–5199, R5201, R5205, R5238).

Carapace. The available material (Figs 3, 4) suggests that the carapace had a length of up to 70 cm (see Costals below), a nuchal notch extending laterally up to peripheral II (see Nuchal below), and that deep grooves decorated the neural-costal contacts along the posterior half of the shell (see Costals and Neurals below). The carapace is 5 to 6 mm thin along the peripherals and costals, but thickens to 8 mm at the neurals. All parts of

the carapace are evenly covered by distinct tubercles that disarticulate easily (Figs 3, 4).

Neurals. We are able to identify six elements as neurals: WMNM P88808 (Fig. 3a), P49476 (Fig. 3b), P49351 (Fig. 3c), P88809 (Fig. 3h), and P88807 (Fig. 3e). WMNM P88807 is a larger shell fragment that consists of two neural elements in addition to costal remains including two neural elements that are up to 8 mm thick (Fig. 3e). The posteriorly angled orientation of the associated rib heads relative to the neural column suggest that

the elements represent neurals V, VI, or VII. Their outline is hexagonal with short anterolateral sides. The anterior of the two neural shows faint traces of a midline keel, as has also been reported for neurals of *Naomichelys speciosa* (Joyce et al. 2011). WMNM P88808 (Fig. 3a) is the largest available neural, flat, about 5 mm thick, and has a hexagonal outline (i.e., contacts with six surrounding bones are apparent). Its dorsal surface is badly eroded: there are faint traces of an intervertebral sulcus, but only the bases remain of the surface tubercles. The orientation of this element is not clear, but its size suggests that it originates from the anterior half of the shell. WMNM P49351 (Fig. 3c) is only half as long anteroposteriorly as the previous element, but about 7 mm thick. A sharp median depression crosses its surface. WMNM P49476 (Fig. 3b) has similar dimensions to WMNM P49351, but it is only about 4 mm thick and flat. The equilateral, hexagonal outline of the last two elements suggests an origin from the back of the shell. WMNM P88809 (Fig. 3d) is the smallest available neural and only about 2 mm thin. Only the right two thirds are preserved. Its small size and equilateral, hexagonal outline suggest that it originates from the posterior portions of the shell of a juvenile.

Costals. A number of elements can be diagnosed as costals, of which the following seven are the most informative: WMNM P88807 (Fig. 3e), a shell fragment that includes remains of three costals, WMNM P88810, a partial left costal I (Fig. 3f), P88811 (Fig. 3h) and P88812 (Fig. 3g), two large costal fragments, and P49470, the median portion of a midsized costal (Fig. 3i). The dermal portion of these costals is about 4 mm thick. The ribs, when present, are broad, about a quarter of the anteroposterior width of the costal, but only add about 2–3 mm to the thickness of each element. The three costal remains preserved in WMNM P88807 (Fig. 3e) are in articulation with two neurals and, therefore, best document the medial aspect of these elements. The slight posteriorly angled orientation of the ribs suggest that they originate from the mid-posterior part of the shell. All elements have two contacts with the adjacent neurals. The free, medial portion of one costal rib is well preserved. It is relatively narrow, about 2 mm across, and delimits a relatively low costovertebral tunnel. WMNM P88810 (Fig. 3f) can be identified as a partial left costal I by the presence of the articular scar for dorsal rib I. The sulcus between vertebral I and pleural I diagonally traverses the dorsal surface of this element. A rounded anteromedial facet for articulation with the nuchal suggests that the nuchal deeply inserted between the anterior costals. WMNM P88811 (Fig. 3h) is significant, as it possesses intact anterior and posterior margins. The greatest anteroposterior “width” of this element is 56 mm, which is a little greater than the greatest costal width that can be observed for the only known complete skeleton of the helochelydrid *Naomichelys speciosa* (Joyce et al. 2014). Assuming similar proportions, the full carapace may therefore have reached a length of over 70 cm. WMNM P49470 (Fig. 3i) only has an anteroposterior “width” of

3 cm and, therefore, likely originates from the back of the shell of a smaller individual. It is notable for exhibiting a concavity just above the rib head, near its medial articulation with the neurals. Together with the grooved neurals, this suggests some meso-scale sculpturing of the shell surface towards the back of the shell.

Nuchal. Two specimens preserve remains of the nuchal: WMNM P88813, the right half of a large nuchal (Fig. 4a), and WMNM P88814, a smaller nuchal fragment, which remains articulated with remnants of the adjacent right costal I and peripherals I and II (Fig. 4b). The two specimens suggest that a broad nuchal notch was present that was framed by peripherals II, as is typical for helochelydrids (Joyce et al. 2014; Pérez-García et al. 2020a). The oblique anterolateral contact of the nuchal with peripheral I is oriented more to the anterior than the side. There is no evidence for costiform processes. The right portion of a cervical scute is preserved in WMNM P88813 (Fig. 4a). As this specimen broke near the midline, we estimate that the complete cervical was at least twice as wide than long. Lateral to the cervical scute, a sulcus is apparent that delimits the contact between marginal I and vertebral I. There is no evidence for the presence of a prepleural on the nuchal. The skin-scutum sulcus runs on the underside of the nuchal just behind the anterior margin of the bone.

Peripherals. A number of peripherals are preserved, of which we present the six most informative. WMNM P88814 includes a nearly complete right peripheral I articulated with remnants of the adjacent element (Fig. 4b). WMNM P88815 is a first peripheral I as well, but lacks much of its dorsal surface (Fig. 4c). These two elements document that peripheral series articulated with the nuchal laterally along an oblique (WMNM P88814) to straight (WMNM P88815) suture, costal I posteriorly, and peripheral II laterally. The scute-skin sulcus runs diagonally across the underside of the peripheral, thereby bridging the location of this sulcus near the margin of the shell at the nuchal with the deep location on the second peripheral. Although damaged, these bones also document that the visceral cavity extends all the way from the bridge region to the medial fifth of peripheral I, as had previously been documented for other helochelydrids (Joyce et al. 2014; Pérez-García et al. 2020a). WMNM P88816 is a relatively large peripheral element that we tentatively interpret as the right peripheral XI, as it displays a small, but elongate facet on its visceral side best interpreted by reference to *Naomichelys speciosa* (Joyce et al. 2014) as the articulation site for thoracic rib IX (Fig. 4h). This element shows faint traces of an intermarginal scute sulcus and documents that the visceral cavity extends posteriorly from the bridge region to reach the pygal. The visceral cavity of *Helochelydra nopcsai*, therefore, extended all the way from the medial fifth of peripheral I to the pygal, much as in *Aragoichersis lignitesta* (Pérez-García et al. 2020a), but also *Pleurosternon bullockii* (Joyce et al. 2022). However, three finger-like pockets within the cavity of WMNM P88816 suggests that the visceral cavity is not developed evenly across the

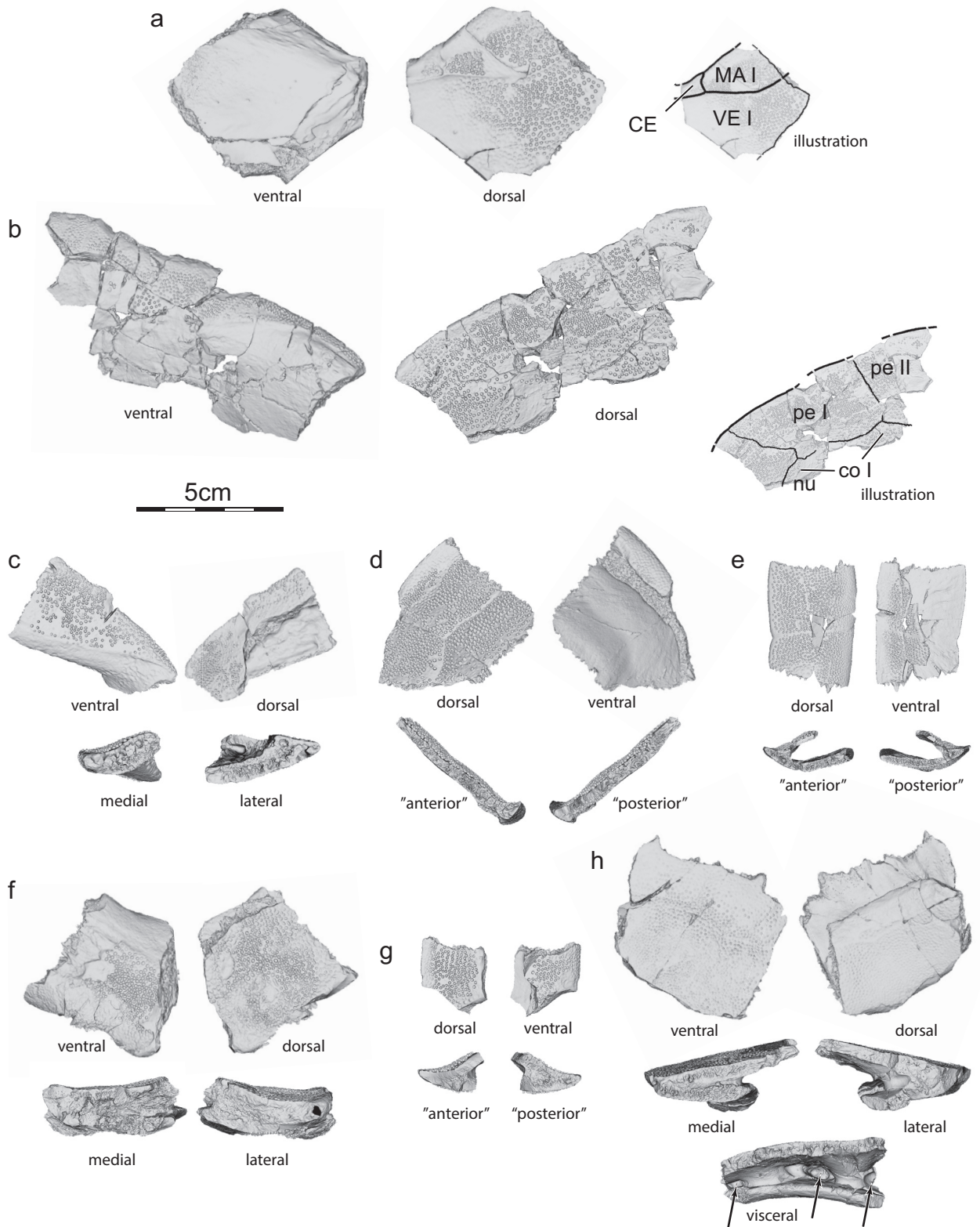


Figure 4. Nuchal and peripheral remains of *Helochelydra nopcsai* from the Early Cretaceous (late Barremian – early Aptian) of Balve, North Rhine-Westphalia, Germany. All images were obtained from CT generated 3D models. (a) WMNM P88813, a partial nuchal; (b) WMNM P88814, a carapacial fragment consisting of remnants of a nuchal, rights peripheral I, remnants of right peripheral II, and remnants of right costal I; (c) WMNM P88815, a partial right peripheral I; (d) WMNM P49051, a partial bridge peripheral; (e) WMNM P88817, a partial bridge peripheral; (f) WMNM P41690, a partial right peripheral XI; (g) WMNM P47259, a partial peripheral; (h) WMNM P88816, a partial left peripheral XI. Anatomical direction are placed in quotes for elements with uncertain orientation. With the exception of the illustrations, all specimens are to scale. *Abbreviations:* CE = cervical scale; co = costal; MA = marginal scale; nu = nuchal; pe = peripheral; VE = vertebral scale.

shell (see arrows in Fig. 4h). The waning visceral cavity combined with minor asymmetries suggest that WMNM P41690 is a damaged right peripheral X as well (Fig. 4f). As the most anterior and most posterior peripherals show evidence of a visceral cavity, it is not possible to identify the serial identity of the damaged, remaining peripheral elements. Three notable remains, WMNM P47259 (Fig. 4g), P49051 (Fig. 4d), and P88817 (Fig. 4e) nevertheless document variable development of a low gutter. WMNM P49051 and P88817 furthermore highlight that the dorsal and ventral branches that make up each peripheral are thin-walled and meet each other just medial to the edge of the carapace. The peripherals of the bridge region are therefore extremely fragile.

Epiplastron. The only available epiplastron, WMNM P88818, is near complete, but mineral precipitations on the external surface partially conceal its sulci (Fig. 5b). The epiplastron formed the anterior aspects of the transversely oriented anterior plastral lobe. The epiplastron has a convex posteromedial contact with the entoplastron. The epiplastron hereby slightly underlaps the entoplastron, which, as a result, would have appeared smaller in ventral than in dorsal view. An equally broad contact is present posterolaterally with the hyoplastron. Though damaged, deep pockets along the posterolateral margin of the epiplastron suggest that at least two peg-like processes of the hyoplastron inserted into the epiplastron. A short median contact is furthermore apparent with its counterpart. A notch along the anterior margin of the epiplastron signifies the location of the gular-extragular sulcus. A faint trace of this sulcus can be gleaned on the ventral surface that runs posteriorly from the notch (Fig. 5b). A similar notch for the extragular-humeral sulcus is apparent on the lateral margin of the epiplastron (Fig. 5b). On the dorsal side, the extragular-humeral sulcus veers posteriorly to cross the lateral side of the epiplastron (see arrows in Fig. 5b). Its posterior end is not preserved, as this was likely located on the hyoplastron. As a result of this arrangement, the extragular covered only part of the epiplastron in ventral view, but most of it in dorsal view. The dorsal side of the epiplastron is characterized by a thickened epiplastral lip.

Entoplastron. Two partial entoplastra are available, WMNM P48296 (Fig. 5a) and P88819 (Fig. 5c), of which the former is better preserved. The posterior half of the entoplastron is lacking in either specimen, but comparison with *Helochelydra nopcsai* (NHMUK R171) suggests that the entoplastron was slightly longer than wide. The entoplastron slightly overlaps the epiplastron along its slightly convex anterolateral contact. The posterolateral contact, as far as preserved, broadly underlapped the hyoplastron. Traces of the embryonic interclavicle are apparent on the dorsal side of both available elements, much as in other helochelydrids. The gulars only cover a small triangular surface on the ventral side of WMNM P48296, but about a third of the ventral surface of P88819. The extragulars minutely overlapped both elements. Only a minute entoplastral scute is apparent in WMNM P48296. An entoplastral scute seems to be absent in

WMNM P88819, in which the humeral-gular junction is just about preserved.

Hyoplastron. Two partial hypoplastral remains can be identified with confidence. WMNM P47721 (Fig. 5d), the more complete of the two, documents the lateral margin of the anterior plastral lobe, just posterior to the articulation of the hyoplastron with the epiplastron, while WMNM P88820 (Fig. 5e) documents a segment slightly further to the back. The two fragments combined indicate that the skin-scute sulcus is barely located on the visceral side of the hyoplastron, but converges with its margin towards the back. Indeed, the sulcus terminates in WMNM P88820 near the margin, which suggests that this element broke at the humeral-pectoral sulcus. The resulting lip is only lightly developed towards the back, as seen in WMNM P88820, but becomes pronounced anteriorly to form a finger-like process that inserted anteromedially into the epiplastron, as seen in WMNM P47721.

Two additional, fragmentary specimens, WMNM P48226 (Fig. 5f) and P88821 (Fig. 5h), exhibit radiating, pin-like tubercles on their visceral sides that are reminiscent of those found on the hyoplastron of *Naomichelys speciosa*, but they may also represent remains of the mesoplastra or hypoplastra. A third fragment, WMNM P88822 (Fig. 5g), is a fragment of the bridge that may similarly represent part of the hyo- or hypoplastron. A rib-like thickening on the visceral side of this fragment is the remnants of a buttress. A series of clearly delineated sulci form the outlines of at least two inframarginals, two marginals, and the neighboring plastral scutes.

Mesoplastron. No mesoplastral remains could be identified as such.

Hypoplastron. We are able to identify at least three remains as hypoplastra, WMNM P88823 (Fig. 5i), P88825 (Fig. 5j), and P88824 (Fig. 5k), all of which preserve the thickened inguinal notch, but can be recognized as hypoplastra by remnants of the xiphiplastral articulation. WMNM P88823, the best of the three preserved elements, documents the transverse contact with the mesoplastron and the slightly oblique posterior contact with the xiphiplastron, which is dorsally stabilized by two xiphiplastral processes that dorsally cover the hypoplastron and a hypoplastral process that dorsally covers the xiphiplastron (Fig. 5i). The relatively intact medial margin suggests that central and posterior plastral fontanelles are present (see arrows in Fig. 5i) and that the hypoplastra only contacted one another along rib-like processes that radiate from the inguinal notch, features otherwise found in *Naomichelys speciosa* (Joyce et al. 2014), but not in the holotype of *Helochelydra nopcsai* (NHMUK R171). The relatively small size of this specimen opens the possibility, however, that these are juvenile features. As preserved, the abdominal/femoral sulcus crosses the hypoplastron diagonally from the inguinal notch to the central plastral fontanelle, but otherwise runs posterior from the notch to meet with the skin-scute sulcus on the dorsal side (Fig. 5i). In this area, the hypoplastron is thickened to nearly 2 cm in

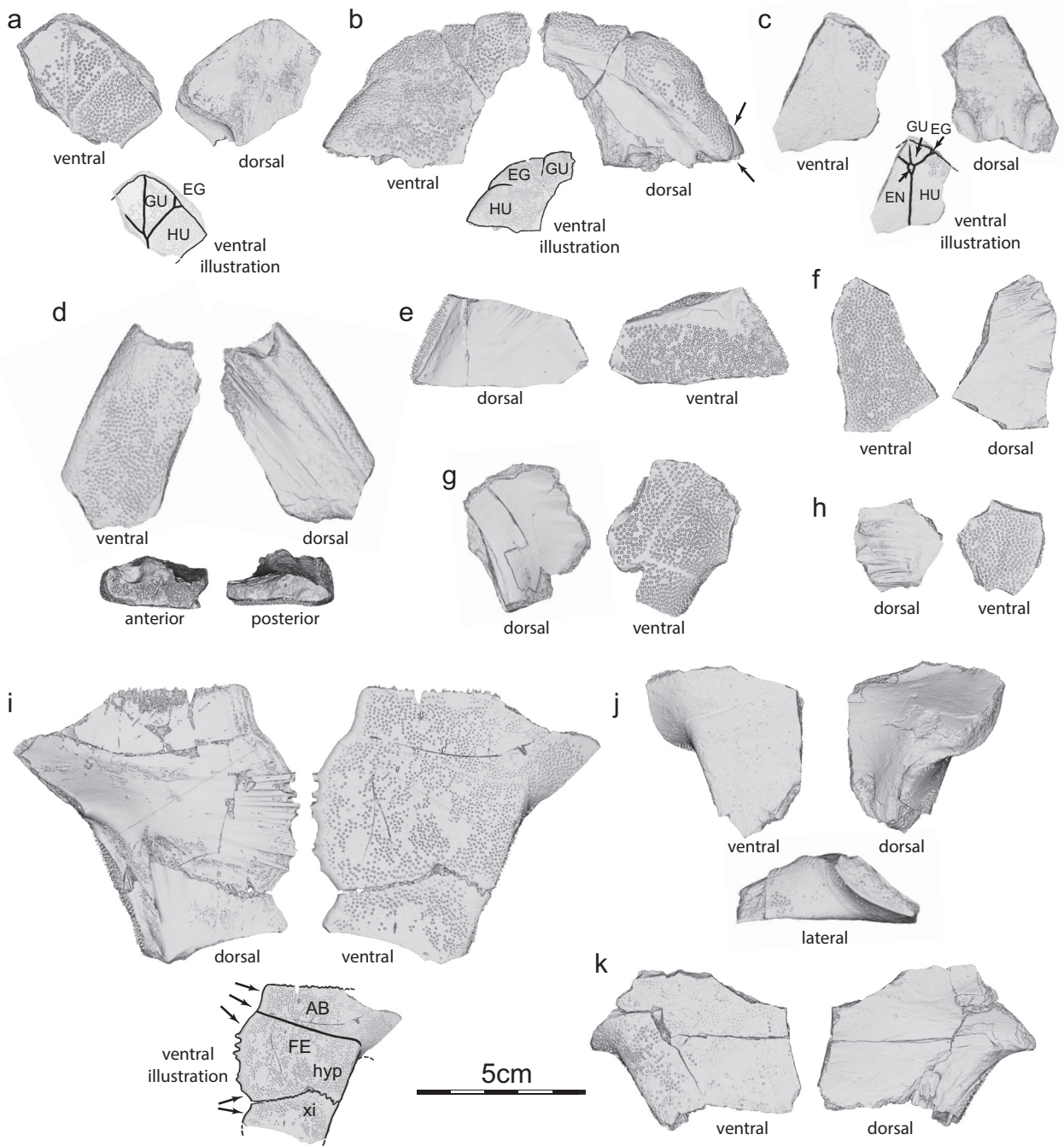


Figure 5. Plastral remains of *Helochelydra nopcsai* from the Early Cretaceous (late Barremian – early Aptian) of Balve, North Rhine-Westphalia, Germany. All images were obtained from CT generated 3D models. (a) WMNM P88819, a partial entoplastron; (b) WMNM P88818, a right epiplastron; (c) WMNM P48296, a partial entoplastron; (d) WMNM P47721, a partial right hyoplastron; (e) WMNM P88820, a partial left hyoplastron; (f) WMNM P48226, a plastral fragment; (g) WMNM P88822, a plastral fragment; (h) WMNM P88821, a plastral fragment; (i) WMNM P88823, a partial left hypo- and xiphiplastron; (j) WMNM P88825, a partial right hypoplastron; (k) WMNM P88824, a right partial hypoplastron. With exception of the illustrations, all specimens are to scale. Abbreviations: AB = abdominal scale; EG = extragular scale; EN = entoplastral scale; FE = femoral scale; GU = gular scale; HU = humeral scale; hyp = hypoplastron; xi = xiphiplastron.

the smallest available specimen (WMNM P88823), but reaches 2.5 cm in the largest (WMNM P88825). In the area of the notch, the skin-scute sulcus runs onto the dorsal side of the hypoplastron to form a semi-lunate lip, but runs near parallel to the margin once it reaches the xiphiplastron (Fig. 5j).

Xiphiplastron. The remnants of a xiphiplastron are preserved in WMNM P88823 attached to the hypoplastron (Fig. 5i). Its contact with the hypoplastron is described above, as is the development of the skin-scute sulcus. A comparison with *Naomichelys speciosa* suggests that the xiphiplastron broke close to the femoral-anal sulcus. The

anal scute, therefore, did not cross the hypoplastra-xiphoplastral suture.

Granicones. More than 150 granicones are available for study (Fig. 6). With few exceptions (see below), all granicones are singular, conical elements that consist of a flat base, which anchored the element into the skin, and an apex, which protruded from the body (Joyce et al. 2014). The external surface of all elements is covered by surface texture that closely mirrors that of the shell. A qualitative assessment suggests that three morphotypes are present: cones (ca. 35%), hooks (ca. 43%), and plates (ca. 22%). As the name implies, cones are conical elements where the apex is situated above the base (e.g., Fig. 6: P88864, P88873). These elements tend to be smaller. Hooks greatly resemble cones, but the apex is offset beyond the surface of the base (e.g., Fig. 6: P88922, P88856). Plates, finally, resemble hooks in that the base is offset from the base, but that are notably flat (e.g., Fig. 6: P88939, P88921). These tend to be the largest available elements. Our morphometric analysis (see below) suggests that these morphotypes do not populate discrete parts of the morphospace, but rather grade into each other. We nonetheless retain this terminology for convenience. As all elements were found in isolation, we do not know which parts of the body they once covered. A complete skeleton of *Naomichelys speciosa* that includes numerous articulated granicones, however, suggests that plates covered the external surfaces of the lower limbs while the spur-like hooks were located on the walking surfaces of the limbs (Joyce et al. 2014).

A total of five elements deviate strongly from the three morphotypes described above (Fig. 6). Two of these (WMNM P88935 and P88940) resemble large hooks by having an apex that is offset relative to the base, but the base in itself is not flat and round, but rather folded along the long axis of the element. We speculate that this type of element may have covered folds on the outside of the limbs. The three other unusual granicones are remnants of compound granicones. WMNM P88974 consists of a single, conical apex, but open sutures on at least one side of its base suggest that it was laterally sutured to at least one more granicone. WMNM P88964 consists of two conical apices that are broadly sutured to one another at their bases. Although the outline of the jointly formed base is somewhat angular, the element appears to be intact. WMNM P88962 also consists of two conical apices, but numerous angularly arranged sutures on both sides of the jointly formed base suggest that it formally articulated with at least two, but likely up to five additional granicones, to form a compound element with at least four to seven apices.

PCA of all measurements indicates that 65.7% of the overall variance can be explained by size or allometric differences between specimens, explained by PC1 (Table 1). No differentiation of morphotypes is apparent based on size differences alone. Our morphospace plot of size-adjusted principal components (Fig. 7) shows that PC2, which explains 71.9% of shape variation after correcting for size, is the only principal component along

which separate clusters of specimens may be determined, as plated granicones plot at low PC2 values with minimal overlap of specimens pre-assigned to other morphotypes. Cones and hooks have broad overlap across PC3 (20% of variance; Fig. 7a) and PC4 (8.0% of variance; Fig. 7b). The absence of separation for these morphotypes and the broad spread of values across PC3 can be explained by shape variation within the pre-assigned hook or cone condition. For example, hooks exist that have large basal measurements but low tip height (Table 1), such as WMNM P88873 (Fig. 7a), the positive extreme point on PC3, but simultaneously hooks exist that have high tip heights compared to relatively small bases (e.g., WMNM P88864, which plots at low PC3 values for the hooked morphotype; Fig. 7a). Similarly, cones with strongly asymmetrical bases plot at extreme negative PC3 values (e.g., WMNM P88940), whereas cones with similar tip offset but symmetrical bases plot at extreme positive PC3 values (e.g., WMNM P88921). The relatively close association in morphospace of hooks like WMNM P88873 and cones like WMNM P88921 is thus primarily caused by similar base dimensions paired with low tip heights (Table 1), regardless of their difference in tip offset which is the primary distinction of cones and hooks based on

Table 1. PCA results (n = 136).

	PC1	PC2	PC3	PC4
Eigenvalues	2.628	0.987	0.275	0.110
Proportion of total variance explained	0.657	0.247	0.069	0.028
Proportion of shape variance explained	–	0.719	0.200	0.080
Eigenvector coefficients				
height	0.170	0.963	-0.155	0.140
minimum base	0.575	-0.010	0.551	0.597
maximum base	0.591	0.045	0.229	-0.772
tip offset	0.540	-0.24	-0.788	0.166

qualitative comparisons.

Cranium. A three-dimensionally preserved, partial, left parietal (WMNM P88806) is the only skull bone in the sample (Fig. 8). The anterolateral and medial margins of its dorsal plate, which formerly contacted the left postorbital and the right parietal, are intact, but the anterior and posterior margins show signs of damage. Striations on the posteromedial side of the element, contained within the area that constituted the cavum cranii, could plausibly represent the articulation area with the supraoccipital, which is usually overlain by the parietal in this area. A short posterolateral facet may represent the former contact with the left squamosal. A comparison with IWCMS 1998.21, a complete *Helochelydra nopcsai* skull from the Isle of Wight (Joyce et al. 2011), suggests that only the anterior half of the element is preserved. The two specimens likely originated from individuals of the same size, as WMNM P88806 has an anteroposterior length of about 2.7 cm, while the equivalent area measures about 2.8 cm in IWCMS 1998.21. The two skulls differ notably in that WMNM P88806 exhibits clear cranial sulci which outline at least 12 polygonal cranial scutes. Their great number, however, obscures homology

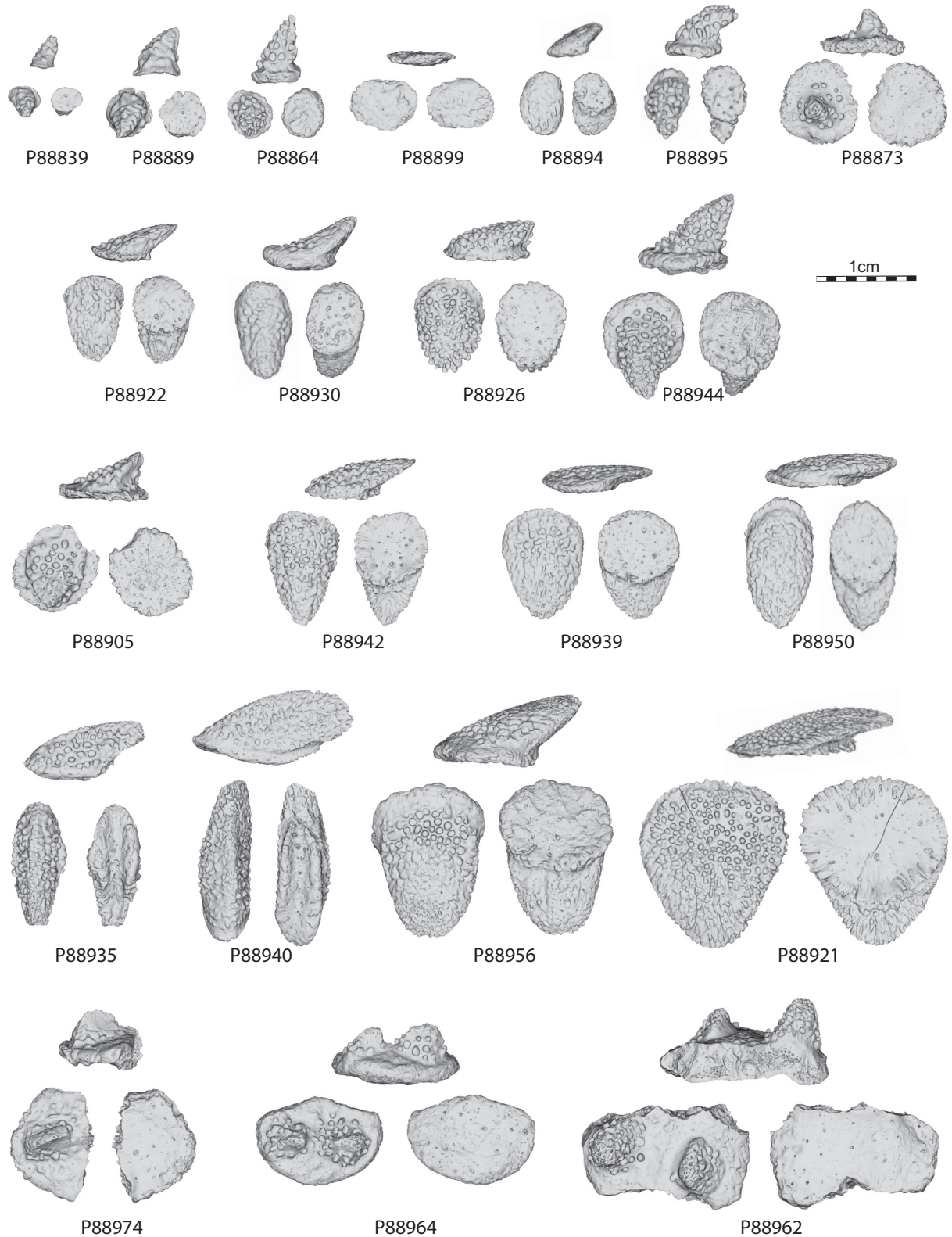


Figure 6. A selection of granicones, *Helochelydra nopcsai* from the Early Cretaceous (late Barremian – early Aptian) of Balve, North Rhine-Westphalia, Germany. All images were obtained from CT generated 3D models. All specimens are shown to scale in lateral (top), apical (bottom left), and basal view (bottom right) and associated with their WMNM catalog number. Specimens were in part chosen to highlight the morphological extremes highlighted by the PC plots (see Fig. 7).

with the cranial scutes of other Cretaceous turtles, as these typically exhibit only four scutes in the equivalent area (Sterli and de la Fuente 2013; Evers et al. 2021). On the ventral

side, traces remain of the heavily damaged descending process. What remains is an outwardly convex crest of bone that documents the greatest width of the cavum cranii.

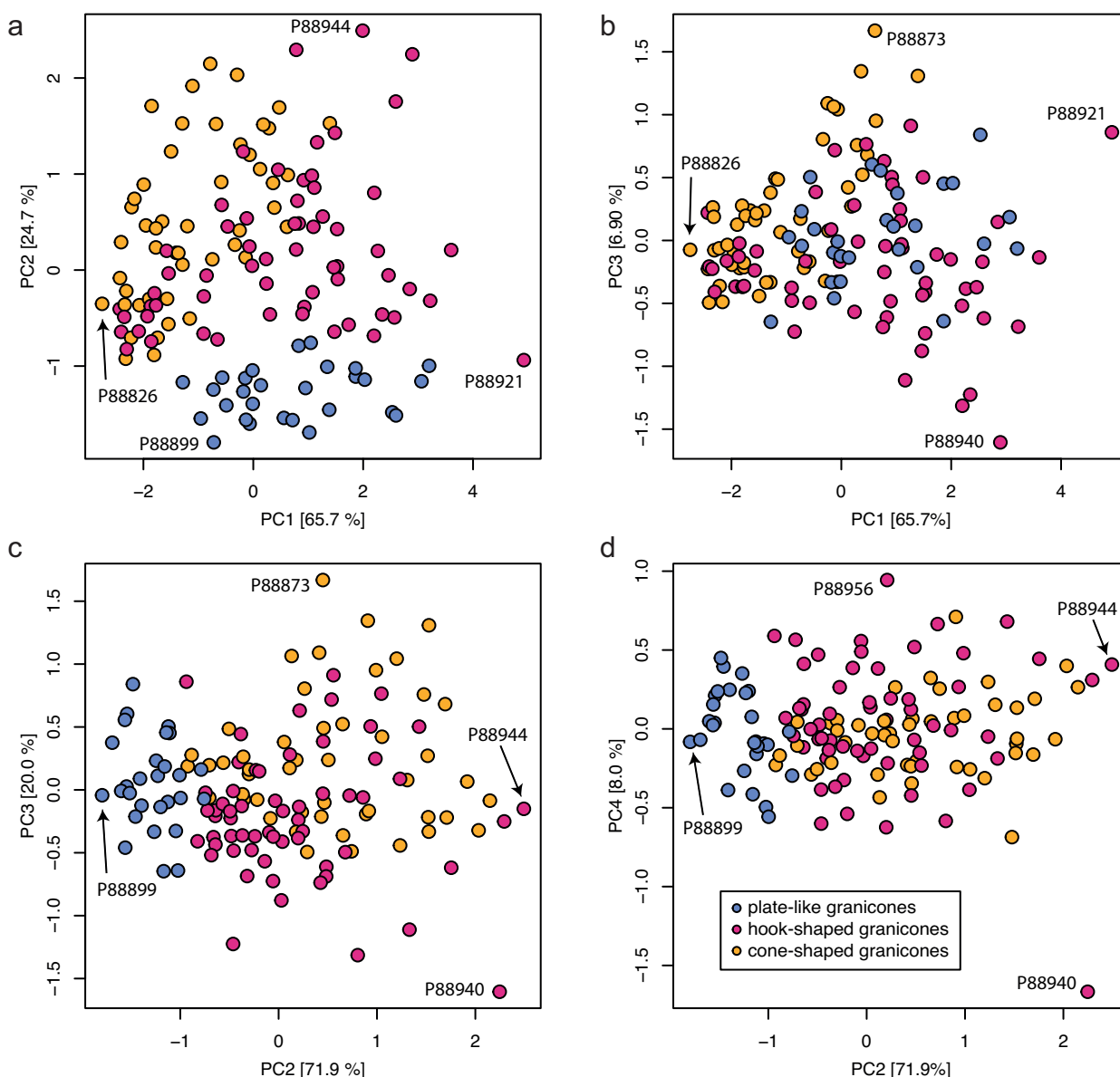


Figure 7. Morphospaces of four granicone measurements from PCA ordination ($N = 165$). (a, b), bivariate morphospaces including size variation. (c, d), morphospaces corrected for size and allometry. A, PC1 vs. PC2. B, PC2 vs. PC3. C, PC2 vs. PC3. D, PC2 vs. PC4. The proportion of variance explained by PC axes are indicated in the axis labels, whereby values in A, B represent total variance (including size) and values in B, C represent shape variance (re-scaled to exclude PC1). An identical plot with unique point labels is provided in Suppl. material 2.

Discussion

Alpha taxonomy

The vast majority of helochelydrid remains cannot be identified rigorously, in part because the true diversity of helochelydrid turtles is not yet understood, but also because fragmentary remains rarely yield diagnostic characters beyond shell surface texture. For these reasons, Joyce et al. (2014) developed a preliminary taxonomy that is focused on shell surface texture, but further recommends assigning material to named taxa based on biogeographic and temporal considerations. Using these criteria, the fossil turtle material presented herein can be assigned to *Helochelydra nopcsai*, as it closely mirrors its

shell surface texture consisting of evenly spaced tubercles that easily dislocate, as it originates from sediments broadly coeval with the type stratum (i.e., Barremian–Albian), and because northern Germany and southern England are typically reconstructed to have been part of the same depositional system at that time (e.g., Aguado et al. 2022; Sanjuan et al. 2022).

Although comparisons are limited, we are able to highlight two notable differences between the new material from Balve and previously described postcranial (Nopcsa 1928; Lapparent de Broin and Murelaga 1999) and cranial material (Joyce et al. 2011) from the Wessex Formation of England. First, while the only available entoplastron from the Wessex Formation exhibits are relatively large entoplastral scutes, the two entoplastra

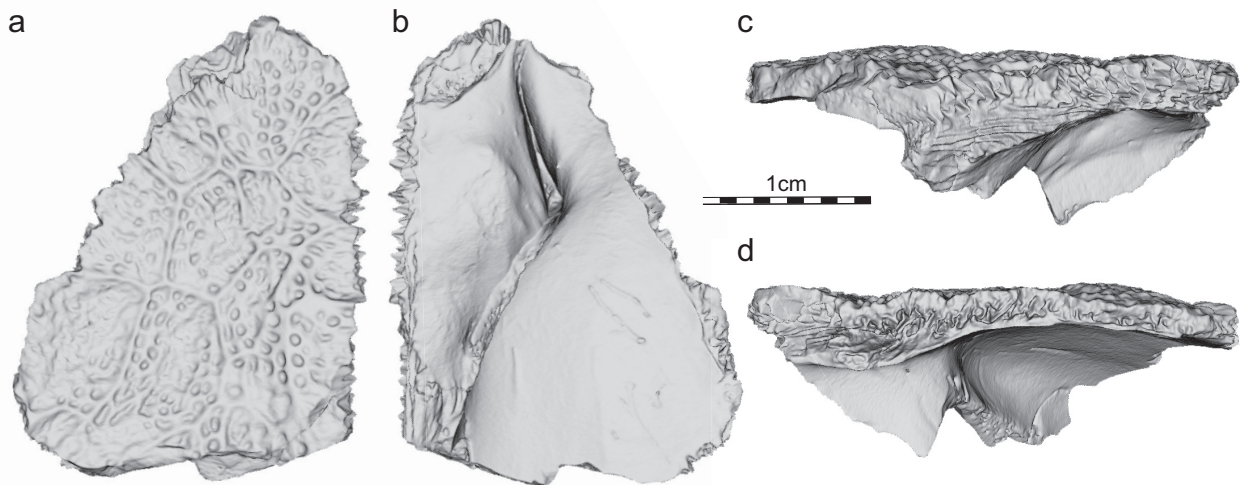


Figure 8. *Helochelydra nopcsai* from the Early Cretaceous (late Barremian – early Aptian) of Balve, North Rhine-Westphalia, Germany. WMNM P88806, a partial parietal in dorsal (a), ventral (b), medial (c), and lateral view (d). All images were obtained from CT generated 3D models.

from Balve appear to have no, or only a small entoplastral scute. And second, while the only available skull from the Wessex Formation lacks evidence of cranial scutes, the parietal fragment from Balve is clearly marked by numerous cranial scute sulci.

Large entoplastral scutes have been reported for some helochelydrids, notably *Naomichelys speciosa* and *Solemys* spp. (Hay 1908; Lapparent de Broin and Murelaga 1999; Joyce et al. 2014; Tong et al. 2023), but this scute is relatively small to absent in others, including not only *Aragoichersis lignitesta* and *Plastremys rutteri* (Pérez-García et al. 2020a; Joyce 2022) but also *Helochelydra nopcsai*. As the scutes of other turtles are known to vary widely, including the entoplastral scute of specimens referred to *Naomichelys speciosa* (Hay 1908; Ostrom 1970; Joyce et al. 2014), we here attribute the observed differences to intraspecific variation, as we find the difference between a small and very small entoplastral to absent entoplastral scute to be minor.

We are unaware of any studies that explicitly document variation to the development of cranial scute sulci in turtles. We are therefore unable to assess if the difference we observe in the development of cranial scute sulci has taxonomic differences. We suspect nonetheless that cranial scute sulci are developed more distinctly in juvenile material, perhaps suggesting that the parietal from Balve originates from a less mature individual.

Morphology

The type material of *Helochelydra nopcsai* is a partial skeleton that remains poorly described to date. Though fragmentary as well, the new material from Balve yields important new insights regarding the morphology of helochelydrids in general and *Helochelydra nopcsai* specifically. We here focus on two characters: the expansion of the visceral bridge cavity to the front and back of the shell and the presence and development of granicones.

Expansion of the visceral bridge cavity

In the vast majority of turtles, the peripherals are modified into two basic shapes: while the peripherals anterior and posterior to the bridge are flat, as they only connect to the carapacial disk medioventrally, the bridge peripherals are V-shaped in cross section to allow articulating with the carapace dorsolaterally and the plastron ventrolaterally. As a result, the visceral cavity of the shell is laterally defined by the bridge peripherals. Lapparent de Broin and Murelaga (1999) documented for the first time that the visceral cavity of the late Late Cretaceous helochelydrid *Solemys gaudryi* and *Solemys vermiculata* extends from the bridge region to the most lateral aspects of the nuchal. The anterior peripherals therefore exhibit a V-shape: the dorsal branch remains articulated with the carapace while the ventral branch creates a shelf that projects towards the visceral cavity. Joyce et al. (2014) extended this observation to the late Early Cretaceous helochelydrid *Naomichelys speciosa*, highlighting that this feature may be a more general feature of helochelydrids. More recently, Pérez-García et al. (2020a) documented that the visceral cavity not only extends anteriorly, but also posteriorly in the late Early Cretaceous helochelydrid *Aragoichersis lignitesta*. The presence of a visceral cavity that extends along the full peripheral margin of the shell, however, was soon after documented as well for the early Cretaceous compsemeydids and pleurosternids *Peltochelys duchastelii*, *Pleurosternon bullockii*, and *Tongemys enigmatica* (Joyce et al. 2022). The presence of this character is particularly surprising for *Pleurosternon bullockii*, as this taxon had historically been known from numerous shells, but never been shown to display this feature (e.g., Owen 1853; Lydekker 1889; Milner 2004; Guerrero and Pérez-García 2021). The primary reason for this oversight is because this taxon is typically preserved as complete, but flattened shells. The anterior and posterior peripherals are therefore compressed to obscure the presence of a cavity. The presence of this cavity is nevertheless

clearly revealed in relatively rare disarticulated remains of this taxon, which allow viewing the peripherals in cross section, but also hinted at as a step-like ridge also apparent in compressed individuals (Joyce et al. 2022).

Our limited sample of peripherals from Balve documents that the visceral cavity of *Helochelydra nopcsai* not only extends from the bridge anteriorly to peripheral I, but also posteriorly to peripheral XI. While the anterior extension looks to be continuous, the posterior extension is achieved through a series of pockets best documented for peripheral XI. It is unclear to us if these pockets are developed in other helochelydrids as well.

We here also note that the step-like ridge apparent in many individuals of *Pleurosternon bullockii* is apparent in the posterior peripherals of *Naomichelys speciosa* as well. We therefore speculate that the visceral cavity of this taxon is more extensive than noted by Joyce et al. (2014).

The phylogenetic relevance of this relatively novel character complex has not yet been explored in full, in part as its distribution remains poorly documented, but it provides evidence for the moment for the hypothesis that helochelydrids are a subclade of *Paracryptodira*, perhaps closely linked with pleurosternids (Rollot et al. 2021, 2022a, b). However, the possible presence of similar expansions of the visceral cavity into the anterior or posterior peripherals of Triassic turtles (pers. comm. Tomasz Szczygielski 2023) suggests that this feature may also be plesiomorphic for the group.

Granicones

A preliminary assessment of the turtle fauna from Balve suggests that four turtles are present, in particular the enigmatic *Chitracephalus dumonii*, the small compsemydid *Peltochelys duchastelii*, a new species of pleurosternid, and *Helochelydra nopcsai*, the focus of this study. Our visual inspection of all granicones from Balve concludes that all display the same surface texture, regardless of shape or size, which closely mirrors the shell surface texture of *Helochelydra nopcsai*. We, therefore, conclude with confidence that *Helochelydra nopcsai* is the only taxon at Balve that possessed osteoderms.

To date, helochelydrid granicones (i.e., osteoderms) have only been reported from a relatively small number of localities. A handful of conical elements were initially described during the 19th century from the Early Cretaceous (Berriasian) Purbeck Limestone Formation of England (Owen 1878; Barrett et al. 2002). Despite their greater age, these broadly correspond in their morphology with the cone-shaped granicones we here report from Balve. A single granicone was previously reported from the Early Cretaceous (Barremian) Wessex Formation of England (Sweetman, 2007), which, unsurprisingly, resembles closely the cone-shaped granicones we here report from Balve. This supports its taxonomic assignment to *Helochelydra nopcsai* (Joyce et al. 2011). A large sample of granicones found in articulation with a skeleton of the Early Cretaceous *Naomichelys speciosa*

(Barrett et al. 2002; Joyce et al. 2014) also resembles those from Balve by variously consisting of cones, hooks, and plates. This may suggest particularly close phylogenetic relationships between *Helochelydra nopcsai* with *Naomichelys speciosa*.

A small number of additional granicones have been reported from other formations that strongly deviate in their morphology from those from Balve. Lapparent de Broin and Murelaga (1999) referred a single late Late Cretaceous (Maastrichtian) element to *Solemys vermiculata* that resembles the granicones of *H. nopcsai* and *N. speciosa* by being covered by a helochelydrid surface texture, but differs by looking to be a compound element consisting of sutured plates, not cones. Pérez-García et al. (2020b) similarly referred an early Late Cretaceous (Cenomanian) element from Spain to *Plastremys lata*, which differs from the granicones of *H. nopcsai* and *N. speciosa* by having a less distinct surface texture and by looking to be a composite element consisting of two unevenly sized cones. Future finds may prove these differences to have taxonomic significance.

The dearth of material is surprising given that helochelydrids broadly occur from throughout the Cretaceous of North America and Europe. We suspect that three factors may play a role. First and foremost, the notable absence of granicones in the well-preserved skeletons of *Aragoichersis lignitesta* (Pérez-García et al. 2020a) suggest that granicones may perhaps not be present in all helochelydrids. Second, we suspect that few continental localities are systematically screen washed for small sized fossils, such as granicones. And, third, even if small sized fossils are systematically collected, we would not be surprised if the granicones either remain unidentified as such or unreported. We hope that the large set of images and 3D models associated with this contribution will ease their identification and comparisons in the future.

Paleoecology

The paleoecology of helochelydrids is generally assumed to be terrestrial because they are mostly found in continental sediments, exhibit shell bone density similar to extant tortoises, and because osteoderms are otherwise only associated with terrestrially adapted turtles, including, among others, the Late Triassic *Proganochelys quenstedtii*, Late Cretaceous nanhsiungchelyid *Basilemys* spp., the Pleistocene meiolaniform *Meiolania platycephs*, and extant testudinids (Lapparent de Broin 1999; Joyce et al. 2011, 2014; Scheyer et al. 2015). Yet, the best preserved helochelydrid skull, that of *Helochelydra nopcsai*, lacks characteristics typical of terrestrial turtles, such as an inflated nasal cavity (Paulina-Carabajal et al. 2017), but instead possesses broad triturating surfaces, which are otherwise mostly associated with aquatic feeding preferences (Foth et al. 2017; Hermanson et al. 2022). Although Joyce et al. (2014) attempted to resolve

this conundrum by suggesting that *H. nopcsai* may have fed on hard terrestrial food items, such as grubs and snails, additional insights are called for to further resolve this question. It should also be noted that osteoderms are ubiquitously known in aquatic non-turtle reptiles, such as phytosaurs, crocodyliforms, or placodonts (Romer, 1956).

The taphonomic setting of the Balve fissure fill deposits is still under investigation. Fissure fills often create taphonomic filters that prefer terrestrial versus aquatic taxa. An informal census of several hundred shell fragments from Balve concludes that less than 1% of finds represent *Chitracephalus dumonii*, about 10% *Peltochelys duchastelii*, about 35% the new species of pleurosternid, and then the remaining 45% *Helochelydra nopcsai*. The remains of *Helochelydra nopcsai* are notable for being particularly fragile, but complete, but this only suggests to us that these remains were not transported, not that this turtle was necessarily terrestrial versus aquatic. The presence of unambiguously aquatic versus terrestrial taxa (Lanser and Heimhofer 2015; Schwermann et al. 2018; Skutschas et al. 2020; Martin et al. 2021, 2022; Hornung et al. 2023) conversely suggests that the fissure fauna at Balve is mixed. We, therefore, conclude that we cannot gain further insights regarding the paleoecology of this animal using taphonomic considerations.

Data availability

All specimens described herein are housed at the LWL-Museum of Natural History, Münster, Germany. 3D mesh models are available at MorphoSource (<https://www.morphosource.org/projects/000497160>).

Author contributions

WGJ designed the study, CT scanned specimens, illustrated specimens, compiled figures, and wrote a primary draft. SWE performed the morphometric study. SR obtained all measurements of granicones. YR segmented CT data and exported 3D mesh models. AHS organized field work and curated specimens. All authors wrote, read, and approved the manuscript and contributed to editing.

Competing interests

The authors declare that they have no conflicts of interest.

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Supplementary material 1

Granicone measurements taken as part of this study

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Data type: table (excel file)

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Supplementary material 2

Morphospaces of four granicone measurements from PCA ordination

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Data type: figure (pdf file)

Explanation note: Morphospaces of four granicone measurements from PCA ordination (N = 165). A–B, bivariate morphospaces including size variation. C–D, morphospaces corrected for size and allometry. A, PC1 vs. PC2. B, PC2 vs. PC3. C, PC2 vs. PC3. D, PC2 vs. PC4. The proportion of variance explained by PC axes are indicated in the axis labels, whereby values in A–B represent total variance (including size) and values in B–C represent shape variance (re-scaled to exclude PC1). In contrast to fig. 5, specimen labels are provided for all datapoints.

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