

Turtles from the Early Cenomanian paralic deposits (Late Cretaceous) of Charentes, France.

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ABSTRACT - A turtle fauna including at least five taxa is described from the Early Cenomanian paralic deposits of Charentes. In addition to an indeterminate pleurodire (cf. Dortokidae), cryptodires are mainly represented by a solemydid. The solemydids are terrestrial turtles which are especially abundant in the only estuarine assemblage studied, where they are parautochthonous. Turtle remains are more fragmented and more abraded in coastal assemblages, indicating longer transport and sea-floor residence time before burial.

Key words : Turtles, Solemydidae, Taphonomy, Late Cretaceous, Cenomanian, Charentes, France

Les tortues des dépôts paraliques du Cénomanién Inférieur (Crétacé Supérieur) des Charentes -

Les restes de tortues des dépôts paraliques du Cénomanién Inférieur des Charentes, incluant au moins cinq taxons, sont décrits. Associés à un pleurodire indéterminé (cf. Dortokidae), les cryptodires sont surtout représentés par un solemydidé. Cette dernière famille de tortues terrestres est particulièrement abondante dans le seul assemblage estuarien étudié, où elle est considérée comme un élément parautochtone. Les restes de tortues deviennent plus fragmentaires et plus abrasés dans les assemblages littoraux, indiquant un transport et un temps de résidence sur le fond avant enfouissement plus longs.

Mots clés : Tortues, Solemydidae, Taphonomie, Crétacé Supérieur, Cénomanién, Charentes, France

INTRODUCTION

The Cenomanian coastal and estuarine deposits of Charentes (Departments of Charente and Charente-Maritime), southwestern France, have yielded a rich fauna of fishes, amphibians, reptiles and mammals (Vullo, 2007; Vullo & Néraudeau, 2008). All of the assemblages described here have been collected from vertebrate microfossil sites, except for the locality of “Fouras Bois-Vert” where relatively large elements are present (Néraudeau et al., 2003). Turtle remains occur in most Early Cenomanian localities and consist mainly of isolated shell fragments. The material studied here comes from six localities (Fig. 1), included stratigraphically in lithological subunits B1 and B2 (*sensu* Néraudeau et al., 1997). These localities are: “Les Renardières” at Tonnay-Charente (subunit B1); “Fouras-Vauban” and “Fouras Bois-Vert” at Fouras (subunit B2); “Traslemaine” and “La Buzinie” at Champniers (subunit B2); “Montagan” at Mainxe (subunit B2). The “Fouras Bois-Vert” site, which has

yielded the most complete and best preserved material, consists of estuarine glauconitic sand and clays which are rich in wood, amber, and bones (Néraudeau et al., 2003). Other sites correspond to sandy-clayey lenses containing abundant bioclasts and lithoclasts deposited in coastal marine environments (Néraudeau et al., 2005; Vullo et al., 2005, 2007a; Vullo, 2007; Vullo & Néraudeau, 2008). The Early Cenomanian age of subunits B1 and B2 is indicated by the presence of the benthic foraminifers *Orbitolina plana concava* and *O. conica* (Néraudeau et al., 1997). Only the most significant turtle specimens are studied in the present paper. Less significant material from other localities has been omitted together with the only turtle specimen (an indeterminate pleural plate) collected in the earliest late Cenomanian deposits of Madame Island.

Although the study material is fragmentary, its description provides further information concerning the poorly known turtle fauna from the Cenomanian and improves our current knowledge of the mid Cretaceous continental turtle

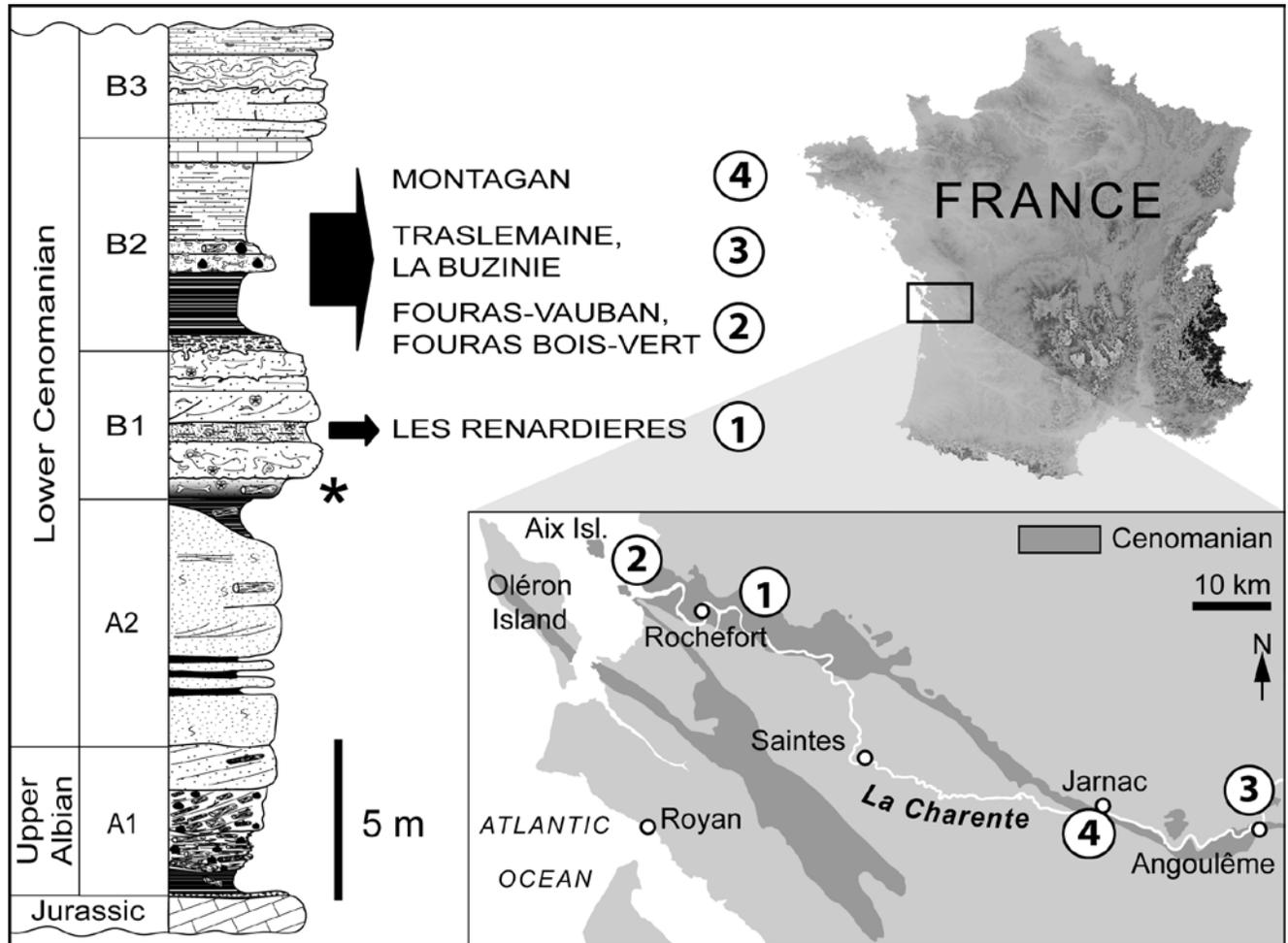


Figure 1 - Geographical and stratigraphic positions of the Early Cenomanian localities treated in this study. The asterisk shows the stratigraphic position of the earliest occurrence of turtles (indeterminate forms) within the Charentes series (assemblages of Font-de-Benon and Aix Island: see Vullo, 2007).

fauna in Europe. We also discuss here the taphonomy and the palaeoecology of these turtles, in an attempt to elucidate their habitat within a wide range of possible paralic environments.

All studied turtle specimens (except the ischium from La Buzinie which is from the private collection of Thierry Lenglet, Mirambeau, France) are unnumbered and provisionally housed in the collections of the Laboratory of Palaeontology, University of Rennes 1, France. They will be stored in the Musée d'Angoulême, where permanent catalogue numbers will be assigned.

SYSTEMATIC PALAEONTOLOGY

Order Chelonii Latreille, 1800
 Suborder Pleurodira Cope, 1868
 Family cf. Dortokidae Lapparent de Broin & Murelaga, 1996

Genus and species indeterminate
 (Figures 2, 3.2)

Material: two incomplete specimens, attributed to a left pubis and a left ischium.

Localities: pubis from Les Renardières (Charente-Maritime) and ischium from La Buzinie (Charente).

Description: The ischium and the pubis, 16 and 20 mm long respectively, share some characters and probably belong to the same taxon. Both show a ventral scar corresponding to a sutured connection with the xiphiplastron. They are strongly compressed laterally, with relatively sharp anterior and posterior margins, and are wide mesiolaterally in relation to their height.

The left pubis (Figs. 2.1, 3.2) has a pectineal process which is well developed antero-medially to posterolaterally, forming an elliptical suture surface of suture with the xiphiplastron ventrally. The pubis height is relatively short and the margin between the xiphiplastral suture and the acetabulum is more concave, and more inclined posterolaterally in com-

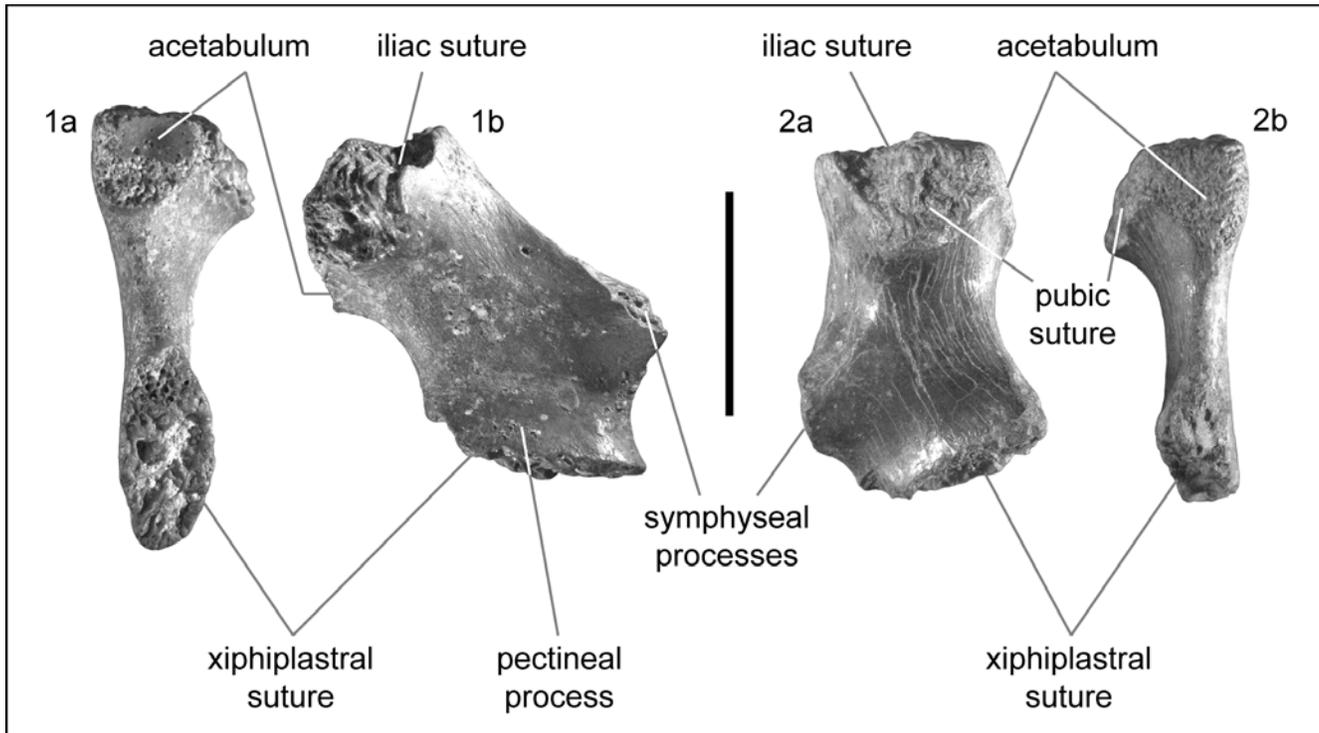


Figure 2 - Pelvic bones of cf. *Dortokidae*. **1**: left pubis from Les Renardières in infero-external (a) and posterior (b) views. **2**: left ischium from La Buzinie in posterior (a) and infero-external (b) views. Scale bar: 1cm.

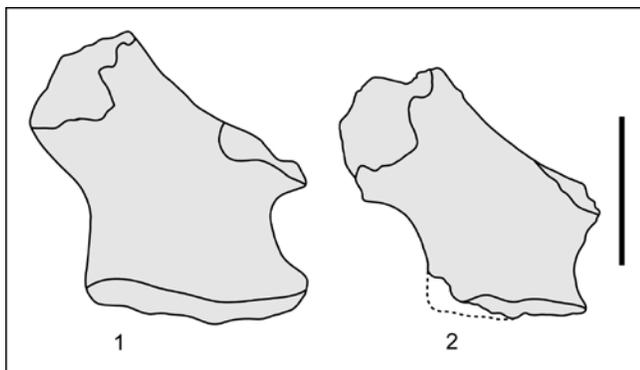


Figure 3 - Comparison between the pubis of *Dortoka vasconica* (**1**) and the pubis of Les Renardières (**2**), in posterior views. Scale bar: 1cm.

parison with *Dortoka vasconica* (Fig. 3.2). The dorsal part of the ischium and ilium junction is well developed. The medial process bearing the pubic symphysis is broken at its base.

The left ischium (Fig. 2.2) is short and wide, and the medial process bearing the ischiadic symphysis is broken at its base. The surface of the ventral xiphiplastral suture is elongated, and somewhat rectangular in shape. The acetabular part is relatively long and the surface of the suture with the pubis is important.

Discussion: The presence of pleurodire turtles in the Cenomanian of Charentes is attested by the discovery of the pubis and ischium described above, bearing a suture scar characteristic of a pelvic girdle sutured to the plastron. These two bones resemble the pubis and ischium of *Dortoka*, a pleurodire genus from the Campanian-Maastrichtian of France and Spain (Lapparent de Broin & Murelaga, 1999: pl. 2, figs. 15a, b, 16). The latter are relatively robust and short, with pronounced concave anterior and posterior surfaces below the medial part of the pubis. However, the Charentes pubis has a narrower pectineal process and a smaller xiphiplastral suture scar. In addition, the base of the pubic symphysis is more ventrally located. The ischiadic suture appears wider in *Dortoka* than in the La Buzinie ischium. Lapparent de Broin & Murelaga (1999: pl. 4, fig. 12) figured a second pleurodire pubis which they referred to the bothremydid genus *Polysternon* (Pelomedusoides, Podocnemidoidea). This incomplete pubis, which is more extended dorsoventrally (as in other Podocnemidoidea) with less concave anterior and posterior margins and a narrower pectineal process, is clearly distinct from our specimen. The Paleocene dortokid described from Romania, *Ronella*, has a pubis which is also similar to our specimen in respect of its general morphology; like the French form it is also robust, long for its height and possesses concave edges along the pectineal process (Lapparent de Broin et al., 2004: pl. 2, fig. 6), but it is longer dorsoventrally than in the Charentes specimens and *Dortoka*.

On the basis of pubis morphology, the pleurodire

turtle from Charentes appears to lie closer to dortokids than to the podocnemidoids (i.e., bothremydids and podocnemidids). The African Pelomedusoides Pelomedusidae, unknown outside of the African domain (Lapparent de Broin, 2000a), also have less robust pelves than dortokids and possess some unique additional characters (Lapparent de Broin & Murelaga (1999: pl. 12). The Dortokidae is a European family of undefined phyletic position in relation to the Pelomedusoides and the Chelidae, which is known from the Barremian to the Late Paleocene (Lapparent de Broin et al., 2004), while the Bothremydidae are unknown (up to now) before the Senonian in Europe. Together, the families are the only pleurodires known in Europe during the Cretaceous (Lapparent de Broin, 2001).

Amongst the shell material collected in Charentes, no specimen can be assigned definitely to a pleurodire.

Suborder Cryptodira Cope, 1868

Family Solemydidae Lapparent de Broin & Murelaga, 1996

Genus and species indeterminate A

(Figures 4, 5, 8.3)

Material: about ninety shell fragments.

Localities: Les Renardières, Fouras-Vauban, Fouras Bois-Vert (Charente-Maritime), Traslemaine, Montagan, La Buzinie (Charente).

Description: The shell is represented by fragmentary to complete dorsal carapacial plates (peripherals, pleural fragments and neurals), fragments of the plastron (hyoplastron and hypoplastron), and items of undetermined location. Most of the specimens have been studied and figured in a master thesis presented by one of us (N. D.) in 2001. The anatomical locations of the most complete plates have been accomplished by reference to the reconstruction of the carapace of *Solemys vermiculata* from the Campanian of Laño, Spain, given by Lapparent de Broin & Murelaga (1999) (Fig. 5: note that the individual shape of each specimen does not coincide exactly with those of the model). A partial right hyoplastron (Figs. 4.1, 5.2) is preserved as a lateroanterior fragment, laterally bordering the anterior lobe. It corresponds to the segment located between the epiplastron and the humeropectoral sulcus (partly preserved) and is recognized by its lateral free border, covered by the dorsal ornamented part of the humeral scute which is flanked medially by a dorsal longitudinal thickening. The regular ventral ornamentation consists of small rounded and close-set, non-radially oriented granulations (Fig. 8.3).

A partial left hypoplastron (Figs. 4.2, 5.2) is represented by the lateral part situated in the inguinal notch. The lateral free border is covered dorsally by the ornamented part of the abdominal scute. The dorsal longitudinal thickening, medial to this part of the scute, is emphasised by a fine ridge lying against the scute border. The base of the hypoplastral (i.e., inguinal) buttress is preserved. The ventral ornamentation is composed of weak and fine granulations and vermiculations, which are aligned in stripes.

A specimen of a neural, probably the fourth, (Figs. 4.3, 5.1), is hexagonal in outline with short sides in front. It shows medial longitudinal thickening, which indicates that a longitudinal medial carina was present along the carapace. The neural is ornamented by fine longitudinal granulated ridges, which radiate from the front.

A fragmentary medial part of a right pleural 1 is preserved. Dorsally, it shows the junction of the vertebral scutes 1 and 2 and the costal 1 scutes (Figs. 4.4a, 5.1), and displays a decoration of small, close-set granulations/vermiculations. Ventrally, (Fig. 4.4b) the free extremity of thoracic rib 2 is preserved. Rib 2 is wide anteroposteriorly and protruding ventrally. Along its anterior border, the groove of the thoracic rib 1 attachment is present for the full length of the preserved pleural part, i.e. nearly half the width of the full pleural 1, as in *Solemys*; this is a relatively long attachment of the first to the second rib, especially in comparison to most modern cryptodires where the first rib is much reduced in width.

A left pleural 5 is represented by the medial part, showing the junction of vertebral scutes 3 and 4 and the costal 3 scutes (Fig. 5.1).

A right pleural 8 (Figs. 4.5, 5.1) represents the fusion of a pleural 8 and a primitive pleural 9, bearing two well developed thoracic ribs ventrally, as in *Solemys vermiculata* (Lapparent de Broin & Murelaga, 1999, pl. 6, 5a, b) and various primitive cryptodires.

Two peripheral 3 fragments, left (Figs. 4.6, 5) and right (Figs. 4.7, 5) are present in the collection. Ventrally, the part of the plate covered by the marginal scute (Figs. 4.6b, c, 4.7b) protrudes and is curved above the visceral face of the dorsal part of the plates, forming a ventral lip extending between the hyoplastral (i.e., axillary) buttress as far as the nuchal. This is a distinctive feature present in *Solemys* (Fig. 5.2) (Lapparent de Broin & Murelaga, 1999), and somewhat similar to the condition in *Proganochelys* (Gaffney, 1990, fig. 75).

A left peripheral 10 is also preserved (Fig. 5). The pleurals and peripherals show close-set, rounded granulations which are more or less aligned and united in vermiculations, according to location.

Discussion: The general morphology of the elements described above agrees with that of *Solemys*. However, as vertebral scutes 3 and 4 are relatively wider than those of *S. vermiculata* (used as model for the reconstruction) for an identical pleural 4 length, the Charentes solemydid A represents at least another species and probably also belongs in another genus. The medial carina is identical to that in the Spanish species, but the radiating stripes of the neurals are distinctive to the Charentes specimens. The ornamentation is of the same type (close granulations; Fig. 8.2, 8.3) but the French material has fewer vermiculations and slightly coarser granulations as a whole.

The family Solemydidae and the genus *Solemys* were erected by Lapparent de Broin & Murelaga (1996) for Late Cretaceous (Campanian-Maastrichtian of France and

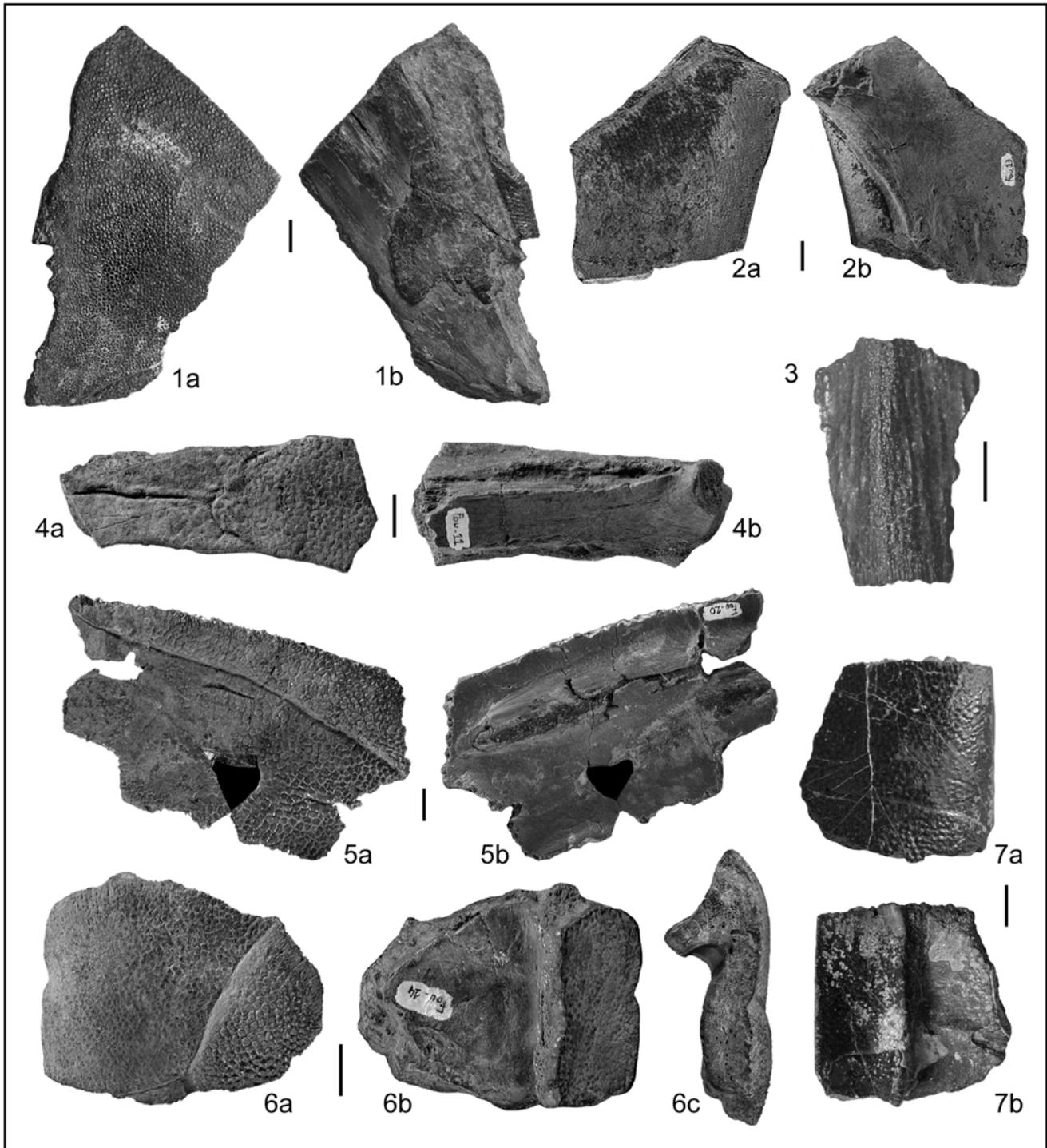


Figure 4 - Shell fragments of decorated cryptodires. 1-7: Solemydidae gen. et sp. indet. A from Fouras-Bois Vert : 1 : right hyoplastron in ventral (a) and dorsal (b) views ; 2 : left hypoplastron in ventral (a) and dorsal (b) views ; 3 : neural in dorsal view 4 : medial fragment of right pleural 1 in dorsal (a) and ventral (b) views ; 5 : right pleural 8-9 in dorsal (a) and ventral (b) views ; 6 : left anterior peripheral in dorsal (a), ventral (b), and posterior (c) views ; 7 : right anterior peripheral in dorsal (a) and ventral (b) views. Scale bars : 1 cm.

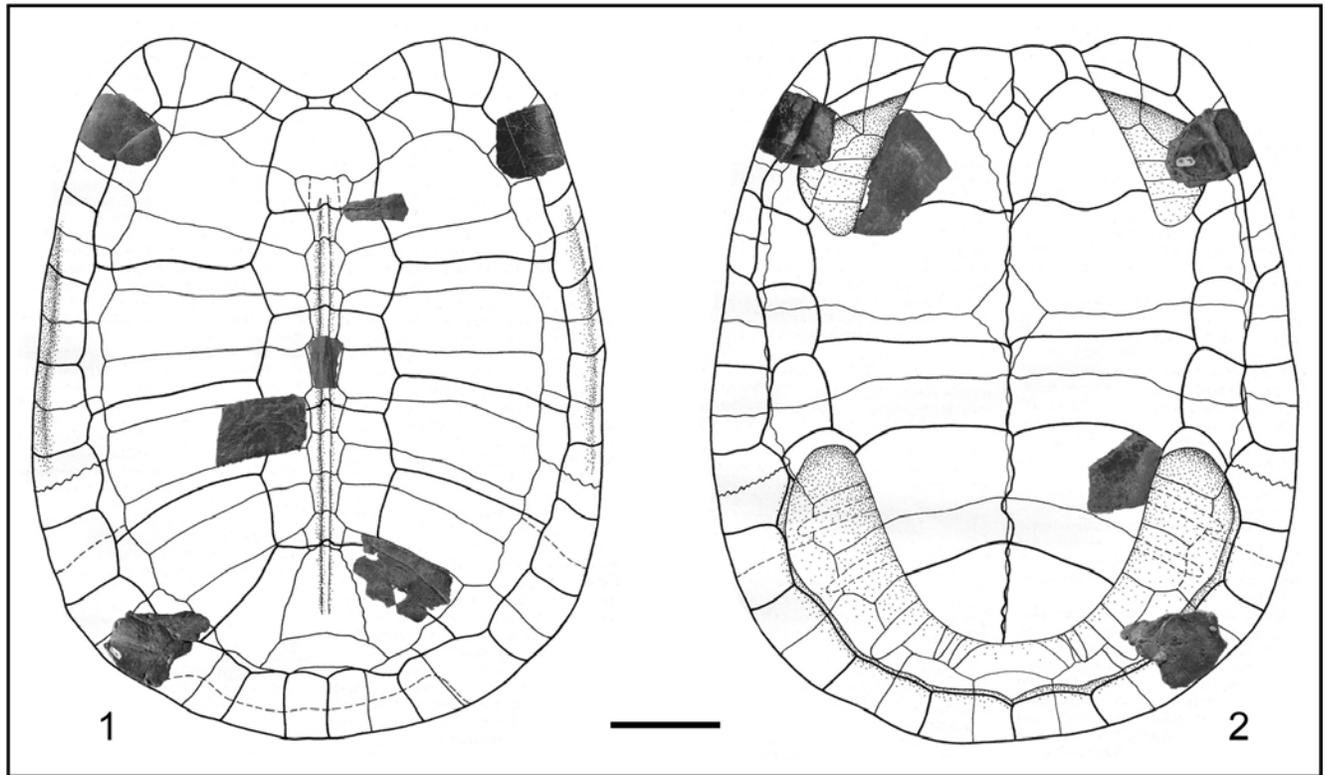


Figure 5 - Anatomical positions of solemydid (Solemydidae gen. et sp. indet. A) shell fragments from Fouras-Bois Vert. **1**: carapace in dorsal view. **2**: carapace and plastron in ventral view. Scale bar: approximately 10 cm.

Spain) turtles with a granulated-vermiculated decoration. These primitive cryptodires, with transversal mesoplastra, are characterized principally by their large size (up to 80 cm long), the anterior peripheral ventral lip, their particular granulo-vermiculated ornamentation and the presence of a well developed epiplastral lip. Lapparent de Broin & Murelaga (1996) included two other genera in this family: *Helochelydra* and *Naomichelys* (type species from the Early Cretaceous of Isle of Wight, England, and the Late Jurassic, Morrison Formation of Montana, North America, respectively), sharing with *Solemys* the presence of an apomorphic entoplastral scute (Lapparent de Broin & Murelaga, 1999, fig. 14). These authors (Lapparent de Broin & Murelaga, 1999) also referred *Plastremys lata* and *Trachydermochelys* spp., from the Cambridge Upper Greensand (late Albian), and *Helochelys*, from the Lower Greensand (early Albian) of Germany, to the Solemydidae. Lapparent de Broin & Murelaga (1999) tentatively placed some French and English specimens from the Jurassic-Cretaceous boundary, formerly erroneously assigned to the genus *Tretosternon* Owen, 1842 (a presumed senior synonym of *Pleurosternon*, after the very precise description of the decoration by Owen, the types of which are lost) to the Solemydidae. “*Trachyaspis*” *turbulensis* from the Spanish Wealden was also recognized as a solemydid. Lapparent de Broin & Murelaga (1999) showed that *Plastremys lata* could belong to *Trachydermochelys*,

and they remarked that *Helochelys* seems to have the same ornamentation pattern as *Helochelydra*, consisting of isolated tubercles (Fig. 8.1), although individual tubercles are possibly not as small or as high as those in *Helochelydra*. This last character allows the Charentes solemydid A to be distinguished from both latter genera. *Trachydermochelys rutteri* also has a decoration made up of more isolated tubercles than in *Solemys*, but the individual units are clearly larger than those found in *Helochelydra*, *Naomichelys* and (possibly) *Helochelys*. Because of the shape of the peripheral plates, it seems that the solemydid A from Charentes had a domed shell, like *Trachydermochelys* (about 22 cm high for 47 cm wide) (Andrews, 1920) but contrary to *Solemys* which has a more flattened carapace (about 16 cm high for 57 cm wide) (Lapparent de Broin & Murelaga, 1999). Although our material is rather fragmentary, it is possible to suggest that the Charentes solemydid A and *Trachydermochelys* are two closely related forms, which are temporally close and have a similar carapace (size, shape), but with a distinct ornamentation. Because many elements are missing in *Trachydermochelys* on the one hand (unprepared ventral border preventing observation of the possible presence of a ventral peripheral lip, no preservation of the entoplastral anterior part preventing assessment of the possible presence of an entoplastral scute), and the entoplastron has not been found in Charentes on the other hand, any assertion is possible.

Genus and species indeterminate B

(Figure 6.1)

Material: one shell fragment.

Localities: Montagan (Charente).

Description: This fragment, coming from an indeterminate part of the shell, shows isolated round protruding tubercles (about 1,5 mm in diameter), separated by a flat surface.

Discussion: Among solemydids, this distinctive decoration of well isolated tubercles is present in the genus *Helochelydra* (Fig. 8.1), known from Early Cretaceous deposits in Europe (Purbeck and Wealden beds: Lapparent de Broin & Murelaga, 1999), in *Naomichelys speciosa* Hay, 1908, from the Late Jurassic of USA, and possibly also in the poorly known German genus *Helochelys* (observation based on the original drawings of Meyer, 1856: Lapparent de Broin & Murelaga, 1999). This ornamentation clearly contrasts with the closely-spaced, larger tubercles, and the granulo-vermiculations found in *Solemys* or the Charentes solemydid A (Fig. 8.2). This single specimen could therefore indicate that another solemydid is present in the Cenomanian of Charentes, lying closer to the *Helochelydra* group than to the group possessing a *Solemys*-like decoration (see above). In any case, the tubercles are not as minute, are relatively less high and not as widely spaced as in *Helochelydra*. They are rather similar to the decoration of some fragments of “*Trionyx*” *bakewelli* Mantell, 1827, a poorly known form from the Wealden beds of England which shows low isolated tubercles as well as vermiculations and closer tubercles according to location on the preserved carapace plates. This form, later erroneously named “*Tretosternon*” *bakewelli* by Owen, has been assigned (Milner, 2004) to *Helochelydra*, without any evidence because shell parts are lacking, in particular, the entoplastron and the difference in the ornamentation: the species has to be considered as being an indeterminate genus of solemydid. For the same reason, as long as the solemydid A from Charentes is not better known by more complete shell material, and in particular by the plastron, it is not possible

to be certain that the form B is a distinct taxon, closer to *Helochelydra*, *Helochelys* or “*Trionyx*” *bakewelli* and even *Trachydermochelys rutteri*. In the same way, fragments proceeding from the Campanian of Canada (Peng et al., 2001; Brinkman et al., 2004) and assigned to *Naomichelys* should be provisionally referred to Solemydidae gen. et sp. indet. or to aff. *Naomichelys* (according to the decoration), as have been identified more carefully similar fragments from the Turonian (Rylaarsdam et al., 2006), Santonian (Brinkman, 2003), and Campanian (Demar & Breithaupt, 2006) of North America. Although these specimens are decorated with more or less small and more or less isolated tubercles, they do not display decisive diagnostic elements such as the entoplastral scute and the epiplastral and peripheral lips.

Family ?Carettochelyidae Boulenger, 1887

Genus and species indeterminate

(Figure 6.2)

Material: a few shell fragments.

Localities: Les Renardières (Charente-Maritime), La Buzinie (Charente).

Description: Some small shell fragments (pleural plates?) displaying a particular sculpture pattern, corresponding to an undulating and varnished surface. The ornamentation consists of very shallow pits, wider than the punctiform pits of pleurosternids and adocids, isolated by flattened intervening anastomosing ridges, in addition to the bright aspect of the surface. The shell is thought to belong to a small form.

Discussion: Such an ornamentation is very similar to that of some parts of the shell of Eocene European carettochelyids (Broin, 1977). During the Mesozoic, this family is known as early as in the Late Jurassic-Early Cretaceous of China, in the Early Cretaceous of Laos and Thailand, and in the Late Cretaceous of Uzbekistan, Mongolia and Japan (see Broin, 1977, 1987; Meylan & Gaffney, 1992; Hirayama et al., 2000; Lapparent de Broin, 2004; Tong et al., 2006). In addition, it is worth noting that some small shell fragments from the Campanian of Villeveyrac (France) have an identi-

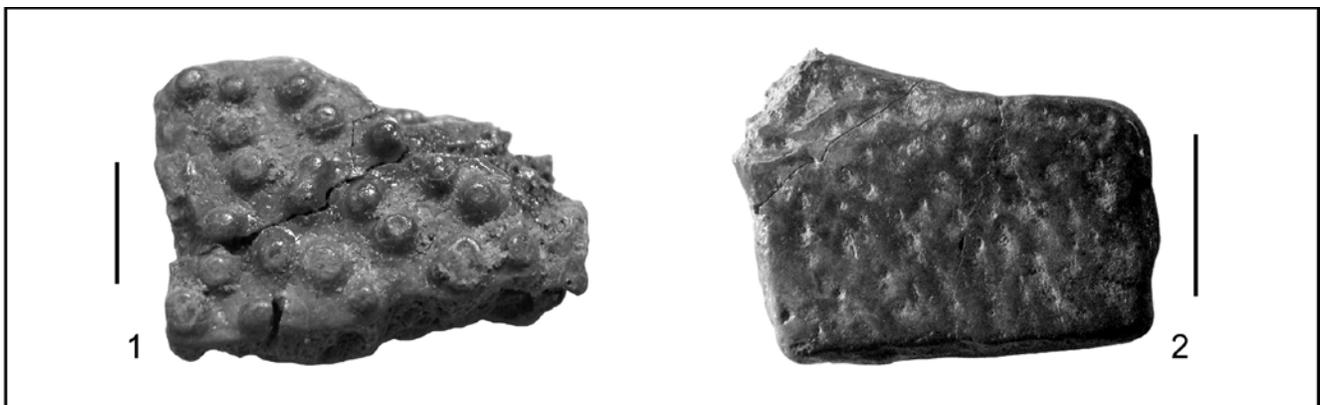


Figure 6 - Shell fragments of decorated cryptodires. 1: Solemydidae gen. et sp. indet. B from Montagan, ?pleural fragment in dorsal view. 2: ?Carettochelyidae from La Buzinie, ?pleural fragment in dorsal view. Scale bars: 5 mm.

cal ornamentation and ought also to be referred to the Carettochelyidae (F. de Lapparent de Broin, pers. observation): this locality, part of the Campanian-Maastrichtian beds of France and Spain, includes a solemydid and a dortokid (Lapparent de Broin & Murelaga, 1999) as in Charentes, in addition to the pleurodire *Polysternon* (Buffetaut et al., 1996). Several groups of Mesozoic turtles are ornamented with weak pits, but among them the ornamentation of the Charentes fragments is appropriate only for the carettochelyids. However, their assignment to this latter family remains hypothetical.

Family, genus and species indeterminate
(Figure 7)

Material: Three peripheral plates.

Localities: Les Renardières, Fouras Bois-Vert (Charente-Maritime).

Description: The three specimens share a similar morphology. The bone surface is nearly flat and smooth. The distal border is sharp. Two of the three peripheral plates, probably posteriors, show a medial border with a pit for the reception of the extremity of the pleural rib (Fig. 7.1b): the contact between peripheral and pleural plates is therefore ligamentous, with fontanelles possibly remaining between the pleural disc and the peripherals up to an advanced age of the animal. The surface is marked by numerous small, irregular grooves which are more or less dichotomous.

Discussion: this type of loose plate connection and the style of plate decoration, sometimes qualified as “chelydroid in aspect” by comparison with the Chelydridae, is frequently found in several unrelated cryptodire turtles such as various chelonoids, Chelydridae and other forms, in the Mesozoic and Cenozoic of Europe (Lapparent de Broin,

2001). The presence of true chelydrids is indicated when the anterior peripherals bear a groove ventrally for the long nuchal processes and the humerals meet the femorals (Broin, 1977; Lapparent de Broin, 2000b), two features that are not visible in Charentes material.

TAPHONOMY, PALAEOECOLOGY AND PALAEO-BIOGEOGRAPHY

Based on sedimentological and palaeontological features, the depositional environments of the different localities treated here have been defined in previous studies (Néraudeau et al., 2003, 2005; Vullo, 2007; Vullo et al., 2005). The palaeoenvironment of “Fouras Bois-Vert” (where bones are preserved in mudstones) corresponds to a tidally influenced outer estuary, while other localities (where bones are preserved in sandstones) indicate a marginal marine setting (e.g., tidal flat, nearshore shallow waters). It is worth noting that the turtle material collected in the Cenomanian of Charentes displays different taphonomic signatures according to the depositional environment (Table 1). Two parameters are considered here: the size of the fragments and the state of abrasion. The shell fragments from “Fouras Bois-Vert” are relatively large (up to 12 cm), while they are smaller (1 to 5 cm) in other localities. Similarly, fragments are generally well abraded (worn ornamentation, blunt edges) in all the localities, except at “Fouras Bois-Vert” where they are mostly fresh. Brand et al. (2000) also noted that turtle bones from a series of fluvial/lacustrine sedimentary units (Eocene of Wyoming) were more abraded in sandstone channels than in fine-grained sediments (e.g., mudstones). Fragmentation and abrasion are more marked for the remains deposited in

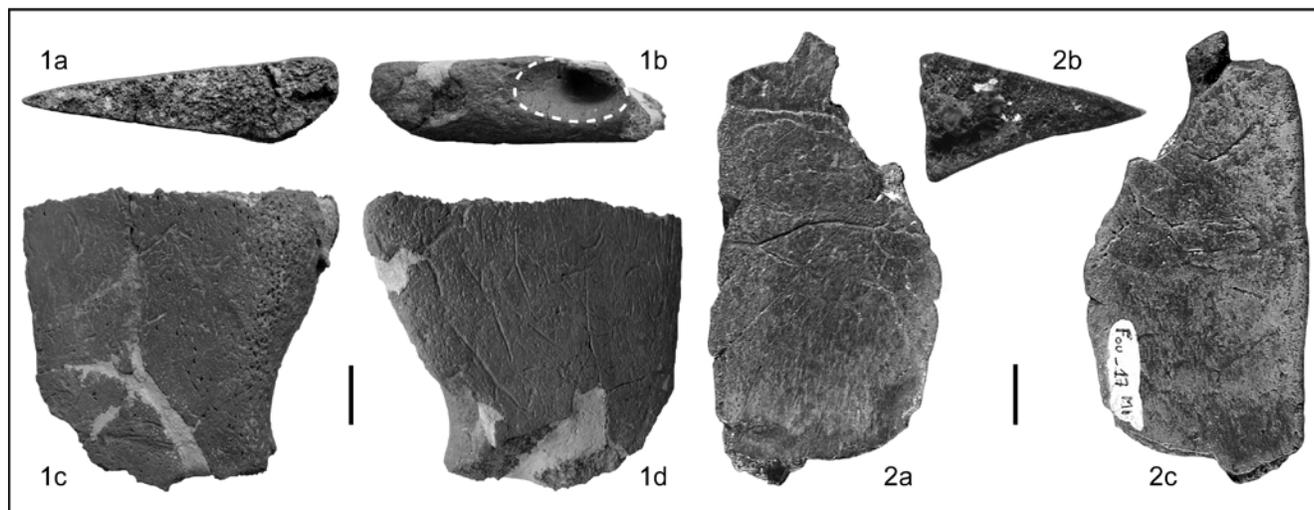
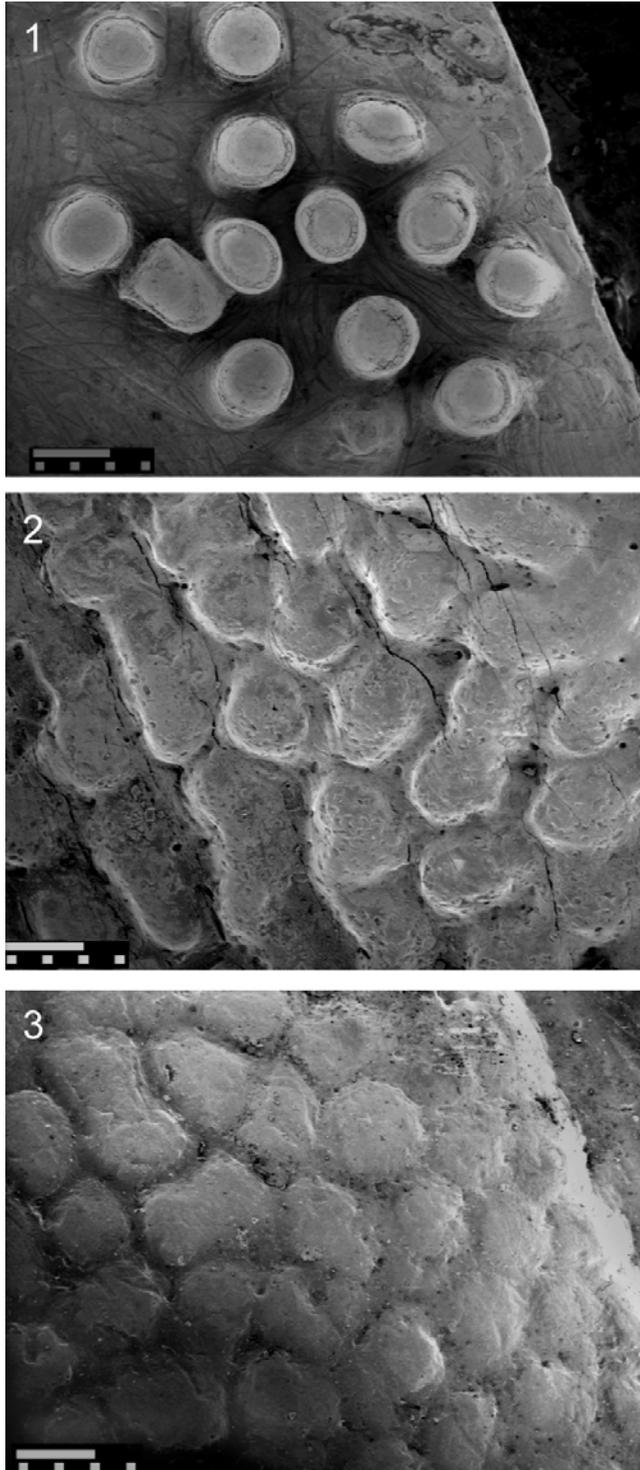


Figure 7 - Shell fragments of “chelydroid” cryptodires. **1**: Cryptodira indet. from Les Renardières, peripheral in ?anterior (a), medial (b; the position of the pit is marked by the dashed line), and ventral or dorsal (c, d) views; **2**: Cryptodira indet. from Fouras-Bois Vert, peripheral in dorsal (a), anterior or posterior (b), and ventral views (c). Scale bars: 1 cm.

coastal shallow water, suggesting longer transport and sea-floor residence time before burial. By contrast, the “Fouras Bois-Vert” assemblage corresponds to a short-term accumulation that contains mainly parautochthonous elements. In this locality, solemydid turtles are represented by numerous angular shell fragments, associated with euryhaline lamniform sharks, aquatic snakes, pterosaurs, iguanodontoid dinosaurs, and abundant conifer wood (Néraudeau et al., 2003).



After Lapparent de Broin & Murelaga (1999), solemydids are considered as rather terrestrial turtles that lived close to fresh water environments. Brinkman et al. (2004) have suggested a coastal habitat for the indeterminate solemydid (attributed to *Naomichelys*) from the Campanian of Canada, without specifying whether it really came into salt water or not. Other solemydids from the Cretaceous of North America have been found in fluvial, estuarine, deltaic, lagoonal or coastal deposits (Hirayama et al., 2000; Brinkman, 2003; Rylaarsdam et al., 2006). This indicates that members of this group were present in varied habitats, from inland to sea-shore environments. Solemydids found in the Cenomanian of Charentes probably lived in a paralic forest of conifers, from whence their skeletal remains were regularly collected by a river and deposited downstream in the estuary mouth or transported up to the coastal marine settings. Lastly, it is worth noting that a third kind of preservation can be observed in the vertebrate assemblage from the base of the unit B1 in Aix Island (Fig. 1). This coastal marine grey limestone has yielded numerous indeterminate turtle shell fragments (the presence of solemydids in this assemblage remains highly uncertain) that are mostly characterized by a relatively large size (up to about 10 cm) (Néraudeau et al., 2009). However, unlike the assemblage of “Fouras Bois-Vert”, the bones are often strongly abraded and subject to bio-erosion (perforations of boring bivalve molluscs). These taphonomic observations indicate that this assemblage probably accumulated in a rather quiet environment (limiting the fragmentation), and that the sedimentation rate may have been relatively low (favouring long-term abrasion and bio-erosion). The time of residence of turtle shells on the bottom before they were buried was sufficient (several months or years) to allow pholadid molluscs to develop and to make borings (Tapanila et al., 2004).

The turtle fauna studied here appears to include three families (i.e., cf. Dortokidae, Solemydidae, ?Carettochelyidae) that are commonly associated in the Late Cretaceous of southwestern Europe, and in particular in the continental Campanian of Villeveyrac (southern France). However, dortokids and solemydids are present as early as the Early Cretaceous in western Europe, represented by indeterminate forms and *Helochelydra* (Lapparent de Broin & Murelaga, 1999; Lapparent de Broin et al., 2004; Milner, 2004). If the identification of carettochelyids is confirmed, this would be the earliest occurrence of the group in Europe, although they are well represented during the Eocene. Carettochelyids, known as early as the Jurassic-Cretaceous boundary in China (Broin, 1977; Broin, 1987; Meylan & Gaffney, 1992; Lapparent de Broin, 2004) occur in the Cenomanian

Figure 8 - Detail (SEM photographs) of the shell decoration. **1**: *Helochelydra* (Early Cretaceous of the Isle of Wight). **2**: *Solemys* (Campanian of Villeveyrac). **3**: Solemydidae gen. et sp. indet. A from the Early Cenomanian of Fouras-Bois Vert. Scale bars : 1 mm.

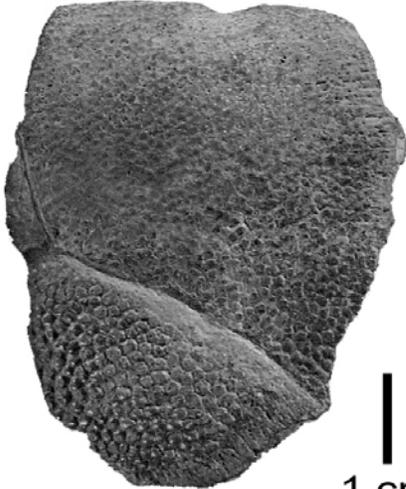
Localities	<i>Les Renardières Fouras-Vauban La Buzinie Traslemaine Montagan</i>	<i>Fouras Bois-Vert</i>
Depositional environment	<i>marginal marine setting</i>	<i>outer estuary</i>
Fragmentation degree	<i>high (1-5 cm)</i>	<i>moderate (5-10 cm)</i>
Abrasion degree	<i>moderate to high</i>	<i>nil to low</i>
Example		

Table 1 - Taphonomic features of the solemydid shell fragments from the Early Cenomanian of Charentes.

of Central Asia, where several vertebrate taxa have affinities with those recovered in Charentes (e.g., basal hadrosaurs, troodontids). Carettochelyids are tropical freshwater turtles with flexible paddles which allow them to swim across sea-arms and along the coasts to reach new territories in freshwater streams, besides their potential for continental dispersion (Renous et al., 2008). It must be noted that all of the turtles here studied belong to Laurasian continental forms, but dortokids are European endemics and solemydids are unknown in Asia. The Bothremydidae, pleurodires of Northern Gondwana origin which developed in Northern Africa and are associated with the former taxa during the European Late Cretaceous, seem to be absent in the Charentes assemblages, although several other taxa of Gondwanan affinities have been collected (e.g., the hybodont shark *Tribodus*, *Hama-*

dasuchus-like ziphodont crocodylians, carcharodontosaurid theropods, and the primitive snake *Simoliophis*) (Vullo et al., 2005, 2007b; Vullo, 2007; Vullo & Néraudeau, 2008). Although vicariant splits might have occurred in some groups during the Early Cretaceous, a selective faunal spreading across the Tethyan region seems to have occurred. The question remains as to whether this pattern of spread is also true for the bothremydids. They seem to have been able to take a marine route along the sea shores, as suggested by the first littoral bothremydids found in the Cenomanian of Israel and well adapted to coastal habits (Lapparent de Broin & Werner, 1998): perhaps their absence from the deposits in Charentes is due to taphonomic bias (e.g., fragmentation) involving the lack of diagnostic material. The considerable distance from the site of their geographical origin in the Middle East up to

Western Europe (i.e., bothremydids would not have reached the western islands of the European archipelago, and would have been really absent from the Cenomanian vertebrate fauna of Charentes) may argue against the taphonomic hypothesis, however.

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REFERENCES

- Andrews, C. W. 1920. Note on two new species of fossil tortoises. *The Annals and Magazine of Natural History*, 5, series 9, 25: 145-151.
- Brand, L. R., Goodwin, H. T., Ambrose, P. D. & Buchheim, H. P. 2000. Taphonomy of turtles in the Middle Eocene Bridger Formation, SW Wyoming. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 162: 171-189.
- Brinkman, D. B. 2003. A review of nonmarine turtles from the Late Cretaceous of Alberta. *Canadian Journal of Earth Sciences*, 40: 557-571.
- Brinkman, D. B., Russell, A. P., Eberth, D. A. & Peng, J. 2004. Vertebrate palaeocommunities of the lower Judith River Group of southeastern Alberta, Canada, as interpreted from vertebrate microfossil assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 213: 295-313.
- Broin, F. de. 1977. Contribution à l'étude des Chéloniens. Chéloniens continentaux du Crétacé et du Tertiaire de France. *Mémoires du Muséum National d'Histoire naturelle*, Paris, C, 38: 1-366.
- Broin, F. de. 1987. Lower vertebrates from the Early-Middle Eocene Kuldana Formation of Kohat (Pakistan): Chelonia. *Contributions from the Museum of Paleontology*, the University of Michigan, 27: 169-186.
- Buffetaut, E., Costa, G., Le Lœuff, J., Martin, M., Rage, J.-C., Valentin, X. & Tong, H. 1996. An Early Campanian vertebrate fauna from the Villeveyrac Basin (Hérault, Southern France). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 1996: 1-16.
- Demar, D.G. Jr., Breithaupt, B.H., 2006. The nonmammalian vertebrate microfossil assemblages of the Mesaverde Formation (Upper Cretaceous, Campanian) of the Wind River and Bighorn basins, Wyoming; pp. 33-53 in Lucas, S. G. & Sullivan, R. M. (eds.), *Late Cretaceous vertebrates from the Western Interior*. *New Mexico Museum of Natural History and Science Bulletin*, 35.
- Gaffney, E. S. 1990. The comparative osteology of the Triassic turtle *Proganochelys*. *Bulletin of the American Museum of Natural History*, 194: 1-263.
- Hirayama, R., Brinkman, D. B. & Danilov, I. G. 2000. Distribution and biogeography of non-marine Cretaceous turtles. *Russian Journal of Herpetology*, 7: 181-198.
- Lapparent de Broin, F. de. 2000a. African chelonians from the Jurassic to the Present. A preliminary catalogue of the African fossil chelonians. *Palaeontologia Africana*, 36: 43-82.
- Lapparent de Broin, F. de. 2000b. Les Chéloniens de Sansan. *Mémoires du Muséum national d'Histoire naturelle, Paris*, 183: 219-261.
- Lapparent de Broin, F. de. 2001. The European turtle fauna from the Triassic to the Present. *Dumerilia*, 4: 155-216.
- Lapparent de Broin, F. de. 2004. A new Shachemydinae (Chelonii, Cryptodira) from the Lower Cretaceous of Laos: preliminary data. *Comptes rendus Palevol*, 3: 387-396.
- Lapparent de Broin, F. de & Murelaga, X. 1996. Une nouvelle faune de chéloniens dans le Crétacé supérieur européen. *Comptes Rendus de l'Académie des Sciences, Paris*, série IIA, 323: 729-735.
- Lapparent de Broin, F. de & Murelaga, X. 1999. Turtles from the Upper Cretaceous of Laño (Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Alava*, 14 (Núm. Espec. 1): 135-211.
- Lapparent de Broin, F. de, Murelaga Bereikua, X. & Codrea, V. 2004. Presence of Dortokidae (Chelonii, Pleurodira) in the earliest Tertiary of the Jibou Formation, Romania: Palaeobiogeographical implications. *Acta Palaeontologica Romaniaae*, 4: 203-215.
- Lapparent de Broin, F. de & Werner, C. 1998. New late Cretaceous turtles from the Western Desert, Egypt. *Annales de Paléontologie*, 84: 131-214.
- Mantell, G. A. 1827. *Illustrations of the geology of Sussex: containing a general view of the geological relations of the south-eastern parts of England; with figures and descriptions of the fossils of Tilgate Forest*. Lupton Relfe, London.
- Meyer, H. Von. 1856. *Helochelys Danubina*, aus dem Grünsande von Kelheim in Bayern. *Palaeontographica*, 4: 96-105.
- Meylan, P. A. & Gaffney, E. S. 1992. *Sinaspideretes* is not the oldest trionychid turtle. *Journal of Vertebrate Paleontology*, 12: 257-259.
- Milner, A. R. 2004. The turtles of the Purbeck Limestone Group of Dorset, southern England. *Palaeontology*, 47: 1441-1467.
- Néraudeau, D., Thierry, J. & Moreau, P. 1997. Variation in echinoid biodiversity during the Cenomanian-Early

- Turonian transgressive episode in Charentes. *Bulletin de la Société géologique de France*, 168 : 51-61.
- Néraudeau, D., Allain, R., Perrichot, V., Videt, B., Lapparent de Broin, F. de, Guillocheau, F., Philippe, M., Rage, J.-C. & Vullo, R. 2003. Découverte d'un dépôt paralic à bois fossile, ambre insectifère et restes d'Iguanodontidae (Dinosauria, Ornithopoda) dans le Cénomanién inférieur de Fouras (Charente-Maritime, Sud-Ouest de la France). *Comptes Rendus Palevol*, 2 : 221-230.
- Néraudeau, D., Vullo, R., Gomez, B., Perrichot, V. & Videt B. 2005. Stratigraphie et paléontologie (plantes, vertébrés) de la série paralic Albien terminal-Cénomanién basal de Tonnay-Charente (Charente-Maritime, France). *Comptes rendus Palevol*, 4 : 79-93.
- Néraudeau, D., Vullo, R., Gomez, B., Girard, V., Lak, M., Videt, B., Depré, E. & Perrichot, V. 2009. Amber, plant and vertebrate fossils from the Lower Cenomanian paralic facies of Aix Island (Charente-Maritime, SW France). *Geodiversitas*, 31 : 13-27.
- Owen, R. 1842. Report on British fossil reptiles. Part II. *Report of the British Association for the Advancement of Science*, 1841 : 60-204.
- Peng, J., Russell, A. P. & Brinkman, D. B. 2001. Vertebrate microsite assemblages (exclusive of mammals) from the Foremost and Oldman formations of the Judith River Group (Campanian) of southeastern Alberta: an illustrated guide. *Provincial Museum of Alberta, Natural History Occasional Paper*, 25 : 1-54.
- Renous, S., Lapparent de Broin, F. de, Depecker, M., Davenport, J. & Bels, V. 2008. Evolution of locomotion in aquatic turtles; pp. 97-138 in Wyneken, J., Godfrey, M. H. & Bels, V. (eds.), *Biology of Turtles*. CRC Press, Taylor & Francis Group, Boca Raton, Florida.
- Rylaarsdam, J. R., Varban, B. L., Plint, A. G., Buckley, L. G. & McCrea, R. T. 2006. Middle Turonian dinosaur paleoenvironments in the Upper Cretaceous Kaskapau Formation, northeast British Columbia. *Canadian Journal of Earth Sciences*, 43 : 631-652.
- Tapanila, L., Roberts, E. M., Bouaré, M. L., Sissoko, F. & O'Leary, M. A. 2004. Bivalve borings in phosphatic coprolites and bone, Cretaceous-Paleogene, northeastern Mali. *Palaios*, 19 : 565-573.
- Tong, H., Claude, J., Buffetaut, E., Suteethorn, V, Naksri, W. & Chitsing, S. 2006. Fossil turtles of Thailand: an updated review; pp. 183-194 in Lü, J., Kobayashi, Y., Hunag D., Lee Y. (eds), *Papers from the 2005 Heyuan International Dinosaur Symposium*, Geological Publishing House, Beijing.
- Vullo, R. 2007. Les vertébrés du Crétacé supérieur des Charentes (Sud-Ouest de la France): biodiversité, taphonomie, paléoécologie et paléobiogéographie. *Mémoires de Géosciences Rennes*, 125 : 1-302.
- Vullo, R. & Néraudeau, D. 2008. Cenomanian vertebrate assemblages from southwestern France: a new insight into the European mid-Cretaceous continental fauna. *Cretaceous Research*, 29 : 930-935.
- Vullo, R., Cappetta, H. & Néraudeau, D. 2007a. New sharks and rays from the Cenomanian and Turonian of Charentes, France. *Acta Palaeontologica Polonica*, 52 : 99-116.
- Vullo, R., Néraudeau, D. & Lenglet, T. 2007b. Dinosaur teeth from the Cenomanian of Charentes, western France: evidence for a mixed Laurasian-Gondwanan assemblage. *Journal of Vertebrate Paleontology*, 27:931-943.
- Vullo, R., Néraudeau, D., Allain, R. & Cappetta, H. 2005. Un nouveau gisement à microrestes de vertébrés continentaux et littoraux dans le Cénomanién inférieur de Fouras (Charente-Maritime, Sud-Ouest de la France). *Comptes Rendus Palevol*, 4 : 95-107.