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Original Article

OXFORD

A revision of the fossil turtles of the Late Jurassic locality of Canjuers, France, and description of a new thalassochelydian species

Gaël E. Spicher[1,2,*], Walter G. Joyce[2], Pierre Gueriau[3,4], Karin Peyer[5], Vincent Reneleau[5], Jérémy Anquetin[1,2]

[1]JURASSICA Museum, Porrentruy 2900, Switzerland
[2]Department of Geosciences, University of Fribourg, Fribourg 1700, Switzerland
[3]Institute of Earth Sciences, University of Lausanne, Lausanne 1015, Switzerland
[4]IPANEMA UAR 3461, Université Paris-Saclay, CNRS, Ministère de la Culture, UVSQ, MNHN, Saint-Aubin 91192, France
[5]CNRS UMR 7207, CR2P, Muséum National d'Histoire Naturelle, Paris 75005, France

*Corresponding author. JURASSICA Museum, Route de Fontenais 21, Porrentruy 2900, Switzerland. E-mail: gael.spicher@unifr.ch

Abstract

The Tithonian (Late Jurassic) limestones of Canjuers (Var, France) represent one of the most important Late Jurassic fossil localities in Europe, yielding an exceptional invertebrate and vertebrate fauna that includes a small number of thalassochelydian turtles, representing the youngest Jurassic turtle fauna known from Europe. Despite the significance of this locality, the turtle material has received limited attention, with most studies dating back more than three decades. Here, we re-examine the turtle specimens from Canjuers using modern imaging techniques to improve the visualization of morphological details. Two specimens represent a new species, described here as *Caesaria templaria* gen. nov. et sp. nov., characterized by a medium-sized skull, short snout, well-developed pygal bone lacking a pygal notch, posterior peripherals broader than long from peripheral VII onward, wide vertebral scutes, and undulated intervertebral scute sulci. A third specimen is referred to *Solnhofia parsonsi* based on skull outline, elongate snout, large skull, and reduced costo-peripheral fontanelles; minor differences from previously described material are interpreted as taxonomically irrelevant. A fourth specimen represents a juvenile individual, but its poor preservation precludes precise identification. Collectively, the Canjuers' turtles provide new insights into Late Jurassic thalassochelydian diversity through the recognition of a new species.

Keywords anatomy, Eurysternidae, multispectral imaging, Testudinata, Thalassochelydia, Tithonian

Introduction

The Late Jurassic (Tithonian) lithographic limestones of Canjuers (Var, south-eastern France) represent one of the most significant Mesozoic *Lagerstätten* in Western Europe. Scientific interest in this site dates back to the 1970s, following the preliminary work of Ginsburg and Mennessier (1970), who first highlighted the exceptional preservation of vertebrate fossils, particularly turtles, crocodilians, and fish, from this locality. Over the years, numerous articulated specimens were recovered, including representatives of Compsognathidae, Pterosauria, Teleosauridae, Pleurosauridae, Sapheosauridae, and other members of Neosphenodontia (Fabre 1973, 1974a, b, 1981, Buffetaut 1980, Fabre *et al.* 1982, Dupret 2004, Peyer 2006). Despite this exceptional diversity, the Canjuers' *Lagerstätte* remains comparatively understudied relative to other Late Jurassic fossil localities, especially in regard to its vertebrate assemblage.

Among the key vertebrate components of the Canjuers' fauna are turtles, which have so far received only limited attention (Fabre *et al.* 1982, Broin 1994). These turtles were previously assigned to the clade Thalassochelydia, a group of basal marine turtles that inhabited the shallow epicontinental seas and archipelagos of Europe and South America

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during the Late Jurassic (Anquetin *et al.* 2017). It should be noted that *Thalassochelydia* probably represent a stem-based turtle clade (Evers and Benson 2019). Historically, thalassochelydians were divided into the poorly circumscribed families 'Eurysternidae' Dollo, 1886, 'Plesiochelyidae' Baur, 1888, and 'Thalassemydidae' Zittel, 1889. The monophyly of these groups remains unconfirmed, but these names are still used in the literature for convenience (Anquetin *et al.* 2017). In contrast, the monophyly of the clade *Thalassochelydia* has been repeatedly confirmed (Evers *et al.* 2019, Evers and Benson 2019, Gentry *et al.* 2019). The clade *Thalassochelydia* probably encompasses the clade Sandownidae as well, which probably derived from 'eurysternids' (Evers and Joyce 2020, Joyce *et al.* 2021), hence significantly extending the stratigraphical record of thalassochelydians.

The first 'eurysternid' turtles were described from the Tithonian Plattenkalks of southern Germany, particularly the historic localities of Solnhofen, Eichstätt, and Kelheim (Meyer 1839a, b, 1860, 1864). Their exceptional preservation allowed these fossils to be among the first extinct turtles distinguished from living taxa and assigned to newly established species (Anquetin *et al.* 2017). During the 19th and early 20th centuries, additional species were named from material in Germany, France, and Switzerland (Wagner 1861, Rütimeyer 1873a, b, Zittel 1877, Lydekker 1889, Oertel 1915, 1924), but many were based on incomplete or poorly diagnostic remains. Long-standing taxonomic uncertainty was further compounded by the destruction or loss of type specimens during World War II (Anquetin *et al.* 2017). Although recent systematic revisions have clarified several aspects of thalassochelydian taxonomy (e.g. Joyce 2000, 2003, Anquetin and Joyce 2014, Anquetin *et al.* 2017), a comprehensive synthesis encompassing all European localities is still lacking.

In this context, the turtle material from Canjuers is of particular importance. Three specimens have been previously discussed in the literature (Fabre *et al.* 1982, Broin 1994), but none have been described in detail. Fabre *et al.* (1982) provisionally referred one of the specimens to aff. *Solnhofia* sp., whereas Broin (1994) identified the presence of new species of *Eurysternum* and *Solnhofia*, and an indeterminate plesiochelyid [this one being the specimen mentioned by Fabre *et al.* (1982)]. A fourth specimen from Canjuers was never mentioned in the literature. The present study provides detailed morphological descriptions of these turtles and evaluates their taxonomic affinities within Thalassochelydia, contributing to a broader re-evaluation of Late Jurassic marine turtles and highlighting the significance of the Canjuers' *Lagerstätte* in reconstructing their evolutionary history.

Institutional abbreviations: BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; DMA, Dinosaurier Museum Altmühltal, Denkendorf, Germany; JME, Jura-Museum, Eichstätt, Germany; LF, Lauer Foundation for Paleontology, Science and Education, Wheaton, Illinois, United States of America; MDC, Musée des Confluences, Lyon, France; MNHN, Muséum national d'Histoire naturelle, Paris, France; NMB, Museum für Naturkunde Berlin, Germany; NMS, Naturmuseum Solothurn, Switzerland; TM, Teyler Museum, Haarlem, Netherlands.

Materials and methods

Material and geological setting

The four known turtle specimens from Canjuers (MNHN.F.CNJ76, MNHN.F.CNJ77, MNHN.F.CNJ82, and MNHN.F.CNJ174) are housed at the Muséum National d'Histoire naturelle in Paris. The first three specimens were excavated between 1965 and 1971 by the Ghirardi family, who collected numerous fossils in the 1960s and 1970s from quarries they owned in the Les Bessons area (Peyer *et al.* 2014). Part of their private fossil collection (including the turtles) was acquired by the MNHN in 1983 (Peyer *et al.* 2014). MNHN.F.CNJ174 was discovered during an excavation led by S. Wenz, a former palaeontologist at the MNHN, in 1971 and integrated into the MNHN fossil collection in 1983. Each specimen is compressed on to a single calcareous slab, which is typical for the lithographic limestone unit of the locality of Canjuers (Peyer *et al.* 2014). No counterparts are known for any of the four specimens, but MNHN.F.CNJ82 is preserved with two dissociated costal and neural fragments (see descriptions for more details). Although MNHN.F.CNJ76, MNHN.F.CNJ77, and MNHN.F.CNJ82 have been the subject of previous studies (see: Fabre 1982, Broin 1994), MNHN.F.CNJ174 remains undescribed.

A thorough examination of the geology and historical background of the Canjuers' locality can be found in Peyer *et al.* (2014). The Canjuers' *Lagerstätte* is a small area situated at an altitude of 860 m on a dry plateau named 'Plateau de Canjuers', north of Aups, in the Var Department (Provence-Alpes-Côte d'Azur region), and represents one of the most significant Late Jurassic fossil deposits in France (Fabre *et al.* 1982, Roman *et al.* 1994, Peyer *et al.* 2014). The area that comprises the *Lagerstätte* is known as 'Les Bessons', named after a former farm that once stood close to the *Lagerstätte* (Peyer *et al.* 2014). The deposits are dated to the Early Tithonian *Mucronatum* Zone (149.2 ± 0.7 Mya) (Atrops 1994). Accordingly, the turtle assemblage from Canjuers represents the youngest known Jurassic turtle fauna in Europe. Within the Les Bessons area, 10 separate quarry sites have been identified, all exposing finely layered lithographic limestones (Peyer *et al.* 2014). The sediments outcropping in the Les Bessons area are part of the 'Calcaire Blancs de Provence' Formation, which spans approximately 1 km^2 and has a thickness of 12 m, with lithographic limestone deposits delimited by coral reef formations (Peyer *et al.* 2014). According to Peyer *et al.* (2014), the quarries of Les Bessons consist of three distinct stratigraphic units: lithographic limestones *sensu stricto* at the base, overlain by bioclastic limestones, and capped by sub-lithographic limestones. The exact stratigraphic positions of the fossil turtles described here were not documented during collection by the Ghirardi family (Peyer *et al.* 2014). Nevertheless, they are inferred to originate from the lithographic limestone *sensu stricto*, based on slab lithology and the fact that this unit yields the majority of fossils at the site (Peyer *et al.* 2014). The preservation of articulated skeletons was facilitated by rapid burial in a shallow, muddy lagoon, where microbial films (found as fossils in Canjuers; Peyer *et al.* 2014) provided

a stabilizing medium, slowed soft-tissue decay, and limited bone disarticulation. Comparable Late Jurassic *Lagerstätten* characterized by exceptional preservation, similar depositional environments, and the recovery of fossil turtles, include Cerin in France (Bernier *et al.* 2014), and Solnhofen (Seilacher *et al.* 1985) and Wattendorf (Fürsich *et al.* 2007) in southern Germany.

UV photography and multispectral luminescence imaging

To enhance the visibility of the bones and to reveal features potentially invisible under normal lighting, such as soft tissues, we employed UV photography and multispectral imaging. UV photographs were collected using a Canon EOS 90D camera equipped with a pale-yellow optical UV filter (Kodak Wratten 2 2B) under illumination by a U1c 6 W 365 nm UV LED flashlight (Jaxman).

Multispectral imaging is complementary to optical and UV photography in allowing for the collection of a series of reflection and luminescence images across spectral ranges from violet to near-infrared. Although a relatively recent addition to paleontological methods, it has already successfully enhanced morphological contrasts or revealed new details in a wide range of fossils (Brayard *et al.* 2019, Klug *et al.* 2019, Robin *et al.* 2021, Brito *et al.* 2024, Saleh *et al.* 2024, Daley *et al.* 2025, Lynch *et al.* 2026), and can also yield information on, and derived from, the composition of fossil tissues (Lustri *et al.* 2024). The multispectral imaging system used in this study consists of a low-noise 4.2-megapixel CMOS camera (ORCA-Flash4.0 LT PLUS, Hamamatsu) with a high sensitivity range spanning from 350 to 900 nm. Attached to the camera is a UV-VIS-IR 60 mm 1:4 Apo Macro lens (CoastalOptics), in front of which a filter wheel equipped with eight interference band-pass filters (Semrock) is installed to capture images within specific spectral ranges from 472 ± 15 to 935 ± 85 nm. Specimens were illuminated by two sets of 16 LED lights with wavelengths ranging from 365 to 770 nm (CoolLED pE-4000), directed on the sample through a liquid light-guide fibre each, positioned to ensure homogeneous illumination of the field of view. The resulting greyscale 16-bit digital images are processed with ImageJ software (Schneider *et al.* 2012), including stacking, illumination homogenization, image alignment, and the generation of false-colour RGB composite images. The figured false-colour images are accompanied by an RGB diagram indicating the illumination–detection couples used, defined by their central illumination (x) and detection (d) wavelengths.

Anatomical nomenclature

Anatomical terminology in this study follows the nomenclatural frameworks established by Zangerl (1969) and Gaffney (1972, 1979).

Systematic palaeontology

Testudinata Klein, 1760 (*sensu* Joyce *et al.*, 2020)

Thalassochelydia Anquetin *et al.*, 2017 (*sensu* Joyce *et al.*, 2021)

Caesaria gen. nov.

urn:lsid:zoobank.org:act:99D01407-2F27-44F8-B737-498BD5121F92.

Type species: *Caesaria templaria* gen. nov. et sp. nov.

Etymology: The name *Caesaria* is used in apposition and refers to Julius Caesar. During Antiquity, the Canjuers' Plateau was known as *Campus Julii* ('plain of Julius Caesar'), a name associated with the passage of Julius Caesar through the Canjuers' Plateau during the Gallic campaigns and from which the name 'Canjuers' is derived. The generic name thus references the historical origin of the name of the type locality.

Diagnosis: Same as for the species.

Caesaria templaria gen. nov. sp. nov. (Figs 1–4)

Zoobank registration: urn:lsid:zoobank.org:act:0EEEC13C-F84-4128–8098-C18048E45A63.

Etymology: The specific name *templaria*, used as a noun in apposition, refers to an important medieval Templar stronghold located at Comps-sur-Artuby, the village adjacent to the Les Bessons area where the fossils were discovered.

Holotype: MNHN.F.CNJ77, an almost complete specimen preserved on a lithographic limestone slab, including a complete shell, skull, a few partial cervical vertebrae, and limb elements (Figs 1, 2).

Referred specimen: MNHN.F.CNJ174, a poorly preserved specimen with a nearly complete shell and some skull elements (Fig. 3).

Type horizon and locality: Late Jurassic (Early Tithonian) lithographic limestone unit of the Canjuers' locality, Var, France.

Diagnosis: Thalassochelydian turtle with the following combination of characters: a medium-sized skull for eurysternids (~20% of carapace length); short snout; moderately developed upper temporal emarginations; trapezoidal nuchal with a distinct nuchal notch; posterior peripherals broader than long starting at peripheral VII; presence of a pygal bone (contrasting with *Eurysternum wagleri*); absence of a pygal notch; retention of small, reduced costo-peripheral fontanelles in medium-sized individuals for eurysternids; wide median cervical scute; wide vertebral scutes; radial shell ornamentation on vertebral scutes; undulated intervertebral scute sulci; and well-developed lateral plastral fontanelles.

Remarks: *Thalassochelydia* are primarily diagnosed by cranial characters (Anquetin *et al.* 2017, Evers and Benson 2019). Regarding the shell, all thalassochelydians appear to possess three cervical scutes (Anquetin *et al.* 2017), a condition we observed in the specimens described here. Based on the presence of these three cervical scutes, and the strong morphological similarity to *Eurysternum wagleri* and *Solnhofia parsonsi*, we refer this newly described taxon to Thalassochelydia. Given the poor preservation of MNHN.F.CNJ174, we consider it more appropriate to refrain from designating this specimen as a paratype and instead to consider it merely as a referred specimen.

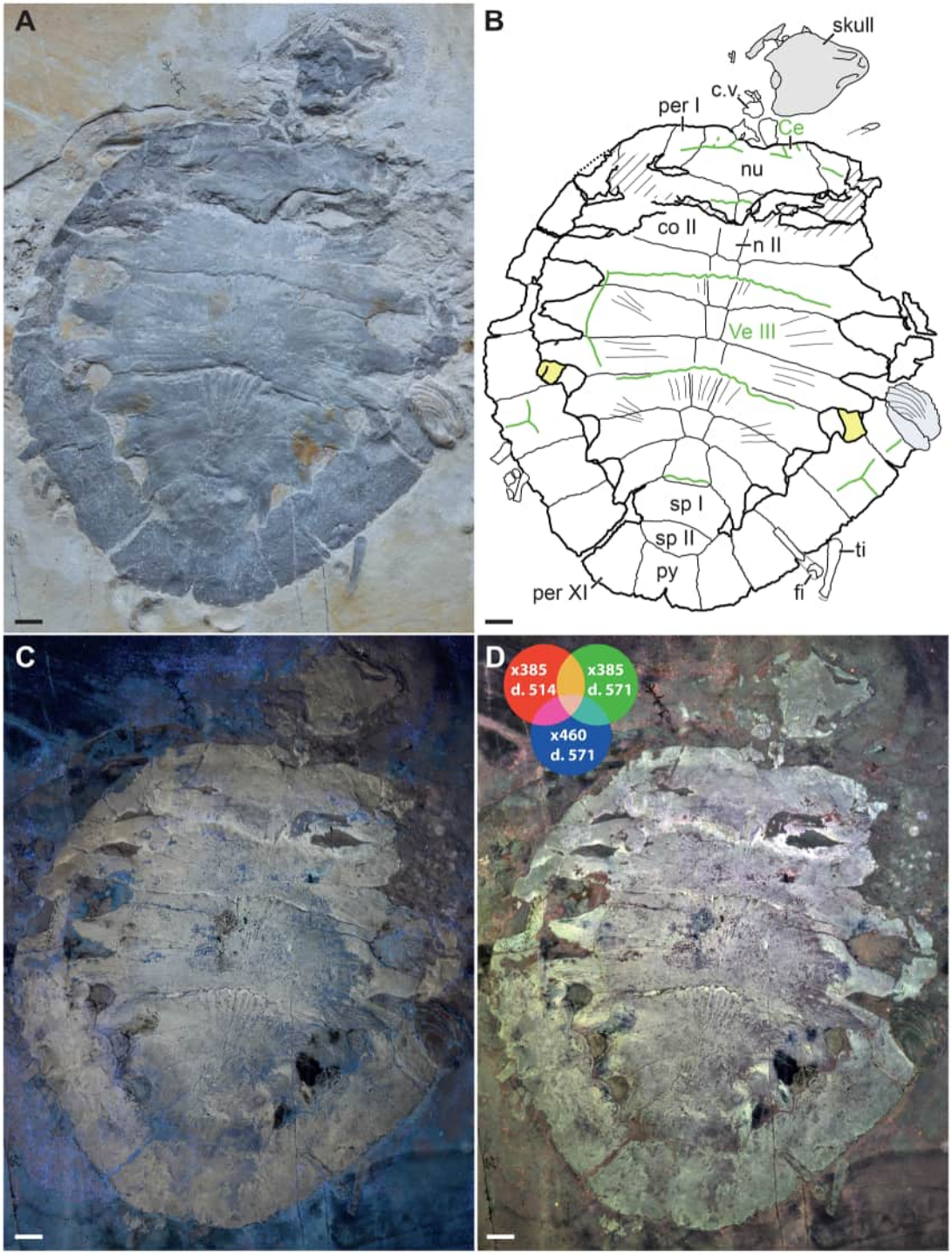

Figure 1 MNHN.F.CNJ77 (*Caesaria templaria* gen. nov. et sp. nov.) from Canjuers. A, photograph; B, interpretative line drawing; C, UV-light photograph; D, false colour multispectral image. Abbreviations: Ce, cervical scute; co, costal; c.v., cervical vertebrae; fi, fibula; n, neural; nu, nuchal; per, peripheral; py, pygal; sp, suprapygal; ti, tibia; Ve, vertebral scute. Dashed lines indicate outlines visible based on impressions on the matrix. The cranial material is indicated by grey areas (located at the anterior end of the specimen) and the plastral elements are indicated by yellow areas (visible through the costoperipheral fontanelles of the shell), whereas hatched surfaces represent areas where the original exposed bony surface has been lost. Scute sulci are indicated by thicker green lines. A brachiopod preserved with the turtle is indicated in light blue (located along the right margin of the shell). In D, *x* corresponds to the projected light wavelength (in nm), and *d* to the band-pass filter used for detection (in nm). Scale bar equals 1 cm.

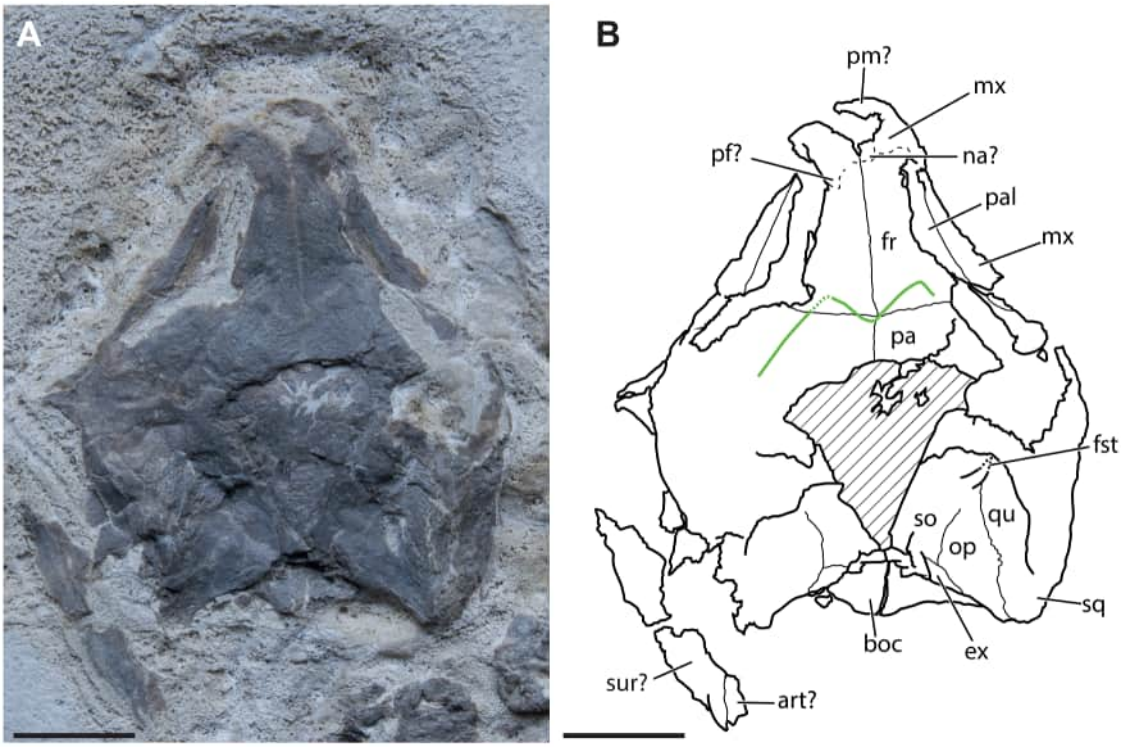

Figure 2 Cranium of MNHN.F.CNJ77 (*Caesaria templaria* gen. nov. et sp. nov.) from Canjuers. A, photograph; B, interpretative line drawing. Abbreviations: art, articular; bo, basioccipital; ex, exoccipital; fr, frontal; fst, foramen stapedio-temporale; mx, maxilla; na, nasal; op, opistothic; pa, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; qu, quadrate; so, supraoccipital; sq, squamosal; sur, surangular. Cranial sulci are indicated by thicker green lines and uncertain sutures with dashed lines. Hatched surfaces represent areas where the original exposed bony surface has been lost. Scale bar equals 1 cm.

Solnhofia Gaffney, 1975

Type species: Solnhofia parsonsi Gaffney, 1975.

Included valid species: Solnhofia parsonsi Gaffney, 1975 and *Solnhofia brachyrhyncha* Anquetin and Püntener, 2020.

Diagnosis: See Anquetin and Püntener (2020).

Solnhofia parsonsi Gaffney, 1975

Holotype: TM 4023, a cranium with lower jaw.

Referred specimens: DMA-JP-2004/005 (Augustin *et al.* 2023); NMS 8741 (Gaffney 1975); JM SCHA 70 (Joyce 2000); and MNHN.F.CNJ82 (Broin 1994; this study) (Figs 5–7).

Occurrence: Late Kimmeridgian of Solothurn, Canton of Solothurn, Switzerland (Gaffney 1975); Late Kimmeridgian of Painten (Augustin *et al.* 2023) and Schamhaupten, Bavaria, Germany (Joyce 2000); Early Tithonian of Solnhofen, Bavaria, Germany (Parsons and Williams 1961, Gaffney 1975); and Early Tithonian of Canjuers, Var, France (Broin 1994, this study).

Revised diagnosis: A species of *Solnhofia* characterized by the following combination of characters: the presence of an enlarged skull (always 40% of carapace length), the skull longer than broad, an elongated and slender snout, contribution of the palatine to the upper triturating surface, less developed processus pterygoideus externus (compared to *Solnhofia brachyrhyncha*), a condylus mandibularis located at the level of the occipital plane, small ventral exposure of the parabasisphenoid (compared to *Solnhofia brachyrhyncha*), a longer than broad mandible with an elongated mandibular symphysis, reduced to closed costo-peripheral fontanelles, broad nuchal forming a wide nuchal notch, hyoplastra and xiphiplastra that are about as wide as long, small semi-lunate lateral plastral fontanelles, and oval central plastral fontanelle.

Thalassochelydia indet

Studied specimen: MNHN.F.CNJ76, a partial skeleton with little bone preserved (Fig. 8).

Remarks: Given the extremely poor preservation of this specimen, no diagnostic characters are visible. Nevertheless, based on its general resemblance to *Solnhofia* (see Discussion), we refer this specimen to Thalassochelydia.

Description

Caesaria templaria

General

MNHN.F.CNJ77, the holotype, is nearly complete and preserved in dorsal view, with the overall body outline well defined (Fig. 1). The shell and skull are articulated, whereas the vertebrae and limb elements are largely disarticulated (Figs 1, 2). The complete, pentagonal shell measures 224 mm

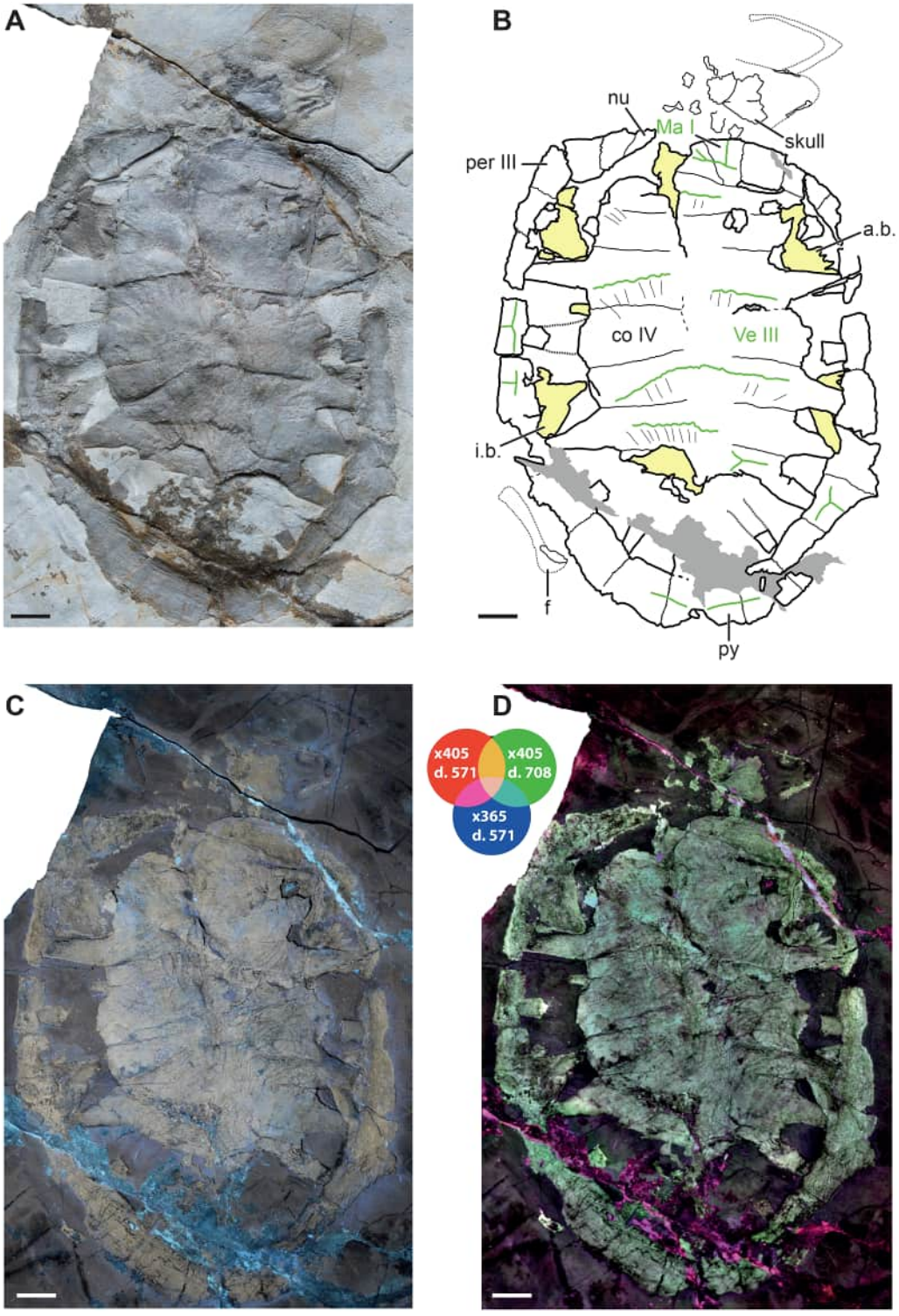

Figure 3 MNHN.F.CNJ174 (*Caesaria templaria* gen. nov. et sp. nov.) from Canjuers. A, photograph; B, interpretative line drawing; C, UV-light photograph; D, false colour multispectral image. Abbreviations: a.b., axillary buttress; co, costal; f, femur; i.b., inguinal buttress; Ma, marginal scute; nu, nuchal; per, peripheral; py, pygal; Ve, vertebral scute. Dashed lines indicate outlines visible based on impressions on the matrix. Blots of glue are indicated by grey areas (located posteriorly on the shell) and plastral elements are indicated by the yellow areas (visible through the costoperipheral fontanelles of the shell), whereas hatched surfaces represent areas where the original exposed bony surface has been lost. Scute sulci are indicated by thicker green lines. In D, *x* corresponds to the projected light wavelength (in nm), and *d* to the band-pass filter used for detection (in nm). Scale bar equals 1 cm.

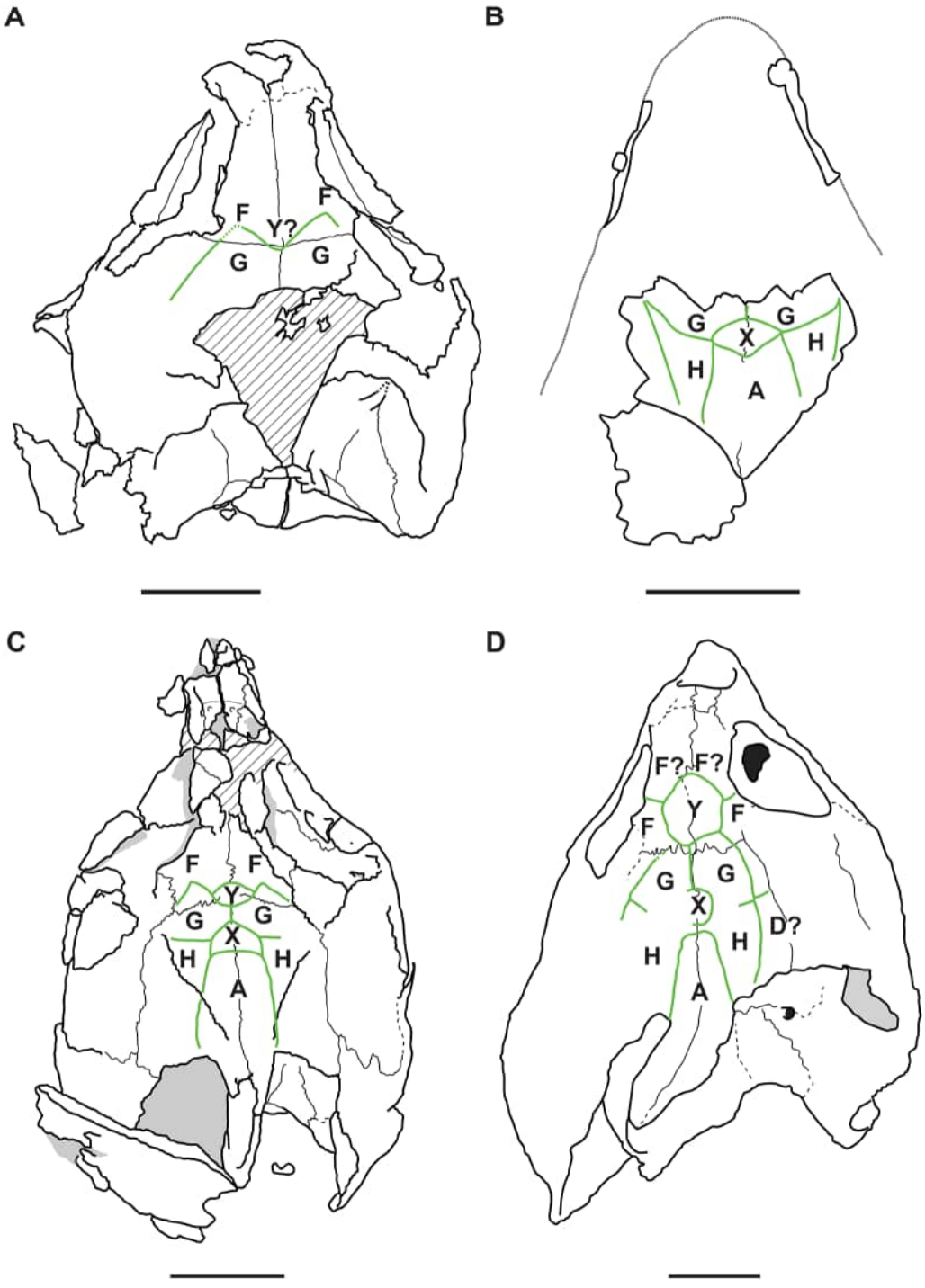

Figure 4 Interpretative line drawing of selected skulls with cranial scute pattern. A, cranium of MNHN.F.CNJ77 (*Caesaria templaria* gen. nov. et sp. nov.) from Canjuers; B, cranium of MNHN.F.CNJ174 (*Caesaria templaria* gen. nov. et sp. nov.) from Canjuers; C, cranium of MNHN.F.CNJ82 (*Solnhofia parsonsi*) from Canjuers; D, cranium of NMS 8741 (*Solnhofia parsonsi*) from Solothurn. Capital letters identify the different scutes. Cranial sulci are indicated by thicker green lines. Dashed lines indicate uncertain sutures. Grey (shaded) areas indicate regions lacking bony material, whereas hatched surfaces represent areas where the original exposed bony surface has been lost. Note that in (B), the dotted line represents the outline of the skull impression on the matrix. Scale bar equals 1 cm.

along the midline and 213 mm at its greatest width. The shell margin between peripherals VII and XI is straight, unlike the slightly concave condition seen in *Eurysternum wagleri* (Anquetin and Joyce 2014). MNHN.F.CNJ174, the referred specimen, consists primarily of an almost complete but heavily damaged shell, exposed in dorsal view (Fig. 3). Portions of the plastron are visible through fenestrations and breaks in the carapace. Cranial and mandibular fragments, along with small bone pieces and an impression of the left femur, are also present. The preserved carapace length, from the anterior margin

of the nuchal to the broken posterior edge of the pygal, is approximately 150 mm, probably close to the original length given the minimal damaged to the pygal. The maximum width, measured at the level of the seventh pair of peripherals, is approximately 119 mm but may have been slightly broader near the eighth pair, but these are poorly preserved.

The preserved shell outline is oval in MNHN.F.CNJ174, contrasting with the more pentagonal shape of MNHN.F.CNJ77 and *Solnhofia parsonsi* (Joyce 2000, Anquetin *et al.* 2017, Augustin *et al.* 2023). The posterior margin is, however, damaged and partially missing. Importantly, the shell bones show no sign of mediolateral compression, as indicated by the thoracic ribs, which remain properly articulated with the peripherals. A prominent fissure extends across the posterior region of the carapace and was infilled with plaster during restoration, partially obscuring the fossil surface.

Skull

Cranial bones: The cranium of MNHN.F.CNJ77 is preserved in dorsal view with a well-defined outline. It is taphonomically compressed and damaged in several areas, obscuring many anatomical details (Figs 2, 4A). The posteromedial portion of the skull roof is missing. The skull is sub-pentagonal, tapering anteriorly into a short blunt snout (Fig. 2). The preservation of MNHN.F.CNJ174, by contrast, is poor as only a triangular portion of the skull roof, formed by the paired parietals, remains identifiable (Figs 3, 4B). Posterior to the parietals, several unidentifiable bone fragments are probably cranial in origin. The anterior skull outline is visible as an impression forming a V-shaped contour with straight anterolateral margins (Figs 3, 4B). Thin bone strips along this impression, probably from the maxillae, are still present. As MNHN.F.CNJ77 preserves the skull more completely, the following description primarily refers to that specimen.

The snout of MNHN.F.CNJ77 is notably short and blunt compared to the elongated and pointed snout of *Solnhofia parsonsi* (Gaffney 1975, Joyce 2000, Augustin *et al.* 2023). The greatest skull width occurs just posterior to the orbits, narrowing slightly toward the posterior tips of the squamosals. The skull measures 45.7 mm in length and 38.4 mm in width, whereas in MNHN.F.CNJ174 the distance from the snout tip to the posterior margin of the parietals is approximately 31 mm. The skull length represents ~20.0% of the shell length in MNHN.F.CNJ77 and ~20.8% in MNHN.F.CNJ174, consistent with most eurysternids (Lapparent de Broin 1996, Anquetin *et al.* 2017) but markedly lower than the characteristic ~40% value of *Solnhofia parsonsi* (Broin 1994, Lapparent de Broin 1996, Anquetin *et al.* 2017) and the ≥25% value in *Solnhofia brachyrhyncha* (Anquetin and Püntener 2020). The skull length-to-width ratio of MNHN.F.CNJ77 is ~1.19, intermediate between that of *Solnhofia parsonsi* (1.30–1.45) and *Solnhofia brachyrhyncha* (1.10; Anquetin and Püntener 2020), although the latter is based on incomplete, deformed material. Nevertheless, this ratio for MNHN.F.CNJ77 should be interpreted with caution, since flattening of the skull may have influenced its value. The interorbital space is about a third of the width of the skull at the orbits. The orbits were thus mostly oriented dorsolaterally.

Due to crushing, few sutures are discernible in MNHN.F.CNJ77. The maxillae, frontals, parietals, opisthotics, supraoccipital, and quadrates can be confidently identified. Anteriorly, the nasals, premaxillae, and a small portion of the left prefrontal may also be present, but the region is heavily damaged, and bone contacts are unclear. The relationships between the nasals, prefrontals, and frontals thus remain uncertain.

Most of the anterior skull roof of MNHN.F.CNJ77 is formed by the frontals, which meet the parietals posteriorly along a straight suture (Fig. 2). The temporal region is poorly preserved and lacks visible sutures. On the left side of the cranium, the posterior part of the temporal surface extends far enough to clearly overlie the foramen stapedio-temporale in dorsal view. On the right side, this region is broken, exposing the foramen, whose margin is partly formed by the quadrate. In this area, the opisthotic is sub-triangular in dorsal view, contacting the supraoccipital medially, the quadrate anterolaterally, and the squamosal posterolaterally. Although the parietal, supraoccipital, and quadrate can be partially identified, their complete morphology cannot be reconstructed due to damage and the absence of visible sutures. The posterior process of the squamosal is short, ending slightly posterior to the condylus occipitalis, unlike in *Solnhofia* spp., where the squamosal protrudes posteriorly far beyond this level (Gaffney 1975, Joyce 2000, Anquetin and Püntener 2020, Augustin *et al.* 2023).

At the posterior end of the skull, small portions of the basioccipital and exoccipitals are preserved. The exoccipitals are only faintly visible in dorsal view, contacting the opisthotics laterally and the supraoccipital medially.

Cranial scutes: In MNHN.F.CNJ77, the poor preservation and loss of much of the cranial roof prevent a detailed reconstruction of the cranial scute pattern. Nevertheless, some faint sulci are discernible (Fig. 4A). Owing to the limited homology criteria for cranial scutes in turtles, their identification relies on comparison with taxa exhibiting well-documented scute patterns (Sterli and de la Fuente 2013, Evers *et al.* 2021, Spicher *et al.* 2024). The anterior margins of the paired G scutes are traceable, and the lateral margin of the left G scute, separating it from the adjacent F scute, is also visible. Anteriorly, the G scutes are pointed, as in *Solnhofia parsonsi* (MNHN.F.CNJ82), contacting the F scutes anterolaterally. The G scutes probably contact a single Y scute anteromedially, although this feature cannot be clearly confirmed. The pointed anterior margins of the G scutes suggest a partial encirclement of the posterior portion of the Y scute. The median sulcus between the G scutes and all posterior sulci are not preserved.

In MNHN.F.CNJ174, several cranial sulci are preserved on the parietals (Fig. 4B). A midline A scute is present posteriorly, longer than wide, followed anteriorly by a lens-shaped X scute. This anatomy contrasts with MNHN.F.CNJ82 (here assigned to *Solnhofia parsonsi*, see below), where the X scute is sub-triangular (Fig. 4C). In MNHN.F.CNJ174, the X scute bears a convex anterior margin and a pointed posterior projection that inserts into the A scute, unlike the concave posterior margin of MNHN.F.CNJ82. This anatomy further contrasts with some specimens of *Solnhofia parsonsi*, such as NMS 8741, in which the A and X scutes do not contact each

other but are separated by the medial junction of the paired H scutes (Fig. 4D). Sub-triangular and anteroposteriorly elongated paired H scutes flank the A and X scutes laterally in MNHN.F.CNJ174 (Fig. 4B). Medially, they contact the A scute along a straight suture, while their anteromedial corners meet the lateral margins of the X scute. Anteriorly, only the posterior portions of the paired G scutes are preserved. They contact each other medially, the X scute posteromedially, and the H scutes posterolaterally.

Mandible: A long, isolated bone fragment is preserved along the posterior left side of the skull in MNHN.F.CNJ77 (Fig. 2). Although its identification is uncertain, it may represent part of the left mandibular ramus. A visible suture divides this bone fragment into a longer anterior and a smaller posterior element, tentatively corresponding to the surangular and articular, respectively. Given the incomplete and damaged state of the specimen, this interpretation remains speculative. In MNHN.F.CNJ174, a shallow V-shaped impression likely represents the mandible (Fig. 3). The imprint shows slender, nearly straight rami and a short, pointed symphysis. The preserved length of the mandible is approximately 28 mm.

Axial skeleton

Several small bone fragments in the cervical region probably correspond to cervical vertebrae, but their preservation is too poor to allow anatomical description (Fig. 1).

Shell

Nuchal: The nuchal is complete in MNHN.F.CNJ77 but only partially preserved in MNHN.F.CNJ174 (Figs 1, 3). It is broad and trapezoidal, its posterior margin being distinctly longer than its anterior margin (Fig. 1). A shallow median nuchal notch is present anteriorly (Fig. 1), resembling the condition in *Eurysternum wagleri* (Anquetin and Joyce 2014) and *Solnhofia parsonsi* (Joyce 2000), but differing from the more rounded, less expanded notch of *Idiochelys fitzingeri* (Lortet 1892).

Neurals: In MNHN.F.CNJ77, eight neurals are preserved, although their outlines are faint (Fig. 1). The neurals I and II and V and VI are incomplete (Fig. 1). The outline of neurals I and II is unclear. Neurals III to VII exhibit a hexagonal outline, neural IV being the smallest element. Neural VIII is large and has an irregular trapezoidal outline with a shorter anterior margin (Fig. 1). In MNHN.F.CNJ174, the neural region is too poorly preserved to assess its morphology, with the exception of the left margin of the fourth neural (Fig. 3).

Suprapygals: MNHN.F.CNJ77 preserves two suprapygals (Fig. 1). The first is large and sub-trapezoidal, wider than long, with a straight anterior and a concave posterior margin (Fig. 1). It articulates posteriorly with a smaller, lens-shaped second suprapygal, the posterior margin of which is more strongly curved (Fig. 1). MNHN.F.CNJ174 lacks preserved suprapygals, except possibly a small fragment of the left posterolateral corner of the second suprapygal (Fig. 3). The presence of two suprapygals in MNHN.F.CNJ77 aligns with the general condition of thalassochelydians, although variation in number and shape is known (e.g. Joyce 2000, Anquetin and Joyce 2014, Augustin *et al.* 2023).

Pygal: The pygal is well preserved in both MNHN.F.CNJ77 and MNHN.F.CNJ174 (Figs 1, 3). It is nearly square, with slightly abraded posterior margins in both specimens (Figs 1, 3). In MNHN.F.CNJ77, a small triangular indentation on the posterior margin probably represents damage rather than a genuine pygal notch (Fig. 1). This apparent absence of pygal notch contrasts with *Eurysternum wagleri*, as already documented by Broin (1994), where a true pygal notch is present formed by the absence of a pygal element (Anquetin and Joyce 2014).

Costals: In MNHN.F.CNJ77, the costals are articulated and well-preserved, except for costals I and II that show localized damage (Fig. 1). In MNHN.F.CNJ174, the costals are relatively well preserved but exhibit frequent damage, particularly along their distal margins and in the posterior part of the carapace (Fig. 3). In MNHN.F.CNJ77, all costals are ossified for at least two-thirds of their length (Fig. 1). The lateral costal portions expose the thoracic ribs, which form costo-peripheral fontanelles that are largest anteriorly and gradually diminish posteriorly, becoming nearly closed behind the eighth costal (Fig. 1). Fontanelles are more extensively developed in MNHN.F.CNJ174 (the smaller specimen) (Fig. 3). In MNHN.F.CNJ77, the left first costal appears to lack contact with the first peripheral, but this absence of contact is likely an artefact of preservation, given the damaged irregular outline of the costal (Fig. 1). In MNHN.F.CNJ174, the first costal appears to contact the first and probably also the second peripheral, but this arrangement is also uncertain. The degree of ossification of the costals in both specimens exceeds that of comparably sized individuals of *Eurysternum wagleri* (Anquetin and Joyce 2014). In both MNHN.F.CNJ77 and MNHN.F.CNJ174, each costal contacts a single peripheral laterally following the symplesiomorphic pattern (i.e. costal n only contacts peripheral n + 2) (Figs 1, 3).

Peripherals: Both specimens exhibit 11 pairs of peripherals (Figs 1, 3), with MNHN.F.CNJ77 preserving all peripherals except the anteriormost and the right anterolateral ones (Fig. 1), whereas MNHN.F.CNJ174 preserves all 11 peripherals on each side of the carapace, although only a few are complete (Fig. 3). The morphology of the first peripheral is noteworthy for being longer than wide (Figs 1, 3), a condition also reported for MB.R.2894 [*Palaeomedusa testa* of Joyce (2003)]. However, the morphology of the first peripheral appears to vary even within a single specimen (right versus left) and probably also changes with ontogeny, especially in relation to the closure of the anterior fontanelles and the completion of ossification in the anterior peripherals and costals. In MNHN.F.CNJ174, the second peripheral is roughly square (Fig. 3), whereas peripherals III–XI are distinctly quadrangular in both specimens (Figs 1, 3). Peripherals III–VII are longer than wide, whereas peripherals VIII–XI are wider than long (Figs 1, 3), a condition also observed in *Solnhofia parsonsi* (Augustin *et al.* 2023) and to a lesser extent in *Eurysternum wagleri*, where the transition occurs around peripheral VIII. In both specimens, the outer margins of the posterior peripherals are slightly abraded

(Figs 1, 3), suggesting that they were originally broader. Peripheral XI is trapezoidal, with a slightly shorter anterior than posterior margin (Figs 1, 3).

Cervical scutes: Although faint, the cervical scutes are well preserved in MNHN.F.CNJ77 (Fig. 1). Three are identifiable, though the lateral sulcus of the left cervical remains uncertain (Fig. 1). In MNHN.F.CNJ174, only the lateralmost portion of the right lateral cervical scute is preserved (Fig. 3). The presence of three cervicals matches the thalassochelydian condition (Anquetin *et al.* 2017). The central cervical is trapezoidal and substantially wider than the two oblique, quadrangular lateral scutes (Fig. 1).

Vertebral scutes: In MNHN.F.CNJ77, five vertebral scutes are preserved, though incompletely (Fig. 1). Each is relatively wide, covering more than two-thirds of the costal width and extending to the costo-peripheral fontanelles (Fig. 1). The fifth is markedly smaller and narrower than the others (Fig. 1). The sulcus between vertebral scutes III and IV appears to align medially with the sutures between costals V and VI, which is unusual for turtles (Fig. 1). However, this configuration is most likely taphonomic, resulting from a dorsal displacement of the shell at the level of costal VI on to costal V. In the original condition, the anterior sulcus of vertebral IV would lie just posterior to the suture between costals V and VI, which is unusual among thalassochelydians, as this sulcus is generally situated on costal V (e.g. Anquetin and Joyce 2014, Anquetin *et al.* 2014, 2017, Püntener *et al.* 2015, 2017, 2020, Raselli and Anquetin 2019). Both specimens exhibit distinct radial ornamentation on the vertebral scutes (Figs 1, 3), a feature also present in *E. wagleri* (Anquetin and Joyce 2014) and *Solnhofia parsonsi* (Joyce 2000, Augustin *et al.* 2023).

In MNHN.F.CNJ174, the number and morphology of vertebral scutes are uncertain due to severe posterior damage. The first vertebral scute appears to be very short, whereas the third and fourth display irregular shapes and asymmetrical margins (Fig. 3). The fourth vertebral seems subdivided into two parts, the posterior one being much narrower (Fig. 3). The sulcus separating these two 'sub-fourth' vertebral scutes extends only across costal VI and should not be interpreted as delimiting vertebral V, which normally covers the suprapygal region. The posterior shell is too damaged to assess vertebral V. Overall, the vertebral pattern in MNHN.F.CNJ174 is highly irregular, particularly posteriorly, where bilateral symmetry is disrupted (Fig. 3), probably reflecting a pathological condition.

Pleural scutes: In MNHN.F.CNJ77, pleural scutes are not directly visible, as sulci are mostly absent and the scutes overlie the costo-peripheral fontanelles (Fig. 1). In the posterior half of the shell, where the peripherals are broader, the pleural scutes appear to have covered about half the peripheral width (Fig. 1). However, this pleural anatomy cannot be confidently extrapolated to the entire carapace due to the lack of sulcus preservation anteriorly. In MNHN.F.CNJ174, pleural scutes are similarly indiscernible, largely due to the extensive costo-peripheral fontanelles (Fig. 3). A small sulcus segment is preserved on the right side of the posterior carapace (Fig. 3), adjacent to the subdivided fourth vertebral scute, indicating that the posterior pleural scutes extended over more than half the costal width. This configuration is consistent with the reduced mediolateral width of the posterior element of the fourth vertebral scute, though it probably reflects the abnormal scute arrangement described earlier.

Marginal scutes: In both MNHN.F.CNJ77 and MNHN.F.CNJ174, marginal scute sulci are faintly preserved on some peripherals (Figs 1, 3). Where visible, they indicate that adjacent marginals met approximately at the midpoint of a given peripheral in the posterior carapace (Fig. 1). The preserved sulci suggest that the marginal scutes were longer than wide (Figs 1, 3). The last pair of marginals does not extend on to the last suprapygal (Fig. 3), a condition shared with *Solnhofia parsonsi* (Augustin *et al.* 2023) and *Idiochelys fitzingeri* (Lortet 1892), but differing from *Eurysternum wagleri* (Anquetin and Joyce 2014), which shows a distinct pattern within eurysternids.

Plastron: In MNHN.F.CNJ77, the plastron is mostly concealed, with only two small fragments visible through the fontanelle between costals V and VI, probably representing portions of the inguinal buttresses (Fig. 1). In MNHN.F.CNJ174, the plastron is similarly obscured, but several elements are visible through the costo-peripheral fontanelles and damaged carapace areas (Fig. 3). Short digitations along the right axillary buttress indicate a ligamentous connection between the carapace and plastron. These digitations are short and stout (Fig. 3), resembling those of *Solnhofia parsonsi* (Joyce 2000) and *Idiochelys fitzingeri* (Lortet 1892), and contrasting with the generally longer, more slender buttress extensions in *Eurysternum wagleri* (Anquetin and Joyce 2014). However, given the poor preservation of MNHN.F.CNJ174, it remains uncertain whether this condition is original and whether similar digitations were present on the remaining buttresses. The axillary buttress extends anteriorly at least to the level of the third peripheral, contacting primarily peripherals III–V (Fig. 3). The inguinal buttress articulates with peripherals VII and VIII and may have had a short anterolateral contact with peripheral VI (Fig. 3). Between the buttresses, a large lateral plastral fontanelle is present (Fig. 3). A rib-like element protrudes from beneath the carapace at the level of the left lateral fontanelle, between costals III and IV (Fig. 3). This element is possibly plastral in nature but was displaced postmortem. Additional medial plastral portions are exposed beneath the broken nuchal anteriorly and the left seventh costal posteriorly (Fig. 3), though these provide little morphological information.

Appendicular skeleton

In MNHN.F.CNJ77, limb remains are incomplete and partially broken (Fig. 1). Identifiable elements include the right tibia and fibula, as well as three probable tarsals, one metatarsal, and a zeugopodial element of the left pes. Other fragments are too damaged for reliable identification. The right tibia and fibula are slender, elongated, and slightly constricted at midshaft (Fig. 1). The tibia measures 27 mm in preserved length, with an estimated total length of 29 mm. The fibula measures 31 mm.

In MNHN.F.CNJ174, limb material is largely absent except for the left femur, preserved mainly as an impression with a small proximal fragment near peripherals IX–X (Fig. 3).

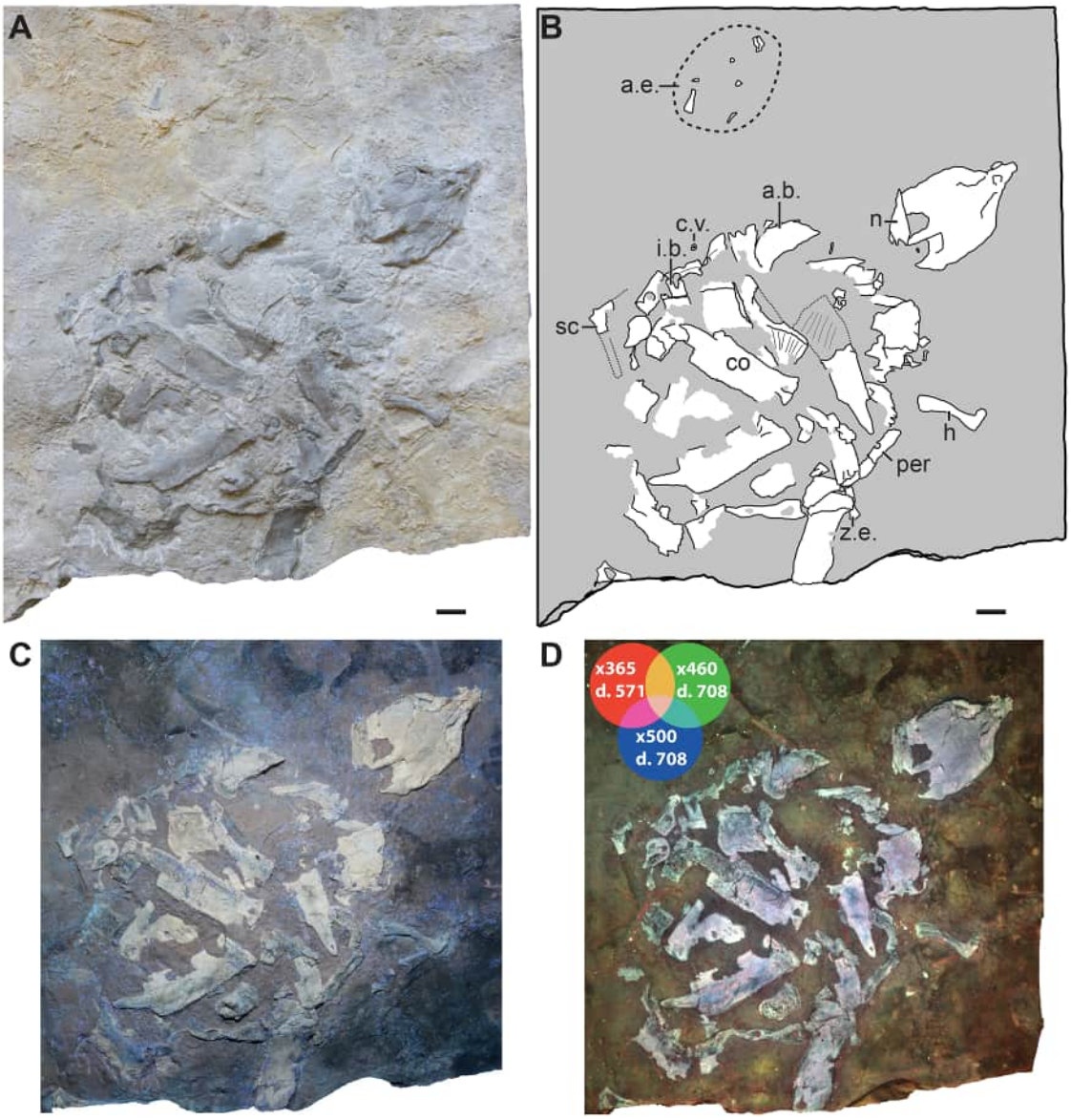

Figure 5 MNHN.F.CNJ82 (*Solnhofia parsonsi*) from Canjuers. A, photograph; B, interpretative line drawing; C, UV-light photograph; D, false colour multispectral image. Abbreviations: a.b., axillary buttress; a.e., autopodial elements; co, costal; c.v., caudal vertebra; h, humerus; i.b., inguinal butress; n, neural; per, peripheral; sc, scapula; z.e., zeugopodial element. The matrix is highlighted in grey. In D, *x* corresponds to the projected light wavelength (in nm), and *d* to the band-pass filter used for detection (in nm). Scale bar equals 1 cm.

The impression indicates a long, slender, and slightly curved element, approximately 31 mm long, 9 mm wide proximally, 3 mm at midshaft, and 6 mm distally. Its proportions and curvature resemble those of eurysternids such as *Eurysternum wagleri* (Anquetin and Joyce 2014), *Solnhofia parsonsi* (Joyce 2000), and *Idiochelys fitzingeri* (Lortet 1892).

Solnhofia parsonsi

General

MNHN.F.CNJ82 consists of a well-preserved and articulated skull associated with numerous disarticulated but well-preserved postcranial elements, including dissociated shell fragments (Figs 5–7). A single, small, isolated caudal vertebra is also preserved, but its condition precludes detailed description (Fig. 5). The postcranial material primarily comprises shell and plastron fragments, along with a few elements of the limbs and pectoral girdle (Fig. 5). All postcranial elements are disarticulated but remain confined to the shell area, so that some lateral peripherals and plastral fragments are approximately in place, as previously noted by Broin (1994).

Skull

Cranial bones: The skull of MNHN.F.CNJ82 is preserved in dorsal view (Figs 5, 6), measuring 57 mm in maximum length and 35.1 mm in maximum width. It retains most of its original outline but is dorsoventrally flattened and exhibits several fractures, particularly in the anterior region (Fig. 6). The skull appears large relative to the shell size, as noted by Lapparent de Broin (1996), suggesting similarity with *Solnhofia parsonsi*,

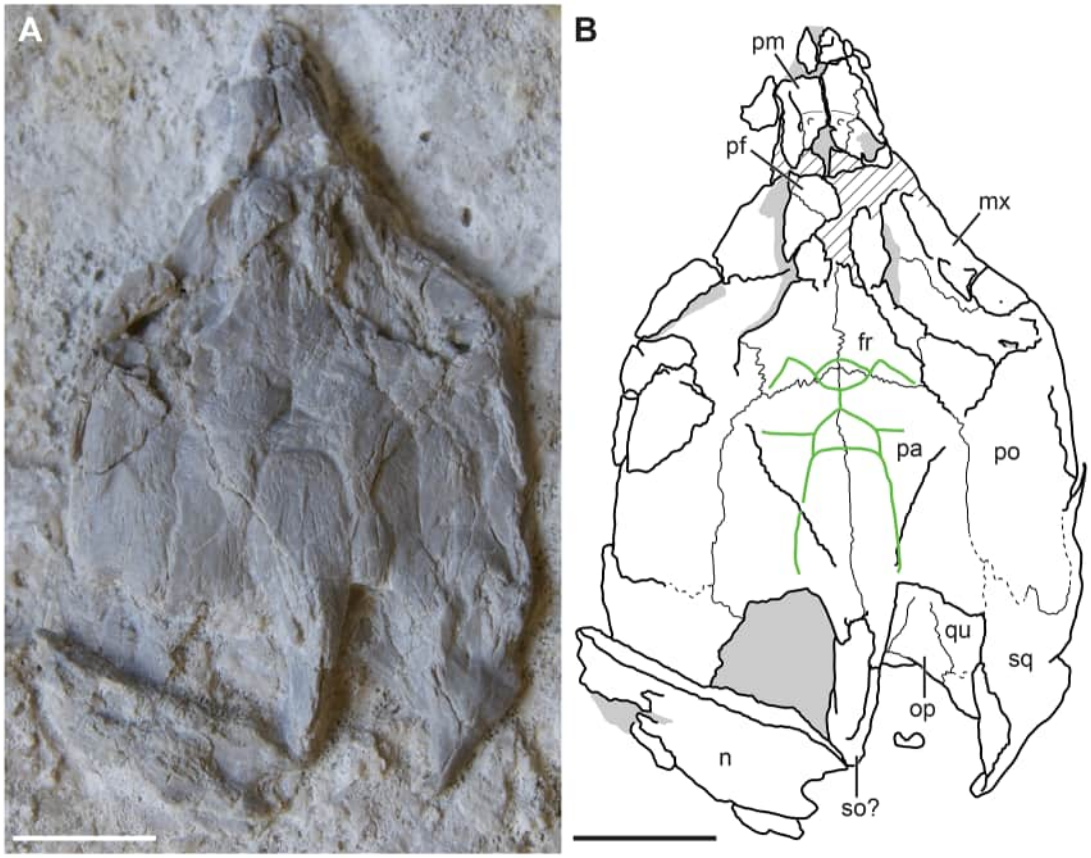

Figure 6 Cranium of MNHN.F.CNJ82 (*Solnhofia parsonsi*) from Canjuers. A, photograph; B, interpretative line drawing. Abbreviations: fr, frontal; mx, maxilla; n, neural; op, opistothic; pa, parietal; pf, prefrontal; po, postorbital; qu, quadrate; so, supraoccipital; sq, squamosal. Dashed lines indicate uncertain sutures. Cranial sulci are indicated by thicker green lines. Grey (shaded) areas indicate regions lacking bony material, whereas hatched surfaces represent areas where the original exposed bony surface has been lost. Scale bar equals 1 cm.

but calculating the relative size of the skull compared to the shell length is not possible due to the disarticulation of the shell. The apertura narium externa is well defined, allowing recognition of the pronounced anterior elongation of the premaxillae that gives the snout a narrow, elongated, and pointed outline (Fig. 6). This condition, already documented by Broin (1994), closely resembles that of *Solnhofia parsonsi* (Gaffney 1975, Joyce 2000) and possibly *Solnhofia brachyrhyncha* (Anquetin and Püntener 2020). The orbits, though slightly deformed, are clearly discernible, positioned immediately posterior to the apertura narium externa and oriented anterodorsolaterally (Fig. 6). Dorsally, the orbital margin is primarily formed by the frontal, whereas the posterior margin is defined by the postorbital (Fig. 6). The anterodorsal margin was probably formed by the prefrontal, but this anatomy cannot be confirmed due to poor preservation in this part of the skull.

As documented by Broin (1994), the upper temporal emarginations are moderately developed (Fig. 6), comparable to *Solnhofia parsonsi* (Gaffney 1975, Evers and Benson 2018, Anquetin and Püntener 2020). The region of the upper temporal emarginations is partially crushed, and sutures in this area are consequently difficult to discern. The upper temporal emarginations are bordered by the supraoccipital medially, the parietal anteriorly and anteromedially, and the squamosal laterally (Fig. 6). As noted by Broin (1994), the postorbital appears to be excluded from the margin of the upper temporal emargination by a parietal–squamosal contact, a condition that contrasts with previous interpretations of *Solnhofia parsonsi*, including the holotype (TM 4023; Evers and Benson 2018; see Discussion). However, given the state of preservation, the sutural relationships in this region cannot be confidently assessed and should be interpreted with caution. As noted by Broin (1994), the frontal–parietal contact is slightly curved anteriorly (Fig. 6). In addition, the suture in MNHN.F.CNJ82 exhibits weak crenulation. This form differs somewhat from the generally straighter and more distinctly crenulated condition observed in other *Solnhofia parsonsi* specimens. However, slight variation in the morphology of the frontal–parietal suture, including the degree of crenulation, is observed in *Solnhofia parsonsi* (Joyce 2000, Evers and Benson 2018, Augustin *et al.* 2023) and the condition in MNHN.F.CNJ82 does not appear unusual within this range. The skull roof bears numerous posteriorly oriented striations and small foramina, concentrated mainly along the midline and extending across the supraoccipital, parietal, and frontal bones.

Cranial scutes: Several cranial sulci are visible across the central region of the skull roof of MNHN.F.CNJ82 (Fig. 4C). For *Solnhofia parsonsi*, cranial scutes are visible in specimen

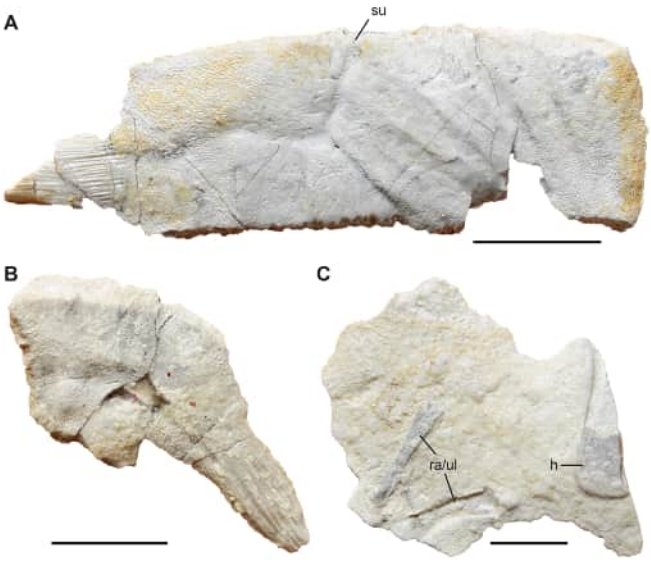

Figure 7 Isolated material of MNHN.F.CNJ82 (*Solnhofia parsonsi*) from Canjuers. A, left costal IV; B, right costal VIII; C, limb elements. Abbreviations: h, humerus; ra, radius; ul, ulna; su, sulcus. Scale bar equals 1 cm.

NMS 8741 (Fig. 4D) and were partially illustrated, though not labelled, by Gaffney (1975).

In MNHN.F.CNJ82, a large, anteroposteriorly elongate midline A scute covers most of the posterior half of the parietals and probably the supraoccipital (Fig. 4C). Anterior to it lies a subtriangular X scute, slightly pointed anteriorly and broader than long, contacting the A scute along a gently concave posterior margin (Fig. 4C). Posterolaterally, it meets large paired H scutes, which also contact the A scute medially (Fig. 4C). Anteriorly, the H scutes contact paired G scutes along a short transverse sulcus (Fig. 4C). The lateral margins of the H and G scutes are not preserved. The G scutes meet medially in front of the X scute and enclose posteriorly a small, lens-shaped Y scute that is wider than long (Fig. 4C). The anterior margin of the Y scute contacts the F scutes (Fig. 4C), whose outlines are unclear. Although the F scutes are not fully visible in MNHN.F.CNJ82, two pairs of F scutes, one anterior and one posterolateral, appear to be common in other turtles exhibiting comparable cranial scute patterns (Evers *et al.* 2021). This configuration may also occur in *Solnhofia parsonsi*, as suggested by specimen NMS 8741 (Fig. 4D). Overall, the cranial scute arrangement in MNHN.F.CNJ82 closely resembles that of *Solnhofia parsonsi* (NMS 8741) (Fig. 4C, D). Nevertheless, despite the general resemblance in the arrangement of the cranial scutes, distinct differences in shape and contacts are present in MNHN.F.CNJ82 compared to *Solnhofia parsonsi* (NMS 8741). The A scute is broader anteriorly and contacts a larger sub-triangular X scute in MNHN.F.CNJ82, whereas the A scute appears to be narrower anteriorly and is separated from a smaller rounded X scute in NMS 8741 (Fig. 4C, D). Another important difference is the large pentagonal Y scute in NMS 8741 (small and lens-shaped in MNHN.F.CNJ82), which impacts the anterior outline of the G scutes and prevents the posterior F scutes from meeting medially (Fig. 4D). We refer the reader to the discussion for details about the significance of these differences.

Shell

Shell bones: The shell elements of MNHN.F.CNJ82 are incompletely preserved and often partially broken, making detailed identification challenging. Several neurals, costals, and peripherals are identifiable with certainty (Fig. 5). Two costal bones, identified as a left costal IV and a right costal VIII, are detached from the main slab (Fig. 7), as mentioned by Broin (1994) and an additional small slab fragment, unmentioned by (Broin 1994), preserves limb material (Fig. 7). Three isolated neurals figured by Broin (1994) could not be relocated and are considered lost. One of these was described as keeled, a feature unknown in *Solnhofia parsonsi*, but this trait cannot be confirmed. According to Broin (1994), all associated fragments were recovered from sediment directly surrounding the main slab, suggesting that they belong to the same. All shell bones are notably thick, contrasting with the thinner condition in MNHN.F.CNJ77 and MNHN.F.CNJ174, as well as in other eurysternids such as *Eurysternum wagleri* and *Parachelys eichstaettensis* (Anquetin *et al.* 2017). This shell thickness is comparable to that observed in *Solnhofia* spp. (Joyce 2000, Anquetin and Püntener 2020, Augustin *et al.* 2023).

On the distal portions of the costals, short rib segments are visible (Fig. 5), and the distal margins are non-sutural, suggesting the potential presence of small costo-peripheral fontanelles as in some *Solnhofia parsonsi* specimens (Joyce 2000, Anquetin and Püntener 2020) and documented by Broin (1994). The partial persistence of these openings indicates that MNHN.F.CNJ82 was not osteologically mature, as adult individuals completely close their fontanelles (e.g. Augustin *et al.* 2023). Several lateral peripherals remain partially articulated and appear relatively narrow (Fig. 5). On the preserved plastral fragments corresponding to the axillary buttresses, numerous small pegs are visible on the articular surface (Fig. 5), indicating the presence of a ligamentous bridge between carapace and plastron, a condition typical of eurysternids and reported in *Solnhofia* spp. (Joyce 2000, Anquetin *et al.* 2017, Anquetin and Püntener 2020). A radial pattern is discernible along the vertebral scute region, a variably present feature in *Solnhofia parsonsi* (Joyce 2000, Augustin *et al.* 2023). A fine, vermicular ornamentation occurs on portions of the carapace but is unevenly distributed (Figs 5, 7). Because this ornamentation is absent on the visceral surfaces of the plates, it is unlikely to be taphonomic in origin. Its irregular distribution may instead indicate a pathological condition. Such ornamentation has not been reported in other specimens attributed to *Solnhofia parsonsi*.

Shell scute sulci: The disarticulated condition of the shell limits interpretation of the scute pattern. On one detached costal, a laterally angled sulcus marking the lateral boundary of a vertebral scute is clearly preserved, together with a transverse sulcus delimiting two pleural scutes (Fig. 7A, B). Based on these sulci, the vertebral scutes of MNHN.F.CNJ82 appear moderately wide (approximately half the costal width), comparable to some *Solnhofia parsonsi* specimens (e.g. DMA-JP-2004/005;

Augustin *et al.* 2023), but narrower than in specimen JM SCHA 70 (Joyce 2000), which exhibits unusually broad vertebral scutes (see Discussion).

Appendicular skeleton

Elements of the appendicular skeleton include a partial scapula, displaced from its anatomical position, a right humerus located anterolateral to the carapace, and an additional small slab fragment, unmentioned by Broin (1994), that preserves limb material (Figs 5, 7). The humerus measures about 30 mm in length and displays a well-developed humeral head. Near the right lateral shell margin, a slender, rod-like bone with a slight midshaft constriction lies partially covered by a peripheral. Its proportions suggest a zeugopodial element, but its precise identity cannot be confirmed (Fig. 5).

Several minute, isolated fragments to the left of the shell may represent autopodial elements (Fig. 5), but their poor preservation precludes identification. A separate slab fragment preserves additional limb remains, including the distal portion of the left humerus, a complete zeugopodial element, and the impression of another (Fig. 7C). Both zeugopodial bones are slender, slightly constricted at midshaft, and dorsoventrally flattened (Fig. 7C). As they are nearly identical in shape, distinguishing between radius and ulna is not possible.

Thalassochelydia indet

General

MNHN.F.CNJ76 is relatively complete but poorly preserved (Fig. 8). It is exposed in dorsal view, with many skeletal elements still in articulation, including the cranium, possible mandibular fragments, the cervical series, part of the hyoid, the plastron, the humeri, the femora, the left tibia, and possible traces of caudal vertebrae. The specimen appears to have been split horizontally, exposing the internal surface of the plastron and the palatal aspect of the skull.

Skull

The skull is preserved in dorsal view and articulated with the postcranial skeleton (Fig. 8). It is triangular in outline, with slightly concave lateral margins and an apparently short snout (Fig. 8). However, given the poor preservation, it remains uncertain whether the short-snouted condition is genuine or taphonomic. Poor preservation prevents precise measurements. However, the skull is estimated to be approximately 43 mm long, the plastron about 78 mm, and the carapace roughly 105 mm in length. Relative to the shell, the skull is proportionally large, as already noted by Broin (1994), and comparable to the condition observed in *Solnhofia parsonsi* (Joyce 2000, Anquetin *et al.* 2017), with a skull representing approximately 41% of the shell length. The posterior outline of the skull is deeply concave, with the squamosal process projecting far posteriorly. Preserved cranial elements include the basioccipital, quadrates, pterygoids, and probable portions of the palatines and vomer, but all are heavily crushed and lack diagnostic details. A portion of the hyoid apparatus is present posterior to the skull, corresponding to the left ceratobranchial I, preserved as a curved, rod-like element. The posterior extremities of the mandibular rami may also be visible, though their identification is uncertain.

Axial skeleton

Cervical vertebrae are only preserved as faint impressions and thin bony sheets, precluding detailed anatomical interpretation. Possible caudal vertebrae are present but too poorly preserved for confident description.

Shell

The carapace appears rounded in outline, as already documented by Broin (1994), but is incompletely preserved (Fig. 8). Its lateral margins can be inferred from impressions of thoracic rib tips and peripheral fragments (Fig. 8). The thoracic rib impressions indicate the presence of large costo-peripheral fontanelles. The plastron is comparatively better preserved but shows weak ossification, particularly along the midline. Thin digitations (peg-like projections) are visible on the axillary and inguinal buttresses of the hyoplastron and hypoplastron, respectively, suggesting a ligamentous bridge with the carapace. Similar digitations are visible on the medial margin of the hyoplastron. A central plastral fontanelle was probably present, though unconfirmed, whereas lateral plastral fontanelles are clearly visible.

Appendicular skeleton

Fragments and impressions of both fore- and hindlimbs are present (Fig. 8). Portions of the humeri are identifiable, and impressions of the femora and tibiae are visible posterior to the shell. However, preservation is too poor to describe their morphology in detail.

Results and discussion

Taxonomic status of MNHN.F.CNJ77 and MNHN.F.CNJ174

Broin (1994) was the first to describe MNHN.F.CNJ77 and proposed that it represents a new species of *Eurysternum*, primarily based on its general skull morphology, short snout, and shell characteristics. Broin (1994) did not include MNHN.F.CNJ174 in her study. Broin (1994) rejected an attribution of MNHN.F.CNJ77 to *Eurysternum wagleri*, because it lacks a pygal bone and instead possesses a well-developed pygal notch. We confirm that both MNHN.F.CNJ77 and MNHN.F.CNJ174 include a distinct pygal bone and, therefore, lack the typical pygal notch of *Eurysternum wagleri*. Broin (1994) further emphasized differences with *Eurysternum wagleri* in cranial morphology, noting notably elongated prefrontals that are longer medially than laterally and proportionally longer than the frontals on the orbital margin. In MNHN.F.CNJ77, the prefrontal region is damaged, and bone contacts are unclear. The relationships between the prefrontals and frontals, based on our observations, thus remain uncertain. In addition, we are unaware of any published description for the skull of *Eurysternum wagleri*. We thus cannot confidently reproduce the observation made and conclusions drawn by Broin (1994) in regard to cranial differences. Broin (1994) further noted that MNHN.F.CNJ77 differs from *Eurysternum wagleri* in having a less constricted posterior shell margin and a broader anterior margin, a condition that we confirm in our observations. Nevertheless, shell outline may be subject

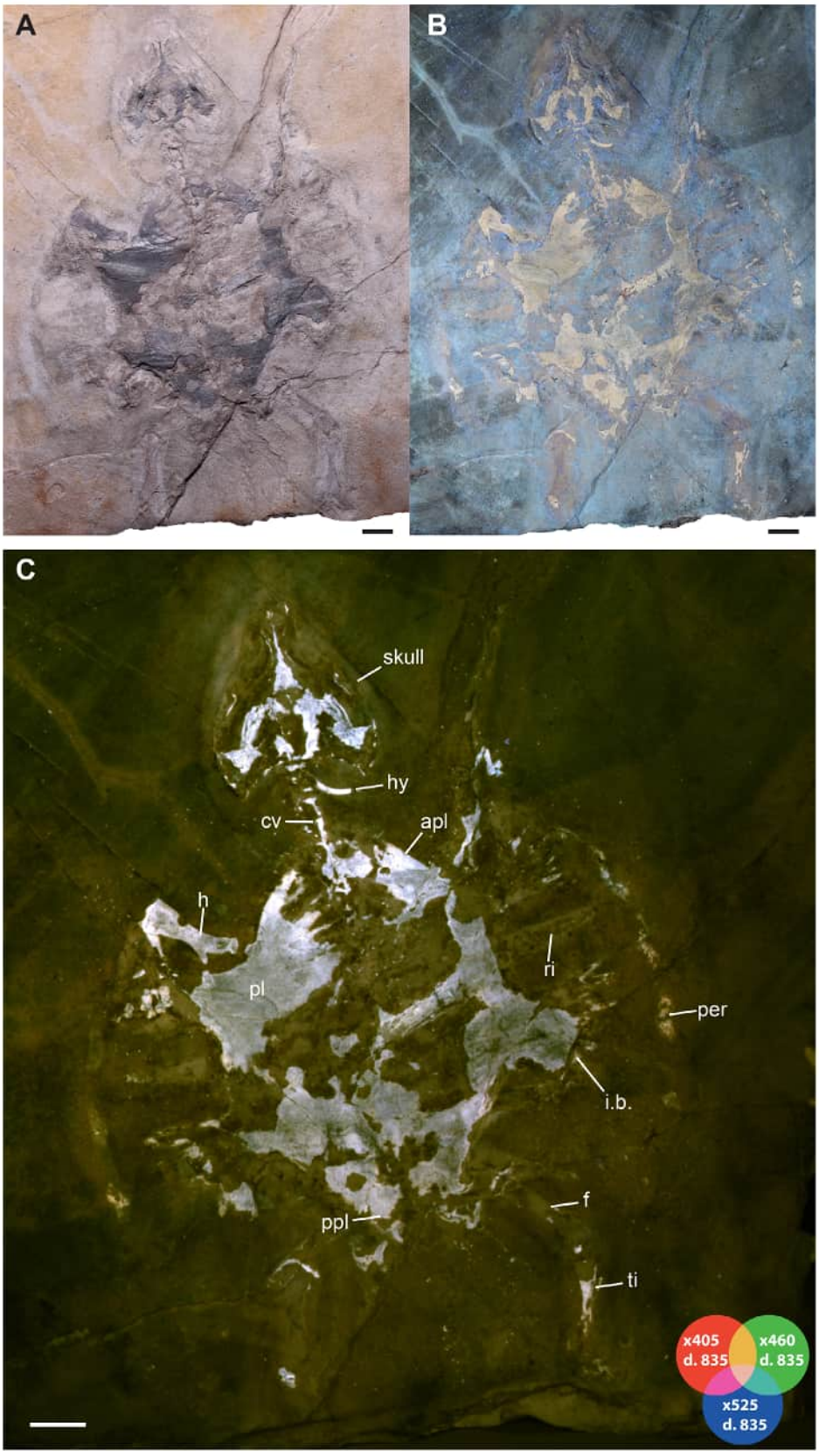

Figure 8 MNHN.F.CNJ76 from Canjuers. A, photograph; B, UV-light photograph; C, false colour multispectral image. Abbreviations: apl, anterior plastral lobe; cv, cervical vertebrae; f, femur; h, humerus; hy, hyoid; i.b., inguinal buttress; per, peripheral; pl, plastron; ppl, posterior plastral lobe; ri, rib; ti, tibia. In D, *x* corresponds to the projected light wavelength (in nm), and *d* to the band-pass filter used for detection (in nm). Scale bar equals 1 cm.

to variation, as seen between the two specimens (see below). Overall, we agree with Broin's (1994) taxonomic conclusion that MNHN.F.CNJ77 cannot be assigned to *Eurysternum wagleri*, mainly based on the presence of a pygal bone.

A referral of these specimens with other named eurysternid taxa can be confidently ruled out as well. MNHN.F.CNJ77 and MNHN.F.CNJ174 lack large body size and the strongly reduced ossification of the costals exposing the broad underlying ribs, as documented in *Achelonia formosa*. They also lack the keeled posterior neurals and reduced costal ossification characteristic of *Chelonides wittei*. An attribution to *Idiochelys fitzingeri* is excluded by the absence of a reduced neural series and the lack of a rounded carapace outline. Likewise, *Palaeomedusa testa* differs in its anteriorly narrow first vertebral scute contacting the cervical scutes only, and *Parachelys eichstaettensis* shows anterolateral contact of vertebral I with marginal I only and has lateral cervical scutes that are triangular in shape (against quandrangular in the specimens discussed here). Finally, *Hydropelta meyeri* possesses unique plastral features not observable here, but the overall resemblance of MNHN.F.CNJ77 and MNHN.F.CNJ174 to *Eurysternum* and *Solnhofia* clearly excludes an affinity with *Hydropelta meyeri*.

Both Canjuers' specimens resemble *Eurysternum wagleri* in exhibiting a similar skull size relative to the shell (roughly 20%), undulated vertebral sulci, and a comparable short-snouted cranial morphology. Besides the absence of a pygal bone, we observe that *Eurysternum wagleri* exhibits a variable pattern in the posterior costals, which contrasts with the condition visible in MNHN.F.CNJ77 and MNHN.F.CNJ174. Starting around costal IV, the costals in *Eurysternum wagleri* may contact either two peripherals (costal n contacting peripherals n + 2 and n + 3) or only the more posterior peripheral (n + 3) (see: Anquetin and Joyce 2014). For example, in BSPG AS I 921, costal VIII contacts peripherals X and XI, whereas in BSPG 1960 VIII 43, it contacts only peripheral XI. This pattern is unique among eurysternids, whereas in MNHN.F.CNJ77 and MNHN.F.CNJ174, the posterior costals consistently contact only the anterior peripheral (costal n contacting peripheral n + 2). Although contacting a single peripheral appears to be the common condition within thalassochelydians (e.g. Meyer 1860, Lortet 1892, Joyce 2000, Anquetin *et al.* 2017, Joyce and Mäuser 2020, Augustin *et al.* 2023), *Eurysternum wagleri* exhibits greater variation, differing from other eurysternids in the posterior costal–peripheral contacts.

The Canjuers' specimens also share several features with *Solnhofia* spp., notably a rounded, subpentagonal shell outline and the presence of posterior peripherals VII–XI that are broader than long. In *Eurysternum wagleri*, this condition usually appears only from peripherals VIII–IX onward. Additional traits such as radial shell ornamentation and a shallow nuchal notch, present in MNHN.F.CNJ77 and MNHN.F.CNJ174, are common to both *Solnhofia* spp. and *Eurysternum wagleri*.

Despite these resemblances, assignment to *Solnhofia* spp. is not supported. Species of *Solnhofia* possess a posteriorly projecting squamosal that extends far beyond the condylus occipitalis, a feature absent in MNHN.F.CNJ77 and MNHN.F.CNJ174. Lateral plastral fontanelles are very small in *Solnhofia* spp., contrasting sharply with the extensive fontanelles of the Canjuers' specimens, which resemble the condition in *Eurysternum wagleri*. Cranially, *Solnhofia parsonsi* typically develops an elongated snout projecting well beyond the apertura narium externa, producing a marked, V-shaped outline in dorsal view. This feature is absent in both Canjuers' specimens. The short-snouted *Solnhofia brachyrhyncha* is more similar in this respect, but MNHN.F.CNJ77 and MNHN.F.CNJ174 differ from it by having proportionally longer frontals, a long and straight parietal–frontal contact, and narrower skulls at the orbital level. Skull proportions also differ: *Solnhofia* spp. have very large skulls relative to carapace length (~40% in *Solnhofia parsonsi*, >25% in *Solnhofia brachyrhyncha*; Broin 1994, Anquetin and Püntener 2020), whereas the Canjuers' specimens are around 20%, matching *Eurysternum wagleri* instead (Broin 1994, Anquetin *et al.* 2017). Their dorsal preservation prevents evaluating the presence of a secondary palate, another key feature of *Solnhofia* spp.. Additionally, their shell bones are thin, unlike the consistently thick shell elements characteristic of *Solnhofia* spp. (Anquetin and Püntener 2020; pers. obs. 02/2025 on JME SCH 70 figured in Joyce 2000). MNHN.F.CNJ82, the only specimen assignable to *Solnhofia parsonsi* from Canjuers, is the only Canjuers' turtle with such thick shell elements, reinforcing this distinction. Vertebral scutes in MNHN.F.CNJ77 and MNHN.F.CNJ174 are proportionally wide, unlike the moderately narrow vertebrals typical of *Solnhofia* spp.. Although one specimen (JME SCH 70) displays unusually broad vertebrals, we regard this condition as exceptional within the genus. Furthermore, vertebral sulci in MNHN.F.CNJ77 and MNHN.F.CNJ174 exhibit pronounced undulations, a feature common in *Eurysternum wagleri* but absent in *Solnhofia* spp. (Anquetin and Joyce 2014).

Taken together, MNHN.F.CNJ77 and MNHN.F.CNJ174 lack the diagnostic traits of *Eurysternum wagleri* (e.g. deep pygal notch) and those of *Solnhofia* spp. (e.g. elongated and pointed snout and large skull-to-shell ratio). Although they share certain features with both taxa, their combined morphology does not correspond with either taxon. We, therefore, erect a new genus and species, ***Caesaria templaria* gen. nov. et sp. nov.**, to reflect this distinctive morphology and to avoid eroding the diagnostic integrity of the genera *Eurysternum* and *Solnhofia*, which exhibit well-defined and distinctive characters (e.g. absence of pygal and large head). We also would like to emphasize that future analyses focusing on phylogeny may ultimately refer this species to either *Eurysternum* or *Solnhofia*, given its general resemblance to both. A close relationship with one of these taxa is at least expected.

Morphological differences between MNHN.F.CNJ77 and MNHN.F.CNJ174

MNHN.F.CNJ174 differs slightly morphologically from MNHN.F.CNJ77 in having a more oval carapace outline and larger costo-peripheral fontanelles. The posterior margin of MNHN.F.CNJ174 is incomplete and damaged, preventing accurate reconstruction of its original shape. Given the preservation of intact thoracic ribs and proper articulation with the peripherals, there is no evidence of strong mediolateral

compression, suggesting that the shell was originally subpentagonal or weakly oval. Additionally, MNHN.F.CNJ174 also exhibits some variation in the morphology of the vertebral scutes, particularly the fourth that is subdivided into two, creating an additional, intermediate scute, which may reflect developmental or pathological irregularities. Regarding the fontanelles, both specimens (MNHN.F.CNJ77 and MNHN.F.CNJ174) retain costo-peripheral fontanelles, which are small and nearly closed anteriorly in MNHN.F.CNJ77, but more open in MNHN.F.CNJ174. Variation in the degree of ossification of these fontanelles is known to be ontogenetic in turtles. In *Eurysternum wagleri*, a slightly neotenic form, large individuals, probably near adult or adult, tend to retain costo-peripheral fontanelles, with complete closure occurring only at full maturity, whereas smaller individuals consistently show proportionally larger openings (Anquetin and Joyce 2014). By contrast, *Solnhofia* spp. specimens consistently exhibit almost closed or fully closed fontanelles, even in small individuals, reflecting a different developmental pattern. The variation observed in MNHN.F.CNJ77 and MNHN.F.CNJ174, both in size and in the degree of closure, aligns well with incomplete ossification: MNHN.F.CNJ174 probably represents a young subadult, whereas the larger MNHN.F.CNJ77, with its small fontanelles, probably corresponds to an older subadult to near-adult individual. Despite these minor differences, MNHN.F.CNJ174 shares a similar morphology with MNHN.F.CNJ77, and both are, therefore, interpreted as belonging to the same new taxon, with the observed variations attributed to taphonomic or pathological processes.

Taxonomic status of MNHN.F.CNJ82

Broin (1994) identified the specimen MNHN.F.CNJ82 from Canjuers as *Solnhofia* sp., primarily because its skull exhibits similarities with that of *Solnhofia parsonsi*. In particular, both share an elongate snout projecting well anterior to the apertura narium externa, formed by the elongation of the premaxillae, and a moderately developed upper temporal emargination. In a subsequent contribution, Lapparent de Broin (1996) emphasized that the relative skull-to-shell size of the Canjuers' specimen is comparable to that of *Solnhofia parsonsi*, reinforcing its attribution to the same genus.

However, Broin (1994) also noted several morphological differences between the Canjuers' skull and *Solnhofia parsonsi*. The parietals contact the squamosals posterolaterally, which is the normal condition observed in most thalassochelydians (Anquetin *et al.* 2017), but contrasts with the condition visible in *Solnhofia parsonsi* and *Jurassichelon oleronensis* (Gaffney 1975, Rieppel 1980, Evers and Benson 2018). In the original description of *Solnhofia parsonsi*, Gaffney (1975) illustrated the lateral margin of the upper temporal emargination as lacking contact between the parietal and squamosal due to a contribution of the quadratojugal. More recently, CT-based segmentation of the holotype by Evers and Benson (2018) likewise suggested exclusion of the parietal–squamosal contact but attributed this condition to a contribution of the postorbital. However, the bone fragment forming the margin of the upper temporal emargination, separated from the main part of the postorbital in that study, is damaged, leaving uncertainty as to whether it truly represents the postorbital or instead an anterior portion of the squamosal. Notably, specimen DMA-JP-2004/005, referred to *Solnhofia parsonsi* by Augustin *et al.* (2023), was interpreted as showing a postorbital contribution to the upper temporal margin. In this specimen, however, upon re-examination, sutural boundaries are poorly discernible in the posterior skull region, and the precise arrangement of the temporal elements remains uncertain. These differing interpretations, combined with the damaged nature of the relevant elements, indicate that the composition of the upper temporal margin is not consistently or unambiguously resolved in *Solnhofia parsonsi* and, therefore, cannot currently be regarded as a reliable taxonomic character, pending discovery of better-preserved material.

Broin (1994) further noted that the frontals of MNHN.F.CNJ82 jointly form a pointed anterior projection between the prefrontals, whereas in *Solnhofia parsonsi* the frontal–prefrontal contact was described as rectilinear (Gaffney 1975). However, as the frontals of most turtles typically form anterior projections underlying the prefrontals, and given that this area is damaged in the Canjuers' specimen as well, the observed morphology may represent such frontal projections rather than a genuine difference from *Solnhofia parsonsi*. Broin (1994) further observed that the frontal contribution to the orbital margin is shorter than that of the prefrontal, and that the elongate snout of MNHN.F.CNJ82 is proportionally narrower than in *Solnhofia parsonsi*. However, differences reported in the contribution to the orbital margin should be treated cautiously, as the frontal–prefrontal region of MNHN.F.CNJ82 is damaged and may not reflect the original morphology, as discussed above for the frontal–prefrontal contact. Likewise, the apparent narrowness of the snout may result from deformation rather than genuine anatomy. Even if original, this feature does not appear strongly distinct and could fall within the range of intraspecific variation. Broin (1994) finally noted that the Canjuers' specimen differs by its smaller shell and overall smaller size. Nevertheless, we do not consider the small body size of MNHN.F.CNJ82 as diagnostic. Size variation in *Solnhofia* is important (e.g. Joyce 2000, Anquetin and Püntener 2020, Augustin *et al.* 2023; unpublished specimens LF 6024 and NMB R2444, which can confidently be assigned to *Solnhofia*) and shows no consistent stratigraphic or geographic trend, probably reflecting intraspecific or ontogenetic variation, sexual dimorphism, or environmentally influenced adult size plasticity. These differences led Broin (1994) to propose that MNHN.F.CNJ82 represents a distinct, smaller species within *Solnhofia*, but she refrained from naming a new taxon in her study.

In addition to the above listed features highlighted by Broin (1994) in MNHN.F.CNJ82 as differing from *Solnhofia parsonsi*, we here also document a few additional morphological differences between MNHN.F.CNJ82 and previously described specimens attributed to *Solnhofia parsonsi*. The cranial scute pattern of MNHN.F.CNJ82 differs markedly from that of NMS 8741, the best-preserved *Solnhofia parsonsi* skull with scutes, particularly an anteriorly broader A scute, a large X scute, which is sub-triangular with a concave posterior margin, a G scute with sharp anterior margins extending around

the posterior half of the Y scute, and a small, lens-shaped Y. However, cranial scute variation is poorly documented in both extant and extinct turtles, and their homology remains uncertain (e.g. Sterli and de la Fuente 2013, Evers *et al.* 2021, Spicher *et al.* 2024). Consequently, we refrain from drawing taxonomic conclusions based on this feature. Similarly, the osseous ornamentation on the shell is unique within *Solnhofia*, but it is irregularly distributed and may reflect individual variation or a potential pathological condition rather than a taxonomically meaningful trait. Likewise, the width of vertebral scutes, previously cited as diagnostic of *Solnhofia parsonsi* (Joyce 2000), is now known to vary (see: Gaffney 1975, Joyce 2000, Augustin *et al.* 2023). MNHN.F.CNJ82 shows moderately wide vertebrals reaching half the length of the costals, consistent with most *Solnhofia parsonsi* specimens (e.g. DMA-JP-2004/005; NMB R2444), whereas JME SCHA 70 alone exhibits exceptionally broad vertebrals and unusual dorsal bosses, probably representing an anomalous or pathological condition (Augustin *et al.* 2023).

Although the apparent exclusion of the postorbital from the upper temporal emargination, resulting in the absence of parietal–squamosal contact, could have taxonomic significance, the configuration of this region is not consistently understood in *Solnhofia parsonsi*, including in the holotype, where the bone contacts are difficult to trace and have been interpreted differently in previous studies (Gaffney 1975, Evers and Benson 2018). In MNHN.F.CNJ82, this region is likewise only weakly discernible due to its state of preservation and partial crushing, preventing a confident assessment of the sutural relationships. Given these uncertainties and the existence of alternative interpretations, this feature cannot be reliably evaluated at present and is, therefore, best treated with caution. We, therefore, do not use it as a basis for taxonomic interpretation until its status is clarified.

After having revised MNHN.F.CNJ82, we agree with Broin (1994) that MNHN.F.CNJ82 is most similar to *Solnhofia parsonsi* and thus can safely be attributed to *Solnhofia*. The morphological similarities highlighted by Broin (1994) clearly correspond to the diagnostic features of the taxon. Although the exact skull-to-shell length proportion in MNHN.F.CNJ82 cannot be measured precisely due to disarticulation (estimated to 44%–45% by Lapparent de Broin 1996), it is evident that the skull is proportionally much larger than in *Eurysternum wagleri* (*c*. 20%; Anquetin and Joyce 2014) or *Idiochelys fitzingeri* [23%–24%; pers. obs. on MDC 20015631 and MDC 20015636, figured in Lortet (1892)], and more comparable to the condition in *Solnhofia* spp., where the proportions reach 25%–40% (Joyce 2000, Anquetin *et al.* 2017, Anquetin and Püntener 2020). Additional features of interest in MNHN.F.CNJ82 are the elongate, pointed snout projecting beyond the apertura narium externa, the large skull relative to shell size, and the reduced costo-peripheral fontanelles, which combined are characteristic of *Solnhofia parsonsi* (Gaffney 1975, Anquetin *et al.* 2017, Anquetin and Püntener 2020).

Although MNHN.F.CNJ82 is stratigraphically the youngest known *Solnhofia* specimen (Mucronatum Zone, Early Tithonian) and exhibits a few differences relative to *Solnhofia parsonsi*, it clearly shares the diagnostic combination of characters of that taxon (see above). We do not interpret the additional differences noted by Broin (1994) or observed here as taxonomically significant, as they fall within the range of intraspecific variation now recognized in *Solngofia parsonsi*, which exhibits substantial morphological variability, especially in the shell (Gaffney 1975, Joyce 2000, Augustin *et al.* 2023). Moreover, no evidence of directional morphological change is observed across its stratigraphic range.

The more notable differences, such as cranial scute pattern variation and the configuration of the upper temporal emargination, are poorly understood or not consistently observable or unambiguously preserved in *Solnhofia parsonsi*, including MNHN.F.CNJ82, due to its strongly crushed skull. Their taxonomic significance, therefore, remains uncertain at present. In addition, only a single disarticulated specimen from Canjuers closely matching *Solnhofia parsonsi* morphology is known, limiting assessment of intraspecific variation versus potential taxonomic significance of these features.

Consequently, although MNHN.F.CNJ82 exhibits some distinct features whose taxonomic significance remains unclear, these are best interpreted cautiously and are not used here as a basis for taxonomic separation. We, therefore, follow Broin (1994) in assigning MNHN.F.CNJ82 to *Solnhofia* and refer it to *Solnhofia parsonsi* rather than to a distinct species, given its conformity with the diagnostic morphology of that taxon.

Taxonomic status of MNHN.F.CNJ76

MNHN.F.CNJ76 was first discussed by Fabre *et al.* (1982), who identified it as being affiliated with *Solnhofia parsonsi* based on skull morphology. Due to the relatively large size of the skull compared to the shell (approximately 40% of shell length), Fabre *et al.* (1982) interpreted the specimen as representing a juvenile individual. Later, Broin (1994) also concluded that MNHN.F.CNJ76 is a juvenile but argued that the specimen could not be confidently assigned to any known species because of extensive erosion. Broin (1994) tentatively noted that the broad snout of MNHN.F.CNJ76 resembles that of *Eurysternum wagleri* but also pointed out that the skull proportion compared to the shell length does not correspond to the proportions observed in juvenile *Eurysternum wagleri* specimens. Consequently, Broin (1994) described MNHN.F.CNJ76 as an indeterminate plesiochelyid turtle. We do not consider the short snout of MNHN.F.CNJ76 to be a reliable feature for comparison with *Eurysternum wagleri*, as suggested by Broin (1994), because of the specimen's poor preservation and weak ossification and because an elongated snout may have been lost or partially broken and still covered by matrix. We are also unaware of any published juvenile specimens referable to *Eurysternum wagleri* that might allow drawing comparisons. Nevertheless, we agree with previous studies that MNHN.F.CNJ76 most likely represents a juvenile individual based on its small size (plastron length ~83 mm), the presence of extremely large lateral plastral and costo-peripheral fontanelles, and the weak ossification along the midline contact between plastral elements. Due to the specimen's poor preservation, no diagnostic characters are available to allow a precise identification, and we, therefore, concur with Broin (1994) that it is currently not possible to assign

MNHN.F.CNJ76 to a specific genus or species. However, we consider the relatively large skull in comparison to the shell length as a potentially significant feature, since this trait is characteristic of the genus *Solnhofia*. Taken alone, however, this character is insufficient to confidently assign the specimen to that genus, particularly given that juvenile skulls are disproportionately larger due to allometric growth. For these reasons, we keep from referring MNHN.F.CNJ76 to a specific taxon.

Conclusion

In conclusion, we provide a detailed revision and description of the turtle specimens from the Late Jurassic (Tithonian) Canjuers Plattenkalk Lagerstätte. One specimen (MNHN.F.CNJ82) can be confidently referred to *Solnhofia parsonsi*, whereas another (MNHN.F.CNJ76) may belong to the same genus or a closely related taxon, although the attribution to the former remains tentative due to its small size and poor preservation. The remaining two specimens (MNHN.F.CNJ77 and MNHN.F.CNJ174) exhibit a combination of morphological characters recognized as being characteristic of a new species, herein designated *Caesaria templaria* gen. nov. et sp. nov. Among Jurassic thalassochelydians, the Canjuers' *Lagerstätte* (Early Tithonian, Mucronatum Zone), represents the latest Jurassic European occurrences of thalassochelydian turtles and contributes to our understanding of their diversity. Nevertheless, It should be noted that thalassochelydians survived the Jurassic/Cretaceous transition with occurrences in the Early Cretaceous and beyond (Hirayama *et al.* 2000, Evers and Benson 2019, Evers and Joyce 2020, Cadena *et al.* 2025).

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Author contributions

Gaël E. Spicher and Jérémy Anquetin designed the study, interpreted the anatomical features, conducted direct, first-hand examinations of the described specimens, and prepared the figures. Pierre Gueriau and Gaël E. Spicher carried out the multispectral imaging. Gaël E. Spicher wrote the first draft of the manuscript. Gaël E. Spicher, Jérémy Anquetin, Walter G. Joyce, Pierre Gueriau, Karin Peyer, and Vincent Reneleau contributed to, read, and approved the final version of the manuscript.

Conflicts of interest

The authors declare that they have no competing interests.

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Data availability

All data supporting the findings of this study are included within the manuscript. No additional datasets or supplementary material are provided.

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