

Shell bone histology of solemydid turtles (stem Testudines): palaeoecological implications

T. M. Scheyer · A. Pérez-García · X. Murelaga

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Abstract Lately, solemydid turtles have been repeatedly recovered as stem Testudines, indicating that they belong to neither one of the two major branches of crown turtles, the Pancryptodira and Panpleurodira. Despite their wide temporal (Late Jurassic to Late Cretaceous) and spatial (North America and Europe) distributions, solemydid turtles are not particularly well known, as exemplified by the fact that only a single skull has been described for the whole group so far. Furthermore, the palaeoecology of solemydid turtles is still contested with hypotheses ranging from semi-aquatic to terrestrial lifestyles. However, the habitat preference of stem Testudines, such as solemydids, is important to understand the evolution and early radiation of the turtle crown, which is primitively aquatic. Here we describe the shell bone microanatomy and histological microstructures of solemydid turtles using a broad sample of taxa of different ages and localities, as well as review previous histological accounts, to elucidate the palaeoecology of the group independent of the geological setting and

gross anatomy of the fossil finds. Our results indicate that Solemydidae share unique histological features pertaining to their strongly ornamented shell bones, which a) in cases allow taxonomic identification of even small shell fragments and b) unambiguously corroborate a terrestrial lifestyle of its members. The latter further supports a terrestrial lifestyle preference of most representatives of the turtle stem.

Keywords Solemydidae · Stem turtles · Bone microstructure · Palaeoecology · Bone ornamentation · Mesozoic

Introduction

Solemydidae are a group of stem Testudines whose members are distributed over Europe and North America from the Late Jurassic (Tithonian) to the Maastrichtian at the end of the Cretaceous (Joyce et al. 2011; Pérez-García et al. 2013). Anquetin (2012) and Joyce et al. (2011) both recovered some representatives of this Laurasian clade of turtles, the North American *Naomichelys speciosa* Hay, 1908 and the European *Helochelydra nopcsai* Lapparent de Broin and Murelaga, 1999 respectively, among other stem representatives of Testudines in their phylogenetic analyses, instead of within the turtle crown (e.g. Lapparent de Broin and Murelaga 1999; Danilov 2005). Only recently, a nicely preserved skull was described for *Helochelydra nopcsai* (Joyce et al. 2011), whereas skulls of other representatives have been found (cf. *Naomichelys* in North America, cf. *Solemys* in Europe) but hitherto remain unpublished. Other solemydid taxa are known only from shell and other postcranial remains.

One of the most obvious diagnostic features of solemydid turtles is their characteristic shell bone surface ornamentation (Lapparent de Broin and Murelaga 1996; 1999; Joyce et al. 2011). This ornamentation consists of high or low tubercles,

T. M. Scheyer (✉)
Paläontologisches Institut und Museum, Universität Zürich,
Karl-Schmid-Strasse 4, CH-8006 Zürich, Switzerland
e-mail: tscheyer@pim.uzh.ch

A. Pérez-García
Centro de Geologia, Faculdade de Ciências da Universidade de
Lisboa (FCUL), Edifício C6, Campo Grande, 1749-016 Lisbon,
Portugal
e-mail: paleontologo@gmail.com

A. Pérez-García
Grupo de Biología Evolutiva, Facultad de Ciencias, UNED, C/Senda
del Rey, 9, 28040 Madrid, Spain

X. Murelaga
Departamento de Estratigrafía y Paleontología, Facultad de Ciencia y
Tecnología, Universidad del País Vasco/EHU, Apartado 644,
48080 Bilbao, Spain
e-mail: xabier.murelaga@ehu.es

and can also include isolated ridges or ridge networks in which the sinuous ridges frequently anastomose. Recently, Joyce et al. (2011) proposed a new diagnosis for the so far identified as valid representatives of Solemydidae, only using the shell bone sculpturing.

The palaeoecology of solemydid turtles is still contested and different hypotheses have been proposed. Marmi et al. (2009) considered at least some species of the Late Cretaceous European *Solemys* Lapparent de Broin and Murelaga, 1996 to have a semi-aquatic lifestyle based on palaeoenvironmental and taphonomic interpretations of the finding, while also providing additional shell bone histological evidence. Joyce et al. (2011), on the other hand, argued for terrestrial habits of solemydid turtles based on anatomical data, such as the presence of limb ossicles. Unfortunately, the described solemydid turtles so far did not include articulated forelimbs, which could otherwise be used to elucidate their palaeoecology, as has been done previously for Triassic stem turtles *Proganochelys quenstedti* Baur, 1887 and *Palaeochersis talampayensis* Rougier, de la Fuente and Arcucci, 1995 (Joyce and Gauthier 2004).

In addition to taphonomic and morphological data, analysis of the microstructure and microanatomy of bones, including an increasing body of shell bone data, presents an independent line of evidence to expound the palaeoecology of fossil turtles (e.g. Scheyer 2007; Scheyer and Sander 2007; Scheyer et al. 2014). Furthermore, even small (shell) bone fragments can be used for histological analysis, even in cases where more complete fossils including limb bones are absent.

In the present study, we thus describe and review the shell bone histology of solemydid turtles with focus on shell bone material from the Late Cretaceous of several sites on the Iberian Peninsula, in comparison to previous histological accounts of the group and to the histological study of material from various countries and ages, to elucidate whether the solemydid taxa share microstructural and internal histological details. These data are then used to elucidate the palaeoecology of solemydid turtles.

Material and methods

The solemydid shell bones (Fig. 1) used in this study includes seven specimens of *Solemys vermiculata* Lapparent de Broin and Murelaga, 1996 and five specimens of *Solemys* sp. from the Spanish sites of Laño (Burgos Province) and Armuña (Segovia Province) respectively, as well as nine samples of Solemydidae aff. *Naomichelys* sp. from Canada and USA. A single shell fragment of *Plastremys lata* Owen in Parkinson, 1881 sensu Joyce et al. (2011; = '*Trachydermochelys phlyctaenus*' of Seeley 1869) from the Early Cretaceous Cambridge Greensand (Cambridge, UK) was included as well. Based on previous works (Pereda Suberbiola and Barrett 1999; Unwin 2001), Joyce et al. (2011, p. 82–83) indicated

that most fossils from the Cambridge greensand deposits are reworked and likely of Albian age.

In addition, the set of thin-sections of Solemydidae aff. *Helochelydra* sp. (MPG-725-3, a peripheral and MPG-725-4, a possible plastron fragment) used in Pérez-García et al. (2013) from Galve (Galve sub-basin, Maestrazgo Basin of the Iberian Range, Teruel Province, Spain), together with additional sections of four specimens (MNCN 59503, including a costal, peripheral and two plastral fragments probably belonging to several specimens) from Barremian strata of another locality of the Maestrazgo Basin (Morella, Morella sub-basin, Castellón Province, Spain) were added for comparison. All taxa and specimens included in the present study are listed in Table 1.

A few sections of the sampled bones of *Solemys vermiculata* (MCNA-15047, a costal fragment; MCNA-15046, a shell fragment) and *Solemys* sp. (UPUAM-14001, a costal fragment) were further modified into black and white images (Fig. 2) to perform a compactness analysis (Table 2) with the program Bone Profiler, Windows-based version 4.5.8 (Girondot and Laurin 2003), to indicate a potential lifestyle based on shell bone microstructures.

Thin sections were studied and images were taken using a LEICA compound microscope DM 2500 M equipped with a LEICA digital camera DFC 420C. Images were then modified into figures using Adobe Creative suite 6 (Photoshop and Illustrator).

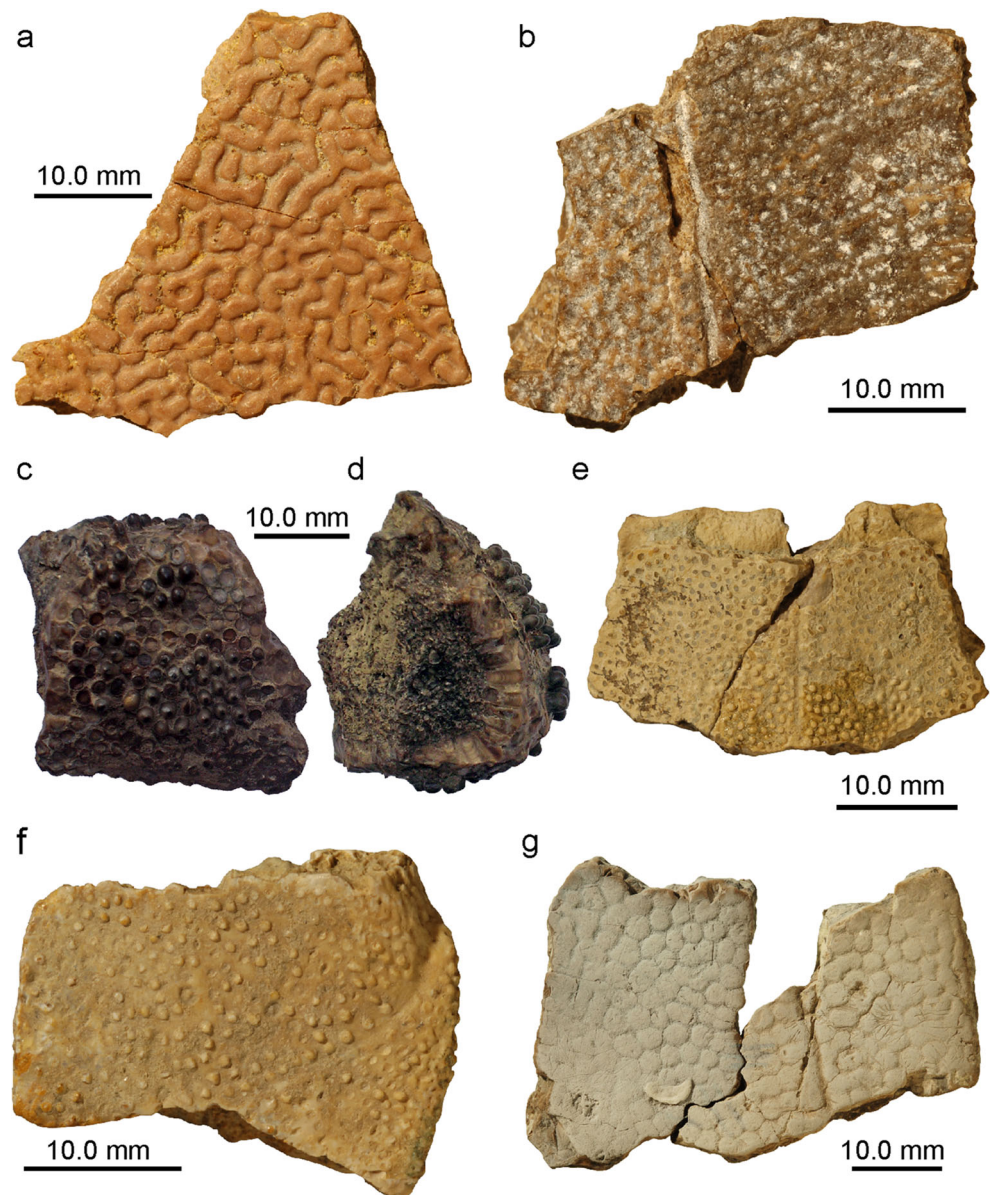
Institutional abbreviations

FM, The Field Museum, Chicago, Illinois, USA; IPS, Institut Català de Paleontologia, Barcelona, Spain; MCNA, Museo de Ciencias Naturales de Alava, Vitoria-Gasteiz, Spain; NHMUK, Natural History Museum, London, UK; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MPG, Museo Paleontológico de Galve, Galve, Teruel, Spain; TMP, Royal Tyrrell Museum of Paleontology, Drumheller, Canada; UPUAM, Unidad de Paleontología, Universidad Autónoma de Madrid, Madrid, Spain.

Previous histological accounts of solemydid turtle bones

The earliest histological description of material now associated to indeterminate members of Solemydidae was given by Owen (1878), who sectioned small conical and ornamented bones, so-called 'granicones', from the Early Cretaceous Purbeck Limestone Formation (UK). Barrett et al. (2002) recognized these bones as sculptured dermal limb ossicles from the limb region of solemydid turtles, similar to those found in specimens of *Naomichelys* from the Early Cretaceous of North America. Owen (1878: 235), in his original

Fig. 1 Selected solemydid taxa used in the present study. **a** *Solemys vermiculata*, costal fragment (MCNA-15047). **b** *Solemys* sp., costal fragment (UPUAM-14001). **c, d** Solemydidae aff. *Naomichelys* sp., peripheral (TMP 90.60.07). **e** Solemydidae aff. *Helochelydra* sp., peripheral (MNCN 59503). **f** Solemydidae aff. *Helochelydra*, plastral fragment (MNCN 59503). **g** *Plastremys lata*, costal fragment (NHMUK R 2251)



description and accompanying image of the sectioned ‘granicone’, hinted at the similarity of the bone matrix to soft tissue structures observable in the “dermal cone of *Moloch*”, i.e. “decussating bands of fibrous tissue, closely matted”. These structures were confirmed by Barrett et al. (2002: 282) who noted an “interwoven mat-like fabric, with the bundles crossing at approximately 90° to each other” in the base of the ‘granicones’. Barrett et al. (2002) further pointed out that, towards the apex, the cortex consists of “bundles of collagen fibrils that run parallel to the outer surface”, the presence of secondary remodelling (i.e. secondary osteons) of cortical bone, as well as that the ornamental tubercles consisted of “loosely bundled collagen fibrils oriented parallel to the outer [bone] surface”.

Enlow and Brown (1957) and Enlow (1969) noted histological details on a turtle shell fragment from the Cretaceous, identified as pertaining to ‘*Trachydermochelys*’, which at the time was thought to be a pleurodiran turtle. Among the characteristic features mentioned are the presence of mostly avascular cortex (unclear whether internal or external or both are meant) composed of numerous bone lamellae and the presence of endosteal Haversian tissue. Unfortunately, neither the text nor the images provide information about the surface ornamentation of the bones. Furthermore, no provenance or other morphological features were provided in Enlow and Brown (1957) and Enlow (1969), which would allow an assessment of the generic assignment or its locality. Whether these bones really belong to “*Trachydermochelys*”

Table 1 Taxon names, specimen numbers, and locality data

Taxon	Specimen number	Locality
<i>Solemys vermiculata</i>	Two neurals (MCNA-15044, MCNA-15054)	Campanian-Maastrichtian, Late Cretaceous, Laño (Burgos Prov.), Iberian Peninsula
	Two costals (MCNA-15047, MCNA-15043)	Campanian-Maastrichtian, Late Cretaceous, Laño (Burgos Prov.), Iberian Peninsula
	One peripheral (MCNA-15045)	Campanian-Maastrichtian, Late Cretaceous, Laño (Burgos Prov.), Iberian Peninsula
	One plastron fragment (MCNA-15048)	Campanian-Maastrichtian, Late Cretaceous, Laño (Burgos Prov.), Iberian Peninsula
	One shell fragment (MCNA-15046)	Campanian-Maastrichtian, Late Cretaceous, Laño (Burgos Prov.), Iberian Peninsula
<i>Solemys</i> sp.	Three costal fragments (UPUAM-14001, UPUAM-14002, UPUAM-14003)	Campanian-Maastrichtian, Late Cretaceous, Armuña (Segovia Prov.), Iberian Peninsula
	Two peripherals (UPUAM-14000, UPUAM-14004)	Campanian-Maastrichtian, Late Cretaceous, Armuña (Segovia Prov.), Iberian Peninsula
Solemydidae aff. <i>Helochelydra</i> sp.	one costal (MNCN 59503)	Arcillas de Morella Fm. (Barremian), Early Cretaceous, Morella (Castellón Prov.), Iberian Peninsula
	One peripheral (MNCN 59503)	Arcillas de Morella Fm. (Barremian), Early Cretaceous, Morella (Castellón Prov.), Iberian Peninsula
	One fragment of hyo- or hypoplastron (MNCN 59503)	Arcillas de Morella Fm. (Barremian), Early Cretaceous, Morella (Castellón Prov.), Iberian Peninsula
	One plastron fragment (MNCN 59503)	Arcillas de Morella Fm. (Barremian), Early Cretaceous, Morella (Castellón Prov.), Iberian Peninsula
	One peripheral (MPG-725-3)	Camarillas Fm. (Lower Barremian), Galve (Teruel Prov.), Iberian Peninsula
	Purported plastral fragment (MPG-725-4)	Camarillas Fm. (Lower Barremian), Galve (Teruel Prov.), Iberian Peninsula
	One costal (FM PR 273)	Antlers Fm. (Albian), Early Cretaceous, Montague County, Texas, USA
Solemydidae aff. <i>Naomichelys</i> sp.	One costal (TMP 90.60.07)	Foremost Fm. (Campanian), Late Cretaceous, Pinhorn Ranch, SE Alberta, Canada
	One peripheral (FM PR 273)	Antlers Fm. (Albian), Early Cretaceous, Montague County, Texas, USA
	One peripheral (TMP 90.60.07)	Foremost Fm. (Campanian), Late Cretaceous, Pinhorn Ranch, SE Alberta, Canada
	One plastron fragment (TMP 2000.16.01)	Foremost Fm. (Campanian), Late Cretaceous, Milkriver, SE Alberta, Canada
	Two shell fragments (TMP 90.60.07)	Foremost Fm. (Campanian), Late Cretaceous, Pinhorn Ranch, SE Alberta, Canada
	Two limb ossicles (FM PR 273)	Antlers Fm. (Albian), Early Cretaceous, Montague County, Texas, USA
	One costal fragment (NHMUK R 2251)	Cambridge Greensand (Albian), Early Cretaceous, Cambridge, UK

Seeley 1869 (Seeley 1869; Marr and Shipley 1904; Andrews 1920) thus cannot be elucidated. Digital images of Enlow's original slides of "*Trachydermochelys*" can be accessed via the *Donald H. Enlow Digital Image Library* on the New York University College of Dentistry homepage (<http://www.nyu.edu/dental/enlow/>).

Scheyer and Sander (2007) classified sectioned material of Solemydidae (aff. *Naomichelys*) among taxa whose histology

indicates terrestrial habits, whereas Scheyer and Anquetin (2008) described the external cortical bone of the same material in comparison to other turtle taxa which exhibit strong surface sculpturing patterns (e.g. *Basilemys*, Trionychidae, Pleurosternidae; see also Scheyer 2007). Scheyer and Anquetin (2008) noted that although a zonation of the external cortical bone into an inner and an outer zone is found in many taxa, some features of the primary shell bone are characteristic

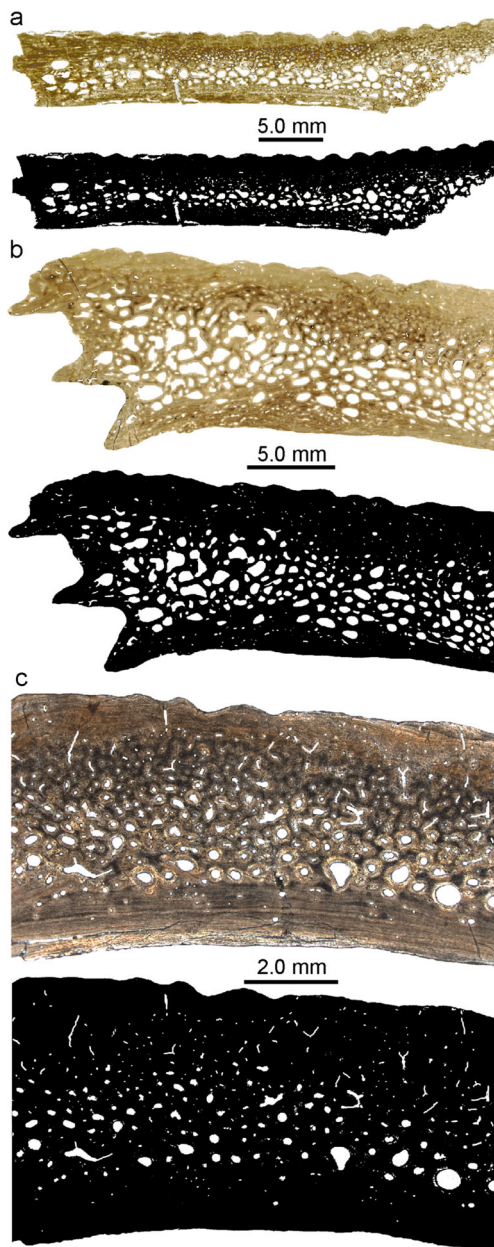


Fig. 2 Sectioned solemydid specimens and resulting binary images used for compactness analysis with Bone Profiler. **a** *Solemys vermiculata*, costal fragment (MCNA-15047). **b** *Solemys vermiculata*, shell fragment (MCNA-15046). **c** *Solemys* sp., costal fragment (UPUAM-14001)

for certain taxa only; as was the case of the highly distinctive pillar-like tubercles well embedded in the surrounding cortical tissue in the sectioned aff. *Naomichelys* fragments.

Recently, Pérez-García et al. (2013) described the bone histology of shell elements (peripheral and a possible plastral fragment) of Solemydidae aff. *Helochelydra* sp. from the Early Cretaceous (Camarillas Formation) from Galve (Galve sub-basin of the Spanish Maestrazgo Basin), whose ornamental tubercles were reported to be “smaller and higher than those of *Plastremys*”. The results of that study are summarized

and incorporated into the respective section on aff. *Helochelydra* below.

Results

Solemys vermiculata and *Solemys* sp. from the Late Cretaceous of Spain

The sampled specimens of *Solemys vermiculata* from Laño and *Solemys* sp. from Armuña share the same histological features, thus they are described in one section, with variation linked to differences in plate shape and size class being pointed out as necessary. All specimens present a diploe structure framed by internal and external compact cortices (Fig. 3a and b). The thickness of the internal cortex ranges from being roughly sub-equal to the external cortex in some elements (e.g. costals MCNA-15047 and UPUAM-14001; neural MCNA-15044) to being greatly reduced in others (e.g. neural MCNA-15054, costal MCNA-15043).

External cortex—The external cortex comprises a more external zone, the ornamental zone, and a more internal zone. The former zone consists of parallel-fibred bone grading into lamellar bone, which is vascularised by a reticular network of primary vascular canals. The characteristic surface ornamentation of valleys and protrusions is well visible in the thin-sections as well, with growth marks in the more external zone extending parallel to the external bone surface. The deeper ornamental trenches seen in some of the specimens (e.g. neural MCNA-15054) are visible as deep incisions between adjacent protrusions in the sections. The more internal zone is composed of interwoven structural fibre bundles (ISF sensu Scheyer and Sánchez-Villagra 2007; Scheyer and Sander 2007; Fig. 3c), extensively vascularized by primary osteons and primary vascular canals. The length and thickness of the fibre bundles varies within the thin-sections. Growth marks are less traceable in this more internally situated zone. There is no distinct transition towards the cancellous bone but a gradual change, indicated by an increasing number of erosion cavities and secondary osteons.

Cancellous bone—Many samples show rather dense interior cancellous bone (Fig. 3a and b), with wide-meshed trabecular bone being restricted to thick interior-most core areas of the shell bones (e.g. neural fragment MCNA-15044, costal MCNA-15047) or adjacent only to the internal cortex (e.g. indeterminate shell fragment UPUAM-14003). In the thicker elements (i.e. neural MCNA-15054, peripherals MCNA-15048, UPUAM-14000) the cancellous bone is generally more extensive, in case of the neural (MCNA-15054) almost reaching the internal bone surface. Even in these thicker shell bones, the majority of the trabeculae are primary, with secondary lamellar bone only lining the vascular spaces. The bone trabeculae are short and thick, whereas the

Table 2 Mean global values of bone compactness parameters as calculated in Bone Profiler. Standard errors (SE) of each parameter are given in brackets

Specimen sampled	Min (SE)	Max (SE)	S:Slope (SE)	P:transition (SE)	Compactness [%]
<i>Solemys vermiculata</i> , costal fragment (MCNA-15047)	0.5768126 (0.009129)	0.9050262 (0.0003297)	0.0962887 (0.0024167)	0.1890038 (0.0060766)	88.4
<i>Solemys vermiculata</i> , shell fragment (MCNA-15046)	0.7047959 (0.0036087)	0.999999 (6.148962e-6)	0.198952 (0.0031944)	0.628011 (0.0063386)	86.4
<i>Solemys</i> sp., costal fragment (UPUAM-14001)	0.7779162 (0)	0.9918489 (0)	0.3631974 (0)	0.0522469 (0)	95.3

intertrabecular spaces are round to ovoid. In the longitudinally sectioned costals MCNA-15043 and UPUAM-14001, the trabecular structure indicating the extension of the rib within the costal plate is faintly distinct from the surrounding cancellous bone.

Internal cortex—The internal cortex consists of parallel-fibred bone, with Sharpey's fibres inserting frequently into the cortical tissue. The transition between interior cancellous core and internal cortex can be quite distinct (Fig. 3a and b), where few scattered larger secondary osteons invade the cortical tissue (e.g. costal UPUAM-14001, neural MCNA-15044, shell fragment UPUAM-14002), or there can be a gradual transition, with almost the complete cortex being pervaded by secondary osteons or erosion cavities (e.g. neural MCNA-15054, shell fragment UPUAM-14004, costal MCNA-15043). The cortical tissue is otherwise vascularised by scattered simple primary vascular canals or primary osteons.

Sutures—Suture zones can be extensive in some samples (e.g. costals UPUAM-14001, MCNA-15047) showing a strong relief composed of well interdigitating, elongated pegs and sockets (see Fig. 2b). In peripheral UPUAM-14000, a deep socket (2 mm wide and 5 mm deep) is present to accommodate the distal rib end of the associated costal plate.

Solemydidae aff. *Helochelydra* sp. from the Early Cretaceous of Spain

Additional sections of some specimens of aff. *Helochelydra* sp. from Morella (MNCN 59503) are used herein to confirm the histological data gained previously from the Lower Barremian material of the Camarillas Formation of the site of Poca, in Galve (Pérez-García et al. 2013). For this reason, we here provide a short summary of the previous findings and add details on the new material where appropriate. The bone samples from both, the Galve and Morella localities reveal diploe structures framed by cortical bone layers (Fig. 4).

External cortex—In all samples the external cortex could be divided into a parallel-fibred external ornamental zone and a thin internal zone in which longitudinally and transversely sectioned fibre bundles form a meshwork. The internal zone of the external cortex is vascularized by reticularly

arranged, primary vascular canals, whereas the external zone is mostly avascular (Fig. 4a and b).

Cancellous bone—The interior parts of a bones are strongly remodelled, so that the trabeculae are all secondary in nature and consist of secondary lamellar bone (Fig. 4a and b).

Internal cortex—The internal cortex is composed of parallel-fibred bone locally grading into lamellar bone. The bone tissue is vascularised by a few simple vascular canals. Towards the interior cancellous bone, successive remodelling of the compact bone into a trabecular meshwork (Fig. 4c) can be observed in a plastral fragment (probably corresponding to a hypoplastron or to a hypoplastron, MNCN 59503).

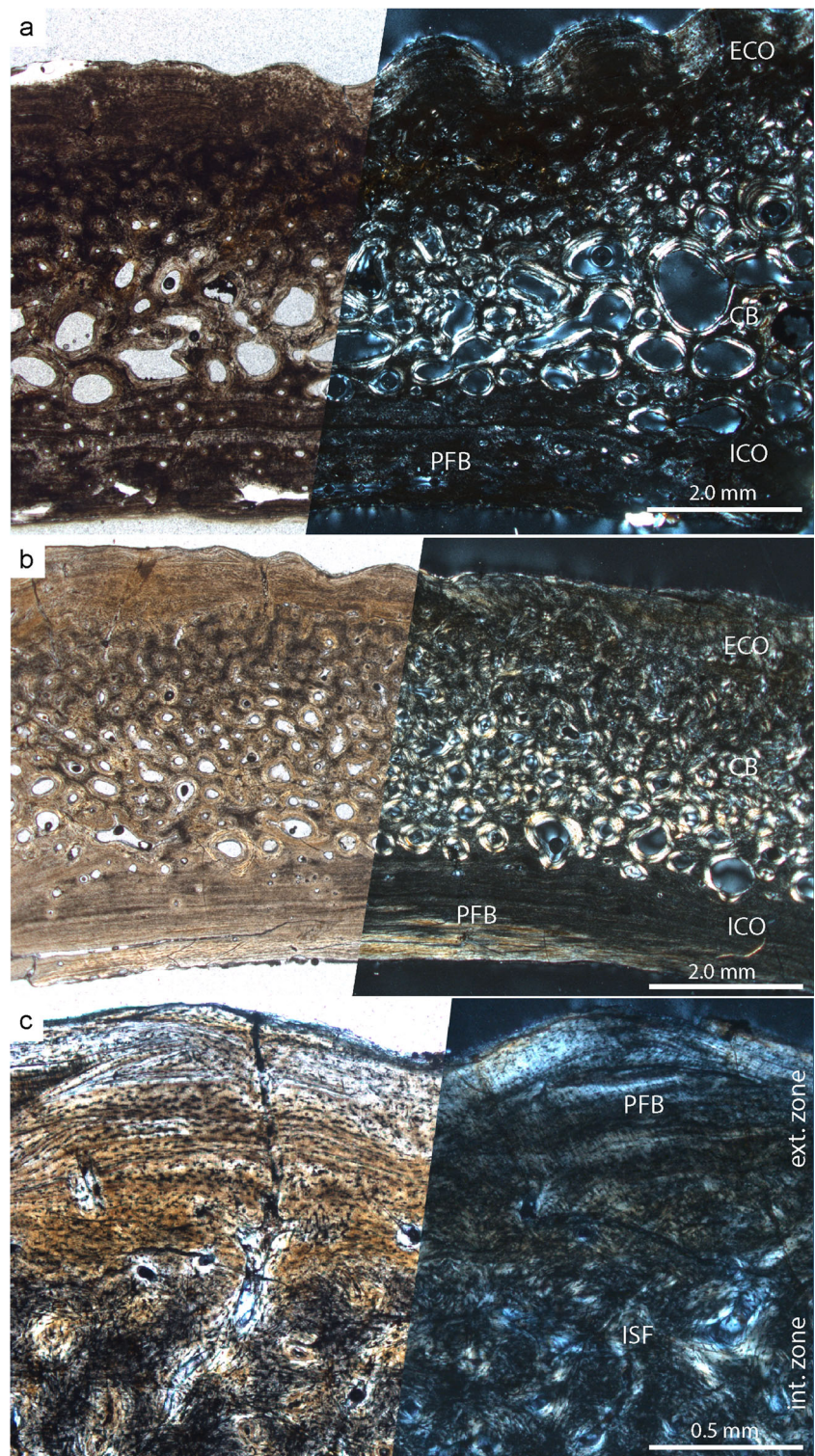
Solemydidae aff. *Naomichelys* sp. from the Cretaceous of North America

In general all elements express a diploe structure and cortices of similar thickness. The external ornamentation consisting of characteristically high and isolated tubercles or columns is seen in all the shell bone sections (Fig. 5). Depending on the bone element that was sampled and its density of tubercles, the adjacent areas, i.e. ornamental valleys, vary in size and extent. The tubercles seen in the limb ossicles (Fig. 5b) are never as distinct and raised as high above the bone surface as can be the case in the shell bones. Indeed, they are more reminiscent of the ornamentation described for the solemydid limb ossicles, the 'granicones', from the Purbeck Limestone Formation (Barrett et al. 2002). Further microstructural differences between the shell bones and limb ossicles are pointed out where necessary.

External cortex—The cortex of the shell bones consists of two zones (Fig. 5d and e), with an outer, ornamental zone being composed of parallel-fibred bone and an inner zone of thick coarse interwoven structural fibre bundles. The tubercular/columnar ornamentation can be seen to originate at the well delimited junction between the outer and inner zone of the cortex. Apart from a few scattered primary vascular canals, the outer zone is avascular, whereas the inner zone is vascularised by scattered short primary vascular canals and primary osteons.

Starting as small pillow-like and pustule-like protrusions, the ornamental tubercles/columns have at first a concentric

Fig. 3 Thin-sections of solemydid specimens shown in normal transmitted (left) and cross-polarized light (right). **a** *Solemys vermiculata*, costal fragment (MCNA-15047). **b** *Solemys* sp., costal fragment (UPUAM-14001). **c** *Solemys* sp., costal fragment (UPUAM-14001), close-up of external cortex. Abbreviations: *CB* cancellous bone; *ECO* external cortex; *ICO* internal cortex; *ISF* interwoven structural fibres; *PFB* parallel-fibred bone



external growth. Adjacent and in between the columns the first layers of parallel-fibred bone are deposited. With continuing growth of the shell plates, the interstitial areas of parallel-fibred bone and the columns grow in external direction until a maximum diameter of the columns is reached. At

the margins of the columns, a tight flexure zone develops where the parallel-fibred bone tissue of the columns and the tissue of the adjacent areas meet. The layers of the latter appear to be dragged externally by the columnar growth. The growth of the external zone of the external cortex is

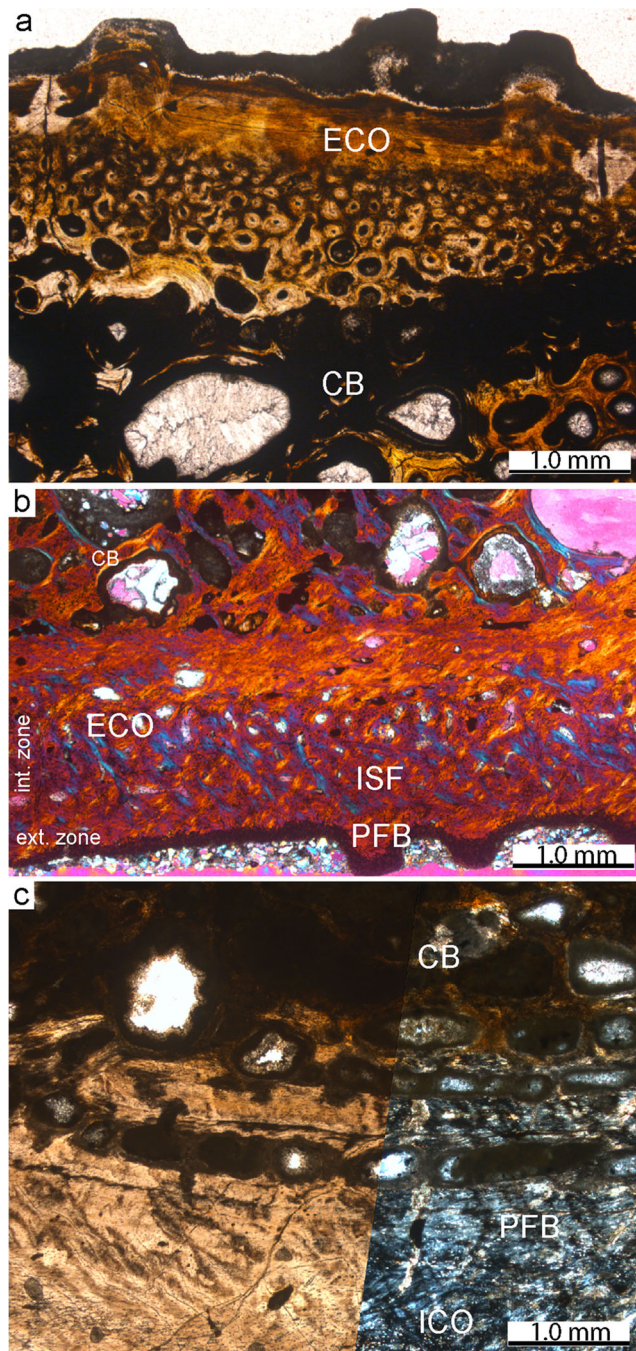


Fig. 4 Thin-sections of Solemydidae aff. *Helochehydra* sp. **a** External cortex and interior cancellous bone of costal (MNCN 59503) in normal transmitted light. **b** Cancellous bone and external cortex of peripheral (MNCN 59503). **c** Internal cortex of plastral fragment (hyo- or hypoplastron, MNCN 59503) in normal transmitted (left) and cross-polarized light (right). Note that image **c** is facing upside-down due to technical constraints. Abbreviations: *CB* cancellous bone; *ECO* external cortex; *ICO* internal cortex; *ISF* interwoven structural fibres; *PFB* parallel-fibred bone

generally well observable due to cyclical growth marks that are present within the parallel-fibred bone of both the columns and the interstitial areas. While the growth marks are widely

spaced at first, the space decreases with continued growth. In the samples of presumably old individuals, the growth marks are tightly spaced adjacent to the external surface of the bone. Adjacent to the external-most layers of interstitial parallel-fibred bone deposited in the ornamental valleys, the columns grow preferentially externally until they protrude from the external bone surface for several millimetres. The growth marks and other histological details are best visible where the plane of sectioning cuts medially through an ornamental column. Bone cell lacunae are generally round in the parallel-fibred bone of the columns, while they are slightly flattened in the parallel-fibred bone of the adjacent areas. In contrast, the external cortex of the limb ossicles is composed of a single undivided unit consisting of ISF. The ornamental tubercles/columns are not protruding far above the surrounding bone surface. As such, the cortex does not possess the clear column-like ornamentation composed of parallel-fibred bone, which is present in the shell bones.

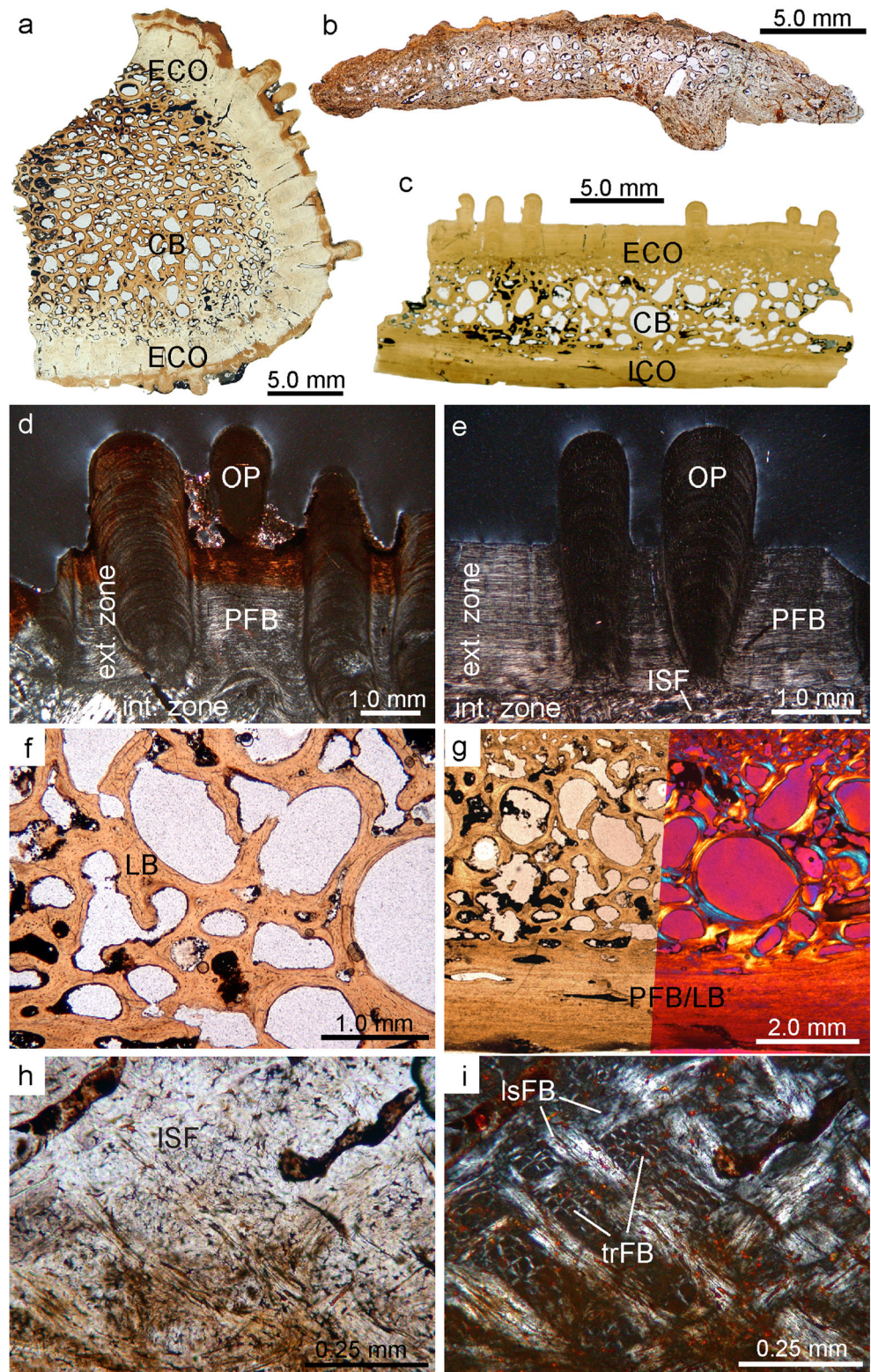
Cancellous bone—In both the shell bones and the limb ossicles, the cancellous bone consists of an irregular arrangement of short thick and longer, more slender trabeculae, with the largest vascular spaces being found in the centre of the interior cancellous bone (Fig. 5c, f and g). Larger secondary osteons are also developed in the more external and more internal regions of the cancellous bone. The trabecular meshwork is primary, however many trabeculae have been secondarily remodelled. The gross of the bone trabeculae constitutes lamellar bone with generally few flattened and elongated bone cell lacunae.

Internal cortex—The internal cortex of the shell bones consists of parallel-fibred bone that can locally grade into lamellar bone (Fig. 5c and g). Bone cell lacunae are slightly flattened and oblong, and distinct growth marks are not observed in the bone matrix. Sharpey's fibres are present in some shell fragments, but they insert more numerous adjacent to the rib bulge in the internal cortex of the costal fragment TMP 90.60.07. Coarse fibre bundles, potentially interwoven structural fibres, are present in the samples from the Albian Antlers Formation, but not in the Cenomanian Formemost Formation. The internal cortex of the limb ossicles is of various thickness in the sampled bones. In both bones, however, it is composed of a regular meshwork of longitudinally and transversely oriented fibre bundles. Among the latter, the delineations of individual fibre bundles are visible as thin bright lines (Fig. 5h and i). Vascularisation in all elements is generally low, with an occasional scattered secondary osteon or a primary vascular canal pervading the tissue, which often open up to the internal bone surface in the limb ossicles.

Plastremys lata from the Early Cretaceous of the UK

The costal fragment showed a compact diploe structure and well developed internal and external cortices of similar thickness (Fig. 6a).

Fig. 5 Thin-sections of Solemydidae aff. *Naomichelys* sp. Images in **a-c** and **f-h** in normal transmitted, **d, e** and **i** in cross-polarised, **d, e** and **i** in cross-polarised light using lambda compensator. **a** Peripheral (TMP 90.60.07). **b** Limb ossicle (FM PR 273). **c** Shell fragment (TMP 90.60.07). **d** Close-up of external cortex and ornamentation in peripheral (TMP 90.60.07). **e** Close-up of external cortex and ornamentation in shell fragment (TMP 90.60.07). **f** Close-up of cancellous bone of shell fragment (TMP 90.60.07). **g** Close-up of cancellous bone and internal cortex of shell fragment (TMP 90.60.07). **h, i** Close-up of cortical bone of limb ossicle (FM PR 273). Abbreviations: *CB* cancellous bone; *ECO* external cortex; *ICO* internal cortex; *ISF* interwoven structural fibres; *LB* lamellar bone; *IsFB* longitudinally sectioned fibre bundles; *OP* ornamentation pattern; *PFB* parallel-fibred bone; *trFB* transversally sectioned fibre bundles



External cortex—Due to preservational bias, the external-most part of the cortex does not show any microstructural details. Only the presence of former vascular spaces can be discerned within the completely altered bone matrix. Towards

the cancellous interior, there appears a wavy border, internal to which the fossil bone matrix is still pristine and its microstructure is well discernible. Here the cortex reveals a meshwork of ISF. The cortex is vascularized by scattered primary osteons.

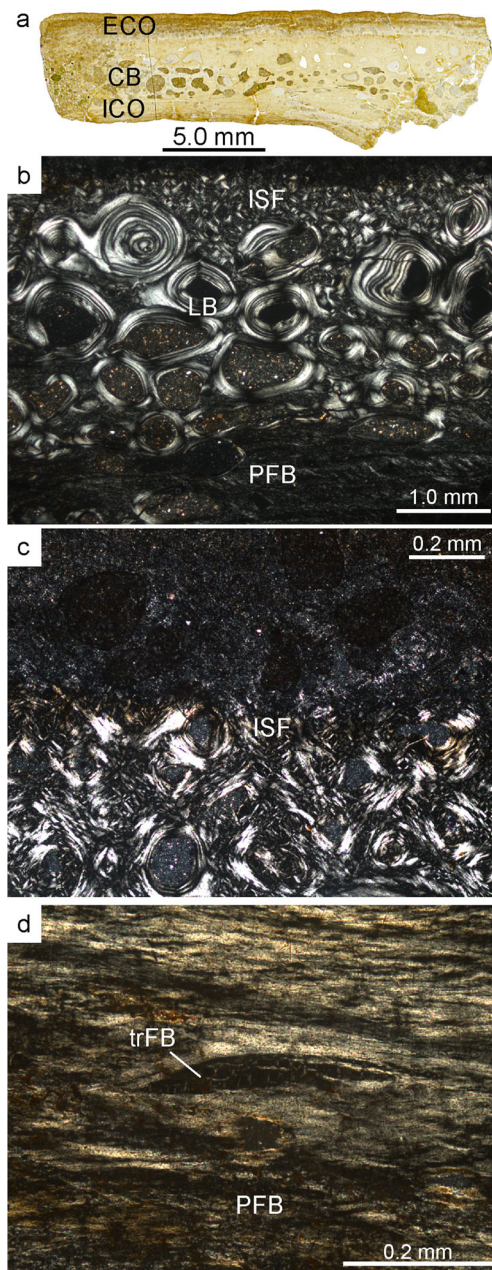


Fig. 6 Thin-sections of *Plastremys lata*. Images in **a** and **d** are in normal transmitted, **b** and **c** in cross-polarised light. **a** Costal fragment (NHMUK R 2251). **b** Close-up of the central part of the section. Note well preserved interior bone tissue. **c** Close-up of the external cortex showing a clear front of bone tissue alteration (upper part of image). **d** Close-up of the internal cortex, consisting of parallel-fibred bone. Abbreviations: *CB* cancellous bone; *ECO* external cortex; *ICO* internal cortex; *ISF* interwoven structural fibres; *LB* lamellar bone; *PFB* parallel-fibred bone; *trFB* transversally sectioned fibre bundles

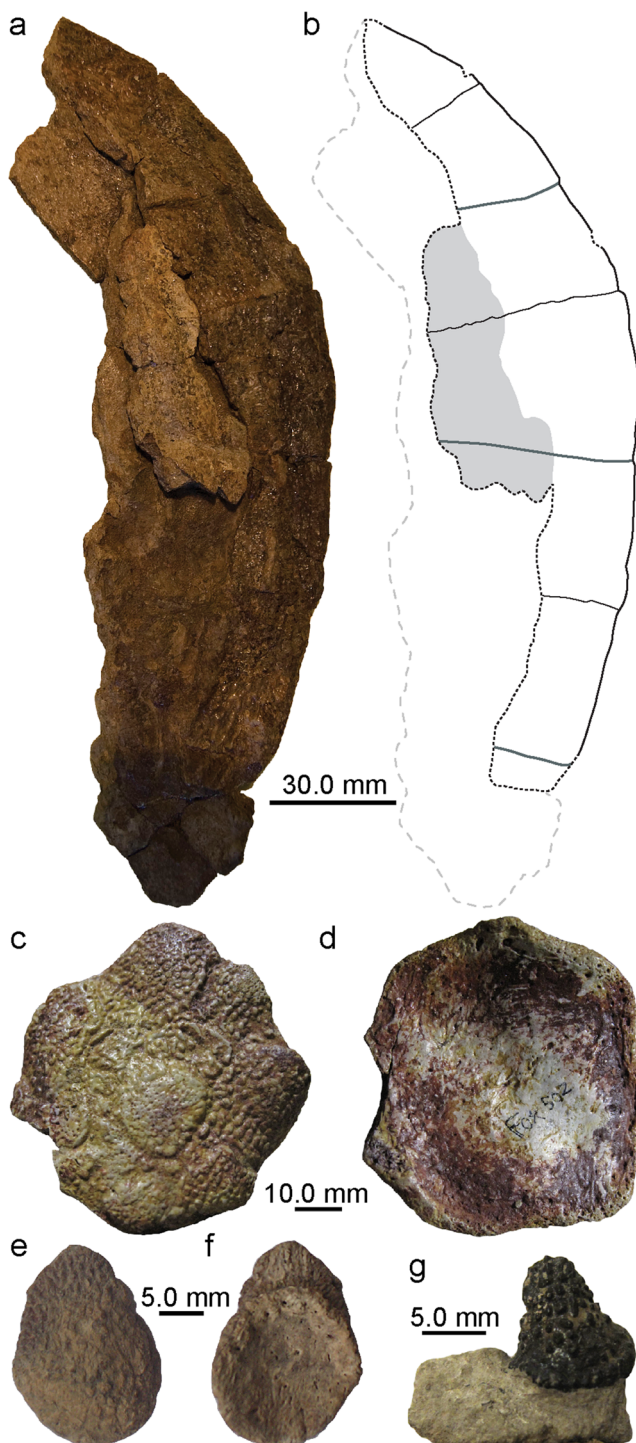
There is no clear transitional zone to the cancellous bone as evidenced by large scattered secondary osteons and erosion cavities lined with lamellar bone (Fig. 6b). Whether the external-most ornamental part of the shell bone consisted of the same ISF matrix as the more internal part cannot be elucidated (Fig. 6c).

Cancellous bone—The vascular spaces in the interior area of the bone are small, round to oval-shaped, mostly lined with lamellar bone, and separated by interstitial primary bone. Only a few small trabeculae formed between adjacent vascular spaces, but those are not secondarily remodelled.

Internal cortex—The cortex is mainly composed of parallel-fibred bone, vascularized by few scattered simple primary vascular canals and primary osteons. Most of the fibres in the bone matrix are transversely sectioned; however, a few well delineated, transversely sectioned fibre bundles are visible as well (Fig. 6d).

Discussion

Solemydid shell bones differ in shape and pattern of ornamentation from that of other ornamented turtles, such as Nanhsiungchelyidae, Adocidae, Trionychidae, and Pleurosternidae. Similarly, solemydid shell bone histology is also different (Scheyer and Anquetin 2008; this paper). Although solemydid samples show the diploe structure typical of many turtle shell bones (Scheyer and Sander 2007), they lack for example any indication of the plywood-like structure typical of trionychid turtles (Scheyer et al. 2007), the distinctive zonation (an inner zone of coarse, irregularly ISF bundles and an outer fine-fibred zone) seen in the external cortices of pleurosternid shell bones, or the spindle-like wavy structures found in nanhsiungchelyid *Basilemys* (Scheyer and Anquetin 2008). Solemydid shell bones show external and internal cortices which are of equal thickness in most taxa, whereas there is some variation in *Solemys* in that the internal cortex can also be reduced in thickness in some specimens. Both the outermost zone of the external cortex and the internal cortex consist of parallel-fibred bone, with the former accommodating the extensive surface ornamentation. As such, the external ornamentation of solemydid shell bones figures also prominently in the thin-sections, as was to be expected already from gross morphology. All solemydid bones thus showed a more or less distinct separation of the external cortical layer in an inner and an outer zone (both zones are variable in thickness). Ornamental valleys and low protrusions were encountered in all samples but in *Naomichelys*, the only taxon in which the high ornamental tubercles are visible as distinct columns in cross-section within a parallel-fibred matrix. Irregularly extending coarse fibre bundles were encountered in all *Naomichelys* specimens from the Albian (both shell bones and limb ossicles) but not from those of the Campanian. The preservation of microstructural details in both sub-samples is generally good, which suggests that these differences are natural.



◀ **Fig. 7** Dorsal view of some peripherals of the specimen of *Solemys* sp. IPS-23008, from the early Maastrichtian of Mina Esquirol (south-eastern Pyrenees, Spain) and selection of solemydid limb ossicles from other localities. **a** Photograph of specimen (IPS-23008). **b** Schematic interpretation of the dorsal region, where the sutures (thin black lines), sulci (thicker gray lines) and the elements interpreted by Marmi et al. (2009) as neurals (shaded grey area) are represented. **c, d** External and internal view of large ossicle of *Solemys* sp. from the Maastrichtian of Fox-Amphoux (France). **e, f** External and internal view of ossicle of Solemydidae aff. *Naomichelys* sp. (FM PR 273; section shown in Fig. 5b). **g** External view of ossicle of *Helochelydra* (Middle Purbeck beds, Durlston Bay, Swanage, Dorset UK; one of the Beckles collection 'granicones', possibly figured on plate XXII, Fig. 3 in Owen 1878; see also Barrett et al. 2002 for more information on 'granicones')

Palaeoecology of solemydid turtles

Scheyer and Sander (2007) argued for a terrestrial lifestyle for Solemydidae (aff. *Naomichelys* sp.) based on the shell bone samples used and reviewed herein. Specifically, the *Naomichelys* bones showed well developed bone cortices framing a rather stout interior cancellous area dominated by short and thick trabeculae, low vascularisation of the cortical bone, and general absence of homogenisation of cortical and cancellous areas. Joyce et al. (2011) similarly argued for terrestrial habits of solemydid turtles in general, based on the presence of limb ossicles in several species from the Early Cretaceous of both North America and Europe, these elements being so far exclusively known in terrestrial turtles. Barrett et al. (2002) further figured a hind limb with ossicles of an almost complete specimen of *Naomichelys* (FM PR 273; the shell of which was first figured by Hirayama et al. 2000), from the Early Cretaceous Trinity Group (Aptian–Albian) of Texas. In addition, a limb ossicle attributable to *Solemys* sp. is known from the Maastrichtian of Fox-Amphoux (France) (plate 11 Fig. 4 in Lapparent de Broin and Murelaga 1999).

In contrast, Marmi et al. (2009), inferred a semiaquatic lifestyle for *Solemys* (specimen IPS 23008) from the Tresp Formation, Mina Esquirol site (NE Spain) based on the interpretation of sedimentary, taphonomic and palaeoenvironmental data. Although Marmi et al. (2009) further performed a preliminary histological analysis on a peripheral fragment of specimen IPS 23008, which largely yielded microstructural details (with the possible exception of a more strongly vascularised internal cortex) typical of terrestrial turtles as described by Scheyer and Sander (2007), the authors choose to disregard this evidence in favour of the aforementioned geological data, pointing out that “histological data alone should be used with caution to elucidate the lifestyle of the Mina Esquirol specimen to avoid erroneous inferences” (Marmi et al. 2009, p. 1311).

One specific point of criticism raised by Marmi et al. (2009: 1310) of the analysis of Scheyer and Sander (2007) was that supposedly “only one fully terrestrial species was tested (*Geochelone pardalis*)” to verify the usefulness of shell

They constitute a potential histological characteristic by which to separate specimens of different geological ages lumped into this ‘wastebasket taxon’. However, this interpretation needs to be confirmed in future studies by incorporating more specimens from different Early and Late Cretaceous localities.

bone histology for lifestyle inference, whereas “other genera included in the ‘terrestrial’ sample were *Cuora* and *Terrapene* that contain some aquatic species. Unfortunately, these authors do not tested if the ‘terrestrial’ histological pattern found in the *Cuora* and *Terrapene* studied species is due to their ecology or if it is genus specific”.

While it is true that only these three taxa were taken as representatives in the main article of Scheyer and Sander (2007), there were several other taxa sampled and listed in the extended appendices besides *Stigmochelys* (*Geochelone*) *pardalis* (see Bell 1828), including at least one other extant fully terrestrial tortoise, *Geochelone elegans* (Schoepff 1795; in Schoepff 1792–1801), one fossil giant tortoise from the Pleistocene, *Hesperotestudo* (*Caudochelys*) *crassiscutata* (Leidy 1889), and one fossil nanhsiungchelyid turtle from the Upper Cretaceous, the terrestrial *Basilemys* Hay 1902 (see Hay 1902: 445). Although it might be arguable that the palaeoecology of fossil species remains ultimately inconclusive because of the lack of direct observation, there is little doubt that in the aforementioned, the taxa are indeed indicative of fully terrestrial habitats (Riggs 1906; Langston 1956; Ernst and Barbour 1989; Brinkman 1998; Meylan and Sterrer 2000; Cisneros 2005).

In addition, direct observation of the specimen IPS-23008, purported peripheral and neural plates “from the edge of an in situ cast of a carapace”, and the field site warrants reinterpretation of some of the observations made by Marmi et al. (2009). There is no evidence available which supports the hypothesis that, prior to the finding of this specimen, it corresponded to a complete fossil shell, but rather constitutes probably only a partially articulate carapace. The elements interpreted by Marmi et al. (2009) as neural plates actually correspond to the dorsomedial region of some of the preserved peripherals of the bridge area (Fig. 7a and b). These peripherals are reinterpreted as belonging to the bridge due to the fact that these plates are composed of two regions, one of them belonging to the dorsal carapace, but the other contacting the plates of the plastron (as can be observed in Fig. 7a and b). The mould did not allow recognition of any element corresponding to the plastron, but it only corresponds to a probably partial carapace. Furthermore, although Marmi et al. (2009) indicated that this specimen was affected by little bone abrasion, the abrasion is very well visible in the ventral region of the preserved elements (see Fig. 2b in Marmi et al. 2009). Thus, we consider that no evidence provided previously for the Mina Esquirol *Solemys* specimen actually supports an aquatic lifestyle for this taxon.

Taphonomic studies on the site of Laño support the identification of Solemydidae as terrestrial taxa. This locality yields a fossil vertebrate assemblage (which includes members of Osteichthyes, Lissamphibia, Lepidosauria, Testudinata, Crocodyliformes, Dinosauria, Pterosauria and Mammalia) in an alluvial depositional system (Pereda-Suberbiola et al.

2000), in which turtle remains are by far the most abundant in terms of identified specimens and minimum number of individuals. *Solemys* remains from that depositional environment exhibit the most weathering/abrasion (thus widest transport) of any preserved taxa, indicating that these turtles were allochthonous elements in this alluvial system.

In addition, observed compactness values of *Solemys vermiculata* and *Solemys* sp. shell fragments gained by Bone Profiler analysis ranged between 86 and 95.3 %. These values lie well above the values gained from purportedly aquatic fossil turtle shell bones (Pérez-García et al. 2012; Scheyer et al. 2014) and tortoise limb ossicles (Scheyer and Sander 2009), and they are comparable to compactness values of long bones of animals living in terrestrial environments (e.g. Canoville and Laurin 2010).

In summary, solemydid turtle shell bones have a well-developed diploe, a strong external surface ornamentation that consists either of separated tubercles (of various height, pattern and size) or of ridges and valleys, as well as a clear separation of the external cortex into two zones in which the outer one consists of parallel-fibered bone and which incorporates the extensive ornamentation. *Solemys vermiculata* is well separable from the other solemydids studied based on the vermiculate surface pattern, whereas the aff. *Naomichelys* and aff. *Helochelydra* material, on the other hand, can be separated based on the combination of external bone structures (e.g. tubercular length and patterns of distribution of tubercles on the shell bones) and histology, or, if the ornamental trabeculae are eroded, based on the histological evidence linked to the ornamentation alone. Within Solemydidae, both external ornamentation and the internal bone structures are thus valuable sources of information, which can be used for systematic purposes and even small shell bone fragments can be assigned to the group using these data. Given the combined histological evidence of shell bones, as well as the presence of limb ossicles (Fig. 7c, d, e, f and g) known now for a variety of solemydid taxa, a terrestrial lifestyle for the solemydid group is well supported. All this evidence further corroborates the hypothesis that, with the possible exception of the Chinese *Odontochelys semitestacea* (Li et al. 2008) and some post-Early Jurassic forms (i.e. *Eileanchelys waldmani* Anquetin, Barrett, Jones, Moore-Fay and Evans, 2009 and *Herckerochelys romani* Sukhanov, 2006; Scheyer et al. 2014; also *Condorchelys antigua* Sterli, 2008; Cerda et al. 2015), the majority of stem turtles showed terrestrial habitat preference (e.g. Joyce and Gauthier 2004; Scheyer and Sander 2007; Sterli et al. 2007).

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