



# The shell and pelvic anatomy of the Late Jurassic turtle *Platychelys oberndorferi* based on material from Solothurn, Switzerland

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**Abstract** *Platychelys oberndorferi* is a stem pleurodire from the Late Jurassic of Europe. The majority of informative specimens originate from the Late Jurassic (late Kimmeridgian) Turtle Limestones exposed north of the city of Solothurn, Switzerland, but these findings remain poorly documented despite their global importance for understanding the evolution of pleurodire turtles. The available material of this species from this locality currently consists of five shells, one of which is associated with two cervical and one caudal vertebrae and a second with two caudal vertebrae and a phalanx, and 16 fragments mostly found in close proximity to one another but representing at least two different individuals. The Swiss material documents variation in the shape of the dorsal protuberances formed by the vertebrae, the number of supramarginals, the presence of a preneural, the orientation and lateral contacts of the neurals, fusion of neural VIII with suprapygial I, fusion of suprapygial II with the pygal, and the shape of the anal notch. All documented variation falls within the range of variation observed in material from the Late Jurassic (early Tithonian) type locality of Kelheim, Germany, and their referral to *Platychelys oberndorferi* is therefore confirmed. The utility of confluent plastral fontanelles in diagnosing the sexes is refuted. However, two specimens document substantial differences in anal notch morphology, which are confirmed to be consistent with sexual dimorphism,

with females having a shallow but broad anal notch framed by rounded xiphialstral processes, whereas males have a narrow anal notch that is framed by pointed xiphialstral processes.

**Keywords** Testudines · Pan-Pleurodira · Platychelyidae · Jurassic · Morphology

## Abbreviations

BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, USA
NHMUK	Natural History Museum, London, United Kingdom
NMB	Naturhistorisches Museum Basel, Basel, Switzerland
NMS	Naturmuseum Solothurn, Solothurn, Switzerland

## Introduction

Turtles (*Testudinata*) are one of the primary clades of extant amniotes with about 350 currently recognized species (TTWG 2014). All phylogenies currently agree that the clade of extant turtles is comprised of two crown clades: side-necked turtles (*Pleurodira*) with a primary distribution in the southern continents and hide-necked turtles (*Cryptodira*) with a global distribution (e.g., Crawford et al. 2015). While the cryptodiran stem lineage has an exceptionally rich fossil record throughout the Jurassic and Cretaceous of Asia (e.g., Sukhanov 2000; Rabi et al. 2010), the pleurodiran stem lineage is restricted to a small clade,

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*Platychelyidae*, which is restricted to the Late Jurassic to Early Cretaceous of the Caribbean, Mexico, Europe, and South America (Cadena and Joyce 2015; López-Conde et al. 2016).

The clade *Platychelyidae* is currently hypothesized to consist of five species: *Platychelys oberndorferi* Wagner 1853 from the Late Jurassic of Europe, *Notoemys laticentralis* Cattoi and Freiberg 1961 from the Late Jurassic of Argentina, *Notoemys oxfordiensis* (de la Fuente and Iturralde-Vinent 2001) from the Late Jurassic of Cuba, *Notoemys tlaxiacoensis* López-Conde et al. 2016 from the Late Jurassic of Mexico, and *Notoemys zapatocaensis* Cadena and Gaffney 2005 from the Early Cretaceous of Colombia. Of these five platychelyids, *Platychelys oberndorferi* was the first to be discovered and is known from relatively rich material, particularly from Switzerland, but the morphology of this taxon remains poorly described.

The first specimen of *Platychelys oberndorferi* was a partial carapace that was described by Wagner in 1853 from the Late Jurassic (early Tithonian) of Kelheim, Germany, in the eastern margin of the greater Solnhofen area. Three additional specimens have since been reported from the region, in particular a near complete carapace (Wagner 1861) and a partial carapace (Lydekker 1889) from the Late Jurassic of Kelheim and a well-preserved anterior plastral lobe from nearby Zandt (Zittel 1877). No other specimens have since been reported from the greater Solnhofen area, with exception of an exquisitely preserved skeleton held in a private collection (Karl and Tichy 2006). The type specimen unfortunately appears to have been destroyed during World War II (Cadena and Joyce 2015).

The first known Swiss specimens of *Platychelys oberndorferi* were discovered in near-synchrony with the German material. Rütimeyer (1859a, b) initially reported fossil material from Late Jurassic (late Kimmeridgian) sediments exposed near the city of Solothurn under the informal name *Helemys*, but soon after referred these specimens to *Platychelys oberndorferi* (Rütimeyer 1867, 1873), a decision that has been followed universally ever since (e.g., Bräm 1965; Mlynarski 1976; Gaffney et al. 2006; Cadena and Joyce 2015; Anquetin et al. 2017). All then available Swiss material was described in detail by Bräm (1965), but this contribution is of limited utility given that it only includes photographs for two out of five specimens and a composite reconstruction rather than illustrations of the individual specimens. Lapparent de Broin (2001, fig. 1) more recently provided an illustration of a shell, but this represents a composite of at least two specimens as well. Several additional specimens were recovered during excavations near Solothurn during the 1980s, but all are shell fragments that were found in isolation, though in general proximity (Meyer 1994). Although some of these fragments were sectioned for

histological study (Scheyer and Sander 2007; Scheyer 2009), the external morphology of these fragments has never been documented.

*Platychelys oberndorferi* was included in the first computer analysis of fossil turtle relationships, which concluded it to be a stem pleurodire (Gaffney et al. 1991). A number of subsequent analyses did not treat this fossil as a separate terminal, but rather utilized it to reconstruct the morphology of the ancestral stem pleurodire (e.g., Gaffney 1996; Hirayama et al. 2000; Gaffney et al. 2007). With the advent of species-level analyses, however, *Platychelys oberndorferi* once again featured prominently (e.g., Gaffney et al. 2006; Joyce 2007; Anquetin 2012) thereby affirming its status as one of the most important fossil turtles. Given that the available descriptions are limited in their utility, the vast majority of researchers are still forced to visit the relevant collections in Germany and Switzerland. The primary goal of this contribution is to provide (simpler) a comprehensive description of all available Swiss material of *Platychelys oberndorferi*. This work is complementary to the recent, detailed description and analysis of two cervical vertebrae that were found in association with one of the Swiss specimens described herein (Anquetin et al. 2017).

## Geological settings

All articulated shell material presented herein was collected over the course of the nineteenth century in commercial quarries located just north of the city limits of Solothurn, Switzerland. Given that all specimens were collected and sold by the quarry workers, the exact strata from which they were collected are not known. It appears certain, however, that all specimens were retrieved from several fossil-rich layers that are locally known as the *Solothurner Schildkrötenkalke* (i.e., Solothurn Turtle Limestones), which corresponds to the uppermost member of the Reuchenette Formation. This assertion is generally supported by many isolated fragments that were collected from these layers during formal excavations organized by the Department of Geosciences of the University of Bern in the 1980s at the St. Niklaus quarry just north of Solothurn and that also yielded a rich accompanying marine fauna known to the late Kimmeridgian in age (Meyer 1994).

## Materials

We here focus on describing the five shells and fragments of *Platychelys oberndorferi* that are housed at NMS and NMB. Additional specimens referable to this taxon are

known from BSPG, NHMUK, and MCZ, but these were not included herein, as these were collected from the Late Jurassic platy limestone quarries of the Solnhofen Region in southern Germany.

NMB So.596 (Figs. 1, 2, 3): This specimen is a complete carapace and partial plastron. The anterior margin and right posterior third of the plastron are not preserved. The left pelvis was illustrated by Rütimeyer (1867, pl. III, fig. 2). The specimen at that time was filled with sediment, preventing a visceral view, but was later prepared completely to reveal much of the internal anatomy, cervicals VI and VIII, and a caudal vertebra. The cervical vertebrae of NMB So.596 were briefly mentioned in several papers (Lapparent de Broin and Murelaga 1999; Lapparent de Broin 2001; de la Fuente and Iturrealde-Vinent 2001), but were only described recently together with the caudal (Anquetin et al. 2017). We refer the reader to this contribution for all aspects pertaining to the anatomy of these elements, as we see no need to provide redundant descriptions herein.

NMS 8685 (Fig. 4): This specimen is a complete carapace, but the plastron is not preserved. Sediment infill blocks the visceral view. NMS 8685 was previously depicted in dorsal view in a lithograph provided by Rütimeyer (1867, pl. III, fig. 1).

NMS 8686 (Figs. 5, 6, 7): This specimen consists of a complete carapace, a nearly complete plastron, two caudal vertebrae cataloged under the numbers NMS 8687 and NMS 8688, and a phalanx cataloged under the number NMS 8690. The right anterior portion of the anterior plastral lobe is not preserved. The left pelvis is intact but shifted anteriorly whereas the right pelvis is missing the acetabular region. Bräm (1965) provided photographs of the shell in dorsal (pl. 1, fig. 1), ventral (pl. 1, fig. 2), and lateral views (pl. 1, fig. 6), and of the two caudal vertebrae (pl. 1, figs. 3 and 4), which he interpreted to be cervicals. These photographs indicate that the acetabular region on the right pelvis was fully preserved in situ and has since fallen out. Lapparent de Broin (2001, fig. 1) provided an illustration of this specimen, but numerous deviations from the actually preserved morphology highlight that this is likely a composite.

NMS 8691 (Fig. 8): This specimen consists of the posterior two-thirds of a carapace in dorsal view and the displaced partial right half of the associated plastron in visceral view. The plastron of NMS 8691 appears to have been used by Rütimeyer (1867) to help reconstruct the shell of *P. oberndorferi*.

NMS 8692 (Fig. 9): This specimen is a partial carapace only lacking its right lateral margins. This specimen was photographed in ventral view by Bräm (1965). No dorsal view of NMS 8692 has been figured, although information from the dorsal view was apparently used to help create the composite illustrated by Lapparent de Broin (2001).

Disarticulated specimens (Figs. 10, 11): Systematic excavations at the St. Niklaus quarry combined with the re-identification of specimens in existing collections yielded 17 disarticulated shell bones that were identified herein by direct reference to the 5 available shells. The elements from the St. Niklaus quarry are from the same size class and some are even articulated with each other, in particular two pairs of peripherals (Fig. 10h–k). However, the presence of two partial left xiphplastra indicates that these fragments derive from at least two individuals (Fig. 11d). Three of these elements, in particular a left costal VI (NMS 22076a; Fig. 10c), a right peripheral VII (NMS 22070; Fig. 10i), and a left hypoplastron (NMS 22076b; Fig. 11e), were embedded in resin and sectioned for histological analysis (Scheyer and Sander 2007; Scheyer 2009).

## Systematic paleontology

**Testudines** Batsch 1788

**Pan-Pleurodira** Joyce et al. 2004

**Platychelyidae** Bräm 1965

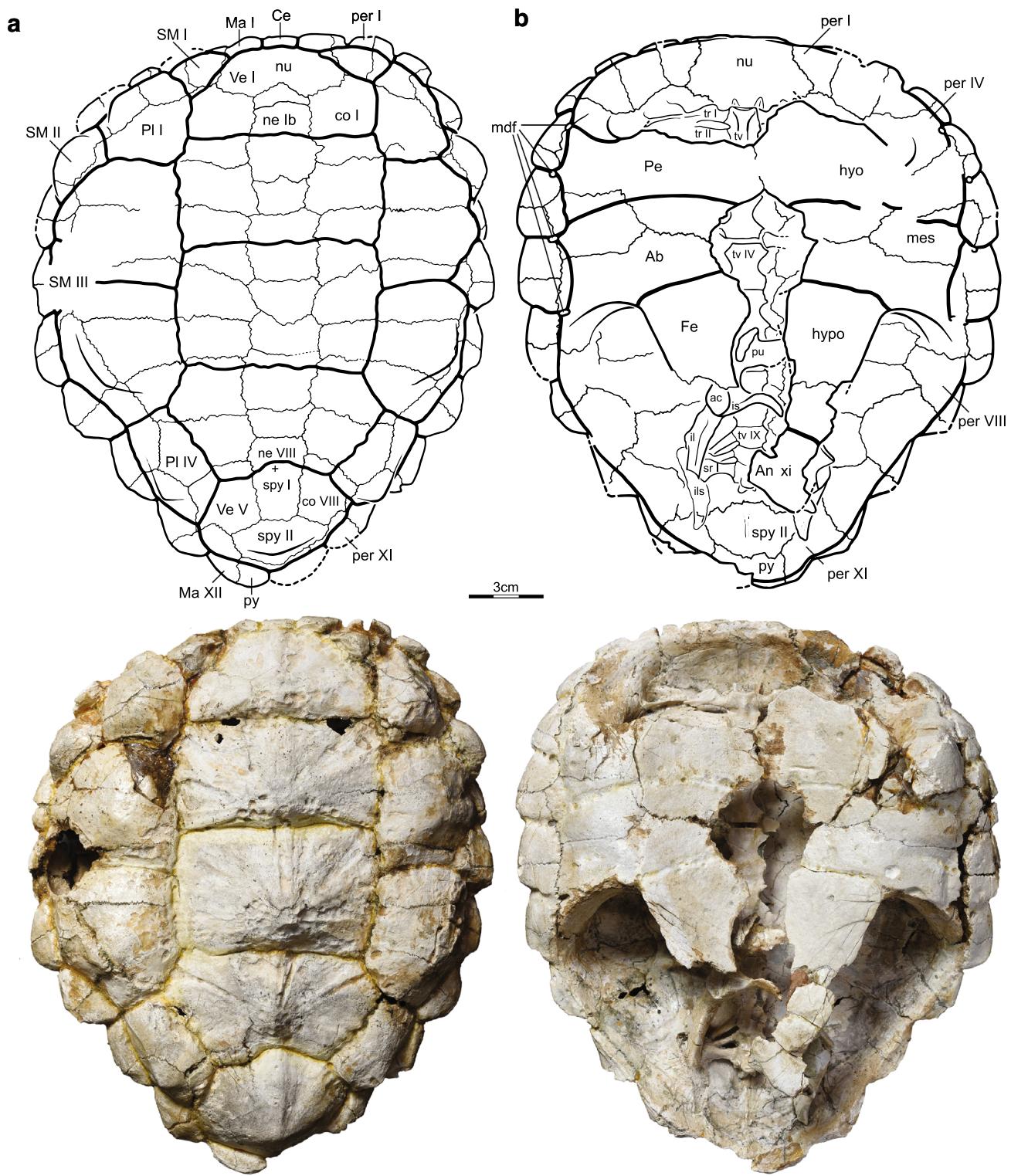
***Platychelys oberndorferi*** Wagner 1853

**Type specimen:** A near complete carapace (Wagner 1853, pl. 1; Meyer 1860, pl. 18.4), formerly housed at BSPG, but now lost (Cadena and Joyce 2015).

**Type locality:** Late Jurassic (Tithonian) of Kelheim, Germany (Wagner 1853; Cadena and Joyce 2015).

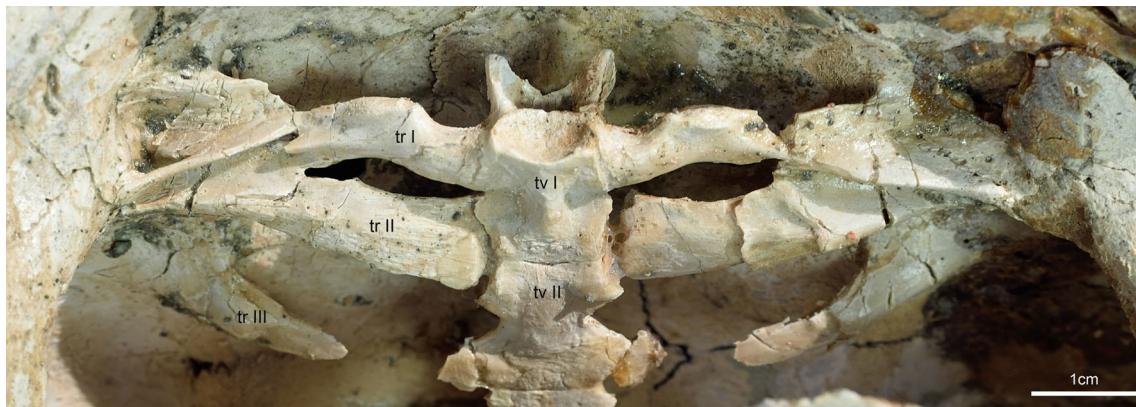
## Description

**Carapace:** In dorsal view, the carapace of *Platychelys oberndorferi* is generally round, but it tapers posterior to the contact of peripheral V and VI, creating a teardrop shape (Figs. 1a, 4, 5a, 8, 9a). The margin of the carapace is relatively smooth anteriorly but becomes increasingly more serrated towards the posterior. The carapace is sculptured on the dorsal surface in the form of three discontinuous keels. The median keel is created by well-developed protuberances that are situated at the posterior edges of vertebral scutes I–V and that form the centers of radial striations. Isolated costals reveal that the keels are massive in cross section (Fig. 10a). The lateral protrusions similarly correspond to pleural scutes I–IV. Dorsal sculpting is also created by the presence of three pyramidal supramarginals, with supramarginal I protruding dorsally and supramarginals II and III dorsolaterally. The size of the median and lateral protuberances varies between specimens. They are particularly pronounced in NMS 8691 and NMS 8685 (Figs. 4, 8), but more subdued in NMB So.596 and NMS 8692 (Figs. 1, 9). The position of the median protuberances on the vertebrals in relation to the intervertebral sulci also



**Fig. 1** NMB So.596, *Platychelys oberndorferi*, Late Jurassic (Kimmeridgian) of Solothurn, Switzerland. Photographs and illustrations of the shell in **a** dorsal and **b** ventral view. *Ab* abdominal scute, *ac* acetabulum, *An* anal scute, *Ce* cervical scute, *co* costal, *Fe* femoral scute, *hyo* hyoplastron, *hypo* hypoplastron, *il* ilium, *ils* iliac scar, *is*

ischium, *Ma* marginal scute, *mdf* musk duct foramen, *mes* mesoplastron, *ne* neural, *nu* nuchal, *Pe* pectoral scute, *per* peripheral, *Pl* pleural scute, *pu* pubis, *py* pygal, *SM* supramarginal scute, *spy* suprapygial, *sr* sacral rib, *tr* thoracic rib, *tv* thoracic vertebra, *Ve* vertebral scute, *xi* xiphiplastron



**Fig. 2** NMB So.596, *Platychelys oberndorferi*, Late Jurassic (Kimmeridgian) of Solothurn, Switzerland. Photographic detail of the anterior thoracic column. *tr* thoracic rib, *tv* thoracic vertebra

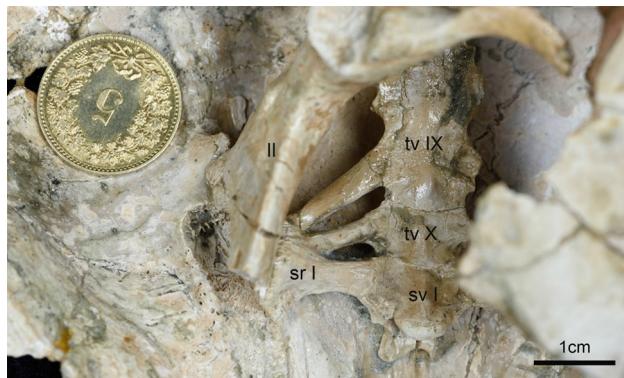
varies. In specimens NMB So.596, NMS 8685, and NMS 8686, the protuberances are more centrally located on the vertebrals and radiate outwards in all directions (Figs. 1, 4, 5), whereas in specimens NMS 8691 and NMS 8692 the protuberances begin sharply at the sulcus and radiate anteriorly only (Figs. 8, 9). The inflated marginals produce additional protuberances.

**Nuchal:** The nuchal is completely preserved in all specimens with the exception of NMS 8691 (Figs. 1a, 4, 5a, 8, 9a). The nuchal is roughly rectangular to hexagonal, up to twice as wide than long, and has lateral sutures that taper medially towards the anterior margin of the carapace. The nuchal contacts neural I posteriorly, costal I posterolaterally, and peripheral I anterolaterally in all specimens. The nuchal shares an additional contact with peripheral II in NMS 8685 (Fig. 4). Neural I deeply intrudes into the nuchal in NMB So.596 creating an anteriorly pointing triangular suture (Fig. 1a). The suture between the nuchal and neural I is otherwise anteriorly concave in NMS 8686, NMS 8692, and NMB So.596, and is straight in NMS 8685. The cervical and the marginals that cover the nuchal heavily sculpt its anterior margin.

**Neurals and pygals:** The Solothurn material of *Platychelys oberndorferi* has eight neurals of varying size and shape in an alternating pattern: neural I is large, neural II is small, neural III is large, neurals IV and V are small, neural VI is large, neural VII is small, and neural VIII is large once again (Figs. 1a, 4, 5a, 8, 9a). Most of the neurals share a lateral contact with their respective costals and a small contact with the previous or following costal, usually the previous one. There is, however, much variation in the five specimens from Solothurn. Specimens NMS 8692 and NMB So.596 have an additional, horizontal suture dividing neural I into a small anterior and large posterior portion (Figs. 1a, 9a). This creates a small, rectangular

“preneural”, but if this additional suture is ignored, the shape and contacts of the eight neurals are nearly identical to those of the other specimens. We thus label the anterior two elements ‘Ia’ and ‘Ib’ for specimens NMS 8692 and NMB So.596 in the figures, but discuss them combined as neural I when making comparisons with other specimens. In most specimens, neural VIII is fused with suprapygal I, creating a long element that we term neural VIII/suprapygal I. Complete fusion occurs on all specimens except for NMS 8692 where the suture is reduced but visible (Fig. 9a). NMS 8691 has additional sutures within neurals III and VIII (Fig. 8). These sutures run parallel to the anteroposterior axis, do not appear to create new neurals, and are thus likely a pathology of that specimen.

Neural I is the largest of the set, longer than wide, and roughly rectangular. It shares sutures with costals I and II laterally and with the nuchal anteriorly. Neural II is roughly rectangular, wider than long, and only contacts costal II laterally, with the exception of specimen NMS 8686 where neural II contacts costal III posterolaterally as well (Fig. 5a). Neural III is large and rectangular, ranging from nearly equidimensional in NMB So.596, NMS 8685 and NMS 8686 (Figs. 1a, 4, 5a) to longer than wide in NMS 8691 and NMS 8692 (Figs. 8, 9a). Neural III contacts costal II anterolaterally and costal III laterally. The contact of neural III with costal IV varies greatly between specimens. In specimens NMB So.596 and NMS 8692, there is no contact between neural III and costal IV (Figs. 1a, 9a). In specimens NMS 8686 and NMS 8685 contact is asymmetrical, with only left posterolateral contact in NMS 8686 and only right posterolateral contact in NMS 8685 (Figs. 4, 5a). Finally, neural III contacts costal IV posterolaterally on both sides in NMS 8691 (Fig. 8). This difference of contacts is largely due to variation in the shape of neural III. Specimen NMS 8691 is unique in having a very wide neural III that expands posterolaterally on both sides and thus neural III shares a relatively broad contact with costal



**Fig. 3** NMB So.596, *Platychelys oberndorferi*, Late Jurassic (Kimmeridgian) of Solothurn, Switzerland. Photographic detail of the sacrum. *il* ilium, *sr* sacral rib, *sv* sacral vertebra, *tv* thoracic vertebra

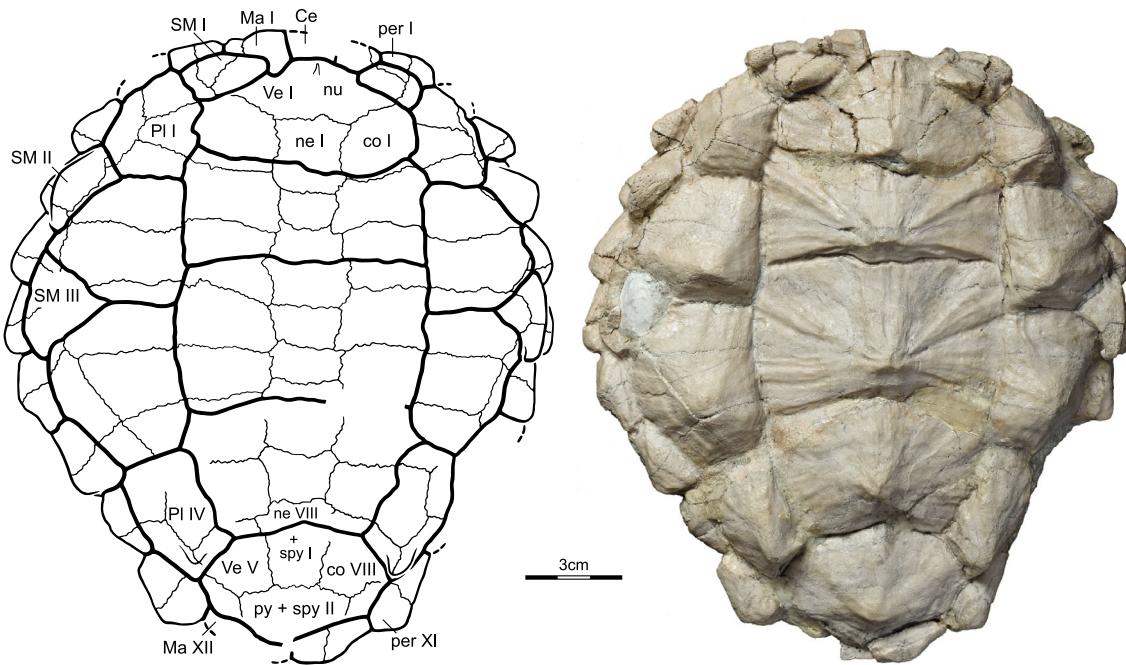
IV. Neurals IV and V are small, rectangular, and wider than long. Neural IV contacts costal IV laterally, as well as costal III anterolaterally in NMB So.596, NMS 8692 (Figs. 1a, 9a), in the right side of NMS 8686 (Fig. 5a), and in the left side of NMS 8685 (Fig. 4). Neural V contacts costal IV anterolaterally and costal V laterally in all specimens. Neural VI resembles neural III in that it is large, rectangular, and equidimensional to slightly longer than wide. Neural VI contacts costal V anterolaterally, costal VI laterally, and costal VII posterolaterally in all specimens apart from NMB So.596, where neural VI and costal VII do not share a sutural contact (Fig. 1a). Neural VII is very similar to neutrals IV and V in shape in that it is small, rectangular, and wider than long. Neural VII shares a lateral contact with costal VII in all specimens as well as an anterolateral contact with costal VI in NMB So.596 (Fig. 1a). Neural VIII/suprapygial I is large and hexagonal, longer than wide, and narrower posteriorly than anteriorly. In specimen NMS 8691, where a division is apparent between neural VIII and suprapygial I, neural VIII is very small, rectangular, wider than long, and contacts costal VII anteromedially to anterolaterally and costal VIII laterally (Fig. 8).

The bones that occupy the pygal region in the available material vary among specimens. Specimen NMB So.596 has a clear transverse suture dividing the region into a pygal and a suprapygal of roughly equal rectangular portions (Fig. 1a). This condition is also hinted at in NMS 8692 in the form of a long horizontal fracture not apparent in the illustration that runs within a sulcus and that may actually represent a suture as well (Fig. 9a). The pygal and suprapygal of the remaining specimens are fused into one large element, with no visible trace of a suture.

**Costals:** *Platychelys oberndorferi* has eight pairs of costals, with the series completely preserved in NMB So.596, NMS 8685, and NMS 8686 (Figs. 1a, 4, 5a), but not in NMS 8691, where the majority of costal I and the right anterior

margin of costal II is missing (Fig. 8), and NMS 8692, where all the costals on the right side of the carapace are partially or completely absent (Fig. 9a). A complete neural series prevents any medial contact of the costals. All eight costals are rectangular in shape and much wider than long with the exception of costal VIII, which tapers posteromedially and is slightly longer than wide. NMS 8692 is missing much of the distal portions of the carapace and only preserves costal–peripheral contacts with peripherals I–III and VIII–XI on the left side (Fig. 9a). Specimen NMS 8691 is missing a large portion of the anterior carapace and the costal–peripheral contacts prior to costal III are not preserved (Fig. 8). On the other four specimens, one or both sides of the carapace have most of the costal–peripheral contacts intact (Figs. 1a, 4, 5a, 9a). All costal–peripheral contacts are accounted for between the five available specimens, although no single carapace preserves all of these contacts. The medial portion of the costals that is covered by the vertebrals is relatively flat, but the distal portion that is covered by the pleurals is greatly domed. This condition differs from the vast majority of other turtles, in which the costals are rounded to flat elements in transverse section.

A complete neural series prevents any medial contact of the costals. All eight costals are rectangular in shape and much wider than long with the exception of costal VIII, which tapers posteromedially and is slightly longer than wide (Figs. 1a, 4, 5a, 8, 9a). The costals share sutural contacts with both neutrals and peripherals. For neural contacts, see the previous section. Costal I deviates from the rectangular form of the other costals in having an enlarged anteromedial portion and shares a suture with the lateral portion of the nuchal. Costal I contacts peripherals I–IV in all specimens except NMS 8685, where neither peripheral I or peripheral IV contact costal I due to the presence of a reduced peripheral I in this specimen (Fig. 4). Costal II contacts peripherals IV and V on all specimens and additionally peripheral III in NMS 8685 (Fig. 4). Costal III contacts peripherals V and VI in all specimens. Costal IV contacts peripherals VI and VII in all specimens. Costal IV also contacts peripheral VIII posterolaterally in NMS 8686 and NMS 8691 (although the contact between right costal IV and right peripheral VIII is obstructed in dorsal view by lateral protuberances) (Figs. 5a, 8), and asymmetrically in NMS 8685, as only the left costal IV contacts left peripheral VIII (Fig. 4). Costal IV contacts peripheral VIII on the left sides of NMB So.596 and NMS 8692, but since the right costal–peripheral contact of this specimen is poorly preserved in the former and absent in the latter, it is uncertain whether this contact is symmetrical in these specimens (Figs. 1a, 9a). Costal V shares a small anterolateral contact with peripheral VII in the right side of specimen NMS 8685, but no contact between costal V and



**Fig. 4** NMS 8685, *Platychelys oberndorferi*, Late Jurassic (Kimmeridgian) of Solothurn, Switzerland. Photograph and illustration of carapace in dorsal view. *Ce* cervical scute, *co* costal, *Ma* marginal

scute, *ne* neural, *nu* nuchal, *per* peripheral, *Pl* pleural scute, *py* pygal, *SM* supramarginal scute, *spy* suprapygial, *Ve* vertebral scute

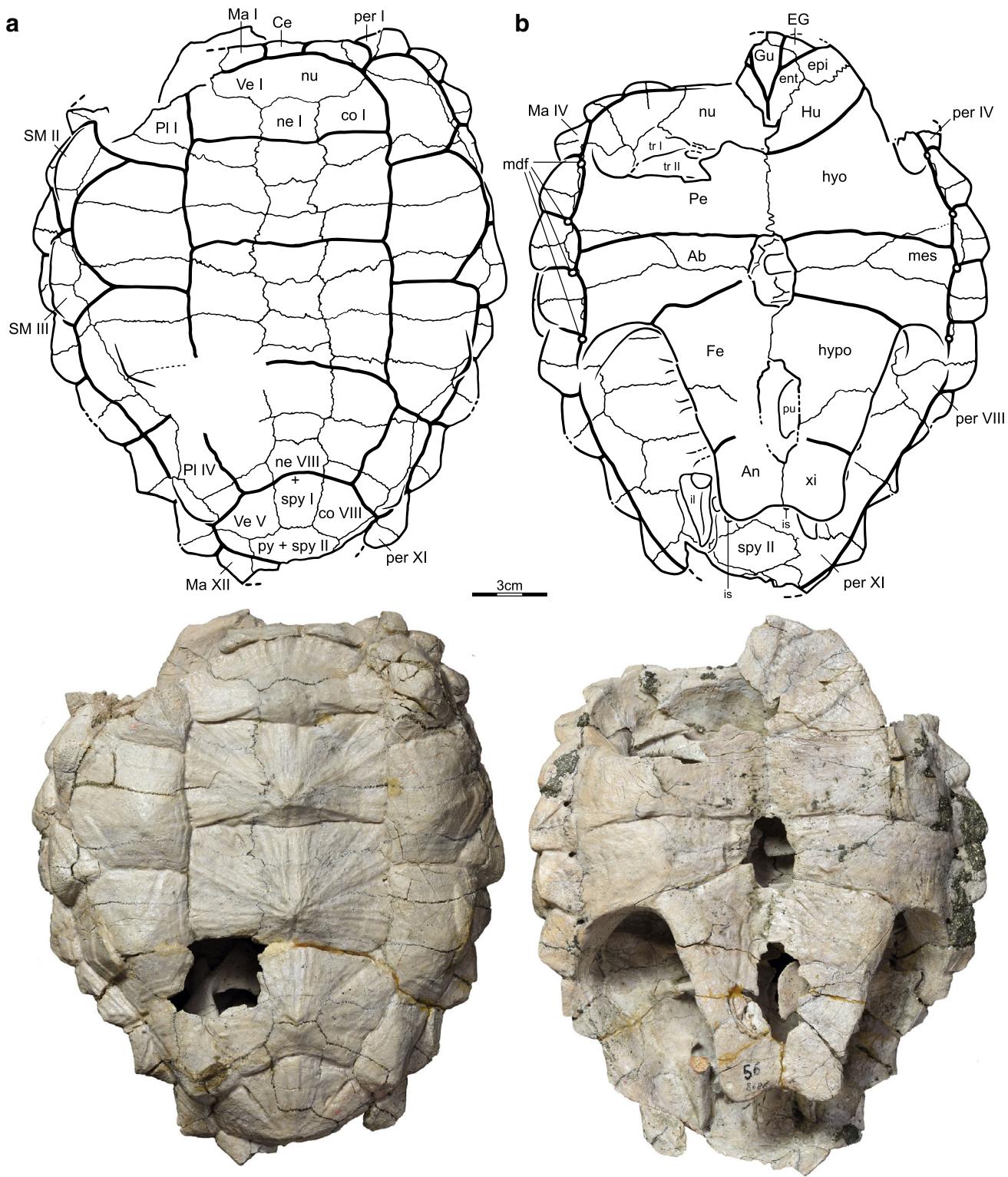
peripheral VII exists in any other specimen (Fig. 4). Although costal V also appears to contact peripheral VII in the right side of specimens NMS 8686 and NMS 8691, this is again an illusion created in the dorsal illustration due to high lateral protuberances (Figs. 5a, 8). Costal V contacts peripheral VIII in all specimens. There is a unique contact between left costal V and left peripheral IX in NMB So.596 (Fig. 1a). Costal VI shares an anterolateral contact with peripheral VIII in specimens NMS 8685, NMS 8686, NMS 8692, and NMS 8691 (Figs. 4, 5a, 9a), but does not contact on the left side of NMB So.596 (Fig. 1). Costal VI contacts peripheral IX in all specimens. Costal VII contacts peripherals IX and X in all specimens. Finally, costal VIII, the smallest of the set, shares sutures with peripherals X and XI and suprapygial II.

**Peripherals:** Eleven pairs of peripherals are present, ranging in shape from equidimensional and rectangular to roughly hexagonal (Figs. 1a, 4, 5a, 8, 9a). The anterior peripherals are less consistent among specimens than the posterior ones due to the high degree of sculpturing in the anterolateral portion of the carapace of NMS 8685 (Fig. 4). Asymmetry also exists in the shapes and sutural contacts of several peripherals in specimens NMB So.596 and NMS 8685 (Figs. 1a, 4). No single specimen has complete preservation of every peripheral. NMB So.596 is the most complete of the specimens and preserves nearly all peripherals with the exception of the anterior margin of left peripheral II, the right lateral portions of left peripherals VI

and VII, and the posterior portion of right peripheral XI (Fig. 1a). Only the posterior portions of left peripherals I–III and left peripherals VIII–XI are visible in NMS 8692 (Fig. 9a). Peripherals II–V are in contact with the hypoplastron, peripherals V and VI with the mesoplastron, and peripherals VI–VIII with the hypoplastron. The surface of all peripherals is highly irregular due to the development of domed carapacial scutes. The medial contacts with the costals are detailed above.

**Cervical scute:** The single cervical scute is not preserved in specimens NMS 8685 and NMS 8691 (Figs. 4, 8) and is only partially preserved in NMS 8692 (Fig. 9a). In specimens NMB So.596 and NMS 8686 (Figs. 1a, 5a) the cervical scute is rectangular and slightly wider than long, although it appears to be much wider than long in dorsal view due to the three dimensionality of this portion of the carapace. The cervical covers a small portion of the nuchal along the midline on the dorsal side of the carapace, but only narrowly covers this element on the visceral side. The cervical contacts marginal I laterally and vertebral I posteriorly.

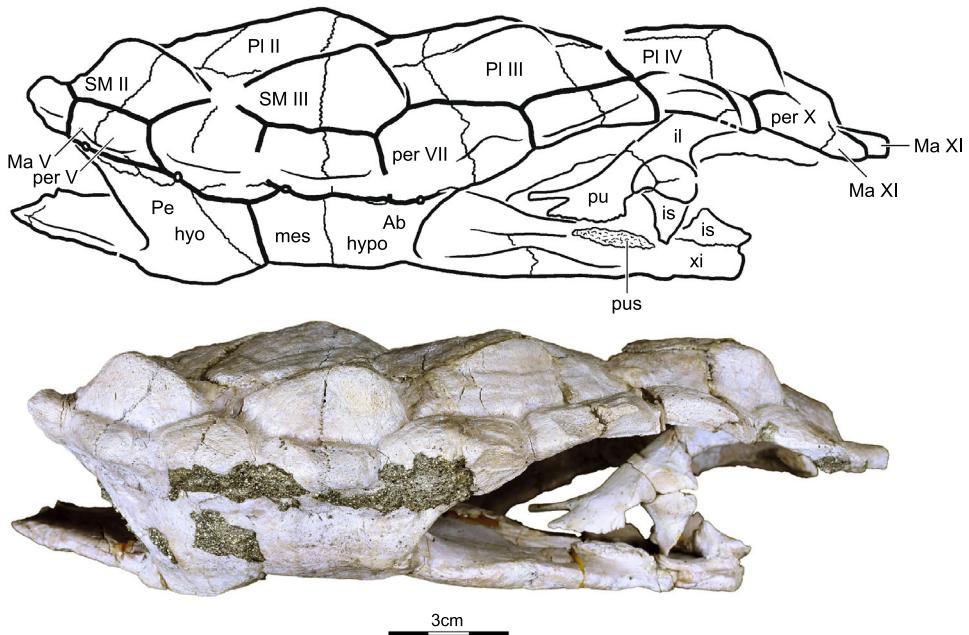
**Vertebrales:** *Platychelys oberndorferi* has five vertebral scutes, clearly preserved in all specimens except NMS 8691 (Fig. 8), where the majority of the anterior portion of vertebral I is not preserved, and NMS 8692 (Fig. 9a), which does not preserve the right half of vertebral I or the right lateral portion of vertebral II. Vertebral I is roughly



**Fig. 5** NMS 8686, *Platychelys oberndorferi*, Late Jurassic (Kimmeridgian) of Solothurn, Switzerland. Photographs and illustrations of the shell in **a** dorsal and **b** ventral view. *Ab* abdominal scute, *An* anal scute, *Ce* cervical scute, *co* costal, *EG* extragular scute, *ent* entoplastron, *epi* epplastron, *Fe* femoral scute, *Gu* gular scute, *Hu*

humeral scute, *hyo* hyoplastron, *hypo* hypoplastron, *il* ilium, *Ma* marginal scute, *mdf* musk duct foramen, *mes* mesoplastron, *ne* neural, *nu* nuchal, *Pe* pectoral scute, *per* peripheral, *Pi* pleural scute, *py* pygal, *SM* supramarginal scute, *spy* suprapygial, *tr* thoracic rib, *Ve* vertebral scute, *xi* xiphoplastron

**Fig. 6** NMS 8686, *Platychelys oberndorferi*, Late Jurassic (Kimmeridgian) of Solothurn, Switzerland. Photograph and illustration of the shell in lateral view. *Ab* abdominal scute, *hyo* hyoplastron, *hypo* hypoplastron, *il* ilium, *is* ischium, *Ma* marginal scute, *mes* mesoplastron, *Pe* pectoral scute, *per* peripheral, *Pl* pleural scute, *pu* pubis, *pus* pubic scar, *SM* supramarginal scute, *xi* xiphiplastron



semicircular to rectangular in shape and is wider than long with an arcuate anterior sulcus and a straight posterior sulcus. Vertebral I contacts the cervical anteriorly, marginal I anteriorly, supramarginal I anterolaterally, and pleural I laterally. Vertebral I covers the posterior half of the nuchal, extends halfway across costal I in all specimens, and covers the anterior half of neural I on all specimens except NMS 8685, where vertebral I covers the anterior two-thirds of neural I (Fig. 4). Vertebrals II and III are both similar in size, rectangular, and are wider than long. Vertebral II contacts pleural I anterolaterally and pleural II laterally, covers roughly a third of costals I–III, and covers the posterior portion of neural I, all of neural II and the anterior half of neural III. Vertebral III contacts pleural II anterolaterally and pleural III laterally, covers the posterior half of neural III, the entirety of neutrals IV and V, and the anterior fifth of neural VI. Vertebral III also extends laterally to cover roughly a third of costals III–VI. Vertebral IV is nearly hexagonal in shape, slightly narrower than vertebrals I and II, and wider anteriorly than posteriorly. Vertebral IV contacts pleural III anterolaterally, pleural IV laterally and covers the posterior four fifths of neural VI, all of neural VII and the anterior third of neural VIII. Vertebral IV also covers a large posteromedial portion of costal VI, roughly half of costal VII and a small anteromedial portion of costal VIII. Vertebrals II–IV are wider than the pleurals. Vertebral V is octagonal in specimens NMS 8685, NMS 8686, NMS 8692, and NMB So.596 (Figs. 1, 4, 5a, 9a), but appears heptagonal on specimen 8691 due to a straightened anterior sulcus (Fig. 8). Vertebral V contacts pleural IV anterolaterally, the posterior half of marginal XI posterolaterally, and

marginal XII posteriorly. In NMS 8692 this scute, furthermore, contacts the supracaudal scute posteriorly (Fig. 9a). Vertebral V covers the posterior two-thirds of neural VIII, the posterior portion of costal VIII, and the suprapygals, and the anterior portion of the pygal, at least as inferred from those specimens where the sutures are clear in this region.

**Pleurals:** Four pairs of pleural scutes are clearly visible on all specimens except NMS 8692, which does not preserve the right pleural series (Figs. 1a, 4, 5a, 6, 8, 9a). Right pleural I is also not preserved on NMS 8691 (Fig. 8) and is anteriorly damaged in NMS 8686 (Fig. 5a). All pleurals contact two vertebrals medially: pleural I contacts vertebrals I and II, pleural II contacts vertebrals II and III, pleural III contacts vertebrals III and IV, and pleural V contacts vertebrals IV and V. Pleurals I and II are pentagonal in shape, slightly longer than wide, and have a fairly straight medial edge. Pleural I is strongly keeled on all specimens, especially in NMS 8685 and NMS 8686, where the pleural I is nearly pyramidal (Figs. 4, 5a). In NMB So.596, NMS 8685, and S9692 pleural I contacts supramarginal I anteromedially, the posteriormost portion of marginal II anteriorly, marginals III and IV laterally, and supramarginal II posterolaterally (Figs. 1a, 4, 9a). In NMS 8686 supramarginal I is missing, allowing contact between pleural I and the full length of marginal II, as well as the posterior portion of marginal I (Fig. 5a, 6). Pleural II is larger than pleural I and does not display such a pronounced vertical keeling, although there is fairly strong ridging in the posterior portion of pleural II in specimens NMS 8685 and NMS 8691 (Figs. 4, 8). Pleural II contacts



**Fig. 7** *Platychelys oberndorferi*, Late Jurassic (Kimmeridgian) of Solothurn, Switzerland. **a** SMNS 8688, proximal caudal vertebra, in left lateral, right lateral, dorsal, ventral, anterior, and posterior view, from left to right. **b** SMNS 8687, distal caudal vertebra, in left lateral,

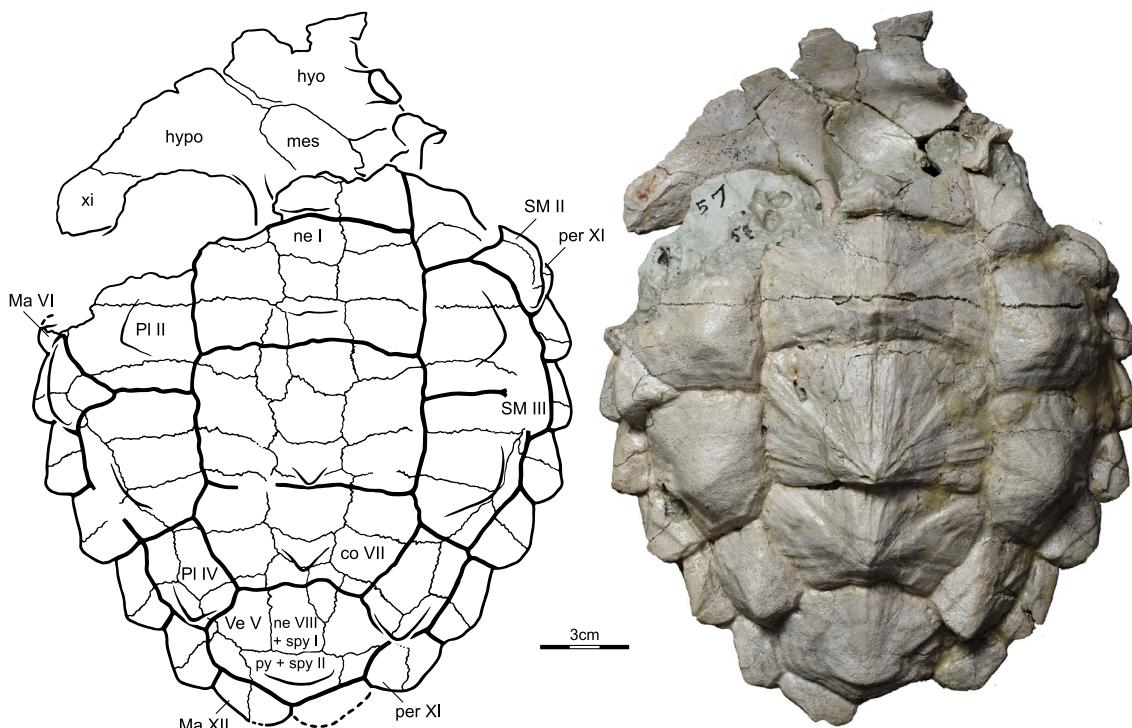
right lateral, dorsal, ventral, anterior, and posterior view, from left to right. **c** SMNS 8690, a phalanx in dorsal, palmar, and lateral views, from left to right. All specimens were found together with NMS 8686 and likely represent the same individual

supramarginal II anterolaterally, marginal VI laterally, and supramarginal III posterolaterally. Its contact with marginals V and VII are completely blocked by supramarginals II and III. Pleural III resembles pleural II in size but is more rectangular and is longer than wide. It contacts supramarginal III anteriorly and marginals VIII and IX laterally. Pleural IV is narrower and more rectangular than pleurals I–III and has very strong posterior ridges on specimens NMS 8685 and NMS 8691 (Figs. 4, 8). Lastly, pleural IV shares a small anterior contact with marginal IX and broad lateral contacts with marginals X and XI.

**Supramarginals:** The available material of *Platychelys oberndorferi* from Solothurn variously exhibits two or three pairs of supramarginals (Figs. 1a, 4, 5a, 6, 8, 9a). The supramarginal located between vertebral I and pleural I, herein termed supramarginal I, is clearly visible in specimens NMB So.596, NMS 8685 and the left anterior margin of NMS 8692 (Figs. 1a, 4, 9a), but is lacking in NMS 8686 (Figs. 5a, 6). The relevant part of the shell is not preserved in NMS 8691 (Fig. 8). Supramarginal I is smaller than the other supramarginals, is wider than long, and ranges in shape from roughly pyramidal in NMS 8692 (Fig. 9a) to more semi-lunate in NMB So.596 and NMS 8685 (Figs. 1a, 4). When present, supramarginal I is located between vertebral I, pleural I, and marginals I and II. This element mostly covers peripheral I, but also laps slightly onto the nuchal, peripheral II and costal I in NMS 8692 and

NMB So.596 (Fig. 1a, 9a). Peripheral I is greatly reduced in NMS 8685 and supramarginal I therefore has a larger overlap onto the nuchal, a minor overlap onto peripheral II, and no clear overlap onto costal I (Fig. 4). Supramarginal II is at least partially present in all specimens: only the right supramarginal II is missing in specimen NMS 8686 (Figs. 5a, 6), whereas only a remnant of the left supramarginal 2 is present in NMS 8692 (Fig. 9a). Supramarginal II is larger than supramarginal I, equidimensional, and consistently pyramidal in shape. It sits between pleurals I and II and marginals IV–VI and mostly covers peripheral IV, with minor overlaps onto peripherals III and IV and costal II. The left supramarginal III is missing in specimen NMB So.596 (Fig. 1a) and both are missing in NMS 8692 (Fig. 9a). Supramarginal III is nearly identical to supramarginal II in size and shape and is located between pleurals II and III and marginals VI–VIII. It evenly covers much of peripherals VI and VII, as well as part of peripheral V in NMS 8685 (Fig. 4), and partially covers a distal portion of costals III and IV.

**Marginals:** The available material of *Platychelys oberndorferi* has 12 pairs of marginals that form increasingly deep serrations towards the posterior of the carapace (Figs. 1a, 4, 5a, 6, 8, 9a). A complete marginal series is only present on the left side of NMB So.596, which also preserves all but marginal XII on the right side (Fig. 1a). Only marginal XI and XII and left marginals VIII and IX



**Fig. 8** NMS 8691, *Platychelys oberndorferi*, Late Jurassic (Kimmeridgian) of Solothurn, Switzerland. Photograph and illustration of the shell in dorsal view. *co* costal, *hyo* hyoplastron, *hypo*

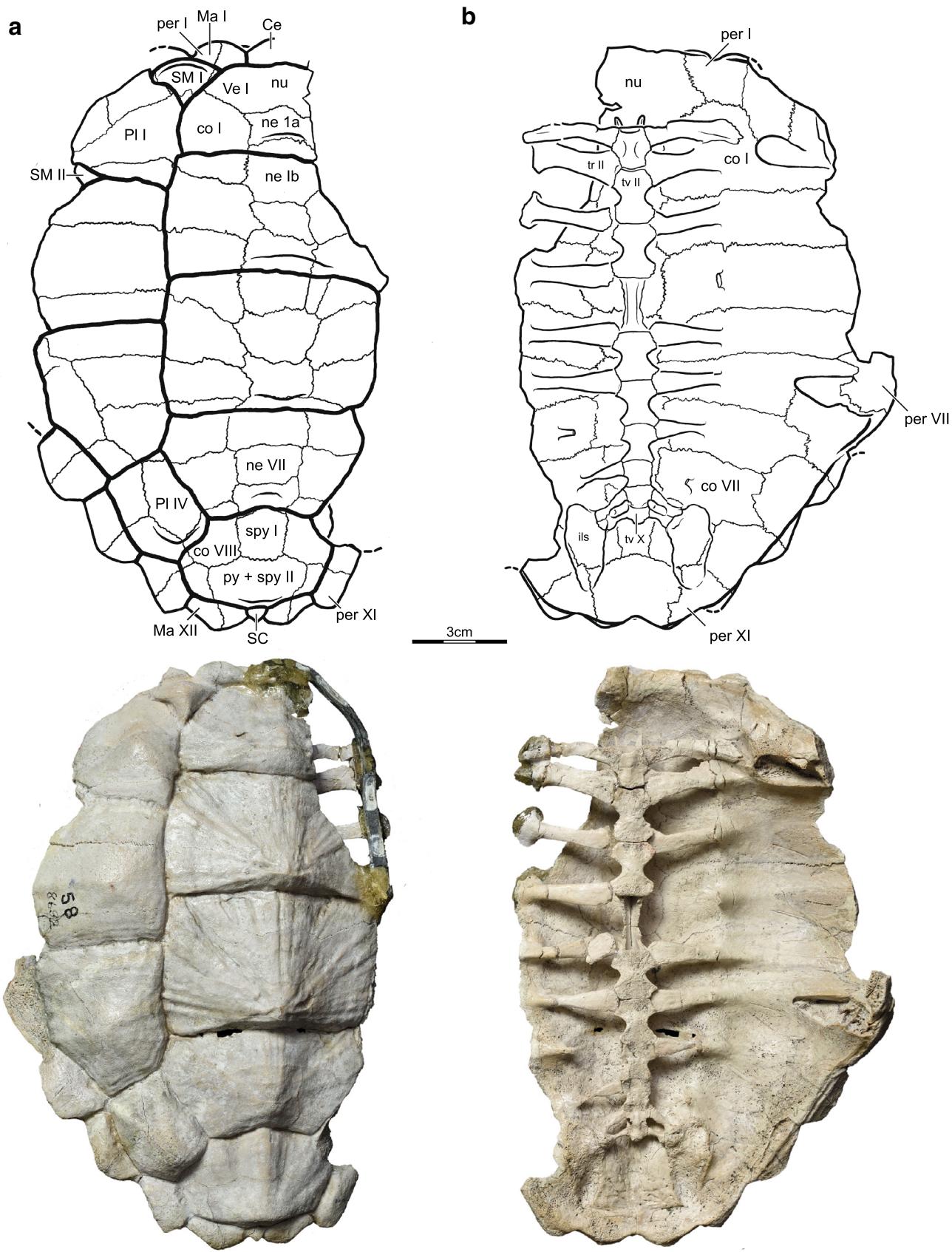
hypoplastron, *Ma* marginal scute, *mes* mesoplastron, *ne* neural, *per* peripheral, *Pl* pleural scute, *py* pygal, *SM* supramarginal scute, *spy* suprapygial, *Ve* vertebral scute, *xi* xiphoplastron

are preserved on NMS 8692 (Fig. 9a), whereas left marginals VI–XII and right marginals III–XII are preserved in specimen NMS 8691 (Fig. 8). Left marginals II–IV, right marginal XII, and the medial half of left marginal XII are not preserved in specimen NMS 8686 (Figs. 5a, 6). Finally, specimen NMS 8685 does not preserve marginals III, right marginals IX and X, or left marginal XII (Fig. 4). The contacts between the marginals and pleurals and supramarginals are described above.

A small triangular scute situated between the marginals XII is visible in specimen NMS 8692 (Fig. 9a). For simplicity, we name this element the supracaudal, though no homology is implied with the similarly named scute in extant tortoises (Testudinidae), which represents the medially fused marginals XII. This appropriate region is unfortunately damaged in all other specimens and it is therefore unclear if this scute is unique to NMS 8692 or occurs universally in *Platychelys oberndorferi*.

**Plastron:** Relatively complete plastra are only present in specimens NMB So.596 and NMS 8686 (Figs. 1b, 5b, 6). Only minor fragments are associated with NMS 8695 and the entire plastron is missing in NMS 8692 (Figs. 4, 9). The lateral portion of the right half of the plastron is visible but displaced anteriorly in NMS 8691 (Fig. 8). The plastron of NMS 8686 is nearly fully complete but

does not preserve parts of the anterior plastral lobe, in particular the left epiplastron (Fig. 5b). The plastron on NMB So.596 is far less complete and is missing all plastral elements above the anterior third of the hyoplastron and the right side below the hyoplastral–xiphoplastral suture (Fig. 1b). The plastra of both NMB So.596 and NMS 8686 display a slight central concavity, but this is likely an artifact of minor crushing, not necessarily a sign of sexual dimorphism. In NMS 8686, a central plastral fontanelle is developed between the hyoplastra and hypoplastra and a separate, xiphoplastral fontanelle of similar dimensions is apparent between the hyoplastra and xiphoplastra (Fig. 5b). The presence of separate central and xiphoplastral fontanelles is confirmed by both available disarticulated hypoplastra, NMS22075 and NMS22076b (Fig. 11c, e). These plastral fontanelles appear to be better developed in NMB So.596 and they may have even been confluent, but this is difficult to ascertain with confidence as the specimen is damaged in the relevant region (see hypoplastra below) (Fig. 1b). The plastron is connected to the carapace by way of a well-developed osseous bridge with well-developed axillary and inguinal buttresses. The axillary buttresses have a thickened end that inserts into the distal portions of costal I, nearly articulates with thoracic rib I, and contacts



**Fig. 9** NMS 8692, *Platychelys oberndorferi*, Late Jurassic (Kimmeridgian) of Solothurn, Switzerland. Photograph and illustration of carapace in **a** dorsal and **b** visceral view. *Ce* cervical scute, *co* costal, *il* iliac scar, *Ma* marginal scute, *ne* neural, *nu* nuchal, *per* peripheral, *Pl* pleural scute, *py* pygal, *SC* supracaudal scute, *SM* supramarginal scute, *spy* suprapygial, *tr* thoracic rib, *tv* thoracic vertebra, *Ve* vertebral scute

peripheral II (Fig. 9b). The inguinal buttress, in contrast, broadly contacts the distal portions of peripheral VIII and the anterior quarter of peripheral VIII (Fig. 9b). The contact with costal I is confirmed by the two available isolated costals (Fig. 10a, b). The anterior margin of the plastron is not completely preserved in any specimen, but appears to have been rounded and slightly protruding beyond the anterior rim of the carapace. The posterior plastral lobe is slightly shorter and narrower than the anterior lobe and contains a wide and fairly shallow, U-shaped anal notch at the posterior margin that shows some variability (see below).

**Plastral bones:** NMS 8686 has a single, medially situated entoplastron near the anterior margin of the plastron (Fig. 5b). The entoplastron is prevented from touching the edge of the anterior plastral lobe due to a narrow anteromedial contact of the epiplastra. The entoplastron contacts the epiplastra anteriorly and the hyoplastron posterolaterally. The posterior epiplastral process is damaged, but appears to have been reduced as in most crown turtles. Two small pits are developed on the visceral side of the entoplastra for the ligamentous attachment with the shoulder girdle (not figured).

A single epiplastron is preserved on the left side of NMS 8686, but the anterior margin is partially damaged (Fig. 5b). The epiplastra share a poorly developed contact with each other anteromedially and share a broad medial contact with the entoplastron and a relatively small posterior contact with the hyoplastron. A pair of roughened pits is developed on the visceral side between the epiplastra and entoplastron that correspond in their placement to the epiplastral processes found in more basal turtles. However, there is no evidence for ossified epiplastral processes.

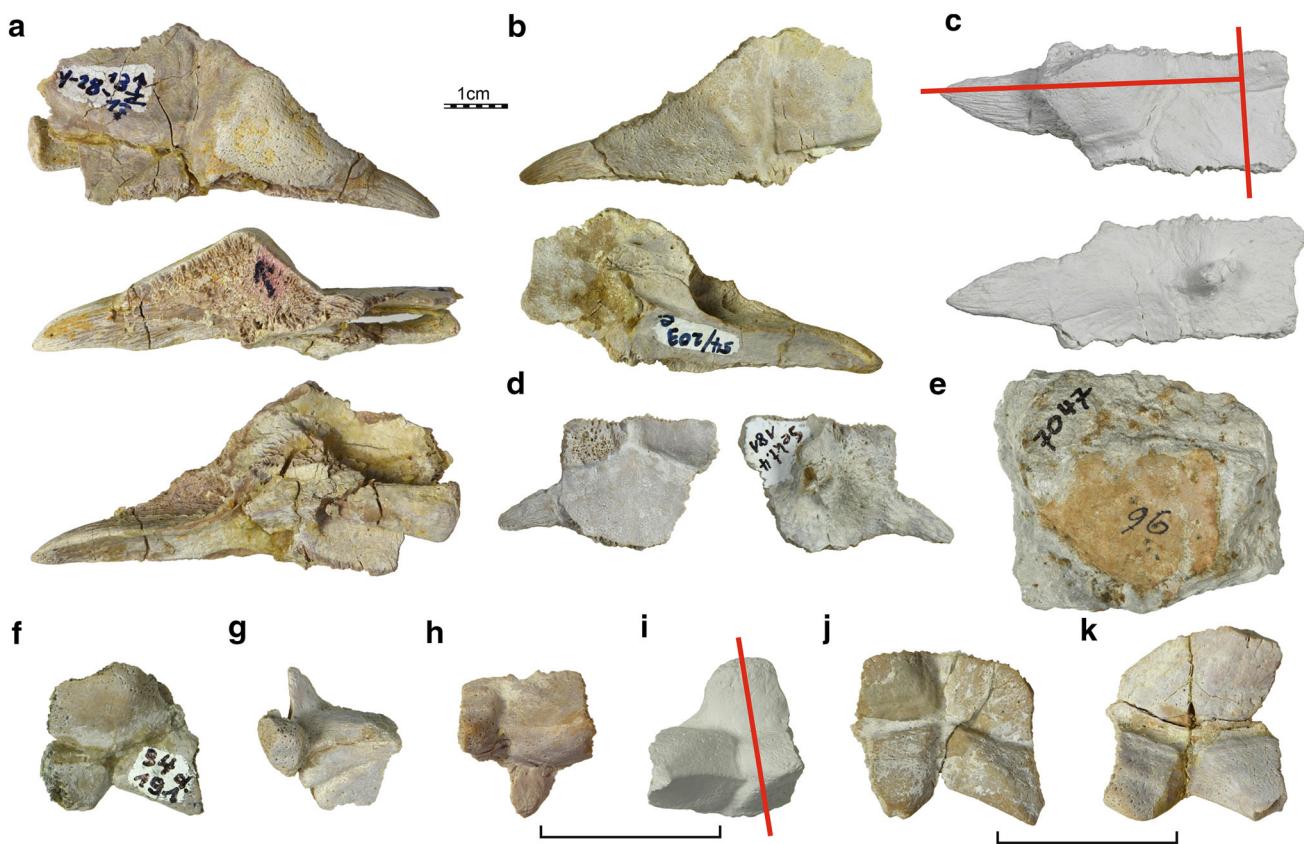
The hyoplastra form most of the anterior plastral lobe and contact the epiplastra anteriorly, the entoplastron anteromedially, the mesoplastra posterolaterally, and hypoplastra posteriorly, contribute to the anterior half of the central plastral fontanelle posteromedially, and contact one another medially (Figs. 1b, 5b, 6). The hyoplastra form well-developed axillary buttresses that insert distally into the distal aspects of costal I and nearly contact thoracic rib I (Figs. 2, 9b). The buttress has a vertical component that helps form a well-defined visceral cavity along the bridge. The hyoplastra laterally contacts peripherals II–V, of which

the contact with peripherals IV and V and the posterior portion of III are covered by scutes.

A single pair of mesoplastra is preserved in NMB So.596 and NMS 8686 and fragmentary remains of the right mesoplastron are associated with NMS 8691 (Figs. 1b, 5b, 8). The mesoplastron is wider than long and roughly triangular in specimen NMS 8686 (Fig. 5b) and more rectangular with medially tapering edges in NMB So.596 and NMS 8691 (Figs. 1b, 8). The mesoplastron extends medially roughly halfway between the hyoplastron and the hypoplastron and extends laterally to contact peripherals V and VI thereby creating the middle third of the osseous bridge. There is no evidence of lateral plastral fontanelles.

The hypoplastron is best preserved in specimens NMB So.596 and NMS 8686 (Figs. 1b, 5b). The hypoplastron contacts peripherals VI–VIII laterally and thereby creates the posterior third of the osseous bridge. The inguinal buttress is similar in thickness and curvature to the axillary buttress of the hyoplastron and its vertical aspect helps define a well-developed visceral cavity along the bridge. The buttress contacts peripheral VII laterally, peripheral VIII posteriorly, but only contacts the most distal portions of costal V (Fig. 9b). The medial aspects of the hypoplastron are notably thin and easily damaged. The hypoplastra are furthermore shifted relative to one another in all specimens thereby making it difficult to assess the midline contact. The medial aspects of the right hypoplastron of NMS 8686 (Fig. 5b), nevertheless, appear to be relatively intact and align with the preserved midline contacts of the hyoplastra and xiphiplastra. The hypoplastra of this specimen appears to have had a butt contact along one-third of its anteroposterior length that fully separated the central and xiphiplastral fontanelles from one another. This region is better preserved in the two available isolated hypoplastra, NMS22075 and NMS22076b (Fig. 11c, e), which clearly document the presence of a midline contact between the hypoplastra that was sutural in nature and spanned about a third of the length of the hypoplastron. The preserved medial aspects of the left hypoplastron of NMB So.596 (Fig. 1b) also appear to be relatively intact, but there is no evidence of a midline contact with the opposing side. The hypoplastra of this individual therefore appear to lack a midline contact, but damage cannot be ruled out. The posterior contact with the xiphiplastron also shows variation between these two specimens by being angled mediolaterally in specimen NMS 8686 and horizontally in NMB So.596. The hypoplastron otherwise shares an anterolateral contact with the mesoplastron, an anterior contact with the hypoplastron, contributes to the posterior half of the central plastral fontanelle and the anterior half of the xiphiplastral fontanelle posteriorly.

Both xiphiplastra are preserved in specimen NMS 8686, but only the left xiphiplastron is preserved in specimen NMB



**Fig. 10** *Platychelys oberndorferi*, Late Jurassic (Kimmeridgian) of Solothurn, Switzerland. **a** NMS 21729, right costal I in dorsal (top), anterior (middle), and visceral (bottom) view; **b** NMS 40900, left costal I in dorsal (top) and visceral (bottom) view; **c** NMS 22076a, in part, cast of left costal VI in dorsal (top) and visceral (bottom) view, the original was embedded in resin for sectioning and histological analysis (Scheyer and Sander 2007; Scheyer 2009), the approximate section lines are highlighted in red; **d** NMS 22086, right costal VIII in dorsal (left) and visceral (right) view; **e** NMS 7047, carapace fragment in dorsal view; **f** NMS 40897, left peripheral I in dorsal

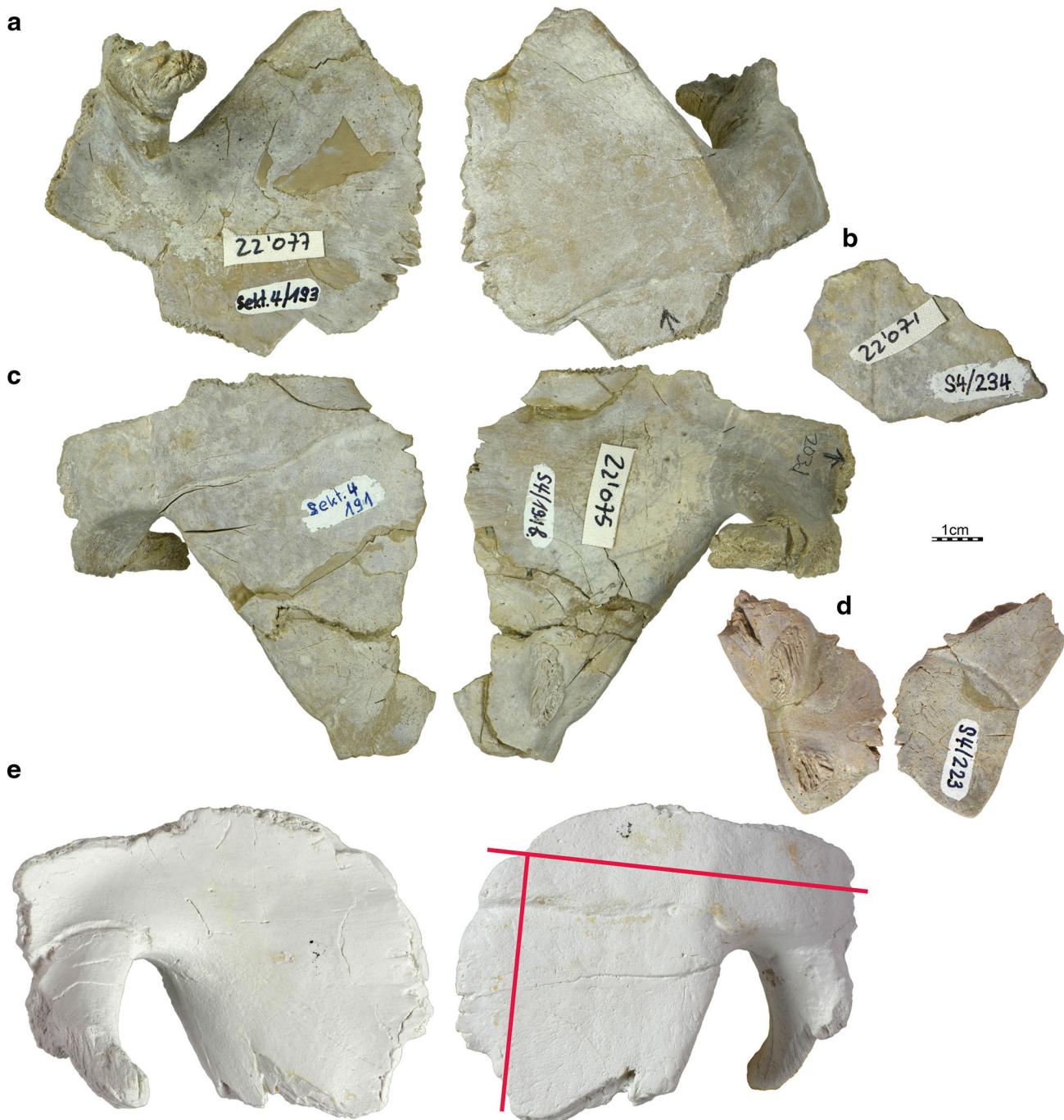
view; **g** NMS 22089, left peripheral VI in dorsal view; **h** NMS 40899, right peripheral VI in dorsal view; **i** NMS 22070, cast of right peripheral VII in lateral view, the original was embedded in resin for sectioning and histological analysis (Scheyer and Sander 2007; Scheyer 2009), the approximate section lines is highlighted in red; **j** NMS 22072, left peripheral IX in dorsal view; **k** NMS 40898, left peripheral X in dorsal view. NMS 40899 articulates with NMS 22070 and NMS 22072 with NMS 40898 and these specimens, therefore, likely originate from the same individual

So.596 (Figs. 1b, 5b). The medial aspects of NMB So.596 are poorly preserved, although the xiphplastra of this element appears to resemble its hyoplastron by being poorly ossified. The midline contact between the xiphplastra is, therefore, relatively short in this specimen and the xiphplastral fontanelle is well developed. In NMS 8686, by contrast, the midline contact between the xiphplastra is much better developed, still intact, and thus the xiphplastral fontanelle is reduced in size. In NMS 8686 the xiphplastra form a shallow, rounded, and wide anal notch with poorly developed and rounded posterior tips. Whereas the relevant area is too damaged in NMB So.596 to be informative, an isolated xiphplastron, NMS 40901, documents a more V-shaped, narrow anal notch with pointed posterior processes (Fig. 11d). The contacts with the pelvis are described below.

**Plastral scutes:** A complete set of plastral scute sulci are preserved in NMS 8686, but only the posterior ones are

preserved in NMB So.596 (Figs. 1b, 5b). There is no evidence of inframarginals in any specimen. The plastral scutes are also well documented on several isolated fragments (Fig. 11).

A single, medially situated gular separates the two extragulars, contributes to the anterior margin of the anterior plastral rim, is longer than wide, and tapers posteriorly (Fig. 5b). The gular contacts the extragulars anteromedially and the humerals posterolaterally. The gular covers the anteromedial portion of the entoplastron and the antero-medial contact of the epiplastra. The anterior rim of the left epiplastron is damaged in NMS 8686 and the left extragular is therefore only partially preserved. The extragular is triangular in shape and shares a broad posterior contact with the humeral in addition to a medial contact with the gular. The extragular covers the middle third of the epiplastron and a small anterolateral portion of the entoplastron.



**Fig. 11** *Platychelys oberndorferi*, Late Jurassic (Kimmeridgian) of Solothurn, Switzerland. **a** NMS 22077, left hyoplastron in visceral (left) and ventral (right) view; **b** NMS 22071, plastral fragment in ventral view; **c** NMS 22075, right hypo- and xiphiplastron in ventral (left) and visceral (right) view; **d** NMS 40901, left xiphiplastron in

visceral (left) and ventral (right) view; **e** NMS 22076b, cast of left hypoplastron, in visceral (left) and ventral (right) view; the original was embedded in resin for sectioning and histological analysis (Scheyer and Sander 2007; Scheyer 2009), the approximate section lines is highlighted in red

The well-preserved left humeral of NMS 8686 is rectangular and angles anterolaterally (Fig. 5b). The humerales are partially separated anteromedially by the gular and extragulars and share a posteromedial contact with its counterpart. The humeral shares a broad

posterior contact with the pectoral that diagonally crosses the hyoplastron. The humeral covers the posterolateral portion of the entoplastron, the posterolateral third of the epplastron, and the anterior portion of the hyoplastron.

The pectoral scute of *Platychelys oberndorferi* is partially preserved in both NMB So.596 and NMS 8686 (Figs. 1b, 5b), although it is only complete on the left side of NMS 8686. The pectoral shares a wide contact with the abdominal posteriorly and contacts marginals V and VI laterally. The pectoral/abdominal sulcus is fairly concave posteriorly in NMB So.596 but straight in NMS 8686. The first two musk duct foramina are located in the sulcus between the pectoral and marginal V and VI. The pectoral covers the majority of the hyoplastron as well as a small anterior portion of the mesoplastron.

The abdominal scute is rectangular, wider than long and shorter than the pectoral (Figs. 1b, 5b). Its medial aspects are not preserved due to the development of a central plastral fontanelle. The abdominal is slightly longer anteroposteriorly in NMB So.596 than in NMS 8686. The abdominal contacts the femoral posteriorly, marginal VI anterolaterally, marginal VII laterally, and marginal VIII posterolaterally. The abdominal/femoral sulcus is angled slightly posterolaterally. The abdominal scute covers the posterior part of the hyoplastron and mesoplastron and a large portion of the hypoplastron.

The femoral scute is completely preserved in NMS 8686 but is poorly preserved on the right side of NMB So.596 (Figs. 1b, 5b). The femoral scute contacts the anal posteriorly and the resulting sulcus is transverse and angled slightly posterolaterally. The femoral covers the posterior portion of the hypoplastron and extends on to the anterior half of the xiphplastra. The anal scute covers the rest of the xiphplastra and is slightly longer than wide.

Four pairs of musk duct foramina are apparent along the sulcus formed between the plastral and carapacial scutes in NMS 8686 and NMB So.596 (Figs. 1b, 5b, 6), but are not preserved in the remaining specimens. The first musk duct foramen is located along the anteromedial margin of marginal V. The position of the second musk duct foramen is varied. In specimen NMB So.596 it is located in the medial portion of the sulcus between marginal V and VI (Fig. 1b), while in specimen NMS 8686, the left second musk duct foramen is in the anteromedial portion of marginal VI but the right second musk duct foramen is in the medial portion of the sulcus between marginal V and VI, as in NMB So.596 (Fig. 5b). The third musk duct foramen is located in the anteromedial margin of marginal VII in NMS 8686 and the right side of NMB So.596, but is located in the medial portion of the sulcus between VI and VII in the left side of NMB So.596. Finally, the fourth musk duct foramen is positioned in the anterior medial third of marginal VIII in the left side of NMS 8686 and the anteromedial corner of marginal VIII in the right side of NMS 8686 and in NMB So.596.

**Internal morphology of the carapace:** Internal features of the carapace are only visible in specimens NMB So.596,

NMS 8686, and NMS 8692 (Figs. 1b, 5b, 9b). The internal view of the carapace is most easily accessible in NMS 8692 because the plastron is missing, but some internal elements are not preserved in this specimen, including the pelvis (Fig. 9b). NMB So.596 preserves all ten thoracic vertebrae, substantial portions of the thoracic ribs, and much of the pelvis (Figs. 1b, 2, 3). NMS 8686 also preserves much of the pelvis and substantial portions of the thoracic ribs, but only thoracic vertebrae II and III are preserved (Fig. 5b). NMS 8692 finally preserves a near complete set of thoracic ribs and vertebrae, but lacks the pelvis (Fig. 9b).

**Thoracic and sacral vertebrae:** The thoracic column consists of ten elements and the sacral column of at least one element. All ten thoracic vertebrae are preserved in NMB So.596 (Fig. 1b). NMS 8692 documents all thoracics except thoracic IV (Fig. 9b), whereas NMS 8686 preserves only thoracic vertebrae II and III (Fig. 5b). Sacral I is preserved only in NMB So.596 whereas sacral II is not preserved in any of the specimens. The articulations between the centra are well preserved whenever centra are preserved. The thoracic vertebrae are attached to the overlying carapace by way of an anteroposteriorly continuous bridge formed by the neural arches. This bridge is about 1.5 cm tall at the first thoracic vertebra but gradually becomes shorter towards the posterior until it disappears at the sacral vertebrae. Small, paired foramina are occasionally apparent along the neural ridge of all specimens that likely represent the exit foramina of the innervation and blood supply to the organs and muscles in these segments (Bojanus 1819). This hypothesis is supported by the fact that the paired foramina of thoracic vertebrae 9 and 10 are larger than the rest, likely due to the larger nerve and blood supply demands of the legs.

Thoracic centrum I is well preserved in specimens NMB So.596 and NMS 8692 (Figs. 2, 9b). Thoracic centrum I is about 20% shorter than thoracic centrum II and is unique among the thoracics in forming an hourglass-shaped ventral ridge instead of being completely flat. Thoracic centrum I has a concave anterior articulation site for the cervical column that faces slightly anteroventrally. The prezygapophyses of thoracic vertebra I protrude anteriorly past the centrum and possess slightly curved facets that are oriented dorsally. The ventral body of thoracic vertebra I is about twice as wide than high anteriorly, but the posterior end of the central body shows no substantial height by being flattened. The first thoracic centrum broadly contacts thoracic rib I anterolaterally and thoracic rib II posterolaterally.

Thoracic centra II–VII are consistent in size, shape, and articulation among specimens (Fig. 9b). They are slightly longer than wide, unusually flat, hourglass-shaped, have straight anterior and posterior articulation sites with one another, and decrease in anteroposterior length towards the

posterior. Thoracic centra II–VII show an anterolateral contact with their own rib and a posterolateral contact with the posterior rib, which increases in size towards the posterior. Thoracic centra VIII–X become increasingly shorter than the more anterior ones and laterally contact their own rib only. Whereas the intercentral joint between thoracic VII and VIII is straight, the more posterior ones become increasingly procoelous, but remain akinetic. The posterior central articulation of thoracic centrum X forms a well-developed and fully kinetic procoelous joint.

Sacral vertebra I is similar in size and shape to thoracic vertebra X and shares a broad lateral contact with sacral rib I, but is fully procoelous (Fig. 3). Two well-preserved postzygapophyses are visible protruding from the posterodorsal margin of the first sacral. These postzygapophyses do not contact the carapace and have lateral-facing, plate-like articular facets.

**Thoracic ribs and sacral rib:** Thoracic rib I is completely preserved in specimens NMB So.596 and NMS 8692 (Fig. 2, 9b), but only the distal portions are available in NMS 8686 (not figured). The head of thoracic rib I is not as anteroposteriorly elongate as those of the other thoracic ribs, but is significantly deeper, almost round in cross section, and articulates medially with the first thoracic vertebra only. The rib is rounded in cross section for the first few proximal millimeters, whereas the distal section is dorsoventrally flattened. The transition from round to flat coincides with a stepping that is apparent in ventral view (Fig. 2) and that creates a notch-like depression along the proximal portion of the bone that likely supported the dorsal process of the scapula. At roughly half its lateral extent, a narrow and pronounced vertical ridge forms along the ventral side of thoracic rib I that becomes progressively taller distally. The distal, sutural articulation with costal I is elongate, is formed both by the horizontal and vertical components of the rib, is about one-third of the length of the rib, and runs parallel with the contact of the costal I with peripherals I and II. Thoracic rib I approaches the most distal tip of the axillary buttress but does not contact it in any specimens. The horizontal plate of thoracic rib I also has an elongate sutural contact with thoracic rib II along roughly half its lateral extent to create an elongate, oval opening between the first and second thoracic ribs. Finally, a small, vertical flange of unknown function is present along the anterior margin of thoracic rib I just lateral to the scapular notch (Fig. 2).

Thoracic rib II is preserved in all specimens where a ventral view of the carapace is available, although its attachment with thoracic vertebrae I and II are not well preserved in NMS 8686 or on the left side of NMB So.596 due to slight compaction (Figs. 2, 5b). Thoracic rib II is the anteroposteriorly broadest of the thoracic ribs. The head is

broad and relatively flat, but not as flat as the following six thoracic rib heads. The second thoracic rib narrows slightly along its proximal third, but then expands and thickens along its articulation with thoracic rib I. A low and broad transverse ridge forms along the distal half of the rib.

Thoracic ribs III–VII are variably preserved in the three specimens where ventral views of the carapace are visible. Specimen NMS 8686 preserves thoracic ribs IV–VI and partially preserves a segment of left thoracic rib III, and the lateral attachment site of thoracic rib VII. Specimen NMS 8692 preserves thoracic ribs III and VI, right thoracic rib IV, left thoracic rib V, and left thoracic rib VII and partially preserves left thoracic rib V, the lateral attachment sites of left thoracic rib IV, and right thoracic rib VII (Fig. 9b). Finally, specimen NMB So.596 preserves only right thoracic ribs VI and VII and the lateral portions of thoracic ribs III–IV and the left thoracic ribs VI and VII (Fig. 1b). Thoracic ribs III–VIII are similar in shape, but decrease in size towards the posterior. These elements display slight ventral doming and have broad and flat heads that become more rounded distally and that insert into their respective costals halfway across the length of the costals.

Thoracic ribs IX and X are preserved in NMS 8692 and NMB So.596 (Figs. 3, 9b) and their attachment sites with the first sacral rib are visible in NMS 8686. The heads of thoracic ribs IX and X are straight, less flat, and much shorter than the previous ribs. Thoracic rib IX points posterolaterally and articulates with the anterior portion of the sacral rib I. Thoracic rib X is oriented only slightly posterolaterally and articulates anterolaterally with thoracic rib IX and laterally with sacral rib I. These two ribs, therefore, contribute indirectly to the sacrum due to their articulation with sacral rib I.

Sacral rib I is only preserved in NMB So.596 (Fig. 3). It is far more robust and rounded than the thoracic ribs. It is narrow at its attachment with sacral vertebra I, round in cross section, and becomes three to four times wider and thicker distally, as in the vast majority of non-pleurodiran turtles. The rib distally inserts into a deep notch formed along the distal margin of the ilium. The lack of a clear attachment site of sacral II with the ilium and the presence of well-developed central and postzygapophyseal attachment sites on sacral vertebra I indirectly support the idea that sacral II functioned like a caudal vertebra in *Platychelys oberndorferi* and, therefore, disarticulated easily after death.

The ten thoracic ribs and the first sacral rib form a substantial costovertebral tunnel that shrinks posteriorly. The tunnel is at its widest and deepest underneath thoracic ribs II–IV and shallows and narrows towards the posterior due to the flattening of the neural spine bridge and the

shortening of thoracic ribs. The tunnel is, therefore, unsubstantial by the time it reaches the sacral column.

**Pelvic girdle:** The pelvis is partially preserved in specimens NMB So.596 and NMS 8686 (Figs. 1b, 3, 5b, 6). The left half of the pelvic girdle is well preserved in NMS 8686 but has slightly shifted anteriorly due to compaction, causing the pubis and ischium to disarticulate from the dorsal surface of the plastron (Figs. 5b, 6). The right half of the girdle only preserves a dorsal portion of the ilium, which articulates ventrally with the carapace, and ventral fragments of the lateral pubic process and the ischium, which remain attached to the dorsal surface of the plastron. Photographs provided by Bräm (1965) show that the right acetabulum of NMS 8686 was fully preserved in situ, revealing that it disarticulated within the last decades. In NMB So.596, the left half of the pelvic girdle remains in situ but does not preserve a large, medial portion of the pubis and a posterior portion of the ischium. The right half of the pelvic girdle in NMB So.596 is highly displaced anteromedially to the point where the ilium was dislocated from its articulation with the ventral body of the carapace and is angled 45° to the anterior (Figs. 1b, 3). The right half of the girdle in NMB So.596 preserves the ventral elements far better than the left side, but a lateral portion of the pubis and the dorsal posterior margin of the ilium are not preserved.

**Ilium:** The ilium articulates proximally with the pubis and ischium to form the dorsal half of the laterally facing acetabulum, which is longer than high (Figs. 1b, 3, 5b, 6). The sutures between these elements remain open in all available specimens. The shaft of the ilium is circular in cross section and slightly tilted towards the posterior. The ilium expands distally to form an anteroposteriorly elongate and thickened fan that is triangular in cross section, with the apex pointing medially. The distal fan articulates with the carapace along a well-developed depression, most easily observed in NMS 8692 (Fig. 9b), that spans from the posterior margin of costal VII across the entire costal VIII to reach the lateral rim of peripheral X and half of the anteroposterior length of peripheral XI. It is apparent from the articulated specimens, however, that the ilium did not sutureally articulate with the carapace, but rather was anchored into this depression by connective tissues. The distal end of the ilium finally articulates with thoracic ribs IX and X and sacral rib I.

**Pubis:** The pubis articulates proximally with the ilium and ischium to form the anteroventral quarter of the acetabulum (Figs. 1b, 5b, 6). The lateral pubic process is anteroposteriorly elongate, oval in cross section and sutured to the visceral margin of the xiphiplastron along an elevated and crenulated surface that is formed by the xiphiplastron, best

visible in the available disarticulated material (Fig. 11c, d). It is not clear whether the two pubes meet at the midline, as only the left medial pubic plate is preserved in NMS 8686 and the right pubic plate is only partially preserved in NMB So.596. However, the medial process of the pelvis is enlarged and plate-like and has a straight median margin, making it plausible that the pubes contacted one another broadly along the midline. There is no evidence of an ossified or calcified epipubic process. The ventral region between the pubis and the ischium is not well preserved in NMS 8686 and NMB So.596, but there is no good evidence for a contact of the pubis with the ischium within the thyroid fenestra.

**Ischium:** The ischium articulates with the ilium and pubis proximally to form the posteroventral quarter of the acetabulum (Figs. 1b, 3, 5b, 6). The medial plate of the ischium forms a flat plate that has dimensions similar to the medial plate of the pubis and broadly contacts its counterpart along the midline. The medial plate sutureally articulates with the xiphiplastron along a suture that runs parallel with the margin of the anal notch, clearly visible in the available disarticulated material (Fig. 11d). The posterolateral margin of the medial plate forms spike like processes that protrude in ventral view beyond the posterolateral margin of the plastron. The ischium, furthermore, forms minute lateral processes, which also protrude beyond the margin of the plastron in ventral view.

## Discussion

**Alpha taxonomy:** All specimens described in this review were collected in limestone quarries located north of the city of Solothurn, Switzerland. The layers from which the turtles were collected are locally known as the *Solothurner Schildkrötenkalke* (Solothurn Turtle Limestones) and are now classified as the uppermost member of the Reuchenette Formation. These layers are known to be late Kimmeridgian in age based on the rich accompanying marine fauna (Meyer 1994). The type locality of *Platychelys oberndorferi*, Kelheim, which yielded a small number of specimens over the course of the last two centuries, is located in the eastern margins of the Solnhofen region of Germany and is dated to be early Tithonian (Cadena and Joyce 2015). Although there is a historic precedence of attributing the Swiss material to *Platychelys oberndorferi* (Rütimeyer 1867, 1873; Bräm 1965), we here take the opportunity to reevaluate this assessment by comparing the Swiss material to the available German specimens, in particular: (1) the holotype consisting of the central portions of a carapace in dorsal view, now lost

(Cadena and Joyce 2015), as figured by Wagner (1853); (2) the anterior lobe of a plastron in ventral view, now lost (Cadena and Joyce 2015), as figured by Zittel (1877); and (3) BSPG ASI1438, a near complete carapace in dorsal view, initially figured by Wagner (1861) and still available for study.

There are some apparent differences between the Solnhofen specimens and particular Solothurn specimens, but all observed differences are found within the Swiss material as well. The degree of dorsal keeling is one such difference: the type specimen appears to have large median keels with apices located at the posterior margin of each vertebral, whereas BSPG ASI1438 appears to have less pronounced and more centrally situated apices. This fits within the natural variation observed in the Swiss material. Additional differences pertain to the sutural contacts between the neurals and the costals, as well as the shape of the neurals. The neural sutures are not well defined in the type specimen, but are clearly visible in BSPG ASI1438. The shape of the first neural agrees with the Solothurn specimens. The second neural shares a posterolateral contact with costal III on both sides, a condition only seen in the left side of NMS 8686. The symmetric contact seen in BSPG ASI1438 is unique but not unexpected, as the shapes of neural II and costal III vary greatly among specimens. The same is true for the shape of neural IV, which is wider anteriorly than any of the Solothurn specimens, but is not unlike the condition seen in NMS 8692 and NMB So.596. Interestingly, neural VII is not drawn in on the illustration of BSPG ASI1438 in Wagner (1861) so it appears to only have seven neurals. However, the shape of “neural VII” is nearly identical to neural VII combined with neural VIII in all the specimens, so it is likely that this suture is not clear in this specimen and was overlooked. Our personal observations of BSPG ASI1438 unfortunately could not clarify this issue, as the relevant portion of the specimen is covered by pen marks.

As there are no systematic differences between the German and Swiss material, we agree with the attribution to the Swiss material to *Platychelys oberndorferi*. Given that the Swiss material consists of five well-preserved specimens and rich isolated remains, as opposed to the three partially preserved specimens from the type locality, of which two are lost, it is clear all future studies will focus on the Swiss material. The German material nevertheless complements the Swiss material and should therefore be always considered. In addition to the differences outlined above, BSPG ASI1438 confirms the presence of a distinct, rectangular suprapygial I above the pygal, which is otherwise only apparent in NMB So.596. The anterior plastral lobe figured by Zittel (1877) is the most complete of any specimen and confirms that the entoplastron is prevented

from reaching the anterior margin of the plastron by a narrow contact between the epplastra, not a broad one as indicated by Lapparent de Broin (2001, fig. 1). The Zittel (1877) plastron is otherwise the only known specimen to document the outline of the anterior plastral lobe, as all other specimens are damaged in this region.

**Thoracic vertebra I:** Extant representative of the two primary clades of turtles, *Pleurodira* and *Cryptodira*, can readily be distinguished by a series of characteristics, but much debate remains of these characteristics are true synapomorphies, symplesiomorphies, or homoplasies. For instance, while extant pleurodires can be differentiated from extant cryptodiodes by the presence of a pterygoid trochlea that guides the adductor jaw muscles around the otic cavity, paleontological data reveal that the otic trochlea seen in cryptodiodes is ancestral to the crown (see Joyce and Sterli 2012 for recent summary). Similarly, while extant pleurodires can be distinguished from extant cryptodiodes by having a pelvis that is suturally attached to the shell, additional paleontology data reveal that sutural pelvises originated multiple times during early turtle evolution (see Joyce et al. 2013 for most recent summary).

Extant pleurodires can also be distinguished from cryptodiodes by the method by which they retract their heads and necks below the shell, in that pleurodires show a horizontal movement, in contrast to the vertical movement apparent in cryptodiodes. Although difference in movement are most apparent from the cervical vertebrae themselves, the morphology of the thoracic vertebra I is useful as well, as its centrum is strongly oriented ventrally in cryptodiode to aid the vertical movement. The centrum of thoracic vertebra I of *Platychelys oberndorferi* is mostly oriented anteriorly, the plesiomorphic condition for all turtles, and it, therefore, was historically unclear if this taxon already achieved the horizontal motion apparent in its more derived cousins. The recent description of the two last cervical vertebrae of NMB So.596 leads to the surprising conclusion that this animal was able to at least partially retract its neck along the vertical plane as in a cryptodiode (Anquetin et al. 2017). We refer the reader to this paper for a more comprehensive discussion.

**Sexual dimorphism:** Although the males of extant pleurodires can readily be distinguished from females of the same species by having much longer and thicker tails, the sexes can only be distinguished using nuances in shell morphology. In particular, males may have less domed shells, a slight concavity to the plastron, or a narrower, more rounded anal notch laterally defined by pointed posterior xiphiplastral processes (Ernst and Barbour 1989). Cadena et al. (2013) recently explored possible sexual dimorphism among the platychelyids *Notoemys laticentralis*, *Notoemys zapotocaensis*, and *Platychelys oberndorferi*. In addition to the characteristics listed above,

Cadena et al. (2013) suggested that males have confluent central and xiphiplastral fontanelles. Along those lines, Cadena et al. (2013) argued that NMS 8686 (Figs. 5, 6) is female because of the presence of a flat posterior plastral lobe, separated central and xiphiplastral fontanelles, and short posterior xiphiplastral processes. This hypothesis is intriguing but difficult to test rigorously based on the available material of *Platychelys oberndorferi*. Although crushing and disarticulation is relatively minor in the material from Solothurn, we see no systematic differences among the five preserved shells that would allow us to distinguish males from females based on doming or plastral concavity. Of four specimens that document the presence and developed of central and xiphiplastral fontanelles, three clearly document that the fontanelles were separated from one another (NMS 8686, NMS22075 and NMS22076b) while one (NMB So.596) is ambiguous. Only two specimens sufficiently preserved the anal notch. NMS 8686 clearly exhibits a shallow anal notch defined by broad and rounded posterior plastral processes. An isolated xiphiplastron, NMS 40901, on the other hand documents an anal notch that is narrower, more V-shaped, and laterally defined by converging and pointed posterior processes. As these differences in anal notch morphology are consistent with those documented for extant pleurodires, especially podocnemidids (Ernst and Barbour 1989), we here tentatively confirm the original identification of Cadena et al. (2013) that NMS 8686 is female, establish NMS 40901 as male, while highlighting that the sex of all remaining specimens remains unclear. In contrast to Cadena et al. (2013), however, we only use anal notch morphology to establish the sexes and question the utility of fontanelle morphology.

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## References

- Anquetin, J. (2012). Reassessment of the phylogenetic interrelationships of basal turtles (Testudinata). *Journal of Systematic Paleontology*, 10, 3–45.
- Anquetin, J., Tong, H., & Claude, J. (2017). A Jurassic stem pleurodire sheds light on the functional origin of neck retraction in turtles. *Scientific Reports*, 7, 42376.
- Batsch, A. J. G. C. (1788). *Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien*. Jena: Akademische Buchhandlung.
- Bojanus, L. H. (1819–1821). *Anatome Testudinis Europaeae*. Vilna: Josephus Zawadzkus.
- Bräm, H. (1965). Die Schildkröten aus dem oberen Jura (Malm) der Gegend von Solothurn. *Schweizerische Palaontologische Abhandlungen*, 83, 1–190.
- Cadena, E. A., & Gaffney, E. S. (2005). *Notoemys zapatocaensis*, a new side-necked turtle (Pleurodira: Platychelyidae) from the Early Cretaceous of Colombia. *American Museum Novitates*, 3470, 1–19.
- Cadena, E. A., Jaramillo, C. A., & Bloch, J. I. (2013). New material of the platychelyid turtle *Notoemys zapatocaensis* from the Early Cretaceous of Colombia; implications for understanding Pleurodira evolution. In D. B. Brinkman, P. A. Holroyd, & J. D. Gardner (Eds.), *Morphology and evolution of turtles* (pp. 105–120). Dordrecht: Springer.
- Cadena, E., & Joyce, W. G. (2015). A review of the fossil record of turtles of the clades *Platychelyidae* and *Dortokidae*. *Bulletin of the Peabody Museum of Natural History*, 56, 3–20.
- Cattoi, N., & Freiberg, M. A. (1961). Nuevo hallazgo de Chelonia extinguidos en la Republica Argentina. *Physis*, 22, 202.
- Crawford, N. G., Parham, J. F., Sellas, A. B., Faircloth, B. C., Glenn, T. C., Papenfuss, T. J., et al. (2015). A phylogenomic analysis of turtles. *Molecular Phylogenetics and Evolution*, 83, 250–257.
- de la Fuente, M. S., & Iturralde-Vinent, M. (2001). A new pleurodiran turtle from the Jagua formation (Oxfordian) of western Cuba. *Journal of Paleontology*, 75, 860–869.
- Lapparent de Broin, F. (2001). The European turtle fauna from the Triassic to the Present. *Dumerilia*, 4, 155–217.
- Lapparent de Broin, F., & Murelaga, X. (1999). Turtles from the Upper Cretaceous of Lanó (Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Alava*, 14, 135–211.
- Ernst, C. H., & Barbour, R. W. (1989). *Turtles of the world*. Washington, DC: Smithsonian Institution Press.
- Gaffney, E. S. (1996). The postcranial morphology of *Meiolania platyceps* and a review of the Meiolaniidae. *Bulletin of the American Museum of Natural History*, 229, 1–166.
- Gaffney, E. S., Meylan, P. A., & Wyss, A. R. (1991). A computer assisted analysis of the relationships of the higher categories of turtles. *Cladistics*, 7, 313–335.
- Gaffney, E. S., Rich, T. H., Vickers-Rich, P., Constantine, A., Vacca, P., & Kool, L. (2007). *Chubutemys*, a new eucryptodiran turtle from the Early Cretaceous of Argentina, and the relationships of the Meiolaniidae. *American Museum Novitates*, 3599, 1–35.
- Gaffney, E. S., Tong, H., & Meylan, P. A. (2006). Evolution of the side-necked turtles: The families Bothremydidae, Euraxemydidae, and Araripemydidae. *Bulletin of the American Museum of Natural History*, 300, 1–698.
- Hirayama, R., Brinkman, D. B., & Danilov, I. G. (2000). Distribution and biogeography of non-marine Cretaceous turtles. *Russian Journal of Herpetology*, 7, 181–198.
- Joyce, W. G. (2007). Phylogenetic relationships of Mesozoic turtles. *Bulletin of Peabody Museum of Natural History*, 48, 1–102.
- Joyce, W. G., Parham, J. F., & Gauthier, J. A. (2004). Developing a protocol for the conversion of rank-based taxon names to phylogenetically defined clade names, as exemplified by turtles. *Journal of Paleontology*, 78, 989–1013.
- Joyce, W. G., Schoch, R. R., & Lyson, T. R. (2013). The girdles of the oldest fossil turtle, *Proterochersis robusta*, and the age of the turtle crown. *BMC Evolutionary Biology*, 13, 266.
- Joyce, W. G., & Sterli, J. (2012). Congruence, non-homology, and the phylogeny of basal turtles. *Acta Zoologica*, 93, 149–159.
- Karl, H.-V., & Tichy, G. (2006). Altmühlatal: Neue Schildkrötenfunde im Plattenkalk. *Biologie in unserer Zeit*, 4, 18–19.
- López-Conde, O. A., Sterli, J., Alvarado-Ortega, J., & Chavarría-Arellano, M. L. (2016). A new platychelyid turtle (Pan-Pleurodira) from the Late Jurassic (Kimmeridgian) of Oaxaca, Mexico. *Papers in Palaeontology*. doi:10.5061/dryad.508g5. (online in advance of print).
- Lydekker, R. (1889). *Catalogue of the fossil reptilia and amphibia in the British Museum (Natural History)*. Part 3, *Chelonia*. London: Longmans.

- Meyer, C. A. (1994). Depositional environment and paleoecology of the Solothurn turtle limestone (Kimmeridgian, northern Switzerland). *Geobios*, 16, 227–236.
- Mlynarski, M. (1976). Testudines. In O. Kuhn (Ed.), *Encyclopedia of Paleoherpetology, Part 7* (pp. 1–133). Stuttgart: Gustav Fischer Verlag.
- Rabi, M., Joyce, W. G., & Wings, O. (2010). A review of the Mesozoic turtles of the Junggar Basin (Xinjiang, Northwest China) and the paleobiogeography of Jurassic to Early Cretaceous Asian testudinates. *Palaeobiodiversity and Palaeoenvironments*, 90, 259–273.
- Rütimeyer, L. (1859a). Notiz über Schildkröten von Solothurn. *Verhandlungen der schweizerischen naturforschenden Gesellschaft*, 43, 57–59.
- Rütimeyer, L. (1859b). Die Schildkröten im Portland-Kalk von Solothurn. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakten-Kunde*, 1859, 366–367.
- Rütimeyer, L. (1867). Die Schildkröten. In F. Lang & L. Rütimeyer (Eds.), *Die fossilen Schildkröten von Solothurn* (Vol. 22, pp. 1–47). Switzerland: Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesammten Naturwissenschaften.
- Rütimeyer, L. (1873). Die fossilen Schildkröten von Solothurn und der übrigen Juraformation. *Neue Denkschrift der Allgemeinen Schweizerischen Naturforschenden Gesellschaft*, 25, 1–185.
- Scheyer, T. M. (2009). Conserved bone microstructure in the shells of long-necked and short-necked chelid turtles (Testudinata, Pleurodira). *Fossil Record*, 12, 47–57.
- Scheyer, T. M., & Sander, P. M. (2007). Shell bone histology indicates terrestrial palaeoecology of basal turtles. *Proceedings of the Royal Society B*, 274, 1885–1893.
- Sukhanov, V. B. (2000). Mesozoic turtles of middle and central Asia. In M. J. Benton, M. A. Shishkin, D. M. Unwin, & E. N. Kurochkin (Eds.), *The age of dinosaurs in Russia and Mongolia* (pp. 309–367). Cambridge: Cambridge University Press.
- von Meyer, H. (1860). *Zur Fauna der Vorwelt. Reptilien aus dem lithographischen Schiefer des Jura in Deutschland und Frankreich*. Frankfurt am Main: Heinrich Keller Verlag.
- Wagner, A. (1853). Beschreibung einer fossilen Schildkröten und etlicher anderer Reptilien-Überreste aus den lithographischen Schiefern und dem grünen Sandsteine von Kehlheim. *Abhandlungen der bayerischen Akademie der Wissenschaften, mathematisch-physikalische Klasse*, 7, 241–264.
- Wagner, A. (1861). Neue Beiträge zur Kenntnis der urweltlichen Fauna des lithographischen Schiefers. 2: Schildkröten und Saurier. *Abhandlungen der bayerischen Akademie der Wissenschaften, mathematisch-physikalische Klasse*, 9, 67–124.
- Zittel, K. A. (1877). Bemerkungen über die Schildkröten des lithographischen Schiefers in Bayern. *Palaeontographica*, 24, 75–184.