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A review of the fossil record of turtles of the clade *Thalassochelydia*

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Abstract

The Late Jurassic (Oxfordian to Tithonian) fossil record of Europe and South America has yielded a particularly rich assemblage of aquatic pan-cryptodiran turtles that are herein tentatively hypothesized to form a monophyletic group named *Thalassochelydia*. Thalassochelydians were traditionally referred to three families, Eurysternidae, Plesiochelyidae, and Thalassemydidae, but the current understanding of phylogenetic relationships is insufficient to support the monophyly of either group. Given their pervasive usage in the literature, however, these three names are herein retained informally. Relationships with marine turtles from the Cretaceous have been suggested in the past, but these hypotheses still lack strong character support. Thalassochelydians are universally found in near-shore marine sediments and show adaptations to aquatic habitats, but isotopic evidence hints at a broad spectrum of specializations ranging from freshwater aquatic to fully marine. A taxonomic review of the group concludes that of 68 named taxa, 27 are nomina valida, 18 are nomina invalida, 18 are nomina dubia, and 5 nomina oblita.

Keywords

Phylogeny, biogeography, *Thalassochelydia*, Late Jurassic, Early Cretaceous

Introduction

Over the course of the last two centuries, rich fossil turtle material has been recovered from Late Jurassic sediments exposed throughout Europe that documents the colonization of the island archipelago and shallow epicontinental seas that covered a large part of that continent at the time by basal pan-cryptodiran turtles. These taxa represent the first unambiguous radiation of crown group turtles into marine environments. The majority of these turtles were traditionally referred to the families Eurysternidae Dollo, 1886, Plesiochelyidae Baur, 1888, and Thalassemydidae Zittel, 1889, but the relationships among these three groups and later groups of marine turtles remain obscure (Joyce 2007; Cadena and Parham 2015). As we find these terms to be useful, we herein place them in quotes to highlight that their monophyly has not yet been rigorously demonstrated. Accumulating evidence suggests that all Late Jurassic coastal marine turtles from Europe form a monophyletic group, which is herein formally named *Thalassochelydia*. With the exception of one species from the Late Jurassic (Tithonian) of Argentina (Fernández and de la Fuente 1988; de la Fuente and Fernández 2011) and a fragment from the putative Early Cretaceous of Switzerland (Pictet and Campiche 1858–1860; Püntener et al. 2014), thalassochelydian turtles are restricted to the Late Jurassic (Oxfordian to Tithonian) of western and central Europe.

“Eurysternids” were initially described from the Tithonian of southern Germany, notably from the lithographic limestone quarries of Solnhofen, Kelheim, and Eichstätt (e.g., Meyer 1839b, 1839c, 1860, 1864). Thanks to their exceptional state of preservation, these were historically among the first fossil turtles to be recognized as truly different from modern faunas and therefore placed in their own taxonomic units (genera). About ten species and seven genera were initially proposed. Unfortunately, despite the amount of well-preserved material that was available, many taxa were based on fragmentary remains. Additional “eurysternids” were subsequently described from France (Thiollière 1851; Meyer 1860; Jourdan 1862) and northern Germany (Maack 1869; Portis 1878). These turtles were extensively studied during the second part of the 19th century and early parts of the 20th century (e.g., Wagner 1861b; Rütimeyer 1873a, 1873b; Zittel 1877a, 1877b; Lydekker 1889b; Oertel 1915, 1924), but taxonomic conclusions varied greatly. After a substantial hiatus, the group has received more attention recently (e.g., Parsons and Williams 1961; Wellnhofer 1967; Gaffney 1975b; Broin 1994; Joyce 2000, 2003; Anquetin and Joyce 2014), but a global revision of the group beyond what is being presented herein is still needed.

“Plesiochelyids” and “thalassemydids” were first described from the Kimmeridgian of Solothurn, Switzerland. At the beginning of the 19th century, limestone quarries around Solothurn started to yield many remains of relatively large turtles. These were collected by Franz Joseph Hugi, who eventually sold his collection to the city and was appointed as first director to the new city museum (Meyer and Thüring 2009). Hugi sent information and specimens to Georges Cuvier in Paris, and some of these were figured in the second edition of his *Recherches sur les ossemens fossiles* (Cuvier 1824; Bräm 1965; Gaffney 1975a). These figured specimens were given various names during the 1830s (Gray 1831; Keferstein 1834; Fitzinger 1835), but these are now nomina oblita. The Solothurn turtles were first thoroughly described by Rütimeyer (1873a), who coined the names *Plesiochelys*, *Craspedochelys*, *Tropidemys*, and *Thalassemys*. In the meantime, “plesiochelyid” taxa had also been described from the Isle of Portland, England (Owen 1842), from the French and Swiss Jura Mountains (Pictet and Humbert 1857; Pictet 1860), from the region of Hannover in Germany (Maack 1869), and from the regions of Le Havre and Boulogne-sur-Mer in northern France (Lennier 1870; Sauvage 1872, 1873).

Initially, Rütimeyer (1873a) recognized 13 species of “plesiochelyids” and “thalassemydids” in Solothurn, although they were at the time classified within Emydidae and Chelydidae. Additional species were subsequently described from northern Germany (Portis 1878; Oertel 1924), northern France (Sauvage 1880; Bergounioux 1937), central western Portugal (Sauvage 1898), southern Germany (Fraas 1903; Oertel 1915), and central southern England (Andrews 1921). Up until the present contribution, there has been no attempt to reevaluate the taxonomy of these turtles at the European scale. Instead, revisionary works focused mostly on the turtles from Solothurn. Bräm (1965) was the first to propose a detailed reassessment of the Solothurn turtle assemblage. Eight of the species initially described by Rütimeyer (1873a) were confirmed as valid and two new species were created. Subsequent authors focused only on part of this assemblage and reached diverging conclusions (Gaffney 1975a; Antunes et al. 1988; Lapparent de Broin et al. 1996). The most recent revision of these turtles concluded the validity of only six species out of the fifteen historically described based on material from the Late Jurassic of the Jura Mountains (Anquetin, Püntener and Billon-Bruyat 2014). This study is, however, far from global as it focused only on a limited geographical region. Since Bräm (1965), new species have been described from southern England (Gaffney 1975a), southern Spain

(Slater et al. 2011), and, more recently, from northwestern Switzerland (Anquetin et al. 2015; Püntener et al. 2015, 2017).

Most thalassochelydians were described during the 19th and early 20th centuries. More than sixty species were named based on material from Switzerland, Germany, England, and France notably, but few attempts were made to synthesize a consistent taxonomy that spanned across the continent. Several reasons may explain this situation. First, the whereabouts of many specimens are uncertain. Second, several species are described based on relatively incomplete material. Third, the amount of literature relating to these turtles is difficult to oversee and some literature is difficult to access. Finally, many specimens, including the types of several species, were destroyed, most as a result of World War II or neglect. A synthetic understanding of these turtles is therefore needed more than ever.

For institutional abbreviations see Appendix 1. Named thalassochelydian genera are listed in Appendix 2.

Skeletal Morphology

Cranium

Cranial material has been described for five species of "plesiochelyids," in particular two crania of *Plesiochelys bigleri* (Püntener et al. 2017), seven crania of *Plesiochelys etalloni* (Gaffney 1975a, 1976; Anquetin et al. 2015; Anquetin and Chapman 2016), one cranium of *Plesiochelys planiceps* (Gaffney 1975a, 1976), one cranium of *Portlandemys gracilis* (Anquetin et al. 2015), and two crania of *Portlandemys mcdowelli* (Parsons and Williams 1961; Gaffney 1975a, 1976; Anquetin et al. 2015). The cranium of "eurysternids" is satisfactorily described only for *Solnhofia parsonsi* based on three skulls from Germany and Switzerland (Parsons and Williams 1961; Gaffney 1975b; Joyce 2000). Crushed, partial cranial remains are known for several other "eurysternids," including *Eurysternum wagleri* (Meyer 1839c; Anquetin and Joyce 2014), *Idiochelys fitzingeri* (Jourdan 1862), *Palaeomedusa testa* (Meyer 1860), and *Parachelys eichstaettensis* (Meyer 1864), but poor preservation prevents any conclusive comparison for the moment. No cranial material is known for "thalassemydids." The cranium is finally known for *Jurassichelon oleronensis* based on a particularly beautifully preserved specimen from France (Rieppel 1980). We show only this specimen (Figure 1), as this is the only known near-complete thalassochelydian skull.

The skull of thalassochelydians is usually longer than wide with moderately developed temporal emarginations. In *Portlandemys mcdowelli* and *Portlandemys gracilis*, the skull is narrower and results in a more acute angle between the two rami of the jaws. The skull of the eurysternid *Solnhofia parsonsi* is macrocephalic, about 40% of the carapace length, and characterized by an elongated snout. The nasals are usually well-developed quadrangular elements, but they are reduced and triangular in *Jurassichelon oleronensis* (Figure 1). These elements contact one another along their entire length and form the dorsal margin of the apertura narium externa. The prefrontals form the anterodorsal part of the orbit and contact one another in the midline for most of their length in most species, although an anteromedial process of the frontals may partly separate the prefrontals posteriorly. In contrast, the frontals contact the nasals anteriorly and fully separate the prefrontals in *Jurassichelon oleronensis* (Figure 1) and *Portlandemys gracilis*. In all species, an anterior process of the frontals contacts the nasals on the ventral surface of the skull roof. The frontals form the posterodorsal margin of the orbit and are proportionally more developed in *Jurassichelon oleronensis*. The parietals are large elements that form most of the skull roof. Because of the moderate development of the upper temporal emargination, there generally appears to be no contact between the parietals and squamosal posterolaterally, except in *Jurassichelon oleronensis*, where the upper temporal emargination is slightly less developed. Cranial scutes are commonly present on the skull roof. The jugal and quadratojugal define a moderately developed lower temporal emargination. The postorbitals are large, elongate elements that form the posterior border of the orbit. The squamosals form the posterodorsal part of the cavum tympani and host a well-developed antrum postoticum.

The triturating surfaces usually consist of a high labial ridge and a well-developed rugose lingual ridge separated by a deep furrow. The triturating surface is broader and more coarsely built in *Portlandemys mcdowelli*. In *Solnhofia parsonsi*, the lingual ridge is reduced and the triturating surface is much wider and flatter forming a true secondary palate, which suggests a durophagous diet. The foramen palatinum posterius remains open posterolaterally in *Plesiochelys* spp. and *Jurassichelon oleronensis*, but it is closed in *Portlandemys mcdowelli* and significantly reduced in *Solnhofia parsonsi*.

The presence of a prominent ventrally-infolding ridge on the posterior surface of the processus articularis of the quadrate is a characteristic uniting all thalassochelydians, including *Jurassichelon oleronensis* (Anquetin et al. 2015). Although the condylus mandibularis is rarely described in detail, this structure may bear some systematic value within the group. The cavum tympani is well developed, especially in *Jurassichelon oleronensis*. The incisura columellae auris

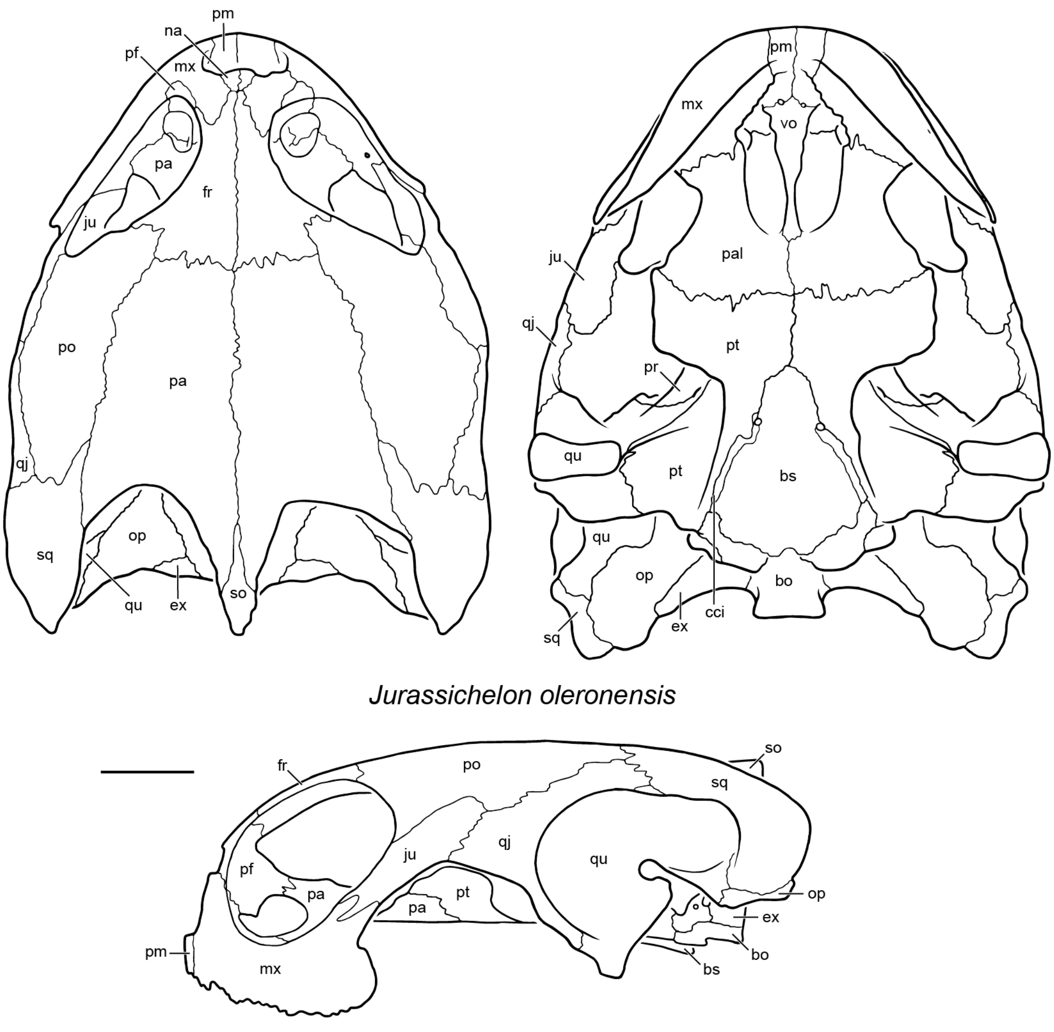

Figure 1 — Cranial morphology of thalassochelydian turtles as exemplified by *Jurassichelon oleronensis* (PIMUZ A/III 514). *Abbreviations:* bo, basioccipital; bs, basisphenoid; cci, canalis carotici internus; ex, exoccipital; fr, frontal; ju, jugal; mx, maxilla; na, nasal; op, opisthotic; pa, parietal; pal, palatine; pbs, parabasisphenoid; pf, prefrontal; pm, premaxilla; po, postorbital; pr, prootic; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer. Scale bar approximates 1 cm.

remains open posteroventrally. The pterygoids extend posteriorly along the basisphenoid and reach the basioccipital in all species. A pterygoid fossa occurs on the posteroventral surface of the pterygoid lateral to the basisphenoid. This fossa is remarkably deep in *Plesiochelys planiceps*, *Portlandemys mcdowelli*, and *Jurassichelon oleronensis*, but notably shallow in *Plesiochelys bigleri*. When its position can be determined, the foramen posterius canalis carotici interni is formed by the pterygoid and opens on or closes to the posterior margin of this bone. Two configurations are observed regarding the canalis caroticus internus. The canal extends deep into the bones in *Plesiochelys planiceps*, *Portlandemys mcdowelli*, and *Portlandemys gracilis*. In contrast, the canalis caroticus internus is superficial in *Plesiochelys etalloni* and *Plesiochelys bigleri* and is open ventrally at least along its anterior half in most specimens (Anquetin et al. 2015). A similar condition is apparently also present in *Jurassichelon oleronensis*.

The ethmoid region is particularly interesting in these turtles. The length of the processus inferior parietalis is reduced in relation to the great development of the foramen interorbitale, a configuration that accommodates enlarged salt-excreting glands in modern marine turtles. The processus inferior parietalis forms most of the anterior and posterior margins of the foramen nervi trigemini. A contact between the processus inferior parietalis and the pterygoid excludes the epipterygoid from the anterior margin of the foramen nervi trigemini. Posteriorly, the parietal covers the prootic anterolaterally, excluding this bone from the posterior margin of the foramen nervi trigemini. This posterior extension of the processus inferior parietalis reaches the quadrate in most species, except *Plesiochelys planiceps*.

The condition in *Solnhofia parsonsi* is apparently similar to that of “plesiochelyids“ and *Jurassichelon oleronensis* (Anquetin et al. 2015).

The processus trochlearis oticum is formed by the quadrate and prootic. This structure is strongly developed in *Plesiochelys planiceps*, *Portlandemys mcdowelli*, and *Solnhofia parsonsi*, but it is relatively reduced in *Plesiochelys bigleri*, *Portlandemys gracilis*, and *Jurassichelon oleronensis* (Figure 1). The development of this structure is intermediate in *Plesiochelys etalloni* and there is possibly a trend towards an increased development of the processus during late ontogenetic stages in this species (Anquetin and Chapman 2016). The foramen stapedio-temporale is large and formed by the quadrate and prootic. There is a contact between the prootic and opisthotic on the dorsal surface of the otic chamber in *Plesiochelys bigleri*, *Plesiochelys planiceps*, *Portlandemys gracilis*, and *Jurassichelon oleronensis*. This contact is reduced or absent in *Portlandemys mcdowelli* and most specimens of *Plesiochelys etalloni*. The posterior development of the crista supraoccipitalis is variable within the group, from short in *Plesiochelys etalloni* and *Jurassichelon oleronensis* (Figure 1) to relatively elongated in *Plesiochelys planiceps* and *Solnhofia parsonsi*.

The morphology of the basisphenoid in the region of the dorsum sellae is of particular interest for the systematics of the group (see Anquetin et al. 2015). All “plesiochelyids” share a unique configuration in which the dorsum sellae is high and does not overhang the posterior part of the sella turcica. As a result, the foramina anterius canalis carotici cerebralis open anterior to the level of the dorsum sellae instead of posteroventral to it, and the surface below the dorsum sellae is well developed and slopes more or less gently anteroventrally. This condition is convergent with the arrangement found in *Pan-Chelonioidea* and might be linked with the adaptation to marine environments, such as the development of hypertrophied salt glands. Interestingly, this unique condition found in “plesiochelyids” is lacking in “eurysternids” and *Jurassichelon oleronensis*, although the latter is possibly intermediate between “eurysternids” and “plesiochelyids.”

The coronoid process is well developed, but, otherwise, the mandible usually has a low profile. Compared to other species, the mandible of *Plesiochelys etalloni* is rather inconspicuous. The triturating surfaces of *Plesiochelys etalloni* are moderately broad, and the labial and lingual ridges are sharp and well defined. In *Plesiochelys planiceps*, the triturating surfaces are narrower than in *Plesiochelys etalloni*. In *Portlandemys* spp., the angle formed by the two rami of the mandible is more acute than in the previous two. The triturating surfaces of *Portlandemys mcdowelli* are broader and more coarsely built, mirroring the condition of the upper jaw, and a dentary hook occurs at the front of the mandible. In contrast, *Portlandemys gracilis* is characterized by much narrower triturating surfaces and a relatively poorly developed lingual ridge. Finally, the triturating surfaces of the mandible of *Solnhofia parsonsi* are flat and notably broad, corresponding to the development of a flat secondary palate in this species.

Shell

The vast majority of thalassochelydians are known from shell material. We therefore refrain from listing all relevant literature and instead refer the reader to the Systematic Paleontology below.

“Plesiochelyids” are relatively large turtles with carapace length reaching up to 55 cm. Their shell is usually moderately domed and completely ossified, although a central plastral fontanelle occurs in some species (Figure 2). “Thalassemydids” were undoubtedly the largest turtles of their time with a carapace length of 70 cm or more, with some individuals possibly reaching 1 m (Pérez-García 2015c). Their shell was apparently much flatter than that of “plesiochelyids.” The carapace of these turtles is usually well ossified, but small costo-peripheral fontanelles may be retained, at least in subadults. The plastron is more reduced with the presence of moderate to large lateral, central, and xiphiplastral fontanelles. Most “eurysternids” are small turtles, often under 20 cm in carapace length, but some species, notably *Eurysternum wagleri* reached larger size (Anquetin and Joyce 2014). The shell was probably relatively flat, although postmortem deformation often precludes a definitive conclusion on that matter. Several species, such as *Achelonia formosa* and *Hydropelta meyeri*, exhibit extensive fenestration of the carapace and plastron, whereas in others, such as *Idiochelys fitzingeri* and *Palaeomedusa testa*, the fenestration is reduced or absent. The bridge is osseous in “plesiochelyids” and “thalassemydids,” forming a fine sutural contact, but mostly ligamentous in “eurysternids,” in which well-developed pegs are present. *Jurassichelon oleronensis* retains small costo-peripheral, lateral plastral, and central plastral fontanelles and exhibits a ligamentous bridge.

The nuchal is trapezoidal in “plesiochelyids” and “thalassemydids.” In “eurysternids,” the nuchal is remarkably wide. A nuchal notch occurs in most species. There are usually eight neurals that are hexagonal in outline with shorter sides facing anteriorly. The only exceptions are *Tropidemys* spp., in which the neurals are strongly keeled and with subequal lateral borders, and *Idiochelys fitzingeri*, in which the neural series is

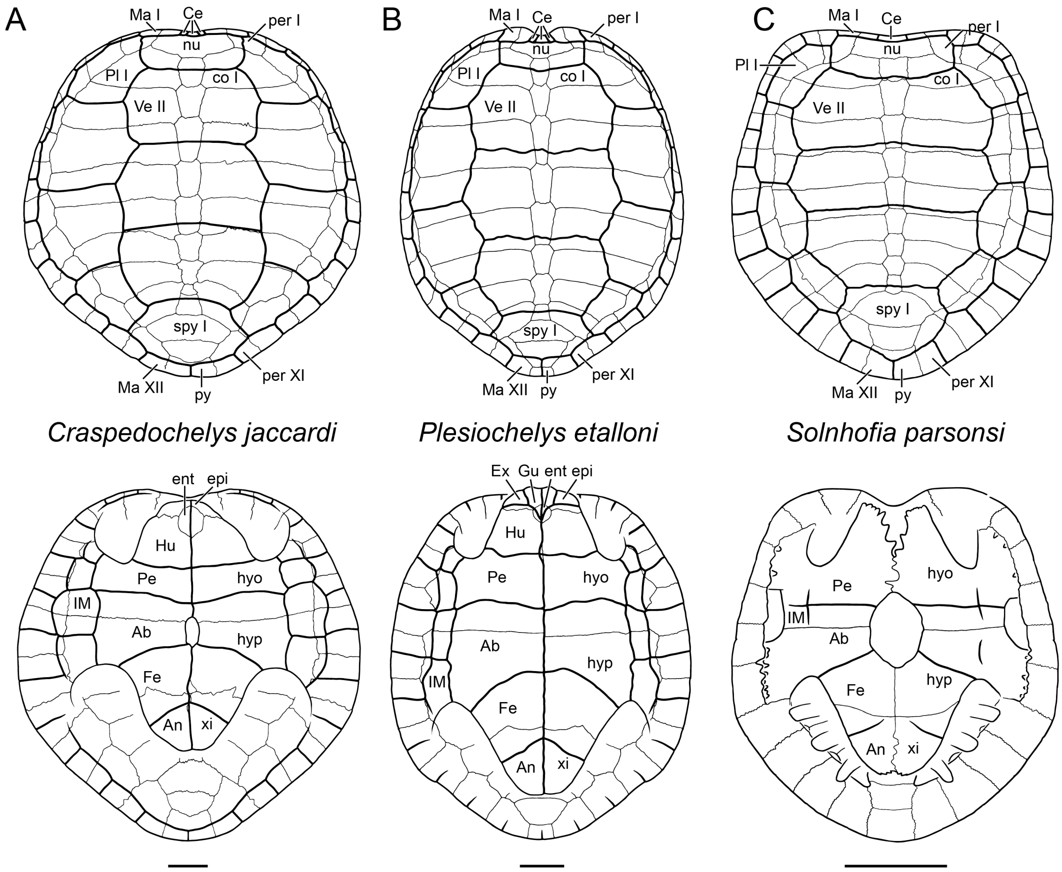

Figure 2 — Shell morphology of thalassochelydian turtles as exemplified by three species. A. *Craspedochelys jaccardi* (idealized drawing of NMS 673). **B.** *Plesiochelys etalloni* (idealized drawing of NMS 669). **C.** *Solnhofia parsonsi* (idealized drawing based on JM SCHA70 and MNB R2441). *Abbreviations:* Ab, abdominal scute; An, anal scute; Ce, cervical scute; co, costal; ent, entoplastron; epi, epiplastron; Ex, extragular scute; Fe, femoral scute; Gu, gular scute; Hu, humeral scute; hyo, hyoplastron; hyp, hypoplastron; IM, inframarginal scute; Ma, marginal scute; nu, nuchal; Pe, pectoral scute; per, peripheral; Pl, pleural scute; py, pygal; spy, suprapygal; Ve, vertebral scute; xi, xiphiplastron. Scale bars approximates 5 cm.

incomplete. The neural series may be interrupted by a medial contact of posterior costals in some individuals of *Plesiochelys etalloni*, *Plesiochelys bigleri*, and *Craspedochelys jaccardi*. In many species, a single medial bone, called the “intermediate” element by Anquetin, Püntener and Billon-Bruyat (2014), is often intercalated between the neural VIII and suprapygal I, which explains why some authors described the presence of three suprapygals in some taxa. There are usually two suprapygal bones, although their outlines and their number are variable. A large pygal notch is diagnostic of *Eurysternum wagleri* and the pygal bone may actually be lacking in this taxon (Anquetin and Joyce 2014).

Three cervical scutes are present in most, if not all, species, but imperfect preservation often hinders correct observation of this feature (see Anquetin, Püntener and Billon-Bruyat 2014). *Jurassichelon oleronensis* is a notable exception as cervicals are apparently lacking in this taxon. Vertebral scutes are usually wider than long and tend to be significantly wider in “eurysternids.” In contrast, these scutes are notably narrow in *Tropidemys* spp. A radiating pattern occurs on the vertebrals in some “eurysternids.” A supernumerary element, the preneural, occurs in several taxa, including *Solnhofia parsonsi* and *Palaeomedusa testa*.

Epiplastra and the entoplastron are unknown in many species, in particular *Eurysternum wagleri*, *Solnhofia parsonsi*, *Thalassemys* spp., and *Jurassichelon* spp., probably because of poor connection with the hyoplastra, although an absence of ossification of these elements cannot be ruled out as an explanation. A central plastral fontanelle occurs in many species, sometimes only as an intraspecific variation (e.g., *Plesiochelys etalloni* and *Plesiochelys bigleri*). Lateral plastral fontanelles are present and usually well developed in all “eurysternids” in which this area is preserved. These fontanelles also occur in *Thalassemys* spp. and *Jurassichelon* spp., but they are generally less developed. A small xiphiplastral fontanelle is also present in some species, notably *Eurysternum wagleri* and *Thalassemys* spp. The posterior plastral lobe is significantly shortened in *Craspedochelys jaccardi*. The plastron of thalassochelydians otherwise conforms to that of basal pan-cryptodires by lacking mesoplastra and by possessing pairs of gulars, extragulars, humerals, pectorals, abdominals, femorals, and anals.

Postcranium

The postcranium is rarely preserved in "plesiochelyids" and "thalassemydids," but occurs more frequently in "eurysternids," mostly because of more favorable preservational conditions in plattenkalk deposits. However, authors have only inconsistently described the available postcranial elements.

Cervical vertebrae are known for several species, including *Idiochelys fitzingeri*, *Jurassichelon oleronensis*, *Palaeomedusa testa*, *Parachelys eichstaettensis*, *Plesiochelys bigleri*, *Plesiochelys etalloni*, *Plesiochelys planiceps*, *Solnhofia parsonsi*, and *Thalassemys hugii*. Centra are relatively short and amphicoelous. The ventral keel is absent or only incipient. The transverse process is short and located anteriorly along the lateral surface of the centrum. The neural arch is moderately high, notably posteriorly. A low neural spine may occur in some cervical vertebrae. The zygapophyses are broadly separated and oriented in a sub-horizontal plane. The tail was probably moderately long (about one-third of the carapace length) and slender in "plesiochelyids," although this is based on only a single individual referred to *Plesiochelys etalloni* (Bräm 1965). Caudals of "thalassemydids" remain unknown at the moment. The tail of "eurysternids" is better known and shows some differences from one taxon to the next. The tail of *Idiochelys fitzingeri* is relatively long and slender and counts more than 22 caudal vertebrae. In *Eurysternum wagleri*, the tail is apparently shorter and stouter, but still counts at least 19 caudal vertebrae. The tail of *Solnhofia parsonsi* is probably intermediate in length between that of *Idiochelys fitzingeri* and *Eurysternum wagleri*. The morphology of the caudal vertebrae is rarely described in detail in the literature, although Bräm (1965) stated that the caudals of *Plesiochelys etalloni* are procoelous.

The pectoral girdle of thalassochelydians is characterized by the presence of a well-developed glenoid neck. The angle formed by the scapular and acromion processes has taxonomic significance for "thalassemydids" (Bräm 1965; Püntener et al. 2015). The pelvic girdle is rarely preserved. A good pelvis is described for *Plesiochelys bigleri* and is characterized by a deep, kidney-shaped acetabulum (Püntener et al. 2017). Complete limbs are mostly known for "eurysternids" and "plesiochelyids." In general, these are characterized by a moderately elongated stylopod, a shorter zeugopod, and a relatively elongated autopod similar in proportion to extant pleurodires and trionychids (Joyce and Gauthier 2004). Well-developed articular surfaces reveal that thalassochelydians did not possess stiffened paddle as in extant marine turtles, but the flippers of *Neusticemys neuquina* were described as having been less mobile than those of trionychids (de la Fuente and Fernández 2011). Two species, *Idiochelys fitzingeri* and *Parachelys eichstaettensis*, are characterized by the unusual manual phalangeal formula of 2-2-3-3-3, whereas a moderate hyperphalangy is known in the pes of *Neusticemys neuquina* (de la Fuente and Fernández 2011). The remaining thalassochelydians apparently possess the plesiomorphic condition of 2-3-3-3-3 for both the manus and the pes.

Phylogenetic Relationships

For most of the 19th century, modern turtles were classified into four groups based on their ecology, as proposed by Duméril and Bibron (1834): Chersites (terrestrial turtles), Elodites (sometimes also Paludines; pond turtles), Potamites (fluvial turtles), and Thalassites (sea turtles). Elodites were further separated into cryptodires ("Cryptodères") and pleurodires ("Pleurodères") based on the orientation of neck retraction, whereas Potamites corresponded broadly to trionychids. Although thalassochelydians were among the first fossil turtles to be recognized as truly different from modern turtles and rapidly placed in their own genera and families, they were still tentatively shoehorned into this ecological classification. Early authors usually referred *Thalassemys*, *Eurysternum*, and *Tropidemys* to cryptodire Elodites, and *Plesiochelys* and *Craspedochelys* to pleurodire Elodites (e.g., Rütimeyer 1873a; Zittel 1889; Lydekker 1889b). Several authors also noted similarities between "thalassemydids" sensu lato (including "eurysternids") and sea turtles (Maack 1869; Fraas 1903), an opinion shared by Bräm (1965) who stated that several characteristics suggest that Cheloniidae could be traced back to thalassochelydians. However, during the first half of the 20th century, thalassochelydians were often tentatively or definitely placed within Amphichelydia, a wastebasket group consisting of several Mesozoic groups (notably Pleurosternidae and Baenidae) supposed to be intermediate between Cryptodira and Pleurodira (Hay 1905; Williams 1950; Kuhn 1964b; Romer 1966).

In a series of papers, Gaffney reevaluated the cranial anatomy of "plesiochelyids" (Gaffney 1975a) and *Solnhofia parsonsi* (Gaffney 1975b) and the classification of the higher categories of turtles based primarily on basicranial characters (Gaffney 1975c). Amphichelydia was rejected as a paraphyletic taxon, and "plesiochelyids" were tentatively included in Chelonioidea based notably on similarities in the region of the dorsum sellae and sella

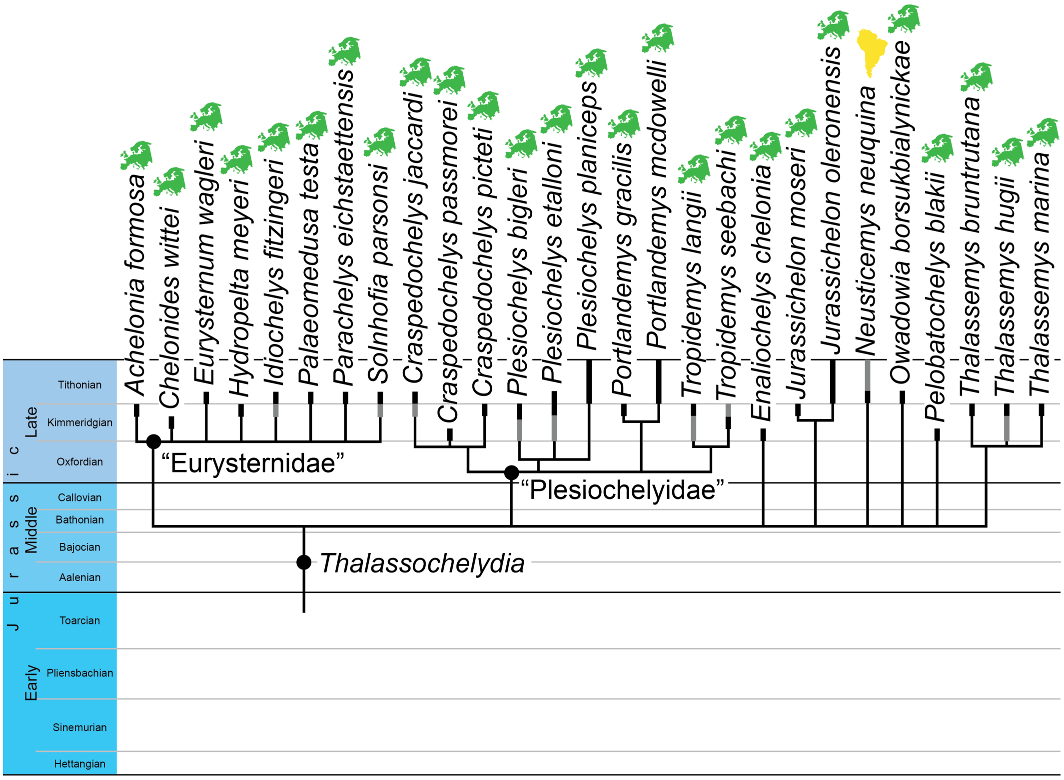

FIGURE 3 — The stratigraphic and biogeographic distribution of valid thalassochelydians. Black lines indicate temporal distribution based on type material. Gray lines indicate temporal distribution based on referred material.

turcica (Gaffney 1975a, 1975c). The latter conclusion was rejected a few years later by Gaffney and Meylan (1988) who proposed that "plesiochelyids" were the most basal known eucryptodires. In this study, the clade Plesiochelyidae included *Plesiochelys* (scored based on *Plesiochelys etalloni* and *Plesiochelys planiceps*), *Portlandemys mcdowelli*, and *Jurassichelon oleronensis* (their "*Thalassemys*"). In all subsequent phylogenetic analyses published up to 2007 in which these turtles were included, "plesiochelyids" formed a single terminal taxon, which prevented a test of their monophyly and internal relationships (Gaffney et al. 1991, 2007; Gaffney 1996; Hirayama et al. 2000). Gaffney et al. (2007) found *Solnhofia parsonsi* to be the sister group of a unified "Plesiochelyidae," hinting to a monophyletic Thalassochelydia. However, subsequent analyses failed to reproduce such a result. Joyce (2007) included an expanded sample by scoring *Plesiochelys etalloni*, *Portlandemys mcdowelli*, *Jurassichelon oleronensis* (his "*Thalassemys*" *moseri*), and *Solnhofia parsonsi* as terminal taxa, but they were found in a paraphyletic arrangement. More recent global phylogenetic analyses of turtles continued to include these species as separate terminal taxa (Danilov and Parham 2006, 2008; Sterli 2010; Anquetin 2012; Rabi et al. 2013; Sterli et al. 2013; Zhou et al. 2014; Zhou and Rabi 2015), but none found them to form a monophyletic group.

More recently, Anquetin et al. (2015) expanded the matrix of Joyce (2007) by including newly developed cranial characters. The resulting phylogenetic analysis, which included *Plesiochelys planiceps*, *Portlandemys gracilis*, and *Tropidemys langii* in addition to the aforementioned taxa, found a monophyletic group uniting "plesiochelyids," *Jurassichelon oleronensis*, and *Solnhofia parsonsi* (Anquetin et al. 2015). We herein propose the name Thalassochelydia to refer to this clade (see Systematic Paleontology; Figure 3). Although preliminary, this study shows that new characters must be sought in order to solve the phylogenetic relationships of this group of turtles.

The relationships within *Thalassochelydia* remain obscure for the moment. "Eurysternids" may be the basalmost members of the group, and *Jurassichelon oleronensis* may be more closely related to "plesiochelyids" than to "eurysternids" (Anquetin et al. 2015). The phylogenetic position of "thalassemydids" is completely unknown since no member of this group has ever been included in a cladistic analysis. "Plesiochelyids" quite probably form a clade, as indicated by several derived cranial features (Anquetin et al. 2015), but the "eurysternids" may well form a paraphyletic group at the base of *Thalassochelydia*. We herein nevertheless retain usage of the terms “Eurysternidae,” “Plesiochelyidae,” and “Thalassemydidae, “ but highlight taxonomic ambiguity through the use of quotes.

In a few studies, thalassochelydian turtles have been found to be closely related to Cretaceous turtles, in particular the Early Cretaceous protostegid *Santanachelys gaffneyi* Hirayama, 1998 and the Early Cretaceous sandownid *Sandownia harrisi* Meylan et al., 2000 (Hirayama 1998; Meylan et al. 2000; Joyce 2007; Mateus et al. 2009; Sterli et al. 2013; Anquetin et al. 2015). If these connections are corroborated by future work, *Thalassochelydia* may become significantly more speciose than presented herein by including species from the Cretaceous and Paleogene. As we find it undesirable to formalize a name that may eventually be shown by future work to be synonymous with the clade *Protostegidae* (sensu Cadena and Parham 2015), we here define *Thalassochelydia* to exclude the protostegid *Protostega gigas* (Cope, 1871; see Systematic Paleontology below).

Paleoecology

Thalassochelydians are generally found in marine sediments associated with abundant marine invertebrates, fishes, and reptiles, notably thalattosuchian crocodylomorphs. “Plesiochelyids” and “thalassemydids” are usually found in relatively open carbonate platform environments (Lapparent de Broin et al. 1996). Hundreds of “plesiochelyid” shells have been found in Solothurn and Porrentruy, Switzerland, but terrestrial fossils are virtually absent from these localities. These turtles have never been found as complete skeletons, but complete shells associated with partial girdles and limbs are relatively common. This suggests limited transport. Therefore, “plesiochelyids” and “thalassemydids” probably lived in these open platform environments. In contrast, “eurysternids” are typically recovered in marginal depositional environments, notably shallow lagoons (Lapparent de Broin et al. 1996). Many examples of subcomplete “eurysternids” are known from German and French plattenkalk localities. Therefore, it can be safely assumed that “eurysternids” were either coastal dwellers or inhabitants of nearby brackish marginal ecosystems (de la Fuente and Fernández 2011; Joyce 2015). The relative abundance of remains referable to *Solnhofia parsonsi* and *Eurysternum wagleri* in southern German plattenkalk localities strongly suggests that these two species at least were actually denizens of these shallow marine environments. This interpretation is apparently supported by a spectacular fossil of *Eurysternum wagleri* in which the stomach area is filled with remains of sea urchins (Joyce 2015).

The morphological evidence that thalassochelydians were adapted to marine conditions is tenuous. Shell fenestration occurs in many species, notably in “thalassemydids” and “eurysternids,” but is usually not as extensive as what can be seen in pan-chelonioids. Limbs are not modified into stiffened paddles, but the manus is somewhat elongated and indicates a good adaptation to life underwater. The large size of the foramen interorbitale, a space that accommodates hypertrophied salt glands in modern marine turtles, has been regarded as a morphological argument supporting an adaptation of thalassochelydians to marine conditions (notably in “plesiochelyids” and *Jurassichelon oleronensis*; see Billon-Bruyat et al. 2005), but this remains to be confirmed.

Billon-Bruyat et al. (2005) analyzed the oxygen isotope composition of a broad selection of thalassochelydian shell bones from the Late Jurassic of western Europe, but uncertainty remains regarding the identification of some analyzed specimens. According to these results, *Jurassichelon oleronensis* and an indeterminate “plesiochelyid” from Solnhofen are characterized by a marine isotopic signature, whereas *Eurysternum* sp. from Canjuers, *Idiochelys fitzingeri* from Cerin, and an indeterminate “thalassemydid” from Solnhofen display values indicating brackish to fresh ambient water (Billon-Bruyat et al. 2005). If these results are to be trusted, they confirm common interpretations that “plesiochelyids” were adapted to more open marine conditions, whereas “eurysternids” notably inhabited more marginal ecosystems. Shell bone histology confirms that thalassochelydians were adapted to life in the aquatic medium. These turtles retain a robust diploe and thickened external compact bone layer, which provided more bone ballast and are usually indicative of neritic forms (Scheyer et al. 2014).

Most thalassochelydians exhibit narrow to slightly broadened triturating surfaces with a high labial ridge and a well-developed rugose lingual ridge. This suggests a main reliance on shearing during food processing and an omnivorous diet possibly including small invertebrates and algae. However, several species depart from this general configuration. For example, *Portlandemys mcdowelli* has more coarsely built triturating surfaces and probably fed on tougher food items. An extensive secondary palate and broadened triturating surfaces are present in *Solnhofia parsonsi* and suggest a durophagous diet. The diverging morphologies of the triturating surfaces of thalassochelydians suggest diverging trophic specializations. Niche partitioning may therefore explain how so many species were able to coexist in the shallow seas of the Late Jurassic.

Paleobiogeography

The oldest records for *Thalassochelydia* are dated from the Oxfordian of Bavaria, Germany and Andalusia, Spain and consist of indeterminate "plesiochelyids" (Kuhn 1949; Slater et al. 2011; Pérez-García 2014). An isolated, poorly preserved costal from the Early Jurassic of Bavaria, Germany was tentatively referred to "thalassemydids" (Schleich 1984), but nothing really supports this conclusion. The Kimmeridgian and Tithonian records of thalassochelydians are more substantial and span from Switzerland, Germany, France, Portugal, Spain, the United Kingdom, Poland, and even Argentina (Figure 4). Although some localities are very productive (e.g., Solothurn and Porrentruy in Switzerland or Kelheim in Germany), material is typically scarce and incomplete in most places, which prevents confident identification and complicates detailed paleogeographical analysis. As a result, 18 out of 26 valid species of *Thalassochelydia* are for the moment known only from their type locality and nearby areas, in particular the southern Jura Mountains in France (*Achelonia formosa*, *Hydropelta meyeri*), the Hannover region of northwestern Germany (*Chelonides wittei*), the lithographic limestone quarries of southern Germany (*Eurysternum wagleri*, *Palaeomedusa testa*, *Parachelys eichstaettensis*, *Thalassemys marina*), the Kimmeridge Clay outcrops of southern England (*Craspedochelys passmorei*, *Enaliochelys chelonia*, *Pelobatochelys blakii*), the Jura Mountains of northwestern Switzerland (*Craspedochelys picteti*, *Plesiochelys bigleri*, *Portlandemys gracilis*, *Jurassichelon moseri*), the Isle of Portland in southern England (*Plesiochelys planiceps*, *Portlandemys mcdowelli*), the Isle of Oléron in western France (*Jurassichelon oleronensis*), and the Neuquén Province in Argentina (*Neusticemys neuquina*). We here recognize fragmentary material from the Kimmeridgian of Poland as representing an indeterminate "plesiochelyid," not an indeterminate helochelydrid as originally described (Borsuk-Białynicka and Młynarski 1968).

Several Kimmeridgian species of "plesiochelyids" and "thalassemydids" are known to occur in several European countries. For example, *Plesiochelys etalloni* is known from the French and Swiss Jura Mountains, northwestern Germany, and southern England (Anquetin, Deschamps and Claude 2014; Anquetin, Püntener and Billon-Bruyat 2014; Anquetin and Chapman 2016; this study). *Tropidemys langii* occurs in northwestern Switzerland and southern England, but incomplete material from northwestern Germany, southwestern France, and central Portugal is probably referable to this species as well (Püntener et al. 2014; Pérez-García 2015a; Anquetin and Chapman 2016). *Tropidemys seebachi* has a more restricted range spanning northern and southern Germany (Karl, Gröning and Brauckmann 2012; Mäuser 2014; Joyce 2015). *Craspedochelys jaccardi* is known from northwestern Switzerland, southwestern France, and possibly central Portugal (Rütimeyer 1873a; Antunes et al. 1988; Lapparent de Broin et al. 1996; Anquetin, Püntener and Billon-Bruyat 2014; this study). *Thalassemys hugii* and *Thalassemys bruntrutana* Püntener et al., 2015 are known from northwestern Switzerland and southern England, and indeterminate "thalassemydids" are also known from the Kimmeridgian of northern France and northwestern Germany (Bergounioux 1937; Pérez-García 2015c; Püntener et al. 2015). This demonstrates that several species of "plesiochelyids" and "thalassemydids" were relatively ubiquitous in western Europe during the Kimmeridgian and were able to navigate openly in the shallow epicontinental sea covering that part of the globe.

The Tithonian record of "plesiochelyids" and "thalassemydids" is more limited. Three species are known exclusively from their type locality: *Plesiochelys planiceps* and *Portlandemys mcdowelli* (Isle of Portland, southern England) and *Thalassemys marina* (Schnaitheim, southern Germany). *Craspedochelys jaccardi* is apparently present in central Portugal (Sauvage 1898; this study). And finally, *Tropidemys* sp. and *Plesiochelys* sp. are signaled in the latest Tithonian of northeastern Spain (Pérez-García et al. 2013).

Compared with "plesiochelyids" and "thalassemydids," "eurysternids" are usually characterized by a more restricted paleobiogeographical distribution, which is probably linked to the fact that they inhabited relatively confined lagoonal to brackish paleoenvironments. *Achelonia formosa* and *Hydropelta meyeri* occur only in the Kimmeridgian of Cerin, France (Thiollière 1851; Meyer 1860; Lortet 1892), whereas *Chelonides wittei* is known only based on few specimens from the Kimmeridgian of Hannover, Germany (Maack 1869; Karl et al. 2007; this study). Similarly, *Eurysternum wagleri*, *Palaeomedusa testa*, and *Parachelys eichstaettensis* appear to occur only in the Solnhofen Archipelago of southern Germany (Meyer 1839a, 1839b, 1854, 1860, 1864; Wagner 1861a; Zittel 1877a; Lydekker 1889b; Joyce 2003; Anquetin and Joyce 2014). *Eurysternum* sp. is signaled from the Tithonian of Canjuers in southeastern France, but preliminary investigations suggest that this is probably a distinct species (Broin 1994). *Solnhofia parsonsi* is known primarily based on specimens from the late Kimmeridgian and Tithonian of Bavaria (Parsons and Williams 1961; Gaffney 1975b; Joyce 2000), but this species is also mentioned in the late Kimmeridgian of Solothurn, Switzerland (Gaffney 1975b), although there are some concerns regarding this assignment (Lapparent de Broin et al. 1996). *Solnhofia* sp. is signaled in the late Kimmeridgian of southwestern

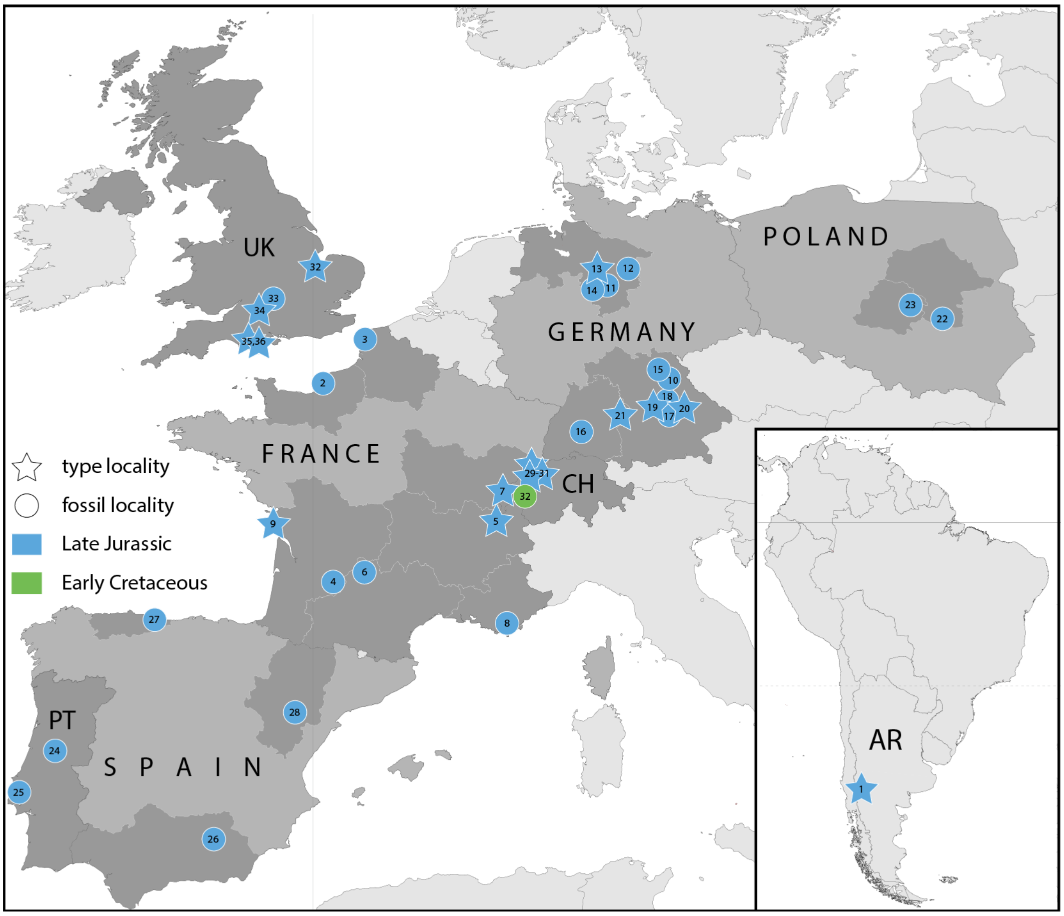

Figure 4 — The global geographic distribution of thalassochelydians in Europe (main box) and South America (inset). Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. Abbreviations: AR, Argentina; CH, Switzerland; PT, Portugal; UK, United Kingdom.

France (Lapparent de Broin et al. 1996) and in the Tithonian of Canjuers, southeastern France (Broin 1994). Finally, *Idiochelys fitzingeri* is known in the late Kimmeridgian of the southern Jura Mountains in France (Jourdan 1862; Rütimeyer 1873a; Lortet 1892) and in the early Tithonian of Bavaria (Meyer 1839a, 1839b, 1840a, 1840b, 1854, 1860; Wagner 1853, 1861b).

The most interesting paleobiogeographical fact about thalassochelydians is undoubtedly the presence of *Neusticemys neuquina*, a species possibly related to "eurysternids," in the Tithonian of Neuquén Province in central western Argentina (Fernández and de la Fuente 1988, 1993; de la Fuente and Fernández 2011). This is the only thalassochelydian known outside Europe. The best way to explain this record is to consider that some thalassochelydians took advantage of the opening of the northern and central parts of the Atlantic Ocean to travel along the coasts of North America or Africa and reach South America, crossing the so-called Hispanic Corridor (Smith 1983) into the Caribbean and making their way south along the western coast of South America. Numerous groups of invertebrates and vertebrates, including platychelyid turtles and thalattosuchian crocodylomorphs (e.g., Bardet et al. 2014; López-Conde et al. 2016), followed similar dispersal roads between the Tethys, Caribbean, and western South America.

Two "classic" thalassochelydians have been reported from the Cretaceous. The first is a small fragment of carapace referable to *Tropidemys* sp. and allegedly found in Valanginian deposits near Sainte-Croix in western Switzerland (Pictet and Campiche 1858–1860; Püntener et al. 2014). However, there are serious doubts regarding the horizon this material comes from and a Kimmeridgian age cannot be ruled out (Rittener 1902; Püntener et al. 2014). An Early Cretaceous age for this fossil must therefore be regarded as highly dubious. The second potential Cretaceous thalassochelydian consists of fragmented remains from the late Albian or early Cenomanian of Uzbekistan. Initially described as a new "thalassemydid" turtle (*Parathalassemys cava* Nessov in

Nessov and Krasovskaya, 1984), this form was more recently referred to Macrobaenidae (Sukhanov 2000). Karl, Tichy and Valdiserri (2012) defended the original identification as a "thalassemydid," but these remains do not exhibit any diagnostic characters of this group, or of *Thalassochelydia* for that matter, and should be disregarded in the future.

Systematic Paleontology

Valid Taxa

See Appendix 4 for the hierarchical taxonomy of thalassochelydians used in this work.

Thalassochelydia (new clade name)

Phylogenetic definition. The name *Thalassochelydia* is here referred to the clade that includes all turtles more closely related to *Eurysternum wagleri* Meyer, 1839c, *Plesiochelys etalloni* (Pictet and Humbert, 1857), and *Thalassemys hugii* Rütimeyer, 1873a, than to *Pelomedusa subrufa* (Bonnaterre, 1789), *Testudo graeca* Linnaeus, 1758, or *Protostega gigas* (Cope, 1871).

Diagnosis. Representatives of the *Thalassochelydia* are currently diagnosed relative to other turtles by the following derived characters: presence of a long posteroventral process of the parietal that forms the posterior margin of the foramen nervi trigemini and excludes the prootic from that foramen, and the development of a ventrally-infolding ridge on the posterior surface of the processus articularis of the quadrate. The presence of three cervical scutes is probably also a diagnostic feature of the group.

Comments. Eucryptodiran turtles from the Late Jurassic of Europe were traditionally classified in several families, in particular Eurysternidae, Plesiochelyidae, and Thalassemydidae, but we are unaware of any higher level name having been proposed to unite all into a group. We here recognize that some information is available that hints at the monophyly of these turtles and we therefore here propose a new name for that group, *Thalassochelydia*, in allusion to their predominantly marine habitat preferences. Increased taxon sampling and the development of new cranial characters recently allowed this group to be supported in a phylogenetic context (Anquetin et al. 2015). In order to avoid potential conflict with the phylogenetic definition of *Protostegidae* Cope, 1872, as recently proposed by Cadena and Parham (2015), our definition of *Thalassochelydia* specifically excludes the species *Protostega gigas* (Cope, 1871).

"Eurysternidae" Dollo, 1886

Diagnosis. "Eurysternidae" is diagnosed as part of *Thalassochelydia* by the full list of characters provided above for that clade. "Eurysternids" are currently differentiated from other thalassochelydians by being thin-shelled and small to moderately sized (carapace length 200 to 400 mm), by the presence of a ligamentous bridge and lateral plastral fontanelles, and a tendency toward the reduction of sutural contacts between the hyoplastra and the anterior plastral elements.

Comments. Since thalassochelydian relationships are still obscure, it is uncertain whether the three traditional families, "Eurysternidae," "Plesiochelyidae," and "Thalassemydidae," correspond to monophyletic groups. As these three names have practical value when it comes to discussing the great diversity of thalassochelydian species, we herein decided to continue their use but highlight their untested monophyly through the use of quotes.

Achelonia formosa Meyer, 1860

[designation of lectotype]

Taxonomic history. *Achelonia formosa* Meyer, 1860 (new species); *Eurysternum crassipes* = *Achelonia formosa* = *Acichelys redtenbacheri* (sic) = *Euryaspis radians* = *Eurysternum wagleri* = *Palaeomedusa testa* Rütimeyer 1873b (synonymy); *Acichelys redenbacheri* = *Achelonia formosa* (?) = *Euryaspis radians* (?) = *Eurysternum crassipes* = *Palaeomedusa testa* Lydekker 1889b (junior synonym); *Eurysternum crassipes* = *Achelonia formosa* Lortet 1892 (synonymy); *Eurysternum wagleri* = *Achelonia formosa* = *Acichelys redenbacheri* = *Aplax oberndorferi* = *Euryaspis radians* = *Eurysternum crassipes* = *Palaeomedusa testa* Fraas 1903 (junior synonym).

Type material. MHNL 20015606 (lectotype), a fragment of the anterior rim of a carapace plus associated partial left forelimb and skull (Meyer 1860, pl. 17.4; Lortet 1892, pl. 2.4); MHNL 20015608 (paralectotype), two isolated manus (Meyer 1860, pl. 17.5; Lortet 1892, pl. 2.6).

Type locality. Cerin, Department of Ain, France (Meyer 1860; Figure 4); Cerin Lithographic Limestones, late Kimmeridgian, Late Jurassic (Enay et al. 1994; Bernier et al. 2014).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Achelonia formosa* can be diagnosed as a "eurysternid" by moderate size and presence of a ligamentous bridge. *Achelonia formosa* can be differentiated from all other "eurysternids" by having well-developed costo-peripheral fontanelles, reduced ossification of the costal bones partly revealing the underlying thoracic ribs, insertion of thoracic rib II between peripherals III and IV, anterior contact of vertebral I with cervical scutes only, a shallow nuchal notch, and stout manual digits.

Comments. *Achelonia formosa* is based on two specimens from the late Kimmeridgian locality of Cerin, France (Meyer 1860). The first specimen (MHNL 20015606) consists of a fragment of the anterior rim of a carapace (partial nuchal, left peripherals I–III, and partial left costal I), parts of the pectoral girdle, remains of the left forelimb, and a crushed skull. The second specimen (MHNL 20015608) consists of two manus exposed in palmar view on a slab of limestone. In a relatively ambiguous statement, Meyer (1860) noted that Victor Thiollière, who communicated this material to him, declared that the two specimens were found at the same time and belonged to the same turtle. It is rather unclear, however, whether Thiollière and Meyer were suggesting that the two remains belong to the same individual or simply pertain to the same species. Rütimeyer (1873a) referred the two specimens to the same taxon, whereas Lortet (1892) clearly stated that the aspect of the sediment suggests they belong to the same animal. However, it is difficult to confirm whether or not the two specimens belong to the same individual since there is no connection between the slabs. For clarity, we designate the first specimen (MHNL 20015606) as the lectotype of *Achelonia formosa*.

Many nineteenth century authors synonymized *Achelonia formosa* with various other forms from the Tithonian of southern Germany. A comparison with *Eurysternum crassipes* (i.e., *Palaeomedusa testa*) is recurrent (e.g., Rütimeyer 1873a; Lortet 1892). The stout features of the manus, the triangular peripheral I, the rapid decrease in width of peripheral III, and the outline of vertebral I were notably mentioned as similarities between these taxa (Rütimeyer 1873a; Lortet 1892) and the lectotype was therefore considered to be a juvenile specimen of *Eurysternum crassipes* (i.e., P*alaeomedusa testa*). However, MHNL 20015606 and the holotype of *Palaeomedusa testa* (BSPG AS I 818) are about the same size (based on the size of the cranium). Additionally, in *Achelonia formosa* the nuchal notch is less developed, the ossification of costal I is much reduced, thoracic rib II inserts between peripherals III and IV (as opposed to the middle of peripheral III in *Palaeomedusa testa*), the upper temporal emargination is less developed, and the orbits are larger and located more laterally, though crushing may have distorted this aspect. All of these features therefore contradict a synonymy between *Achelonia formosa* and *Palaeomedusa testa*.

The characteristics of the lectotype are sufficient to set *Achelonia formosa* apart from other thalassochelydians and therefore support its validity. Based on the apparent presence of three cervical scutes and a ligamentous bridge, this taxon is tentatively referred to "Eurysternidae." However, this species remains poorly known and should be revised in detail.

Chelonides wittei Maack, 1869

[designation of lectotype]

Taxonomic history. *Chelonides wittei* Maack, 1869 (new species); *Chelonides wittei* = *Stylemys lindenensis* (pro parte) Portis 1878 (senior synonym); *Anaphotidemys wittei* Kuhn 1964b (new combination); *Plesiochelys solodurensis* = *Chelonides robusta* = *Chelonides wittei* = *Emys etalloni* = *Plesiochelys langii* = *Plesiochelys minor* = *Stylemys hannoverana* = *Stylonides* [sic] *lindensis* [sic] Karl et al. 2007 (synonymy).

Type material. GZG 773-1 (lectotype), a partial shell (Maack 1869, pl. 33.1, 2; Portis 1878, pl. 17.9, 10; Karl et al. 2007, pls. 2.3, 4); GZG 773-2 to GZG 773-17 (paralectotypes), including a partial skull, shell elements, and some girdle remains (Maack 1869, pl. 33.3–18; Portis 1878, pl. 17.11, 12).

Type locality. Tönniesberg (= Tönjesberg), Hannover, Lower Saxony, Germany (Figure 4); *Pteroceras* layer (= *Aporrhais* layer), middle Kimmeridgian, Late Jurassic (Maack 1869; Karl et al. 2007).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Chelonides wittei* can be diagnosed as a "eurysternid" by the full list of characters provided for that taxon above. *Chelonides wittei* differs from all other "eurysternids" in small size and in the presence of moderate keel on the posterior neurals, small costo-peripheral fontanelles, thoracic ribs that are partly apparent on the dorsal surface of the distal portions of the costal bones, wide vertebral scutes, a large and oval central plastral fontanelle, and elongated and narrow lateral plastral fontanelles.

Comments. Hay (1905) curtly stated that *Chelonides* Maack, 1869 was preoccupied and proposed *Anaphotidemys* as a replacement name, but he did not provide a citation to back up his claim. Many years later, Kuhn (1964b) clarified that *Chelonides* Maack, 1869 appears to be a junior homonym to *Chelonides* Boisduval, 1835, a work that is, however, not cited in the reference list of that paper. Our investigation revealed that *Chelonides* is actually a tribe of nocturnal lepidopterans established by Boisduval in 1840 (Boisduval 1840; Orbigny 1843). Given that the ICZN (1999) only recognizes homonymy within the family group or genus group, we see no case of homonymy and therefore also no need for a replacement name. *Anaphotidemys* Hay, 1905 must therefore be considered a junior synonym of *Chelonides* Maack, 1869.

Chelonides wittei is based on a series of specimens, in particular a partial shell (GZG 773-1), a partial skull (GZG 773-2), and several isolated shell and girdle elements. The full type series is illustrated in Maack (1869, pl. 33.1–18) and referenced in Karl et al. (2007). The partial shell GZG 773-1 was designated as "Hauptvertreter" (main representative) of the species by Maack (1869). This led Karl et al. (2007) to refer to this specimen as the holotype, but this designation is incorrect with regard to current rules of zoological nomenclature (ICZN 1999, art. 74). We here formally designate GZG 773-1 as the lectotype of *Chelonides wittei*. As a result, this specimen now serves as the sole bearer of the name, regardless of the nomenclatural interpretation being applied.

Without diagnostic evidence, Portis (1878) referred additional specimens from northern Germany to *Chelonides wittei*, including some specimens previously referred to *Stylemys lindenensis* and *Stylemys hannoverana* by Maack (1869). According to Karl et al. (2007), all of the specimens mentioned above should be referred to *Plesiochelys solodurensis*, but these authors failed to provide detailed justification for this referral. We find that the paralectotypes and the specimens referred by Portis (1878) are in need of reevaluation. However, the lectotype (GZG 773-1) is clearly different from *Plesiochelys etalloni* and other Late Jurassic forms, justifying the validity of *Chelonides wittei*. Based on the small size of the specimen (carapace length of about 20 cm), the very wide vertebral scutes, the presence of lateral plastral fontanelles, and the ligamentous bridge with peg-like projections, we tentatively refer *Chelonides wittei* to "Eurysternidae." This species differs from other "eurysternids" based on several characteristics of the shell (see diagnosis), including the presence of a moderate keel on the posterior neurals.

Eurysternum wagleri **Meyer, 1839c**

(= *Acichelys redenbacheri* Meyer, 1854)

Taxonomic history. *Clemmys*? *wagleri* Fitzinger 1835 (nomen nudum); *Erysternum* (sic) *wagleri* Meyer 1839a (nomen nudum); *Eurysternum wagleri* Meyer, 1839c (new species); *Eurysternum crassipes* = *Achelonia formosa* = *Acichelys redtenbacheri* (sic) = *Euryaspis radians* = *Eurysternum wagleri* = *Palaeomedusa testa* Rütimeyer 1873b (synonymy); *Eurysternum wagleri* = *Achelonia formosa* = *Acichelys redenbacheri* = *Aplax oberndorferi* = *Euryaspis radians* = *Eurysternum crassipes* = *Palaeomedusa testa* = *Parachelys eichstaettensis* Zittel 1877a (senior synonym); *Eurysternum wagleri* = *Eurysternum crassipes* = *Parachelys eichstaettensis* = *Hydropelta meyeri* Oertel 1915 (senior synonym); *Eurysternum wagleri* = *Acichelys redenbacheri* Anquetin and Joyce 2014 (senior synonym).

Type material. BSPG uncat. (holotype), a partial shell with associated remains of the girdles, limbs, cervical vertebrae, and mandible (Meyer 1839a, no plate number; Anquetin and Joyce 2014, fig. 1), now considered lost (Anquetin and Joyce 2014).

Type locality. Solnhofen, Bavaria, Germany (Meyer 1839a, 1839c; Figure 4); Solnhofen Formation, early Tithonian, Late Jurassic (Schweigert 2007).

Referred material and range. Late Jurassic (early Tithonian) of Denkendorf/Zandt and Solnhofen, Bavaria, Germany (including the lectotype of *Acichelys redenbacheri* Meyer 1854, see Anquetin and Joyce 2014).

Diagnosis. *Eurysternum wagleri* can be diagnosed as a "eurysternid" by the full list of characters provided for this taxon above. *Eurysternum wagleri* differs from all other "eurysternids" by having a pentagonal carapace outline with its greatest width at the level of peripherals VII–VIII and a slightly concave margin between peripherals VIII–XI, a broad trapezoidal nuchal forming a wide nuchal notch, a wide median cervical scute, retention of developed costo-peripheral fontanelles in medium-sized individuals (closed or greatly reduced in adults), a deep pygal notch, a well-developed radiating pattern on vertebrals II–IV, a contribution of vertebral V to the posterior carapace margin, and a wider than long central plastral fontanelle.

Comments. *Eurysternum wagleri* is based on a disarticulated, partial skeleton preserved in ventral view on a slab of limestone that Meyer (1839c) described based on its illustration only. The holotype was originally in possession of George Graf zu Münster of Bayreuth, Germany (Meyer 1839a, 1839c), but was later transferred to Munich (Wagner 1853, 1861b) where it was studied by many individuals (e.g., Maack 1869; Rütimeyer 1873a; Zittel 1877a; Oertel 1915). The holotype is currently missing from the BSPG and is therefore considered lost (Anquetin and Joyce 2014). A poorly crafted cast of this specimen is nevertheless available at the Sedgwick Museum in Cambridge, United Kingdom (Joyce 2003).

The configuration of the holotype reveals relatively little about the anatomy of *Eurysternum wagleri*, with the exception of the presence of a deep pygal notch (Anquetin and Joyce 2014). This probably explains why *Eurysternum wagleri* was synonymized with so many contemporaneous species from the German and French lithographic limestones, most of which are based on fragmentary remains as well. A persistent idea that lasted from Rütimeyer (1873a) to Lapparent de Broin et al. (1996) was that *Eurysternum wagleri* represented the juvenile stage in a growth series ranging from *Aplax oberndorferi* (hatchling) to *Palaeomedusa testa* and *Acichelys redenbacheri* (adults), among others. Joyce (2003) more recently described a subcomplete specimen of *Palaeomedusa testa* (see below) that clearly refutes a synonymy with *Eurysternum wagleri*. Many of the other taxa from this purported ontogenetic series, on the other hand, are too incomplete to allow rigorous assessment (see Invalid and Problematic Taxa below). We therefore here agree with Anquetin and Joyce (2014) that *Eurysternum wagleri* can only be synonymized with *Acichelys redenbacheri*, as these are the only taxa that clearly display the diagnostic pygal notch typical of this taxon.

***Hydropelta meyeri* (Thiollière, 1851)**

Taxonomic history. *Chelone*? *meyeri* Thiollière, 1851 (new species); *Hydropelta meyeri* Meyer 1860 (new combination); *Eurysternum wagleri* = *Eurysternum crassipes* = *Hydropelta meyeri* = *Parachelys eichstaettensis* Oertel 1915 (junior synonym); *Eurysternum* (*Hydropelta*?) *meyeri* Kuhn 1964b (new combination); *Eurysternum wagleri* = *Achelonia formosa* = *Acichelys redtenbacheri* [sic] = *Acrochelys* [sic] *approximata* = *Acrochelys* [sic] *redenbacheri* = *Aplax oberndorferi* = *Changisaurus microrhinus* = *Chelone planiceps* = *Euryaspis radians* = *Euryaspis approximata* = *Eurysternum crassipes* = *Eurysternum ignoratum* = *Palaeomedusa testa* Karl, Tichy and Valdiserri 2012 (junior synonym).

Type material. MHNL 20015611 (holotype), a partial shell (Thiollière 1851; Meyer 1860, pl. 16.9; Lortet 1892, pl. 2.3).

Type locality. Cerin, Department of Ain, France (Thiollière 1851; Figure 4); Cerin Lithographic Limestone Formation, late Kimmeridgian, Late Jurassic (Enay et al. 1994; Bernier et al. 2014).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Hydropelta meyeri* can be diagnosed as a “eurysternid” by the full list of characters provided for that taxon above. *Hydropelta meyeri* differs from all other “eurysternids” by the presence of relatively well-developed costo-peripheral fontanelles, an elongated and pointed anterior plastral lobe, a long posterior entoplastral process, and a large lateral plastral fontanelle.

Comments. *Hydropelta meyeri* is based on a relatively incomplete shell from the late Kimmeridgian lithographic limestones of Cerin, France (Thiollière 1851). The specimen consists of the partial right side of a shell preserved in ventral view and still embedded in a slab of limestone. It was initially misinterpreted as the left side of a shell (Thiollière 1851; Meyer 1860), but Lortet (1892) rectified this error and produced a very nice illustration of the specimen. Oertel (1915) considered *Hydropelta meyeri* to be a junior subjective synonym of *Eurysternum wagleri*, an opinion that was recently supported by Karl, Tichy and Valdiserri (2012). Lapparent de Broin et al. (1996) also suggested a possible synonymy of *Hydropelta meyeri* with *Solnhofia parsonsi*. The latter hypothesis can be safely rejected based on the presence of large costo-peripheral fontanelles and the presence of an extensive fenestration of the plastron in the holotype of *Hydropelta meyeri*, whereas specimens of *Solnhofia parsonsi* of comparable size are characterized by closed, or almost closed, carapacial fontanelles and a reduced plastral fenestration (Joyce 2000). A synonymy with *Eurysternum wagleri* can also be rejected based on plastral morphology, as the hyoplastra of *Hydropelta meyeri* are long and thin anteromedially and form an elongated and pointed anterior plastral lobe (Lortet 1892). The anterior plastral lobe of *Eurysternum wagleri* is shorter and less pointed anteriorly, as in all other known Late Jurassic turtles, and is characterized by the presence of a hyoplastral fontanelle.

The anterior plastral morphology of *Hydropelta meyeri* sets this taxon apart from other Late Jurassic turtles known in Europe and supports its validity. However, the morphology of this taxon remains otherwise poorly known, as it is only represented by the type specimen.

***Idiochelys fitzingeri* Meyer, 1839b**

(= *Idiochelys wagneri* Meyer, 1840b = *Chelonemys plana*
Jourdan, 1862 = *Chelonemys ovata* Jourdan, 1862)

Taxonomic history. *Idiochelys fitzingeri* Meyer 1839a (nomen nudum); *Idiochelys fitzingeri* Meyer, 1839b (new species); *Idiochelys fitzingeri* = *Idiochelys wagneri* Wagner 1853 (senior synonym); *Idiochelys fitzingeri* = *Idiochelys wagneri* = *Aplax oberndorferi* Wagner 1861b (senior synonym); *Idiochelys fitzingeri* = *Idiochelys wagnerorum* = *Chelonemys plana* = *Chelonemys ovata* Rütimeyer 1873b

Chelonemys plana = *Chelonemys ovata* Rütimeyer 1873b (senior synonym).

Type material. BSPG uncat. (holotype), the posterior half of a shell with articulated hind limbs and tail (Meyer 1839b, pl. 7.1; Meyer 1860, pl. 17.2), now considered lost (see below).

Type locality. Kelheim, Bavaria, Germany (Meyer 1839a, 1839b; Figure 4); Solnhofen Formation, early Tithonian, Late Jurassic (Schweigert 2007).

Referred material and range. Late Jurassic (late Kimmeridgian) of Cerin, Department of Ain, France (holotypes of *Chelonemys plana* Jourdan, 1862 and *Chelonemys ovata* Jourdan, 1862, referred specimens of Rütimeyer 1873a and Lortet 1892).

Diagnosis. *Idiochelys fitzingeri* can be diagnosed as a "eurysternid" by the full list of characters provided for that taxon above. *Idiochelys fitzingeri* differs from all other "eurysternids" in the presence of an oval to rounded carapace, a broad nuchal that forms a deep and narrow nuchal notch, a reduction of the neural series, the retention of moderate costo-peripheral fontanelles, a shallow pygal notch, wide vertebrals, sutural contact of the hypoplastra with the anterior plastral elements in adults, a slightly wider than long hyoplastron, a central plastral fontanelle that is wider than long in juveniles and absent in adults, xiphiplastra about as wide as long, a reduced manual phalangeal formula (2-2-3-3-3), and a long tail.

Comments. *Idiochelys fitzingeri* is based on a single, incomplete specimen described from the lithographic limestone quarries of Kelheim, Germany (Meyer 1839b). The holotype of *Idiochelys fitzingeri* originally belonged to George Graf zu Münster of Bayreuth, Germany (Meyer 1839b) but was later transferred to Munich (Wagner 1853), where it was studied by Maack (1869), Rütimeyer (1873a), Zittel (1877a), and Oertel (1915). This specimen is missing from the BSPG collections and must be considered lost. Primarily because of a single highly diagnostic character, the reduction of the neurals, the validity of this taxon has never been questioned. In the past, three taxa from the Late Jurassic of Europe have been synonymized with *Idiochelys fitzingeri*: *Idiochelys wagneri* from Kelheim, Germany as proposed by Wagner (1853) and *Chelonemys plana* and *Chelonemys ovata* from Cerin, France as proposed by Rütimeyer (1873a, 1873b). Although variation is apparent between all these attributed specimens, especially in the number of neurals, none of this variation appears to be systematic, thus justifying the inclusion of all specimens into the same taxon. Unfortunately, both the holotypes of *Idiochelys fitzingeri* and *Idiochelys wagneri* are lost, and, although at least three additional specimens referable to *Idiochelys fitzingeri* were found in the lithographic limestone quarries of Kelheim during the 1840s to 1870s (Meyer 1854, 1861; Rütimeyer 1873a), they were housed in Munich too and did not outlast World War II either. Interestingly, although so many specimens were found in so little time during the nineteenth century in the Kelheim quarries, none have been found since that could be attributed to this taxon. Although the designation of a neotype is currently not necessary, it would also be impossible because no material exists from the type section. The validity of this taxon is nevertheless uncontroversial.

Palaeomedusa testa **Meyer, 1860**

(= *Eurysternum crassipes* Wagner, 1861a)

Taxonomic history. *Palaeomedusa testa* Meyer, 1860 (new species); *Eurysternum crassipes* = *Palaeomedusa testa* Wagner 1861a (objective synonymy); *Eurysternum crassipes* = *Palaeomedusa testa* = *Acichelys redenbacheri* Wagner 1861b (objective and subjective synonymy, respectively); *Palaeomedusa testa* = *Eurysternum crassipes* Meyer 1861 (senior objective synonym); E*urysternum crassipes* = *Achelonia formosa* = *Acichelys redtenbacheri* (sic) = *Euryaspis radians* = *Eurysternum wagleri* = *Palaeomedusa testa* Rütimeyer 1873b (synonymy); *Eurysternum wagleri* = *Achelonia formosa* = *Acichelys redenbacheri* = *Aplax oberndorferi* = *Euryaspis radians* = *Eurysternum crassipes* = *Palaeomedusa testa* = *Parachelys eichstättensis* Zittel 1877a (junior synonym); *Acichelys redenbacheri* = *Achelonia formosa* (?) = *Euryaspis radians* (?) = *Eurysternum crassipes* = *Palaeomedusa testa* Lydekker 1889b (junior synonym); *Palaeomedusa testa* = *Eurysternum crassipes* = *Thalassemys marina* Joyce 2003 (senior synonym).

Type material. BSPG AS I 818 (holotype), partial anterior half of a carapace with skull, articulated cervical series, and complete right and partial left forelimbs (Meyer 1860, pl. 20.1).

Type locality. Kelheim, Bavaria, Germany (Meyer 1860; Figure 4); Solnhofen Formation, early Tithonian, Late Jurassic (Schweigert 2007).

Referred material and range. Late Jurassic (early Tithonian) of Solnhofen, Bavaria, Germany (Joyce 2003).

Diagnosis. *Palaeomedusa testa* can be diagnosed as a "eurysternid" by moderate size and the presence of a ligamentous bridge and lateral plastral fontanelles. *Palaeomedusa testa* differs from all other "eurysternids" by having an oval carapace that is narrow anteriorly, reduced to absent costo-peripheral fontanelles, an anteriorly narrow vertebral I that only contacts the cervicals anteriorly, a shallow nuchal notch, and stout manual digits.

Comments. *Palaeomedusa testa* and *Eurysternum crassipes* are based on the same type specimen and, consequently, are objective synonyms with *Palaeomedusa testa* having seniority (see *Eurysternum crassipes* below). According to Meyer (1860) and Wagner (1861b), this fossil originally belonged to Dr Oberndorfer of Kelheim, Germany, but it was later transferred to the collections in Munich (Zittel 1877a). This is one of the few fossil turtles that survived the effects of World War II. Primarily because of the great influence of Zittel's (1877a) work, this taxon was considered a junior synonym of *Eurysternum wagleri* by most authors and was ignored from taxonomic considerations. Unfortunately, the holotype of *Palaeomedusa testa* consists of an anterior half of a carapace, whereas the most diagnostic traits of *Eurysternum wagleri* are seen in the posterior region. Thus, an objective review of this synonymy long remained difficult. More recently, Joyce (2003) noted a new, complete specimen (MNB R 2894) that overlapped in its anterior carapacial morphology that of the holotype of *Palaeomedusa testa*, but clearly lacked the deep pygal notch of *Eurysternum wagleri*. Since then, the taxon *Eurysternum wagleri* was also revised, which allowed clearer differentiation of the two taxa (Anquetin and Joyce 2014). *Palaeomedusa testa* must thus be considered a valid name. In contrast to Joyce (2003), we refute a synonymy between *Palaeomedusa testa* and *Thalassemys marina* (see below).

Parachelys eichstaettensis Meyer, 1864

Taxonomic history. *Parachelys eichstaettensis* Meyer, 1864 (new species); *Eurysternum wagleri = Achelonia formosa = Acichelys redenbacheri = Aplax oberndorferi = Euryaspis radians = Eurysternum crassipes = Palaeomedusa testa = Parachelys eichstaettensis* Zittel 1877a (junior synonym); *Parachelys eichstaedtensis* Lydekker 1889b (incorrect spelling); *Eurysternum wagleri = Eurysternum crassipes = Hydropelta meyeri = Parachelys eichstaettensis* Oertel 1915 (junior synonym).

Type material. NHMUK OR42888 (holotype), shell fragments, subcomplete right manus, right scapula, coracoid, and humerus (Meyer 1864, pl. 45.1–6), as well as a crushed skull and a complete series of cervical vertebrae (yet undescribed, see below).

Type locality. Eichstätt, Bavaria, Germany (Meyer 1864; Figure 4); Solnhofen Formation, early Tithonian, Late Jurassic (Schweigert 2007).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Parachelys eichstaettensis* can be diagnosed as a "eurysternid" by the presence of a notably thin shell. *Parachelys eichstaettensis* differs from all other "eurysternids" in the reduction of costo-peripheral fontanelles, anterolateral contact of vertebral I with marginal I only, and a reduced manual phalangeal formula (2-2-3-3-3).

Comments. The holotype of *Parachelys eichstaettensis* originally belonged to Dr Krantz of Bonn, Germany (Meyer 1864). In 1871, the specimen was purchased by the British Museum as part of the Van Breda Collection (Lydekker 1889b). The original description of Meyer (1864) is based on limited postcranial material of a single individual: some shell fragments, a subcomplete right manus, and the right scapula, coracoid, and humerus. Acetic acid preparation of the holotype in the 1950s revealed additional material, especially a crushed skull and a complete series of cervical vertebrae. As of today, this new material remains undescribed.

Meyer (1864) diagnosed *Parachelys eichstaettensis* mostly based on the presence of the unique manual phalangeal formula of 2-2-3-3-3. The plesiomorphic phalangeal formula for crown turtles is probably 2-3-3-3-3 for both manus and pes (Sánchez-Villagra et al. 2007; Delfino et al. 2010). Although the phalangeal formula can be used to diagnose taxa, studies on recent species have shown that significant amounts of variation exist (e.g., Minx 1992; Delfino et al. 2010). The same reduced manual phalangeal formula of 2-2-3-3-3 is also present in two specimens from the late Kimmeridgian locality of Cerin, France now referred to *Idiochelys fitzingeri* (Rütimeyer 1873a, pl. 15). However, what is known of the carapace of *Parachelys eichstaettensis*, notably the fact that vertebral I is reduced in width and contacts only marginal I anterolaterally, clearly distinguishes this taxon from *Idiochelys fitzingeri*, as already noted by Lydekker (1889b). We therefore herein consider *Parachelys eichstaettensis* to be valid.

Solnhofia parsonsi Gaffney, 1975b

Taxonomic history. *Solnhofia parsonsi* Gaffney, 1975b (new species).

Type material. TM 4023 (holotype), a partially damaged skull with lower jaw (Parsons and Williams 1961, figs. 2, 7, Type material. TM 4023 (holotype), a partially damaged skull with lower jaw (Parsons and Williams 1961, figs. 2, 7, 10, 11, pl. 4; Gaffney 1975b, figs. 2, 4, 7–16).

Type locality. Solnhofen Region, Bavaria, Germany (Figure 4); horizon unknown, most likely Solnhofen Formation, early Tithonian, Late Jurassic (Regteren-Altena 1967; Gaffney 1975b).

Referred material and range. Late Jurassic (late Kimmeridgian) of Solothurn, Canton of Solothurn, Switzerland (Gaffney 1975b); Late Jurassic (Kimmeridgian/Tithonian) of Schamhaupten, Bavaria, Germany (Joyce 2000).

Diagnosis. *Solnhofia parsonsi* can be diagnosed as a “eurysternid” by the full list of characters provided for this taxon above. *Solnhofia parsonsi* differs from all other “eurysternids” by having an enlarged skull (40% of carapace length), an elongated snout, a complete secondary palate, limited temporal emargination, a smooth triturating surface, absence of a lingual ridge, reduction of the foramen palatinum posterius, massive processi trochlearis oticum that obscure the foramen nervi trigemini in lateral view, a common opening for the foramina anterius canalis carotici cerebralis, an elongate mandibular symphysis, low but short labial ridges on the mandible, a pentagonal carapace with its greatest width at peripheral VII, a broad nuchal that forms a wide nuchal notch, reduced costo-peripheral fontanelles, an evenly rounded posterior margin of the carapace, broad posterior peripherals, a large pygal, wide vertebral scutes, hyoplastra and xiphiplastra that are about as wide as long, semilunate lateral plastral fontanelles, and an oval central plastral fontanelle.

Comments. *Solnhofia parsonsi* is one of the few Late Jurassic turtles from Europe to be based on a skull only (Gaffney 1975b). However, the description of a complete specimen from Schamhaupten, Germany revealed that this taxon is indeed distinct from all other taxa based on shell characters as well (Joyce 2000). According to Lapparent de Broin et al. (1996), the referred skull from Solothurn, Switzerland should be excluded from *Solnhofia parsonsi* and placed in its own species, notably, because the snout appears to be much shorter in this specimen. For Gaffney (1975b), this difference is the result of the deformation that affected the Solothurn skull during fossilization. For the moment, no evidence allows us to give more credit to one interpretation over the other. For the sake of simplicity, we maintain the status quo.

Broin (1994) and Lapparent de Broin et al. (1996) tentatively associated several specimens from the Late Jurassic of France with *Solnhofia parsonsi*. Given that these specimens demand more preparation and further study, we here await a more detailed description to evaluate this claim but confirm the general affinity of this material with *Solnhofia parsonsi*.

“Plesiochelyidae” Baur, 1888

Diagnosis. “Plesiochelyidae” is diagnosed as part of *Thalassochelydia* by the full list of characters provided above for that clade. “Plesiochelyids” are primarily differentiated from all other thalassochelydians by the presence of a high dorsum sellae that does not overhang the sellae turcica, the placement of the foramina anterius canalis carotici cerebralis more anterior than the level of the dorsum sellae, the exclusion of the epipterygoid from the anterior margin of the foramen nervi trigemini (also in *Jurassichelon oleronensis*), a relatively large size (carapace length 400–550 mm), the lack of carapacial fontanelles in adults, an osseous bridge, and, at most, a central plastral fontanelle.

Comments. Among the three family names traditionally used for grouping species within *Thalassochelydia*, “Plesiochelyidae” is the only one for which several derived cranial characters potentially support the monophyly (Anquetin et al. 2015). We nevertheless highlight this name with quotation marks to emphasize that monophyly needs to be further tested in a global phylogenetic context.

Craspedochelys Rütimeyer, 1873a

Type species. *Craspedochelys* picteti Rütimeyer, 1873a.

Diagnosis. *Craspedochelys* can be diagnosed as a “plesiochelyid” by the full list of shell characters provided for that taxon above. *Craspedochelys* is currently differentiated from *Plesiochelys* by the development of a broader and more rounded carapace (usually as wide as long), a shallower nuchal notch (except in *Craspedochelys passmorei*), a higher length/width ratio of the costal bones (4.3–4.8 or more, as opposed to 3.1–3.6 for costal IV), a relatively shorter plastron (incompletely known in *Craspedochelys picteti*), and a proportionally wider hyoplastron. It differs from *Tropidemys* by the absence of a neural keel, elongated neural bones, and wider vertebral scutes.

Comments. *Craspedochelys* is a problematic genus. First, its type species, *Craspedochelys picteti*, is based on a fragmentary shell. Second, the main differences between *Craspedochelys* and *Plesiochelys* are relatively tenuous, being mostly related to shell shape. Gaffney (1975a) seriously questioned these supposed differences and argued that most of them could be explained by individual variations or postmortem compression. Antunes et al. (1988), followed by Lapparent de Broin et al. (1996), reaffirmed the validity of *Craspedochelys*, but most of their arguments where once again based on general shell shape. The arguments of Gaffney (1975a), Antunes et al. (1988), and Lapparent de Broin et al. (1996) were recently reassessed and confronted the available material (Anquetin, Püntener and Billon-Bruyat 2014). This study confirmed most of the conclusions of Lapparent de Broin et al. (1996) and proposed new quantitative characters to separate *Craspedochelys* from *Plesiochelys* (length/width ratio of costal bones and plastral proportions).

Craspedochelys jaccardi **(Pictet, 1860)**

(= *Plesiochelys choffati* Sauvage, 1898)

Taxonomic history. *Emys jaccardi* Pictet, 1860 (new species); *Plesiochelys jaccardi* Rütimeyer 1873a (new combination); *Plesiochelys etalloni* = C*raspedochelys crassa* = *Craspedochelys picteti* = *Plesiochelys jaccardi* = *Plesiochelys sanctaeverenae* = *Plesiochelys solodurensis* = *Stylemys lindensis* [sic] Gaffney 1975a (junior synonym); *Craspedochelys jaccardi* = *Craspedochelys picteti* Antunes et al. 1988 (new combination and senior synonym); *Craspedochelys jaccardi* = *Plesiochelys solodurensis* var. *langenbergensis* Karl et al. 2007 (senior synonym).

Type material. MHNN FOS 977 (holotype), a complete shell (Pictet 1860, pls. 1–3; Lapparent de Broin et al. 1996, pl. 4; Anquetin, Püntener and Billon-Bruyat 2014, fig. 4).

Type locality. Les Hauts-Geneveys, Canton of Neuchâtel, Switzerland (Jaccard 1860; Ayer 1997; Figure 4); "Virgulien supérieur," possibly corresponding to the early Tithonian, Late Jurassic (Jaccard 1860; Lapparent de Broin et al. 1996).

Referred material and range. Late Jurassic (late Kimmeridgian) of Solothurn, Canton of Solothurn, Switzerland (hypodigm of *Plesiochelys jaccardi* by Bräm 1965); Late Jurassic (Kimmeridgian) of Lamothe-Cassel, Lot, France (Lapparent de Broin et al. 1996); Late Jurassic (Tithonian) of Vila Franca do Rosário, Lisbon District, Portugal (holotype of *Plesiochelys choffati* Sauvage, 1898).

Diagnosis. *Craspedochelys jaccardi* is diagnosed as a "plesiochelyid" and a representative of *Craspedochelys* by the full list of shell characters provided for those taxa above. *Craspedochelys jaccardi* differs from all other *Craspedochelys* by having a more rounded carapace with its greatest width at the level of peripheral VII, a higher length/width ratio of the costal bones (4.8 or more, as opposed to around 4.3 for costal IV). In addition, *Craspedochelys jaccardi* differs from *Craspedochelys picteti* by being smaller in size (carapace length 420 mm) and by having an evenly rounded anterior carapacial rim, a contact between costal VIII and peripheral XI present, a wider than long pygal bone, and wider than long hyoplastra and differs from *Craspedochelys passmorei* by having a shallower nuchal notch, epiplastra that reach the lateral margin of the anterior plastral lobe, and a shorter posterior plastral lobe.

Comments. *Craspedochelys jaccardi* is based on a complete shell from the Late Jurassic, possibly early Tithonian, of Les Hauts-Geneveys, Switzerland (Pictet 1860). Since Rütimeyer (1873a), this species was referred to the genus *Plesiochelys*, but Antunes et al. (1988) referred this species to the genus *Craspedochelys*. Although Gaffney (1975a) synonymized this species with *Plesiochelys etalloni*, *Craspedochelys jaccardi* is clearly differentiated from other "plesiochelyids," notably, by a broad, almost rounded carapace and a plastron significantly reduced in length (Anquetin, Püntener and Billon-Bruyat 2014).

Several specimens from the Kimmeridgian of Solothurn, Switzerland, have been referred to *Craspedochelys jaccardi* (Rütimeyer 1873a; Bräm 1965). Although the similarities between these and the holotype of *Craspedochelys jaccardi* are obvious, a few apparent differences (pattern of vertebral scutes, shorter plastron) might warrant a different species for the Solothurn specimens (Anquetin, Püntener and Billon-Bruyat 2014). Lapparent de Broin et al. (1996) similarly described several specimens from the Kimmeridgian and Tithonian of Lot, France that they related to *Craspedochelys jaccardi* or *Craspedochelys* sp., but this material should be reevaluated. At the very least, the specimen described as "*Craspedochelys jaccardi* forme b" (MNHN coll. Dutrieux 2D) corresponds to our concept of C*raspedochelys jaccardi*. The holotype of *Plesiochelys choffati* (MG-LNEG 28) is herein interpreted as a juvenile individual of *Craspedochelys jaccardi* (see below). Finally, the specimen described by Antunes et al. (1988) as *Craspedochelys* cf. *jaccardi* is provisionally considered herein as *Craspedochelys* sp. pending revision.

Craspedochelys passmorei **(Andrews, 1921)**

Taxonomic history. *Tholemys passmorei* Andrews, 1921 (new species); *Plesiochelys passmorei* Kuhn 1964b (new combination).

Type material. NHMUK R5871 (holotype), subcomplete shell with associated postcranial remains, including parts of the girdles, the left humerus, and partial cervical vertebrae (Andrews 1921, figs. 1–3).

Type locality. Swindon, Wiltshire, United Kingdom (Figure 4); Kimmeridge Clay, Kimmeridgian, Late Jurassic (Andrews 1921; Benton and Spencer 1995).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Craspedochelys passmorei* can be diagnosed as a “plesiochelyid” and a representative of *Craspedochelys* by the full list of shell characters provided for those taxa above. *Craspedochelys passmorei* differs from all other *Craspedochelys* by having a hexagonal carapace, with its greatest width between peripherals IV and VII, and a deeper nuchal notch. In addition, *Craspedochelys passmorei* differs from *Craspedochelys jaccardi* by having a lower length/width ratio of the costal bones (around 4.3, as opposed to 4.8 or more for costal IV), reduced epiplastra that do not reach the lateral margin of the anterior plastral lobe, and a longer posterior plastral lobe. It differs from *Craspedochelys picteti* by being smaller in size and by having a less quadrangular anterior carapace, a contact between costal VIII and peripheral XI, a wider than long pygal bone, and wider than long hyoplastra.

Comments. *Craspedochelys passmorei* is based on a single, subcomplete shell from the Kimmeridge Clay of Swindon, United Kingdom (Andrews 1921). Most authors referred this taxon to the “Plesiochelyidae” (Andrews 1921; Kuhn 1964b; Lapparent de Broin et al. 1996; Lapparent de Broin 2001) and Kuhn (1964b) even proposed the new combination *Plesiochelys passmorei*. In contrast, Andrews (1921) and Lapparent de Broin et al. (1996) noted that this form was closer to *Craspedochelys* than *Plesiochelys*. The broad carapace, the length/width ratio of costal IV (4.34), and the proportions of the hyoplastron indeed recall what is known in *Craspedochelys* (sensu Anquetin, Püntener and Billon-Bruyat 2014), which is why we refer this taxon to this genus herein. *Craspedochelys passmorei* is notably characterized by a broad, sub-pentagonal carapace, a shallow, but wide nuchal notch, a broad, short anterior plastral lobe, and an epi-hyoplastral suture strongly concave anteriorly. For the time being, *Craspedochelys passmorei* is only known from the Kimmeridge Clay of Swindon, United Kingdom.

Craspedochelys picteti Rütimeyer, 1873a

(= *Craspedochelys crassa* Rütimeyer, 1873a)

Taxonomic history. *Craspedochelys picteti* Rütimeyer, 1873a (new species); *Craspedochelys picteti* = *Craspedochelys crassa* Bräm 1965 (senior synonym); *Plesiochelys etalloni* = *Craspedochelys crassa* = *Craspedochelys picteti* = *Plesiochelys jaccardi* = *Plesiochelys sanctaeverenae* = *Plesiochelys solodurensis* = *Stylemys lindensis* [sic] Gaffney 1975a (junior synonym); *Craspedochelys jaccardi* = *Craspedochelys picteti* Antunes et al. 1988 (junior synonym).

Type material. NMS 8510 (holotype; formerly NMS 129), left anterior portion of a shell with poorly preserved plastron (Rütimeyer 1873a, pl. 5.1; Anquetin, Püntener and Billon-Bruyat 2014, fig. 3).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Referred material and range. Late Jurassic (late Kimmeridgian) of Solothurn, Canton of Solothurn, Switzerland (hypodigm of Bräm 1965).

Diagnosis. *Craspedochelys picteti* can be diagnosed as a “plesiochelyid” and a representative of *Craspedochelys* by the full list of shell characters provided for those taxa above. *Craspedochelys picteti* differs from all other *Craspedochelys* by having a carapace with a heraldic shield shape, a greater size (up to 550 mm), a reduced or absent contact between costal VIII and peripheral XI, and a smaller and narrower pygal bone. *Craspedochelys picteti* further differs from *Craspedochelys jaccardi* by having a lower length/width ratio of the costal bones (around 4.3, as opposed to 4.8 or more for costal IV), and slightly longer than wide hyoplastra.

Comments. *Craspedochelys picteti* is based on an incomplete, anterior portion of a shell from the Kimmeridgian Solothurn Turtle Limestone, Switzerland (Rütimeyer 1873a; Bräm 1965). As demonstrated by a relatively complete carapace from the same locality, this taxon is characterized by a carapace with the shape of a heraldic shield, which is unique among Late Jurassic European turtles (Bräm 1965; Anquetin, Püntener and Billon-Bruyat 2014). The validity of this species has been questioned several times. Gaffney (1975a) first tentatively synonymized *Craspedochelys picteti* with *Plesiochelys etalloni*, explaining morphological discrepancies by postmortem deformation and individual variation. Antunes et al. (1988) rejected the conclusions of Gaffney (1975a) and proposed instead to synonymize *Craspedochelys picteti* with *Craspedochelys jaccardi*, although they did not revise the material firsthand. Describing new material from the Late Jurassic of France, Lapparent de Broin et al. (1996) partially revised some of the Solothurn specimens and reestablished *Craspedochelys picteti* and *Craspedochelys jaccardi* as distinct taxa, which they differentiated mainly based on size criteria. Only recently was the Solothurn material thoroughly revised and the validity of *Craspedochelys picteti* supported by renewed character observations (Anquetin, Püntener and Billon-Bruyat 2014).

Strangely, *Craspedochelys picteti* has never been reported from elsewhere than Solothurn, where it is known only by a handful of specimens. Anquetin, Püntener and Billon-Bruyat (2014) were able to show that *Craspedochelys picteti* is differentiated from both *Craspedochelys jaccardi* and *Plesiochelys etalloni* based on morphological and morphometric characters. However, *Craspedochelys picteti* and *Craspedochelys jaccardi* exhibit the same tendency toward a broader shell. One possibility to explain the relative rarity of *Craspedochelys picteti* would be that the few Solothurn specimens referred to this species are actually sexual morphs of *Craspedochelys jaccardi*. Sexual dimorphism may be very pronounced in some extant turtles (Pritchard 2008). New material would be necessary to test this hypothesis.

Plesiochelys Rütimeyer, 1873a

Type species. *Plesiochelys solodurensis* Rütimeyer, 1873a.

Diagnosis. *Plesiochelys* can be diagnosed as a “plesiochelyid” by the full list of characters provided above for that group. Based on cranial anatomy, *Plesiochelys* is currently differentiated from *Portlandemys* by a proportionally broader skull, a more obtuse angle between the labial ridges of maxilla and dentary, placement of the foramina anterius canalis carotici cerebralis closer to the level of the dorsum sellae, and a shorter mandibular symphysis. Based on shell anatomy, *Plesiochelys* is currently differentiated from *Craspedochelys* by a more elongated and oval carapace, a deeper nuchal notch, a lower length/width ratio of the costal bones (3.1–3.6, as opposed to 4.3–4.8 or more for costal IV), a relatively long plastron (about 85% to 90% of the carapace length), and a hyoplastron longer than wide and from *Tropidemys* by the absence of a neural keel, elongated neural bones, and wider vertebral scutes.

Comments. As it is now apparent, *Plesiochelys etalloni* is probably the most abundant turtle in Kimmeridgian deposits throughout Europe. For a long time, however, most authors named a new species in each new region, which eventually led to more than 20 species being assigned to this genus (Kuhn 1964b). These species are reassessed herein.

Plesiochelys bigleri Püntener et al., 2017

Taxonomic history. *Plesiochelys bigleri* Püntener et al., 2017 (new species).

Type material. MJSN TCH007-252 (holotype), a nearly complete shell with associated partial cranium and incomplete appendicular skeleton (Püntener et al. 2017, figs. 4, 7, 11, 12); MJSN TCH006-1451 (paratype), isolated partial cranium (Püntener et al. 2017, figs. 5, 6).

Type locality. Courtedoux, Canton of Jura, Switzerland (Figure 4); Lower *Virgula* Marls, Chevenez Member, Reuchenette Formation, late Kimmeridgian, Late Jurassic (Comment et al. 2011, 2015; Püntener et al. 2017).

Referred material and range. Late Jurassic (early and late Kimmeridgian) of the Banné Marls and Lower *Virgula* Marls, Courtedoux, Canton of Jura, Switzerland (Püntener et al. 2017).

Diagnosis. *Plesiochelys bigleri* can be diagnosed as a “plesiochelyid” and a representative of *Plesiochelys* by the full list of characters provided for these taxa above. *Plesiochelys bigleri* differs from other *Plesiochelys* spp. in a lower temporal skull roof, a shallower pterygoid fossa, a reduced processus trochlearis oticum, a more rounded foramen nervi trigemini, and placement of the foramen anterior nervi abducentis anteromedial to the base of the processus clinoideus and of the foramina anterius canalis carotici cerebralis more anteriorly relative to the level of the dorsum sellae. In addition, *Plesiochelys bigleri* differs from *Plesiochelys planiceps* by being smaller in size and by having a lower lingual ridge on the maxilla, a parietal-quadrate contact posterior to the foramen nervi trigemini, a less developed processus trochlearis oticum, a more superficial canalis caroticus internus that may have remained partly open ventrally, and a reduced contribution of the exoccipital to the condylus occipitalis. It differs from *Plesiochelys etalloni* in having a less extensive flooring of the cavum acustico-jugulare by the pterygoid, the absence of complete ossification of the pila prootica, a posterolaterally extending processus paroccipitalis, reduced neural and costal bone thickness, absent or poorly developed epiplastral bulbs, and a more quadrangular anterior margin of the anterior plastral lobe.

Comments. *Plesiochelys bigleri* is typified based on a relatively complete skull-shell association from the late Kimmeridgian of the vicinity of Porrentruy, Switzerland (Püntener et al. 2017), but an isolated cranium (paratype) and 40 additional shells are known from the type locality as well. The shell of *Plesiochelys bigleri* is remarkably similar to that of *Plesiochelys etalloni*, which complicates the differentiation between the two species based only on postcranial remains. These species differ notably in the relative thickness of neural and costal bones and in the presence of epiplastral bulbs. However, *Plesiochelys bigleri* differs from other *Plesiochelys* spp. in several aspects of the cranium. The posterior part of the skull roof is notably reduced in height and the foramina anterius canalis carotici cerebralis are located more anteriorly in *Plesiochelys bigleri* (Püntener et al. 2017).

Plesiochelys etalloni (Pictet and Humbert, 1857)

(= *Emys hugi* Gray, 1831 = *Emys hugii* Gray, 1831 = *Emys trionychoides* Gray, 1831 = *Emys jurensis* Keferstein, 1834 = *Clemmys*? *grayi* Fitzinger, 1835 = *Stylemys hannoverana* Maack, 1869 = *Plesiochelys langii* Rütimeyer, 1873a = *Plesiochelys sanctaeverenae* Rütimeyer, 1873a = *Plesiochelys solodurensis* Rütimeyer, 1873a = *Plesiochelys solodurensis langenbergensis* Oertel, 1924)

Taxonomic history. *Emys etalloni* Pictet and Humbert, 1857 (new species); *Plesiochelys etalloni* Rütimeyer 1873a (new combination); *Plesiochelys etalloni* = *Stylemys lindensis* [sic] Bräm 1965 (senior synonym); *Plesiochelys etalloni* = *Craspedochelys crassa* = *Craspedochelys picteti* = *Plesiochelys jaccardi* = *Plesiochelys sanctaeverenae* = *Plesiochelys solodurensis* = *Stylemys lindensis* [sic] Gaffney 1975a (senior synonym); *Plesiochelys solodurensis* = *Chelonides robusta* = *Chelonides wittei* = *Emys etalloni* = *Plesiochelys langii* = *Plesiochelys minor* = *Stylemys hannoverana* = *Stylonides* [sic] *lindensis* [sic] Karl et al. 2007 (synonymy); *Plesiochelys etalloni* = *Plesiochelys solodurensis* = *Plesiochelys sanctaeverenae* = *Plesiochelys langii* Anquetin, Deschamps and Claude 2014 (senior synonym).

Type material. MAJ 2005-11-1 (holotype), a shell missing a large part of the carapace (Pictet and Humbert 1857, pls. 1–3; Anquetin, Deschamps and Claude 2014, figs. 1, 2, S2, S3).

Type locality. Forêt de Lect, near Moirans-en-Montagne, Jura, France (Pictet and Humbert 1857; Figure 4); Horizon uncertain, late Kimmeridgian or early Tithonian, Late Jurassic (Lapparent de Broin et al. 1996; Anquetin, Deschamps and Claude 2014).

Referred material and range. Late Jurassic (middle Kimmeridgian) of Oker bei Bad Harzburg and Hannover, Lower Saxony, Germany (Maack 1869; Oertel 1924; Karl et al. 2007); Late Jurassic (late Kimmeridgian) of Solothurn, Canton of Solothurn, and Glovelier, Canton of Jura, Switzerland (hypodigm of Anquetin, Deschamps and Claude 2014; Anquetin et al. 2015); Late Jurassic (Kimmeridgian) of England (Anquetin and Chapman 2016).

Diagnosis. *Plesiochelys etalloni* can be diagnosed as a “plesiochelyid” and a representative of *Plesiochelys* by the full list of characters provided for these taxa above. *Plesiochelys etalloni* differs from other *Plesiochelys* spp. in a more extensive flooring of the cavum acustico-jugulare by the pterygoid, the complete ossification of the pila prootica, and a narrow, slit-like foramen nervi trigemini. In addition, *Plesiochelys etalloni* differs from *Plesiochelys planiceps* by a smaller size, a lower lingual ridge on the maxilla, a narrower distance between the lingual ridges of the maxilla at the level of the pterygoid-vomer suture, a more rounded foramen palatinum posterius, a parietal-quadrate contact posterior to the foramen nervi trigemini, a less developed processus trochlearis oticum, a superficial canalis caroticus internus often remaining partly open ventrally, an absent or reduced contribution of the exoccipital to the condylus occipitalis, and the anterior portion of the lingual ridge on the dentary curving medially. It differs from *Plesiochelys bigleri* by having a higher temporal skull roof, a deeper pterygoid fossa, a more developed processus trochlearis oticum, an foramen anterior nervi abducentis located more posteriorly relative to the base of the processus clinoideus, closely set foramina anterius canalis carotici cerebralis located almost vertically below the dorsum sellae, a processus paroccipitalis that extends mainly posteriorly, increased neural and costal bone thickness, presence of epiplastral bulbs, and a more rounded or pointed anterior margin of the anterior plastral lobe.

Comments. *Plesiochelys etalloni* is based on a single shell from the Kimmeridgian or early Tithonian of the French Jura Mountains (Pictet and Humbert 1857). Soon after its original description, this species was recognized in Solothurn, Switzerland along with three other purportedly new species: *Plesiochelys solodurensis*, *Plesiochelys langii*, and *Plesiochelys sanctaeverenae* (Rütimeyer 1873a). Bräm (1965) transferred most of the specimens previously referred to *Plesiochelys langii* to *Plesiochelys etalloni* but still recognized *Plesiochelys solodurensis* and *Plesiochelys sanctaeverenae* as valid taxa. Gaffney (1975a) argued for synonymizing *Plesiochelys solodurensis*, *Plesiochelys sanctaeverenae*, *Plesiochelys jaccardi*, *Craspedochelys picteti*, and *Stylemys lindenensis* with *Plesiochelys etalloni*. In contrast, Lapparent de Broin et al. (1996) considered that *Plesiochelys etalloni* and *Plesiochelys solodurensis* were distinct taxa: the first being limited to the type from the French Jura, and the second encompassing all the *Plesiochelys* specimens from Solothurn. One of the major issues with *Plesiochelys etalloni* was that the holotype specimen was lost to science for about 150 years. The recent rediscovery and redescription of this specimen coupled with a revision of all available material relevant to this question revealed that *Plesiochelys etalloni* is distinct from *Craspedochelys picteti* and *Craspedochelys jaccardi* (Anquetin, Deschamps and Claude 2014; Anquetin, Püntener and Billon-Bruyat 2014). *Plesiochelys etalloni* is known in abundance in Solothurn, Switzerland, where about 30 relatively complete shells enlighten the significant intraspecific variability of this taxon (Anquetin, Püntener and Billon-Bruyat 2014). One of the most striking variable characters is the retention of a central plastral fontanelle in some individuals.

Cuvier (1824) described and figured several specimens from the Late Jurassic of Solothurn, Switzerland. Most of these specimens can now be safely referred to *Plesiochelys etalloni*. However, in the early 1830s, three authors used the specimens described and figured by G. Cuvier as the basis of five new species that are all senior synonyms of *Plesiochelys etalloni*: *Emys hugi* Gray, 1831, *Emys hugii* Gray, 1831, *Emys trionychoides* Gray, 1831, *Emys jurensis* Keferstein, 1834, and *Clemmys*? *grayi* Fitzinger, 1835 (see below). Since none of these five names has been used as valid since Giebel (1847), while *Plesiochelys etalloni* has been in continuous use since Pictet and Humbert (1857), we declare them to be nomina oblita herein (ICZN 1999).

Oertel (1924) referred a series of specimens (GZG 763-1 to GZG 763-8) from the middle Kimmeridgian of Oker, Germany to different species of *Plesiochelys*. However, Karl et al. (2007) recently transferred all of these specimens to *Craspedochelys jaccardi*. Our observations reveal that only two of these specimens (GZG 763-1 and GZG 763-4) are sufficiently preserved to be identified as *Plesiochelys etalloni* herein (see also comments under *Plesiochelys solodurensis langenbergensis* Oertel, 1924).

***Plesiochelys planiceps* (Owen, 1842)**

Taxonomic history. *Chelone planiceps* Owen, 1842 (new species); *Stegochelys planiceps* Lydekker 1889a (new combination); *Plesiochelys planiceps* Gaffney 1975a (new combination).

Type material. OUMNH J.1582 (holotype), cranium lacking temporal roofing, subcomplete mandible, and remains of the hyoids and cervical vertebrae (Owen 1884, pl. 8.1–3; Gaffney 1975a, fig. 15; Gaffney 1976, figs. 1, 2, 8, 9, 13, 15, 16, 33, 34, 44, 46, 47, 49).

Type locality. Isle of Portland, Dorset, United Kingdom (Owen 1842; Gaffney 1975a; Figure 4); Portland Beds, Tithonian, Late Jurassic (Benton and Spencer 1995).

Referred material and range. No specimens have been formally referred to date.

Diagnosis. *Plesiochelys planiceps* can be diagnosed as a “plesiochelyid” and a representative of *Plesiochelys* by the full list of cranial characters provided for these taxa above. *Plesiochelys planiceps* differs from other *Plesiochelys* spp. by its larger size, a higher lingual ridge on the maxilla, the absence of a contact between the parietal and the quadrate posterior to the foramen nervi trigemini, a strongly developed processus trochlearis oticum, a canalis caroticus internus situated deep within bone, a foramen posterius canalis carotici interni opening on the posterior margin of the pterygoid and not visible in ventral view, and each exoccipital forming one-third of the condylus occipitalis. In addition, *Plesiochelys planiceps* differs from *Plesiochelys etalloni* by having a wider distance between the lingual ridges of the maxilla at the level of the pterygoid-vomer suture, an elongated foramen palatinum posterius, and the anterior portion of the lingual ridge on the dentary curving medially (as opposed to anteriorly). It differs from *Plesiochelys bigleri* by having a higher temporal skull roof, a deeper pterygoid fossa, a more developed processus trochlearis oticum, a foramen anterior nervi abducentis located more posteriorly relative to the base of the processus clinoideus, and the foramina anterius canalis carotici cerebralis located almost vertically below the dorsum sellae.

Comments. *Plesiochelys planiceps* is based on a beautifully preserved cranium and lower jaw from the Tithonian of the Isle of Portland, United Kingdom (Owen 1842; Gaffney 1975a). This species was referred to *Plesiochelys* by Gaffney (1975a), who differentiated it from *Plesiochelys etalloni* mainly based on a few characters of the upper and lower jaws. Later, Gaffney (1976) provided a more complete description of the cranial anatomy of *Plesiochelys*, but made only few references to *Plesiochelys planiceps*. Although illustrations were provided by Gaffney (1975a, 1976), the type material of *Plesiochelys planiceps* has still not been described in detail in the literature. Without providing such a description, Anquetin et al. (2015) recently listed cranial characters in which this species differs from *Plesiochelys etalloni* (see Diagnosis, above). There is therefore no doubt regarding the validity of this species.

Portlandemys **Gaffney, 1975a**

Type species. *Portlandemys mcdowelli* Gaffney, 1975a.

Diagnosis. *Portlandemys* can be diagnosed as a "plesiochelyid" by the full list of cranial characters provided above for that taxon. *Portlandemys* is currently differentiated from *Plesiochelys* by a proportionally narrower skull, a more acute angle between the labial ridges of maxilla and dentary, the foramina anterius canalis carotici cerebralis located more anteriorly, and a longer mandibular symphysis.

Portlandemys gracilis **Anquetin et al., 2015**

Taxonomic history. *Portlandemys gracilis* Anquetin et al., 2015 (new species).

Type material. MJSN BSY009-708 (holotype), partial cranium with basicranium and skull roof (Anquetin et al. 2015, figs. 5–9).

Type locality. Courtedoux, Canton of Jura, Switzerland (Figure 4); Lower *Virgula* Marls, Chevenez Member, Reuchenette Formation, late Kimmeridgian, Late Jurassic (Comment et al. 2011, 2015; Anquetin et al. 2015).

Referred material and range. Late Jurassic (late Kimmeridgian) of the Lower *Virgula* Marls, Courtedoux, Canton of Jura, Switzerland (Anquetin et al. 2015).

Diagnosis. *Portlandemys gracilis* can be diagnosed as a "plesiochelyid" and a representative of *Portlandemys* by the full list of cranial characters provided for these taxa above. *Portlandemys gracilis* differs from *Portlandemys mcdowelli* by having a more gracile cranium, a less robustly ossified skull roof and basicranium, a reduced, narrow processus trochlearis oticum formed mostly by the quadrate, a broad contact between nasal and frontal on the dorsal surface of the skull roof preventing a midline contact of the prefrontals, absence of a ridge closing the pterygoid fossa posteriorly, foramen posterius canalis carotici interni located on posterior margin of the pterygoid (barely visible in ventral view) further away from the basisphenoid-pterygoid suture, a raised pedestal on the dorsal surface of the pterygoid contacting the processus interfenestralis of the opisthotic, a basisphenoid ogival in outline in ventral view, a more gracile mandible with a low profile in lateral view, weakly developed lingual ridges on the mandible, a symphyseal region broadly rounded as seen in dorsal view, absence of symphyseal hook, and splenial triangular in shape with extended anterior part.

Comments. *Portlandemys gracilis* is based on a partial cranium (basicranium and skull roof) from the late Kimmeridgian of the vicinity of Porrentruy, Switzerland (Anquetin et al. 2015). This species and the Tithonian *Portlandemys mcdowelli* (type species of the genus) share a unique configuration of the anterodorsal aspect of the basicranium. The surface below the dorsum sellae slopes gently anteroventrally and the foramina anterius canalis carotici cerebralis therefore open a long distance anterior to the level of the dorsum sellae. However, *Portlandemys gracilis* differs from *Portlandemys mcdowelli* in several other aspects of the skull, notably in being more gracile (Anquetin et al. 2015). A mandible from the same stratigraphic level as the holotype was also tentatively referred to *Portlandemys gracilis* (Anquetin et al. 2015). As in *Portlandemys mcdowelli*, this mandible is characterized by an acute angle of the labial ridges, but the triturating surface is markedly different between the two species.

Portlandemys mcdowelli **Gaffney, 1975a**

Taxonomic history. *Portlandemys mcdowelli* Gaffney, 1975a (new species).

Type material. NHMUK R2914 (holotype), cranium lacking both lateral temporal areas and a large part of the left otic region, a partial associated mandible, and possibly unfigured postcranial fragments (Parsons and Williams 1961, figs. 1, 3–6, 9, pls. 1–3; Gaffney 1975a, figs. 13, 14; Gaffney 1976, figs. 6, 7, 10, 11, 17–19, 38, 46, 50).

Type locality. Isle of Portland, Dorset, United Kingdom (Parsons and Williams 1961; Gaffney 1975a; Figure 4); Portland Beds, Tithonian, Late Jurassic (Benton and Spencer 1995).

Referred material and range. Late Jurassic (Tithonian) of the Isle of Portland, Dorset, United Kingdom (Gaffney 1975a; Anquetin et al. 2015).

Diagnosis. *Portlandemys mcdowelli* can be diagnosed as a "plesiochelyid" and a representative of *Portlandemys* by the full list of cranial characters provided for these taxa above. *Portlandemys mcdowelli* differs from *Portlandemys gracilis* by having a more robust cranium, a strong processus trochlearis oticum formed equally by the quadrate and prootic, a midline contact of the prefrontals preventing a nasal-frontal contact on the dorsal surface of the skull roof, the presence of a ridge closing the pterygoid fossa posteriorly, foramen posterius canalis carotici interni located close to the basisphenoid-pterygoid suture on the posteromedial part of the pterygoid, absence of a raised pedestal on the dorsal surface of the pterygoid contacting the processus interfenestralis of the opisthotic, basisphenoid triangular in outline in ventral view, a more robust mandible with a high profile in lateral view, strongly developed lingual ridges on the mandible, a symphyseal region more pointed anteriorly as seen in dorsal view, presence of a strong symphyseal hook, and a more trapezoidal splenial.

Comments. *Portlandemys mcdowelli* is based on a relatively complete cranium plus associated mandible from the Tithonian of the Isle of Portland, United Kingdom (Gaffney 1975a). Two further partial crania were initially referred to this form (Parsons and Williams 1961; Gaffney 1975a), but a recent reevaluation of these specimens revealed that one of them (NHMUK R3163) is not referable to this taxon (Anquetin et al. 2015). The validity of *Portlandemys mcdowelli* has never been questioned, but the postcranial skeleton of this species is not known and it may happen that the shell has already been described under a different name. The study of the undescribed postcranial material registered under the same catalogue number as the holotype specimen in the NHMUK might help with this issue. However, one would first need to ascertain that the skull and the postcranial material are indeed truly associated.

Based on characters of the basicranium (area of the sella turcica and ethmoid region), Gaffney (1975a) referred *Portlandemys mcdowelli* to the “Plesiochelyidae.” Anquetin et al. (2015) followed this conclusion although comparisons are limited because the internal basicranial anatomy of “thalassemydids” and “eurysternids” is poorly known. *Portlandemys mcdowelli* is notably differentiated from the other species referred to the genus *Portlandemys gracilis* (see above) by a skull with robust features, coarse, heavy-built triturating surfaces, and a strongly developed processus trochlearis oticum.

Tropidemys **Rütimeyer, 1873a**

Type species. *Tropidemys langii* Rütimeyer, 1873a.

Diagnosis. *Tropidemys* can be diagnosed as a “plesiochelyid” by the full list of shell characters provided for that taxon above. *Tropidemys* is currently differentiated from all other “plesiochelyids” by particularly thick shell bones, a posteriorly tectiform carapace, a greatly reduced or absent nuchal notch, keeled neurals (more pronounced posteriorly), wide and hexagonal intermediate and posterior neurals with anterolateral sides as long as posterolateral sides, retention of costo-peripheral fontanelles in juveniles (closed in adults), and narrow vertebral scutes.

Comments. *Tropidemys* is an easily identifiable taxon characterized by thick shell bones, a tectiform carapace, and keeled and hexagonal neurals with equally long lateral sides. Consequently, isolated elements of *Tropidemys* sp. have been signaled in many deposits (see Püntener et al. 2014 for a review), but, given that other taxa have tectiform shells as well, it was beyond the scope of the present study to reassess these sparse discoveries.

Tropidemys langii **Rütimeyer, 1873a**

(= *Tropidemys expansa* Rütimeyer, 1873a = *Tropidemys gibba* Rütimeyer, 1873a = *Craspedochelys plana* Rütimeyer, 1873a)

Taxonomic history. *Tropidemys langii* Rütimeyer, 1873a (new species); *Tropidemys langii* = *Tropidemys expansa* = *Tropidemys gibba* = *Craspedochelys plana* Bräm 1965 (senior synonym, lectotype designation); *Tropidemys langii* = *Chelone valanginiensis* = *Stylemys lindensis* [sic] (pro parte) = *Tropidemys expansa* = *Tropidemys gibba* = *Tropidemys seebachi* Karl et al. 2007 (synonymy).

Type material. NMS 8554 (lectotype; formerly NMS 16), posterior part of a carapace (Rütimeyer 1873a, pl. 7.1; Anquetin, Püntener and Billon-Bruyat 2014, fig. 5); NMS uncat. (paralectotypes), an isolated neural and an isolated costal V (Rütimeyer 1873a, pl. 7.3–4). Additional paralectotypes possibly exist but are impossible to identify with certainty based on the original publication.

Type locality. Solothurn, Canton of Solothurn, Switzerland (Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Referred material and range. Late Jurassic (late Kimmeridgian) of Solothurn, Canton of Solothurn, Switzerland (Bräm 1965; Püntener et al. 2014); Late Jurassic (early and late Kimmeridgian) of Courtedoux and Porrentruy, Canton of Jura, Switzerland (Püntener et al. 2014); Late Jurassic (Kimmeridgian) of the Kimmeridge Clay, Weymouth, Dorset, United Kingdom (Lydekker 1889b; Anquetin and Chapman 2016).

Diagnosis. *Tropidemys langii* can be diagnosed as a “plesiochelyid” and a representative of *Tropidemys* by the full list of shell characters provided for those taxa above. *Tropidemys langii* differs from *Tropidemys seebachi* by having five vertebral scutes.

Comments. Rütimeyer (1873a) established *Tropidemys langii* based on a type series consisting of a large fragment of the posterior region of a carapace, several isolated neurals and costals, and several fragments of plastron from the Kimmeridgian of Solothurn, Switzerland. Since no specimen numbers are mentioned in the original publication, it is difficult to be certain as to which specimens are part of the type series, notably, regarding the isolated neurals and costals. Bräm (1965) concluded that all but one of the plastron fragments should be referred to *Thalassemys hugii*, but the remaining specimen (NMS 8651, formerly NMS 19) was subsequently also excluded from *Tropidemys langii* based on comparison with more complete material from the vicinity of Porrentruy (Püntener et al. 2014). Therefore, the large fragment of carapace (NMS 8554, formerly NMS 16) is the only unambiguous syntype. Bräm (1965) incorrectly referred to this specimen as the holotype, but, according to the ICZN rules, this should nevertheless be interpreted as a valid lectotype designation (ICZN 1999, art. 74.5). An isolated neural and costal V are the only known potential paralectotypes as they were illustrated by Rütimeyer (1873a), but no attempt has been made to find them in the NMS collections.

The fragmentary nature of the specimens that Rütimeyer (1873a) had at hand probably partly explains why he recognized three different species of *Tropidemys* in Solothurn. In contrast, Bräm (1965) had access to a subcomplete carapace (NMS 8648, formerly NMS 15) and concluded that only one species was present in Solothurn, for which he, as first reviser, selected *Tropidemys langii* as the senior name. Several new specimens, including plastrons and limb bones, from the Kimmeridgian of Porrentruy, Switzerland were recently described in detail (Püntener et al. 2014).

Lydekker (1889b) referred four specimens from the Kimmeridge Clay of Weymouth, United Kingdom, to *Tropidemys langii*. Anquetin and Chapman (2016) confirmed this attribution for three of these specimens but disagreed with the referral of an isolated hyoplastron, which exhibits a lateral plastral fontanelle (see Püntener et al. 2014 for plastral material of *Tropidemys langii*). A large isolated costal from the Kimmeridge Clay of Weymouth was also recently assigned to *Tropidemys langii* (Anquetin and Chapman 2016).

***Tropidemys seebachi* Portis, 1878**

Taxonomic history. *Tropidemys seebachi* Portis, 1878 (new species); *Tropidemys seebachi = Stylemys lindenensis* (pro parte) Portis 1878 (partial synonymy); *Tropidemys langii = Chelone valanginiensis = Stylemys lindensis* [sic] (pro parte) = *Tropidemys expansa = Tropidemys gibba = Tropidemys seebachi* Karl et al. 2007 (junior synonym); *Tropidemys seebachi* Karl, Gröning and Brauckmann 2012 (lectotype designation).

Type material. GZG 769-1 (lectotype), articulated anterior part of a carapace, including four neurals and five incomplete costals (Portis 1878, pl. 15.1; Karl, Gröning and Brauckmann 2012, pls. 1.1–3, 2.1, 2); GZG 769-3, GZG 773-20, GZG 773-34, and GZG 773-43 (paralectotypes), isolated costal, hyoplastron, and hypoplastra (Maack 1869, pls. 34.21, 35.35, 36.44; Portis 1878, pl. 15.3–5; Karl, Gröning and Brauckmann 2012, pls. 1.1, 2, 2.3, 4, 2.5, 6).

Type locality. Lindener Berg, Hannover, Lower Saxony, Germany (Karl, Gröning and Brauckmann 2012; Figure 4); *Pteroceras* layer (= *Aporrhais* layer), middle Kimmeridgian, Late Jurassic (Karl et al. 2007).

Referred material and range. Late Jurassic (late Kimmeridgian) of Wattendorf, Bavaria, Germany (Mäuser 2014; Joyce 2015).

Diagnosis. *Tropidemys seebachi* can be diagnosed as a “plesiochelyid” and a representative of *Tropidemys* by the full list of shell characters provided for those taxa above. *Tropidemys seebachi* differs from *Tropidemys langii* by the presence of more than five vertebral scutes.

Comments. Portis (1878) erected *Tropidemys seebachi* based on a series of five specimens, including an anterior part of carapace that was recently designated as the lectotype (Karl, Gröning and Brauckmann 2012). Among the four paralectotypes, three isolated plastral fragments are of questionable affinity, especially considering that they also serve as part of the type series of *Stylemys lindenensis* Maack, 1869 and *Stylemys hannoverana* Maack, 1869 (see below). Portis (1878) transferred these to *Tropidemys seebachi* based on a strong resemblance with plastral material from Solothurn referred to *Tropidemys langii* by Rütimeyer (1873a). However, this attribution of the Solothurn material was recently shown to be incorrect (Püntener et al. 2014), and there is therefore no solid evidence to support the assignment of the three aforementioned plastral elements to *Tropidemys seebachi*.

Tropidemys seebachi is clearly distinguished from *Tropidemys langii* based on a unique pattern of carapacial scutes characterized by the presence of more than five vertebral scutes (Karl, Gröning and Brauckmann 2012; Püntener et al. 2014). A complete specimen from the Kimmeridgian of Wattendorf, Germany (Mäuser 2014, fig. 47; Joyce 2015, fig. 812) confirms that this species is not defined based on abnormal individual variations.

“Thalassemydidae” Zittel, 1889

Diagnosis. As for *Thalassemys* Rütimeyer, 1873a.

Comments. Under the current state of knowledge, it may appear superfluous to maintain the name Thalassemydidae because it is redundant with *Thalassemys* at the moment. However, the phylogenetic relationships of *Thalassemys* spp. with other thalassochelydians have never been properly explored. One of the main reasons for this is the absence of cranial material for thalassemydids. Pending better understanding of thalassochelydian relationships, we maintain the use of the name Thalassemydidae for practical reasons, but, once again highlight its taxonomic ambiguity through the use of quotation marks.

Thalassemys Rütimeyer, 1873a

Type species. *Thalassemys* hugii Rütimeyer, 1873a.

Diagnosis. *Thalassemys* can tentatively be diagnosed as a representative of *Thalassochelydia*, but the presence of three cervicals is suspected in some individuals. *Thalassemys* is currently differentiated from other thalassochelydians by a large size (carapace length greater than 600 mm), absence of nuchal notch, clearly visible linear striations perpendicular to most shell sutures, retention of reduced costo-peripheral fontanelles in adults, an osseous bridge in adults, vertebral scutes with anterolaterally concave and posterolaterally convex margins, lateral plastral fontanelles, a tendency toward the reduction of sutural contacts between hyoplastra and anterior plastral elements, and a wide scapular angle (usually more than 110°).

Comments. The genus name *Thalassemys* was first mentioned by Rütimeyer in 1859 (Rütimeyer 1859), but this genus name was not associated with any specific name. According to the current rules of zoological nomenclature (ICZN 1999, art. 11, 12), the name *Thalassemys* only became available in 1873 when Rütimeyer associated specific names to it (Rütimeyer 1873a). Most previous authors, including ourselves (Anquetin, Püntener and Billon-Bruyat 2014), mistakenly attributed the name *Thalassemys* to Rütimeyer (1859).

Fragmented remains from the late Albian or early Cenomanian of Itemir, Uzbekistan were initially tentatively referred to a new “thalassemydid” turtle, *Parathalassemys cava* Nessov in Nessov and Krasovskaya, 1984 (see also Nessov 1984). Nessov (1997) finally concluded that the affinities of this species were uncertain (see Averianov 2002). According to Sukhanov (2000), this species more probably belongs to Macrobaenidae. In contrast, Karl, Tichy and Valdiserri (2012) concluded that this form should indeed be referred to “thalassemydids” and proposed the new combination *Thalassemys cava* (misspelled *carva*). However, the few remains briefly described and figured by Nessov and Krasovskaya (1984) do not exhibit diagnostic characters of “thalassemydids.” This taxon is therefore not further considered herein.

Thalassemys bruntrutana Püntener et al., 2015

Taxonomic history. *Thalassemys bruntrutana* Püntener et al., 2015 (new species).

Type material. MJSN SCR011-87 (holotype), an almost complete and articulated carapace and associated disarticulated plastron (Püntener et al. 2015, figs. 3–6).

Type locality. Courtedoux, Canton of Jura, Switzerland (Figure 4); Lower *Virgula* Marls, Chevenez Member, Reuchenette Formation, late Kimmeridgian, Late Jurassic (Comment et al. 2011, 2015; Püntener et al. 2015).

Referred material and range. Late Jurassic (late Kimmeridgian) of Solothurn, Canton of Solothurn, Switzerland and Egmont Bight, Isle of Purbeck, Dorset, United Kingdom (hypodigm of Püntener et al. 2015).

Diagnosis. *Thalassemys bruntrutana* can be diagnosed as a representative of *Thalassemys* by the full list of characters provided for that taxon above. *Thalassemys bruntrutana* differs from all other *Thalassemys* by having a more elongated nuchal with strong anterolateral thickening on the ventral surface (difficult to observe in *Thalassemys marina*) and wider vertebral scutes. *Thalassemys bruntrutana* furthermore differs from *Thalassemys hugii* by having a proportionally longer plastron, broader and less inclined xiphiplastra, and a wider scapular angle. It differs from *Thalassemys marina* by having less pronounced lateral plastral fontanelles.

Comments. *Thalassemys bruntrutana* is based on a relatively complete, but partly disarticulated, shell from the late Kimmeridgian of the vicinity of Porrentruy, Switzerland (Püntener et al. 2015). This species differs from *Thalassemys hugii* in several features: more elongated nuchal with strong anterolateral thickening on the ventral surface, wider vertebral scutes, less inclined lateral margin of xiphiplastron, and wider angle between scapular and acromion processes. This form is also present in Solothurn and in the Kimmeridge Clay of southern England (Püntener et al. 2015).

Thalassemys hugii Rütimeyer, 1873a

(= *Thalassemys gresslyi* Rütimeyer, 1873a = *Eurysternum ignoratum* Bräm, 1965)

Taxonomic history. *Thalassemys hugii* Rütimeyer, 1873a (new species); *Thalassemys hugii* = *Enaliochelys chelonia* Lydekker 1889b (synonymy); *Thalassemys hugii* Bräm 1965 (lectotype designation).

Type material. NMS 8595 to NMS 8609 (lectotype; formerly NMS 1), a large carapace plus associated plastral fragments and postcranial elements (Rütimeyer 1873a, pl. 1; Bräm 1965, pl. 7; Anquetin, Püntener and Billon-Bruyat 2014, fig. 6; Püntener et al. 2015, figs. 3, 5, 6). With the exception of the lectotype, it is unclear which other specimens once formed the syntype series.

Type locality. Solothurn, Canton of Solothurn, Switzerland (Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Referred material and range. Late Jurassic (late Kimmeridgian) of Solothurn, Canton of Solothurn, and Courtedoux, Canton of Jura, Switzerland (Püntener et al. 2015); Late Jurassic (Kimmeridgian) of Abington, Oxfordshire, United Kingdom (Pérez-García 2015c).

Diagnosis. *Thalassemys hugii* can be diagnosed as a representative of *Thalassemys* by the full list of characters provided for that taxon above. *Thalassemys hugii* differs from all other *Thalassemys* by having narrower vertebral scutes. *Thalassemys hugii* further differs from *Thalassemys bruntrutana* by having a proportionally wider nuchal without anterolateral thickening on the ventral surface, a proportionally shorter plastron, narrower and more inclined xiphiplastra, and a smaller scapular angle, and differs from *Thalassemys marina* by having less pronounced lateral plastral fontanelles.

Comments. *Thalassemys hugii* is based on a relatively complete carapace with associated plastral and postcranial elements from the Kimmeridgian of Solothurn, Switzerland (Rütimeyer 1873a). The validity of this species has never been questioned. Bräm (1965) used the lectotype of *Thalassemys hugii* to conceptualize the differences between “thalassemydids” and “eurysternids.” The latter were described as having a central plastral fontanelle and a pair of lateral plastral fontanelles, whereas “thalassemydids” only had a central plastral fontanelle. More recently, the presence of a pair of lateral plastral fontanelles was unambiguously demonstrated in *Thalassemys hugii*, contradicting the utility of this simplistic key (Anquetin, Püntener and Billon-Bruyat 2014). The diagnosis of *Thalassemys hugii* was recently refined by Püntener et al. (2015).

Lydekker (1889b) proposed that *Enaliochelys chelonia* was a synonym of *Thalassemys hugii*, although *Enaliochelys chelonia* Seeley 1869 should have had priority over *Thalassemys hugii* Rütimeyer 1873a. However, the type material of *Enaliochelys chelonia* was recently revised, and it appears that this taxon is clearly distinct from *Thalassemys hugii* (Pérez-García 2015b).

Thalassemys marina Fraas, 1903

Taxonomic history. *Thalassemys marina* Fraas, 1903 (new species); *Eurysternum marinum* Maisch 2001 (new combination); *Palaeomedusa testa* = *Eurysternum crassipes* = *Thalassemys marina* Joyce 2003 (junior synonym).

Type material. SMNS 10817 (holotype), a partial carapace with associated steinkern and the right half of a plastron (Fraas 1903, pls. 1–3).

Type locality. Schnaitheim, Baden-Württemberg, Germany (Figure 4); Brenztaloolith, late Kimmeridgian, Late Jurassic (Fraas 1903; Maisch 2001).

Referred material and range. Late Jurassic (late Kimmeridgian) of Schnaitheim, Baden-Württemberg, Germany (Maisch 2001).

Diagnosis. *Thalassemys marina* can be diagnosed as a representative of *Thalassemys* by clearly visible linear striations perpendicular to most shell sutures, retention of reduced costo-peripheral fontanelles, vertebral scutes with anterolaterally concave and posterolaterally convex margins, presence of lateral plastral fontanelles, and a tendency toward the reduction of sutural contacts between hyoplastra and anterior plastral elements. *Thalassemys marina* differs from all other *Thalassemys* by having vertebral scutes with intermediate width and greatly developed lateral plastral fontanelles.

Comments. *Thalassemys marina* is based on a single, partial shell from the late Kimmeridgian of Schnaitheim, Germany (Fraas 1903). Bräm (1965), followed by Maisch (2001), proposed that *Thalassemys marina* should be excluded from the genus *Thalassemys* and referred to *Eurysternum* instead based on the presence of a pair of lateral plastral fontanelles in the holotype (SMNS 10817). However, Anquetin, Püntener and Billon-Bruyat (2014) recently revealed that such lateral plastral fontanelles are actually present in *Thalassemys hugii*, the type species of *Thalassemys* (see above). Consequently, the simple presence of lateral plastral fontanelles must not be considered a diagnostic feature of eurysternids.

Thalassemys marina was thought to represent a valid species of fossil turtle for 100 years until Joyce (2003) proposed this taxon to likely represent a junior synonym of *Palaeomedusa testa*. One of the main characters Joyce (2003) used in support of this synonymy is the presence of a pair of triangular, supernumerary pleural scutes just anterior to the regular pleural I. However, observation of the type specimen (SMNS 10817) reveals that this part of the shell is actually a plaster reconstruction. We therefore refute the proposed synonymy of Joyce (2003) and consider *Thalassemys marina* to be a valid, though poorly diagnosed, taxon.

Incertae Sedis

Comments. Here we list species that may be, or have been proposed to be, closely related to thalassochelydian turtles, but whose exact systematic position is uncertain. Although their relationships are currently obscure, all of these species are valid taxa.

Enaliochelys chelonia Seeley, 1869

Taxonomic history. *Enaliochelys chelonia* Seeley, 1869 (new species); *Thalassemys hugii* = *Enaliochelys chelonia* Lydekker 1889b (synonymy).

Type material. CAMSM J29898 to CAMSM J29955 (holotype), a partial, disarticulated skeleton (Seeley 1869; Pérez-García 2015b, fig. 4).

Type locality. Ely, Cambridgeshire, United Kingdom (Figure 4); Kimmeridge Clay, probably early Kimmeridgian, Late Jurassic (Seeley 1869; Benton and Spencer 1995).

Referred material and range. Late Jurassic (early? Kimmeridgian) of the Kimmeridge Clay, Ely, Cambridgeshire, United Kingdom (Pérez-García 2015b).

Diagnosis. *Enaliochelys chelonia* lacks diagnostic characters of *Thalassochelydia*, but several characteristics may indicate a close relationship with “thalassemydids” (see below). *Enaliochelys chelonia* differs from all other thalassochelydians by its large size (more than 600 mm in carapace length), well-developed costo-peripheral fontanelles, increased width of the rib associated with the last pairs of costals, and wide vertebral scutes.

Comments. *Enaliochelys chelonia* is based on a partial, disarticulated skeleton from the Kimmeridge Clay (Kimmeridgian) of Ely, Cambridgeshire, United Kingdom (Seeley 1869). Following Lydekker (1889b), *Enaliochelys chelonia* was considered a synonym of *Thalassemys hugii*, although the name *Enaliochelys chelonia* should have had priority over *Thalassemys hugii*. Although most subsequent authors overlooked this material, *Enaliochelys chelonia* was more recently considered a nomen nudum by Benton and Spencer (1995) but without further discussion. Although we agree that the description in Seeley’s (1869) catalogue is diminutive, it nevertheless fulfills the minimum requirements for names published prior to 1931 (ICZN 1999) and must be considered available. The type specimen was only recently described and figured in detail (Pérez-García 2015b). *Enaliochelys chelonia* is a large form (carapace length of about 60 cm) characterized by reduced costal bones, the increased width of the rib associated with the last pairs of costals, and wide vertebral scutes. This taxon is therefore clearly distinct from *Thalassemys hugii* and must be considered valid. The affinities of *Enaliochelys chelonia* remain uncertain, although several characteristics (large size, absence of nuchal notch, great scapular angle) may suggest a close relationship with thalassemydids.

Jurassichelon Pérez-García, 2015b

Type species. *Jurassichelon oleronensis* Pérez-García, 2015b.

Diagnosis. *Jurassichelon* can be diagnosed as a thalassochelydian by the full list of characters provided for this clade above. *Jurassichelon* is differentiated from all other thalassochelydians by medium size (350–400 mm in carapace length), the presence of reduced costo-peripheral fontanelles, distally thinning costal bones, vertebral scutes that cover about half of the costals, a mostly ligamentous contact between the hyoplastron and the epi- and entoplastron, and the presence of a small xiphiplastral notch.

Jurassichelon moseri (Bräm, 1965)

Taxonomic history. *Thalassemys moseri* Bräm, 1965 (new species); *Plesiochelys solodurensis* = *Thalassemys moseri* Lapparent de Broin et al. 1996 (junior synonym).

Type material. NMS 9151 (holotype; formerly NMS 618), a partial shell with only the medial part of the carapace preserved (Bräm 1965, pl. 8.2, 3; Anquetin, Püntener and Billon-Bruyat 2014, fig. 7a–d).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Bräm 1965; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Referred material and range. Late Jurassic (late Kimmeridgian) of Solothurn, Canton of Solothurn, Switzerland (see hypodigm of Bräm 1965).

Diagnosis. *Jurassichelon moseri* can be diagnosed as a representative of *Jurassichelon* by the full list of shell characters provided above for that taxon. *Jurassichelon moseri* differs from *Jurassichelon oleronensis* by having thicker shell bones, wider lateral peripherals that are connected to the plastron by a sutural contact, absence of lateral plastral fontanelles, and a reduced, though sutural, midline contact of the plastral elements.

Comments. *Jurassichelon moseri* is based on a relatively complete shell from the Kimmeridgian of Solothurn, Switzerland (Bräm 1965). Bräm (1965) initially identified this turtle as a new species of *Thalassemys*, notably, based on the retention of costo-peripheral fontanelles and the absence of lateral plastral fontanelles. Rieppel (1980) later described a skull-shell association (PIMUZ A/III 514) from the Tithonian of the Isle of Oléron, France that he referred to this taxon. However, he concluded that *Thalassemys moseri* was probably more closely related to *Plesiochelys* than to *Thalassemys hugii* and called for a global revision of the “Plesiochelyidae” and “Thalassemydidae.” Lapparent de Broin et al. (1996) argued that the holotype of *Thalassemys moseri* is characterized by the presence of three cervical scutes, wide vertebral scutes, and an oval central plastral fontanelle and was probably a young individual of *Plesiochelys solodurensis*, the only *Plesiochelys* species they recognized in Solothurn. Therefore, they concluded that *Thalassemys moseri* was a junior synonym of *Plesiochelys solodurensis*. They also provisionally referred the cranium described by Rieppel (1980) to *Plesiochelys* sp., pending revision of the associated shell remains. Based on a thorough revision of the Solothurn turtle assemblage, Anquetin, Püntener and Billon-Bruyat (2014) were able to show that *Thalassemys moseri* was indeed a valid species differing from all other known thalassochelydians, although a referral to the genus *Thalassemys* was certainly incorrect. Nonetheless, following the conclusions of Lapparent de Broin et al. (1996) regarding the invalidity of *Thalassemys moseri* and those of Rieppel (1980) concerning the unique nature of the cranium from the Isle of Oléron, Pérez-García (2015b) proposed the new name *Jurassichelon oleronensis* for the latter material.

Although a new genus name was certainly needed, the first step should have been a proper reassessment of the specimens from Solothurn and the Isle of Oléron in order to determine whether they represent a single taxon or two closely related species. Such a thorough reassessment is still needed and the present study is not the right place. However, based on first-hand observation of the material from Solothurn and the Isle of Oléron, as well as still undescribed material from the Kimmeridgian of Porrentruy, Switzerland, we are in a position to reach some conclusions. The specimens from Solothurn and the material from the Isle of Oléron share several important characteristics that indicate close relationships: the costals are relatively thin distally, the costo-peripheral fontanelles are retained, broad vertebral scutes cover slightly more than half of the costal length, and a sutural contact between the anterior plastral elements and the hyoplastra is absent. However, the specimen from the Isle of Oléron also exhibits notable differences from the Solothurn material: the shell bones are much thinner, the bridge peripherals are reduced to narrow, wedge-shaped elements connected to both costals and plastron by connective tissues, very narrow lateral plastral fontanelle are present, and the midline contact of the hyoplastra is mostly formed by connective tissues. These observations strongly suggest that the material from Solothurn and the specimen from the Isle of Oléron belong to two closely related, but distinct, species. We therefore propose the new combination *Jurassichelon moseri* (Bräm, 1965) for the Solothurn material.

***Jurassichelon oleronensis* Pérez-García, 2015b**

Taxonomic history. *Jurassichelon oleronensis* Pérez-García, 2015b (new species).

Type material. PIMUZ A/III 514, a nearly complete skull and associated partial shell, cervical vertebrae, and postcranial elements (Rieppel 1980, figs. 1–6, 11–17).

Type locality. La Morelière, Isle of Oléron, Charente-Maritime, France (Figure 4); Formation unknown, Tithonian, Late Jurassic (Rieppel 1980).

Referred material and range. No specimens have been referred to date.

Diagnosis. *Jurassichelon oleronensis* can be diagnosed as a representative of *Jurassichelon* by the full list of characters provided above for that taxon. *Jurassichelon oleronensis* differs from *Jurassichelon moseri* in having much thinner shell bones, wedge-shaped, narrow bridge peripherals that are connected to the plastron and the costals by connective tissues, presence of a narrow lateral plastral fontanelle, and midline contact of the hyoplastra mostly formed by connective tissues. Additionally, *Jurassichelon oleronensis* differs from other thalassochelydians in having a low temporal skull roof, large orbits, a narrow interorbital bar, a short, broadly-arched triturating surface, and a high dorsum sellae overhanging the sellae surface, and a high dorsum sellae overhanging the sellae turcica.

Comments. *Jurassichelon oleronensis* is based on a single specimen (PIMUZ A/III 514) from the Tithonian of the Isle of Oléron, France (Rieppel 1980). This specimen represents one of the few skull-shell associations known for thalassochelydians and is therefore regularly included into phylogenetic analyses (e.g., Gaffney and Meylan 1988; Joyce 2007; Sterli 2010; Anquetin 2012; Rabi et al. 2013). Rieppel (1980) originally referred this specimen to *Thalassemys moseri* Bräm, 1965, but pointed out that this species was probably more closely related to *Plesiochelys* than to *Thalassemys hugii*. Lapparent de Broin et al. (1996) concluded that *Thalassemys moseri* was an invalid name (junior synonym of *Plesiochelys solodurensis*) and that the specimen described by Rieppel (1980) should be provisionally referred to *Plesiochelys* sp. However, Rieppel (1980) had clearly established that PIMUZ A/III 514 was more plesiomorphic than *Plesiochelys* and *Portlandemys* for many features of the skull. Based on the conclusions of Rieppel (1980) and Lapparent de Broin et al. (1996), Pérez-García (2015b) proposed the new genus and species *Jurassichelon oleronensis* for PIMUZ A/III 514.

Contradicting the conclusions of Lapparent de Broin et al. (1996), Anquetin, Püntener and Billon-Bruyat (2014) were able to show that *Thalassemys moseri* Bräm, 1965 was indeed a valid species. The taxonomy of *Jurassichelon oleronensis* is therefore dependent on the status of this taxon. Unfortunately, none of the recent studies offered a thorough reassessment of PIMUZ A/III 514 and of the material from Solothurn referred to *Thalassemys moseri*. Preliminary observations were made on all of these specimens for the purpose of the present work and allow us to conclude that the material from Solothurn and the specimen described by Rieppel (1980) represent two separate but closely-related species (see comments for *Jurassichelon moseri*). *Jurassichelon oleronensis* must therefore be considered a valid taxon, but a proper reassessment of all of the material referred to *Jurassichelon* (Oléron, France, Solothurn and Porrentruy, Switzerland) is needed.

Neusticemys neuquina (Fernández and de la Fuente, 1988)

Taxonomic history. *Eurysternum*? *neuquinum* Fernández and de la Fuente, 1988 (new species); *Neusticemys neuquina* Fernández and de la Fuente 1993 (new combination).

Type material. MLP 86-III-30-2 (holotype), posterior part of the carapace with a hyo- and hypoplastron and fragments of the appendicular skeleton (Fernández and de la Fuente 1988, pl. 1; de la Fuente 2007, fig. 3.2e, f); MLP 86-III-30-1 (paratype), anterior fragment of carapace with hyoplastra, anterior part of hypoplastra, and fragments of the pelvic girdle (Fernández and de la Fuente 1988, pl. 2.a, b); MOZ-PV 1106 (paratype), anterior part of a carapace (Fernández and de la Fuente 1988, pl. 2.c).

Type locality. Cerro Lotena, Neuquén, Argentina (Figure 4); Portada Covunco Member, Vaca Muerta Formation, early Tithonian, Late Jurassic (Fernández and de la Fuente 1988; Gasparini et al. 2015).

Referred material and range. Late Jurassic (late middle to late Tithonian), Vaca Muerta Formation, Neuquén, Argentina (Fernández and de la Fuente 1993; de la Fuente and Fernández 2011; Gasparini et al. 1997).

Diagnosis. *Neusticemys neuquina* lacks diagnostic characters of *Thalassochelydia*, but several characteristics may indicate close relationships with "eurysternids" and/or "thalassemydids" (see below). *Neusticemys neuquina* differs from all other thalassochelydians in having a depressed anterolateral carapacial rim, developed costo-peripheral fontanelles, a moderate medial keel along the posterior third of the carapace, large lateral and central plastral fontanelles, a ligamentous bridge, elongation of forelimb and hindlimb, elongation of pedal digit V, and a long tail.

Comments. *Neusticemys neuquina* is based on three shell fragments from the early Tithonian of the Vaca Muerta Formation, Neuquén, Argentina (Fernández and de la Fuente 1988). Additional specimens from the late middle Tithonian (Fernández and de la Fuente 1993; de la Fuente and Fernández 2011) and late Tithonian (Gasparini et al. 1997) of the same formation have since been referred to this taxon. *Neusticemys neuquina* was initially tentatively referred to *Eurysternum* (Fernández and de la Fuente 1988), but more complete specimens and comparison with the material from the Tithonian of southern Germany led Fernández and de la Fuente (1993) to refer this species to a new genus. This species is the only thalassochelydian known outside Europe, but its relationships are still unclear (Fernández and de la Fuente 1993; Gasparini et al. 1997, 2015; de la Fuente 2007; de la Fuente and Fernández 2011). The retention of wide costo-peripheral fontanelles, the ligamentous bridge with axillary and inguinal buttresses forming peg-like projections, and the presence of large lateral and central plastral fontanelles are reminiscent of the condition in some "eurysternids," notably *Eurysternum wagleri*. However, its size (up to around 50 cm in carapace length) and its resemblance with *Thalassemys marina* (notably concerning the morphology of the plastron) could suggest a referral to "thalassemydids." Fernández and de la Fuente (1993) and subsequent authors noted that BSPG 1952 I 113, a carapace from the Late Jurassic of Langenaltheim, Bavaria, Germany, is remarkably similar in morphology with *Neusticemys neuquina*. Interestingly, this specimen is also characterized by the presence of distinct linear striations perpendicular to costals and neurals margins, a thalassemydid feature (e.g., Püntener et al. 2015). New material, including a cranium, from the type locality is currently being described and a preliminary phylogenetic analysis suggests that *Neusticemys neuquina* is closely related to the Late Jurassic *Solnhofia parsonsi* and *Jurassichelon oleronensis*, as well as to the Early Cretaceous *Santanachelys gaffneyi* (de la Fuente et al. 2014). It is more appropriate to wait for the conclusion of this ongoing study before referring *Neusticemys neuquina* to either "Eurysternidae" or "Thalassemydidae."

The anterior carapacial rim of *Neusticemys neuquina* strongly reminds one of the condition in numerous pan-chelonioids with a nuchal projecting forward and a depressed carapace border along the two first pairs of peripherals. A similar condition occurs in some undescribed specimens from the Solnhofen Limestone (see above). *Neusticemys neuquina* is also characterized by a relative elongation of both the fore- and hindlimbs and an elongation of digit V in the pes (de la Fuente and Fernández 2011).

Owadowia borsukbialynickae **Szczygielski et al., 2017**

Taxonomic history. *Owadowia borsukbialynickae* Szczygielski et al., 2017 (new species).

Type material. ZPAL V/O-B/1959 (holotype), a fragment of lower jaw, right coracoid, ilium, and femur (Szczygielski et al. 2017, figs. 2–4).

Type locality. Owadów-Brzezinki Quarry, near Tomaszów Mazowiecki, Łódź Voivodeship, Poland (Figure 4); Kcynia Formation, lower Tithonian, Late Jurassic (Szczygielski et al. 2017).

Referred material and range. No specimens have been referred to date.

Diagnosis. The available material of *Owadowia borsukbialynickae* lacks diagnostic characters of *Thalassochelydia*, but several characteristics of the lower jaw combined with temporal and spatial considerations suggest a close relationship with thalassochelydians (see below). *Owadowia borsukbialynickae* differs from all other thalassochelydians by a narrow and V-shaped lower jaw, a spoon-like symphysis without symphyseal hook, a triturating surface well developed in the symphyseal area but only moderately developed along the mandibular rami, a high and sharp labial ridge, a reduced lingual ridge present only laterally, and a large splenial.

Comments. *Owadowia borsukbialynickae* is based on a partial specimen consisting of the anterior part of a lower jaw, a right coracoid, a right ilium, and a nearly complete right femur (Szczygielski et al. 2017). This material was found in the Tithonian of central Poland alongside remains of other marine reptiles (ichthyosaurians and thalattosuchian crocodylomorphs). The mandible of *Owadowia borsukbialynickae* bears some similarity with that of *Solnhofia parsonsi* and *Portlandemys mcdowelli*, notably, in being narrow and V-shaped and in having a well-developed symphysis (Szczygielski et al. 2017). Because of these similarities and the fact that the specimen was found in deposits formed in a shallow marine environment during the Late Jurassic, *Owadowia borsukbialynickae* is tentatively included in *Thalattochelydia* herein. Given that the body parts that represent this species are not known for the majority of named species from localities further to the west, future finds across Europe will be able to clarify if *Owadowia borsukbialynickae* is a valid species, or simply the junior synonym of a previously named species.

Pelobatochelys blakii **Seeley, 1875**

Taxonomic history. *Pelobatochelys blakii* Seeley, 1875 (new species); *Pelobatochelys blakei* Lydekker 1889b (incorrect spelling); *Tropidemys blakii* Pérez-García 2015a (new combination and lectotype designation).

Type material. NHMUK R.2a (lectotype), central fragment of carapace with neurals IV–VI and fragments of adjoining costals (Seeley 1875, pl. 13.1b; Pérez-García 2015a, fig. 2e–g); NHMUK R.2, NHMUK OR44177a, NHMUK OR44177, NHMUK OR44177b, and NHMUK OR41235 (paralectotypes), fragments of carapace with nuchal, neurals and costals, isolated pygal bone, and isolated peripheral bone (Seeley 1875, pl. 13.1a, c, d; Pérez-García 2015a, figs. 2a–d, 2h–j, 3i–l).

Type locality. Smallmouth Sands, Weymouth, Dorset, United Kingdom (Figure 4); Kimmeridge Clay, early Kimmeridgian, Late Jurassic (Seeley 1875; Benton and Spencer 1995).

Referred material and range. Late Jurassic (early Kimmeridgian) of the Kimmeridge Clay, Weymouth, Dorset, United Kingdom (hypodigm of Pérez-García

Dorset, United Kingdom (hypodigm of Pérez-García 2015a).

Diagnosis. *Pelobatochelys blakii* can be diagnosed as a thalassochelydian by the presence of three cervical scutes. *Pelobatochelys blakii* differs from all other thalassochelydians by having thin and reduced costals that partly reveal the underlying thoracic ribs, elongated and keeled neurals, a waisted neural V, a tendency toward the fusion of posterior neurals, and a fluted pattern on the vertebral scutes.

Comments. *Pelobatochelys blakii* is based on a syntype series consisting of several individuals from the Smallmouth Sands, Kimmeridge Clay, Weymouth, Dorset, United Kingdom (Seeley 1875; Benton and Spencer 1995). *Pelobatochelys blakii* is only known from the carapace and has never been found elsewhere than in the Kimmeridge Clay of Weymouth. Little attention was given to this taxon since its original description, but most authors acknowledged the validity of this species (Lydekker 1889b; Delair 1958; Kuhn 1964b). Lydekker (1889b) considered it to be an intermediate between *Acichelys redenbacheri* and *Tropidemys langii*, whereas Delair (1958) referred *Pelobatochelys blakii* to Acichelyidae. Recently, Püntener et al. (2014) suggested that the material of *Pelobatochelys blakii* was too incomplete to warrant a definitive diagnosis and proposed that this material should be referred to *Tropidemys* sp. based on the presence of keeled neurals. Finally, Pérez-García (2015a) revised the material and proposed the new combination *Tropidemys blakii*. However, the only characteristics that *Pelobatochelys blakii* and *Tropidemys* spp. have in common are the keeled neurals and tectiform carapace. The remaining features are incongruent with a referral to *Tropidemys*, at least as diagnosed by Püntener et al. (2014) and Pérez-García (2015a), in particular the elongated neurals with shorter anterolateral margins, the reduced ossification of the costals, and the very wide vertebral scutes with a unique fluted sculpturing. Until the relationships of this enigmatic turtle are better understood, it is preferable to keep it in its own genus and maintain the use of the name *Pelobatochelys blakii*. This species is notably characterized by the reduced ossification and the thinness of the costals, the keeled neurals, the waisted neural V, the tendency toward the fusion of posterior neurals, and the unique fluted pattern left by the wide vertebral scutes (especially strong anteriorly on each vertebral).

Lydekker (1889b) argued that this taxon could reach large size. He notably described a specimen that shows the contour of the carapace, but not the sutures of the bones (Lydekker 1889b). At the time, this specimen was still in the collection of the recently deceased collector R.F. Damon. The NHMUK collection now houses a specimen (NMHUK R1769) that fairly matches this description and that was purchased from the Damon collection in 1890. NHMUK R1769 is indeed a large fossil that appears to be a tectiform turtle shell. Although this purported shell may belong to *Pelobatochelys blakii*, it should also be kept in mind that *Tropidemys langii*, another turtle with a tectiform shell, is also present in the Kimmeridge Clay of Weymouth, United Kingdom (Anquetin and Chapman 2016). Therefore, the referral of this specimen remains conjectural.

Invalid and Problematic Taxa

Acichelys approximata Wagner, 1856

nomen dubium

Taxonomic history. *Acochelys approximata* Wagner, 1856 (new species, incorrect spelling of genus name); *Euryaspis*? *approximata* Wagner 1861a (new combination); *Euryaspis approximata* Maack 1869 (new combination); *Eurysternum wagleri* = *Euryaspis approximata* Kuhn 1961 (junior synonym).

Type material. NMAG uncat. (holotype), a fragmentary carapace (Wagner 1856; no illustration available), now considered lost (see comments below).

Type locality. Neuburg an der Donau, Bavaria, Germany (Wagner 1856); Tithonian, Late Jurassic (see comments below).

Comments. Although Wagner (1856) explicitly refers to Meyer's (1854) genus *Acichelys*, the genus name is consistently misspelt as "*Acochelys*" throughout the text. Indeed, the specific epithet "*approximata*" was chosen because Wagner (1856) concluded that this taxon closely resembles Meyer's (1854) *Acichelys redenbacheri*. *Acichelys approximata* was described and diagnosed based on a single fragmentary carapace (Wagner 1856), which was never illustrated in the literature. Wagner (1856) states that the holotype originated from a yellowish, dense limestone below the dolomite and lithographic limestone, which is extremely vague. However, given that most deposits exposed in the area of Neuburg an der Donau are Late Jurassic (Tithonian) in age (Meyer and Schmidt-Kaler 1996), it is reasonable to speculate that the type specimen was Tithonian as well.

According to Wagner (1856) and Maack (1869), the holotype of *Acichelys approximata* was in possession of the Naturhistorischer Verein (Natural History Society) of

Augsburg, Germany, but the collections of the Naturhistorischer Verein (now the Naturmuseum Augsburg) were destroyed during an air raid in 1944 (Achtlig, pers. comm., 2002). With the specimen lost, it is impossible to reevaluate what taxon this name objectively refers to or which locality the specimen is from. None of the characters listed by Wagner (1856) are diagnostic at the species level, but rather diagnose eurysternid turtles in general (Joyce 2003; Anquetin and Joyce 2014). The name *Acichelys approximata* is therefore available, but must be considered a nomen dubium.

Acichelys redenbacheri **Meyer, 1854**

nomen invalidum

(junior synonym of *Eurysternum wagleri* Meyer, 1839c)

Taxonomic history. *Acichelys redenbacheri* Meyer, 1854 (new species); *Eurysternum crassipes* = *Acichelys redenbacheri* = *Palaeomedusa testa* Wagner 1861b (synonymy); *Eurysternum crassipes* = *Achelonia formosa* = *Acichelys redtenbacheri* = *Euryaspis radians* = *Eurysternum wagleri* = *Palaeomedusa testa* Rütimeyer 1873b (synonymy, incorrect spelling of species epithet); *Eurysternum wagleri* = *Aplax oberndorferi* = *Achelonia formosa* = *Acichelys redenbacheri* = *Euryaspis radians* = *Eurysternum crassipes* = *Palaeomedusa testa* = *Parachelys eichstaettensis* Zittel 1877a (junior synonym); *Acichelys redenbacheri* = *Achelonia formosa* (?) = *Euryaspis radians* (?) = *Eurysternum crassipes* = *Palaeomedusa testa* Lydekker 1889b (senior synonym); *Eurysternum wagleri* = *Acichelys redenbacheri* Anquetin and Joyce 2014 (junior synonym, lectotype designation).

Type material. MNB R 2440 (lectotype), external mold of the posterior half of a carapace (Meyer 1860, pl. 21.4, 5; Anquetin and Joyce 2014, figs. 5, 6). The paralectotypes are all lost (Anquetin and Joyce 2014).

Type locality. Lithographic limestone quarries of Solnhofen, Bavaria, Germany (Meyer 1854, 1860; Figure 4); Solnhofen Formation, early Tithonian, Late Jurassic (Schweigert 2007).

Comments. *Acichelys redenbacheri* was originally typified based on a series of unrelated specimens from different quarries and strata. The lectotype (MNB R 2440) is from the lithographic limestone quarries of Solnhofen (Tithonian), whereas the paralectotypes are from the *Diceras*-Limestone (late Kimmeridgian to early Tithonian) and lithographic limestone (Tithonian) of Kelheim, Germany (Meyer 1854, 1860). None of these specimens were illustrated in the original publication (Meyer 1854). Only one specimen (MNB R 2440) can be confidently identified as being part of the syntype series and was recently designated as the lectotype of *Acichelys redenbacheri*, whereas the paralectotypes are all considered to be lost (Anquetin and Joyce 2014). Anquetin and Joyce (2014) argued that MNB R 2440 shares several similarities (deep pygal notch, contribution of vertebral V to the posterior carapacial margin, wide vertebral scutes with radiating pattern, carapace tear-drop shaped) with specimens referred to *Eurysternum wagleri* and concluded that *Acichelys redenbacheri* should be considered a junior synonym of this species. We agree with this assessment.

Aplax oberndorferi **Meyer, 1843**

nomen dubium

Taxonomic history. *Aplax oberndorferi* Meyer, 1843 (new species); *Idiochelys fitzingeri* = *Idiochelys wagneri* = *Aplax oberndorferi* Wagner 1861b (junior synonym); *Eurysternum wagleri* = *Achelonia formosa* = *Acichelys redenbacheri* = *Aplax oberndorferi* = *Euryaspis radians* = *Eurysternum crassipes* = *Palaeomedusa testa* = *Parachelys eichstaettensis* Zittel 1877a (junior synonym).

Type material. BSPG uncat. (holotype), a near-complete juvenile specimen (Meyer 1860, pl. 18.2); now considered lost (see below).

Type locality. Lithographic limestone quarries of Kelheim, Bavaria, Germany (Meyer 1843); Solnhofen Formation, early Tithonian, Late Jurassic (Schweigert 2007).

Comments. *Aplax oberndorferi* is based on a single, small individual that measured no more than 6.3 cm from the snout to the tip of the tail (Meyer 1843). The illustration of the holotype depicts a turtle with a carapace that shows almost no signs of ossification of the costals, peripherals, or neurals (Meyer 1860). Meyer (1843) was well aware that many juvenile turtles do not exhibit well-ossified shells, but he brought into consideration that the aforementioned elements are absent in adult leatherback turtles (*Dermochelys coriacea*). In case this specimen represented the juvenile of a dermochelyid turtle, he created the new taxon name *Aplax oberndorferi*.

Since Meyer (1843), an additional subadult turtle was described from the Solnhofen region (figured in Meyer 1860), which Meyer (1854) also attributed to the taxon *Aplax oberndorferi* even though this turtle possesses poorly ossified neurals and costals. Subsequent authors disagreed with Meyer's assessments and synonymized *Aplax oberndorferi* with taxa such as *Idiochelys fitzingeri* (Wagner 1861a; based on the alleged lack of neurals) or *Eurysternum wagleri* (Zittel 1877a, 1877b). Given the loss of the holotype, the lack of morphology apparent from the type illustration, and the many valid adult taxa from the Solnhofen region, it is unclear to what taxon *Aplax oberndorferi* objectively refers to. The possibility that this taxon represents the juvenile of a dermochelyid can be confidently excluded, as the fossil record of this group most certainly does not precede the Late Cretaceous (Joyce et al. 2013). As such, even though the name must be considered available, *Aplax oberndorferi* should be ignored from future considerations as a nomen dubium.

Chelonemys ovata Jourdan, 1862

nomen invalidum

(junior synonym of *Idiochelys fitzingeri* Meyer, 1839b)

Taxonomic history. *Chelonemys ovata* Jourdan, 1862 (new species); *Idiochelys fitzingeri = Idiochelys wagnerorum = Chelonemys plana = Chelonemys ovata* Rütimeyer 1873b (junior synonym).

Type material. MHNL 20015634 (holotype), a near-complete individual, including carapace, skull, cervical series, partial limbs, and tail (Jourdan 1862; Rütimeyer 1873a, pl. 15.a; Lortet 1892, pl. 1.1).

Type locality. Cerin, Department of Ain, France (Jourdan 1862; Figure 4); Lithographic limestones of Cerin, late Kimmeridgian, Late Jurassic (Enay et al. 1994; Bernier et al. 2014).

Comments. *Chelonemys ovata* and *Chelonemys plana* (see below) are based on material from the late Kimmeridgian of Cerin, France. The original publication does not contain any illustration, but rather consists in a brief description of the two species made by Jourdan in 1862 in front of the "Société impériale d'agriculture, d'histoire naturelle et des arts de Lyon," a learned society based in Lyon, France. During this communication, Jourdan (1862) produced a lithograph depicting the three specimens he was aware of from Cerin. One he referred to *Chelonemys ovata*, one to *Chelonemys plana*, and the third to *Idiochelys* sp. (Lortet 1892). After his death, Louis Lortet sent the lithograph to Ludwig Rütimeyer, who published it in his volume on the fossil turtles from Solothurn (Rütimeyer 1873a; Lortet 1892). However, Rütimeyer (1873a) somehow mixed the specimens, attributing the holotype of *Chelonemys ovata* to *Chelonemys plana* and vice versa. This original lithographic plate was irremediably damaged during reproduction (Rütimeyer 1873a). A new one was commissioned and later published by Lortet (1892).

Chelonemys ovata is based on a single, near-complete specimen preserved in dorsal view on a slab of lithographic limestone. Rütimeyer (1873a, 1873b) concluded that *Chelonemys ovata* and *Chelonemys plana* were junior synonyms of *Idiochelys fitzingeri* from the Tithonian of Kelheim, Germany (see above). The holotype of *Chelonemys ovata* (MHNL 20015634) is indeed very similar to the lost holotype of *Idiochelys fitzingeri* and there is no doubt that these two specimens should be referred to the same species.

Chelonemys plana Jourdan, 1862

nomen invalidum

(junior synonym of Idiochelys fitzingeri Meyer, 1839b)

Taxonomic history. *Chelonemys plana* Jourdan, 1862 (new species); *Idiochelys fitzingeri = Idiochelys wagnerorum = Chelonemys plana = Chelonemys ovata* Rütimeyer 1873b (junior synonym).

Type material. MHNL 20015635 (holotype), a near-complete individual consisting of plastron, carapace, skull, complete forelimbs, left hind limb, and tail (Jourdan 1862; Rütimeyer 1873a, pl. 15.b; Lortet 1892, pl. 1.2).

Type locality. Cerin, Department of Ain, France (Jourdan 1862; Figure 4); Lithographic limestones of Cerin, late Kimmeridgian, Late Jurassic (Enay et al. 1994; Bernier et al. 2014).

Comments. *Chelonemys plana* is based on a single subcomplete specimen preserved in ventral view on a slab of late Kimmeridgian lithographic limestone from Cerin, France. When first figured (Rütimeyer 1873a), this specimen (MHNL 20015635) was mislabeled as the holotype of *Chelonemys ovata* (see above). Rütimeyer (1873a, 1873b) concluded that *Chelonemys plana* was a junior synonym of *Idiochelys fitzingeri* from the Tithonian of Kelheim, Germany. The preservation of the specimen in ventral view complicates direct comparison with the holotype of Idiochelys fitzingeri, as the latter is preserved in dorsal view. However, the collection of *Chelonemys* specimens from Cerin provides several indications that Rütimeyer (1873a) was correct (see Lortet 1892). What can be seen of the carapace in MHNL 20015635 is congruent with the morphology of specimens visible only in dorsal view, notably MHNL 20015634 (holotype of *Chelonemys ovata*) and MHNL 20015631. These specimens share the same limb morphology, notably, a remarkable manual phalangeal formula (2-2-3-3-3; but note that this formula is also known in *Parachelys eichstaettensis*, see above). MHNL 20015636, a smaller individual preserved in dorsal view, was also delicately prepared so as to reveal the dorsal surface of its plastron (Lortet 1892, pl. 2.1, 2), which is congruent with that of MHNL 20015635 except for the central plastral fontanelle, which is closed in this larger specimen. This strongly suggests that the *Chelonemys* specimens from Cerin belong to a single taxon and that this taxon is fully equivalent with the type of *Idiochelys fitzingeri*. We therefore confidently synonymize *Chelonemys plana* Jourdan, 1862 with *Idiochelys fitzingeri* Meyer, 1839b.

Chelonia valanginiensis Pictet in Pictet and Campiche, 1858–1860

nomen dubium

Taxonomic history. *Chelonia valanginiensis* Pictet in Pictet and Campiche, 1858–1860 (new species); *Chelone valanginiensis* Maack 1869 (new combination, possibly unintentional); *Tropidemys valanginiensis* Rütimeyer 1873a (new combination); *Tropidemys langii* = *Chelone valanginiensis* = *Stylemys lindensis* [sic] (pro parte) = *Tropidemys expansa* = *Tropidemys gibba* = *Tropidemys seebachi* Karl et al. 2007 (synonymy).

Type material. MCG GEOLREG 16849 (holotype), a partial carapace consisting of four neurals and the proximal part of the associated costals (Pictet and Campiche 1858–1860, pls. 1, 2, 3.1).

Type locality. Sainte-Croix, Canton of Vaud, Switzerland (Pictet and Campiche 1858–1860); formation unknown, possibly Valanginian (but see below), Early Cretaceous (Rittener 1902; Püntener et al. 2014).

Comments. *Chelonia valanginiensis* is based on a small fragment of a large carapace consisting of four neurals (possibly neurals III–VI) still attached to the proximal part of the neighboring costals. A plastron fragment, possibly a hypoplastron, and the distal half of a radius or ulna were also tentatively referred to this taxon (Pictet and Campiche 1858–1860), but these need not necessarily be related to this taxon. All material was collected in the vicinity of Sainte-Croix, Canton of Vaud, Switzerland. Although the description of the fossils from Sainte-Croix was authored by both Pictet and Campiche, a footnote explains that the part on vertebrates was written by Pictet alone and authorship is therefore restricted to him. Based on obvious similarities of the material from Sainte-Croix with specimens from Solothurn, Rütimeyer (1873a) proposed the new combination *Tropidemys valanginiensis*. The material from Sainte-Croix was recently reassessed by Püntener et al. (2014), who concluded that it was indeed referable to *Tropidemys* sp., but otherwise lacked diagnostic characters. *Chelonia valanginiensis* is therefore herein considered to be a nomen dubium.

The material from Sainte-Croix allegedly comes from Early Cretaceous (Valanginian) deposits (Pictet and Campiche 1858–1860), which would be remarkable since other “plesiochelyids” are restricted to the Late Jurassic. However, there are serious doubts from where the material was collected and the Kimmeridgian also occurs in the region of Sainte-Croix (Rittener 1902; Püntener et al. 2014). The occurrence of *Tropidemys*, and by extension of the “Plesiochelyidae,” in the Early Cretaceous must therefore be regarded as highly dubious.

Chelonides robusta Portis, 1878

nomen dubium

Taxonomic history. *Chelonides robusta* Portis, 1878 (new species); *Anaphotidemys robusta* Kuhn 1964b (new combination with substitute name proposed by Hay 1905); *Plesiochelys solodurensis* = *Chelonides robusta* = *Chelonides wittei* = *Emys etalloni* = *Plesiochelys langii* = *Plesiochelys minor* = *Stylemys hannoverana* = *Stylonides* [sic] *lindensis* [sic] Karl et al. 2007 (junior synonym).

Type material. GZG 769-11 (syntype), right costals IV and V (Portis 1878, pl. 18.14); GZG 769-12 (syntype), left hyo- and hypoplastron (Portis 1878, pl. 18.15); GZG 769-13 to GZG 769-19 (syntypes), isolated shell fragments (Portis 1878, not figured).

Type locality. Tönniesberg, Hannover, Lower Saxony, Germany; *Pteroceras* layer (= *Aporrhais* layer), middle Kimmeridgian, Late Jurassic (Portis 1878; Karl et al. 2007).

Comments. *Chelonides robusta* is based on a syntype series consisting of two costals (GZG 769-11), a left hyo- and hypoplastron (GZG 769-12), and isolated shell fragments (GZG 769-13 to GZG 769-19). Portis (1878) distinguished *Chelonides robusta* from *Chelonides wittei* based on characters of the carapace: carapace short and wide; bone unusually thick; vertebral scutes only covering one-third of the costals. However, he considered the material insufficient to warrant proper description. Oertel (1924) proposed transferring the plastral material of *Chelonides robusta* (GZG 769-12) to *Plesiochelys* but expressed some doubts as to whether the remaining material can be retained in *Chelonides*. Similarly, Kuhn (1964b) pointed out that the material was so scarce that a referral to *Chelonides* was questionable. Finally, Karl et al. (2007) referred all material of *Chelonides robusta* to *Plesiochelys solodurensis*, effectively synonymizing the two taxa.

The thickness and shape of the two costals (GZG 769-11) strongly remind us of those of *Tropidemys langii*. However, the preserved vertebral scute is too wide and laterally too pointed to allow a referral to this species. Furthermore, the medial part of the costals is damaged, thereby preventing confirmation of a referral to *Tropidemys langii* or closely related forms. The remainders of the syntype series are too poorly preserved to allow any definitive conclusion. We therefore consider *Chelonides robusta* Portis, 1878 to be a nomen dubium.

***Clemmys*? *grayi* Fitzinger, 1835**

nomen oblitum

(senior synonym of *Plesiochelys etalloni* [Pictet and Humbert, 1857])

Taxonomic history. *Clemmys*? *grayi* Fitzinger, 1835 (unnecessary substitute name for *Emys hugi* Gray, 1831).

Type material. See *Emys hugi* Gray, 1831 (below).

Type locality. See *Emys hugi* Gray, 1831 (below).

Comments. *Clemmys*? *grayi* was apparently proposed by Fitzinger (1835) as a substitute name for *Emys hugi* Gray, 1831, which he possibly considered too close orthographically to *Emys hugii* Gray, 1831, a proposition with which we can only sympathize. Fitzinger (1835) did not explicitly refer to specimens in his contribution, but he clearly stated that his *Clemmys*? *grayi* corresponds to *Emys hugi*. Such an emendation is considered unjustified by the current code of nomenclature (ICZN 1999). As an unnecessary substitute name, *Clemmys*? *grayi* is not valid, but remains available. Like *Emys hugi* (see below), this name is also a senior synonym of *Plesiochelys etalloni* (Pictet and Humbert, 1857). However, *Clemmys*? *grayi* has not been used as a valid name since Giebel (1847; as Emys grayi) and must therefore be considered a nomen oblitum.

***Craspedochelys crassa* Rütimeyer, 1873a**

nomen invalidum

(junior synonym of *Craspedochelys picteti* Rütimeyer, 1873a)

Taxonomic history. *Craspedochelys crassa* Rütimeyer, 1873a (new species); *Craspedochelys picteti* = *Craspedochelys crassa* Bräm 1965 (junior synonym); *Plesiochelys etalloni* = *Craspedochelys crassa* = *Craspedochelys picteti* = *Plesiochelys jaccardi* = *Plesiochelys sanctaeverenae* = *Plesiochelys solodurensis* = *Stylemys lindensis* [sic] Gaffney 1975a (junior synonym).

Type material. NMS 8507 (holotype; formerly NMS 130), a poorly preserved carapace fragment (Rütimeyer 1873a, pl. 9.5, 5b).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. *Craspedochelys crassa* is based on a single carapace fragment that reveals relatively little anatomy. Rütimeyer (1873a) mainly diagnosed *Craspedochelys crassa* based on the greater thickness of the costal bones. However, Bräm (1965) noted much later that this feature is relatively variable within the shell of many individuals from Solothurn and therefore synonymized *Craspedochelys crassa* with *Craspedochelys picteti*, an assessment recently confirmed by Anquetin, Püntener and Billon-Bruyat (2014). We agree with this assessment.

***Craspedochelys plana* Rütimeyer, 1873a**

nomen invalidum

(junior synonym of *Tropidemys langii* Rütimeyer, 1873a)

Taxonomic history. *Craspedochelys plana* Rütimeyer, 1873a (new species); *Tropidemys langii* = *Craspedochelys plana* Bräm 1965 (junior synonym).

Type material. NMS 8500 (holotype; formerly NMS 132), left anterolateral portion of a carapace (Rütimeyer 1873a, pl. 9.1, 2).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. *Craspedochelys plana* is based on a fragmentary piece of carapace. The dorsal surface does not allow precise identification, but Bräm (1965) correctly noted that the axillary buttress forms a crest on the visceral side of costal I, a feature characteristic of *Tropidemys langii* (Püntener et al. 2014). We therefore agree with Bräm (1965) in synonymizing *Craspedochelys plana* with *Tropidemys langii*.

***Cyrtura temnospondyla* Jaekel, 1904**

nomen dubium

Taxonomic history. *Cyrtura temnospondyla* Jaekel, 1904 (new species).

Type material. MNB R1890 (holotype), a series of 14 articulated caudal vertebrae (Jaekel 1904, fig. 6; Kuhn 1964a, fig. 1a; Anquetin and Milner 2015, fig. 2).

Type locality. Locality uncertain, Bavaria, Germany (Jaekel 1904); Solnhofen Formation, early Tithonian, Late Jurassic (Schweigert 2007).

Comments. Jaekel (1904) originally described the holotype of *Cyrtura temnospondyla* as the tail of a temnospondyl amphibian. For 60 years, subsequent workers tended to disagree with this referral, alternatively considering this specimen as undiagnostic (Bergounioux 1955; Huene 1956) or tentatively referring it to turtles, though without discussion (Romer 1956, 1966). In contrast, Kuhn (1964a) reaffirmed the original interpretation of Jaekel (1904). More recently, several authors reached the conclusion that *Cyrtura temnospondyla* was not a temnospondyl amphibian, but remained uncertain regarding its proper identification (Warren and Hutchinson 1983; Schoch and Milner 2000; Maisch and Matzke 2005). Anquetin and Milner (2015) recently reevaluated the holotype and concluded that it can be confidently identified as a turtle tail. However, given the absence of diagnostic characters, C*yrtura temnospondyla* must be considered a nomen dubium.

Emys beaugrandi **Sauvage, 1872**

nomen dubium

Taxonomic history. *Emys beaugrandi* Sauvage, 1872 (new species); *Plesiochelys beaugrandi* Sauvage 1873 (new combination).

Type material. MHNB 215 (holotype), a carapace fragment (Sauvage 1872; Sauvage 1873, unnumbered figure), now considered lost (Vadet and Rose 1986).

Type locality. Delahodde Quarry, Boulogne-sur-Mer, Department of Pas-de-Calais, France (Figure 4); formation unknown, Kimmeridgian, Late Jurassic (Sauvage 1873; Vadet and Rose 1986).

Comments. *Emys beaugrandi* is based on a single specimen from the Kimmeridgian of Boulogne-sur-Mer, France. Sauvage (1872, 1873) only described some parts of the carapace (neurals and costals) and only schematically figured the outline of vertebral II and neural II. It is therefore unclear how complete this specimen was. The specimen was originally housed in the Beaugrand Collection of the Natural History Museum of Boulogne-sur-Mer (MHNB 215), but the museum is now closed and the collections have been dissolved. What remained of Sauvage's turtles was salvaged and is currently under study (Lapparent de Broin, pers. comm., 2014), but this collection apparently does not include the holotype specimen of *Emys beaugrandi*, thereby confirming that the holotype is lost, as already noted by Vadet and Rose (1986). The original diagnosis and description of *Emys beaugrandi* by Sauvage (1872, 1873) are too general to allow a precise identification and this species is therefore herein considered to be a nomen dubium. However, it should be noted that some characteristics of *Emys beaugrandi* evoke "thalassemydids," in particular the anterolaterally diverging lateral sides of vertebral I, the anterolaterally concave and posterolaterally convex outline of vertebral II, the presence of disarticulated costals with strong, protruding rib tip, and the abrupt thinning of the distal parts of the costals.

Emys dollfusii **Lennier, 1870**

nomen dubium

(objective senior synonym of *Plesiochelys normandica* Bergounioux, 1937)

Taxonomic history. *Emys dollfusii* Lennier, 1870 (new species); *Emys dollfussii* Sauvage 1873 (incorrect spelling of species epithet); *Plesiochelys dollfussi* Sauvage 1873 (new combination and incorrect spelling of species epithet); [*Emys dolfusii*] Bergounioux 1937 (nomen dubium and incorrect spelling of species epithet); *Emys dollfussi* = *Plesiochelys normandicus* Bigot 1939 (senior objective synonym and incorrect spelling of species epithet).

Type material. MHNH uncat. (holotype), a fragmentary shell (Lennier 1870, pl. 7.1, 2; Lennier 1887, pl. 22.1, 2; Bergounioux 1937, pl. 1), destroyed during World War II (Lapparent de Broin, pers. comm., 2014).

Type locality. Cap de la Hève, near Le Havre, Department of Seine-Maritime, France (Figure 4); formation unknown, Kimmeridgian, Late Jurassic (Lennier 1870, 1887).

Comments. *Emys dollfusii* is based on a fragmentary shell from the Kimmeridgian of Cap de la Hève, near Le Havre, France (Lennier 1870) that also serves as the holotype of *Plesiochelys normandica* Bergounioux, 1937, as noted by Bigot (1939). There is some ambiguity regarding the year of publication of the original description, as the date of publication is not provided. Lennier (1887) and Bigot (1939) wrote that Lennier's *Etudes géologiques et paléontologiques sur l'embouchure de la Seine* was published in 1863, but several bibliographical repositories date this publication from 1870. We retain the later date herein as it is more conservative. The holotype specimen consists of a large shell lacking most of the distal parts of the costals, the suprapygal area, and the anterior lobe of the plastron. The preservation of this shell was rather poor and most sutures were not visible (Lennier 1870, 1887; Bergounioux 1937). Unfortunately, the specimen was housed in Le Havre and was destroyed during World War II, so it is now impossible to scrutinize its morphology, although photographs published by Bergounioux (1937) reveal some interesting anatomical features. The size and general morphology are consistent with that of “plesiochelyids.” The outline of the carapace was subcircular with a shallow nuchal notch. The plastron was proportionally short, as evidenced by the important post-xiphiplastral space. The xiphiplastra were probably about as wide as long when complete, and they may have defined a small xiphiplastral notch posteromedially. These characteristics are shared by species referred herein to the genus *Craspedochelys*. However, without the type material, it is not possible to find enough characters to diagnose *Emys dollfusii* as a valid species or place it in synonymy with any valid species, which is why it is herein considered a nomen dubium.

Emys dutertrei Sauvage, 1872

nomen dubium

Taxonomic history. *Emys dutertrei* Sauvage, 1872 (new species); *Plesiochelys dutertrei* Sauvage 1873 (new combination); *Plesiochelys dutertrei* Vadet and Rose 1986 (lectotype designation).

Type material. MHNB 212 (lectotype), a carapace fragment (Sauvage 1872; Sauvage 1873, unnumbered figure; Vadet and Rose 1986, pl. 18); MHNB uncat. (paralectotype), an unfigured hyoplastron (Sauvage 1872, 1873; Vadet and Rose 1986).

Type locality. Boulogne-sur-Mer, Department of Pas-de-Calais, France (Figure 4); formation unknown, Kimmeridgian, Late Jurassic (Sauvage 1873; Vadet and Rose 1986).

Comments. *Emys dutertrei* is based on a carapace fragment and a hyoplastron from the Kimmeridgian of Boulogne-sur-Mer, France. This material was only briefly described by Sauvage (1872, 1873). More recently, the carapace fragment was designated as the lectotype of *Emys dutertrei* (Vadet and Rose 1986). This specimen consists only of neurals II and III, partial neurals IV and V, and proximal parts of left costals I–III and right costals I–V. Vertebral scutes are moderately wide and are roughly similar in morphology to those observed in *Plesiochelys etalloni* and *Craspedochelys* spp. A first-hand observation of this material might reveal more information, but for the time being we consider this specimen as undiagnostic at the species level. *Emys dutertrei* is therefore herein considered to be a nomen dubium.

Sauvage (1873) tentatively referred an additional large bone to *Emys dutertrei* that he originally identified as an epiplastron (“épisternal”), but which appears to be a hyoplastron based on the associated description (no illustration). This specimen was found in a different level, possibly lower in the Kimmeridgian. The whereabouts of that specimen are uncertain.

Emys hugi Gray, 1831

nomen oblitum, designation of lectotype

(senior synonym of *Plesiochelys etalloni* [Pictet and Humbert, 1857])

Taxonomic history. *Emys hugi* Gray, 1831 (new species); *Clemmys*? *grayi* = *Emys jurensis* (pro parte) Fitzinger 1835 (unnecessary substitute name, new combination, and partial objective synonymy).

Type material. NMS 8693 (lectotype; formerly NMS 59), a distorted, near-complete shell (Cuvier 1824, pl. 15.4, 5; Rütimeyer 1873a, pl. 12.1, 2; Anquetin, Püntener and Billon-Bruyat 2014, fig. 2); NMS 8738 (paralectotype; formerly NMS 134), a disarticulated, partial skull with associated mandible, hyoid elements, and shell fragment (Cuvier 1824, pl. 15.7; Rütimeyer 1873a, pl. 14.5; Gaffney 1975a, fig. 6; Gaffney 1976, figs. 14, 35–37, 41–43, 48). Gray (1831) also designated the following specimens as parts of the type series: two neurals clearly assignable to Tropidemys langii (Cuvier 1824, pl. 15.8, 9); a pelvis (Cuvier 1824, pl. 15.10); a plastron fragment (Cuvier 1824, pl. 15.11).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Cuvier 1824; Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. Thanks to the work of Kuhn (1964b), we were able to track down the taxonomic history of a series of five species typified in the early 1830s based on material from Solothurn, Switzerland, namely, *Emys hugi* Gray, 1831, *Emys hugii* Gray, 1831, *Emys trionychoides* Gray, 1831, *Emys jurensis* Keferstein, 1834, and *Clemmys*? *grayi* Fitzinger, 1835. Cuvier (1824) identified three distinct species in the Solothurn material sent to him by F.J. Hugi. Gray (1831) proposed the names *Emys hugi*, *Emys hugii*, and *Emys trionychoides* for these three species. Keferstein (1834), probably unaware of the work of Gray (1831), united all the specimens described and figured by Cuvier (1824) under a single name, *Emys jurensis*. Fitzinger (1835) reestablished the names proposed by Gray (1831), which he tentatively referred to the genus *Clemmys*, and proposed *Clemmys*? *grayi* as a substitute name for *Emys hugi*, perhaps because he felt it confusing to have two similarly-spelt turtle species from the same locality. These taxa were described by their respective authors along with a specific reference to specimens described and figured by Cuvier (1824), which means that they are all available names. Some of these, notably *Emys hugi*, had the potential to alter currently established taxonomy. However, all of these species names have not been used as valid since Giebel (1847) and therefore fall under Article 23.9 of the current code of zoological nomenclature (ICZN 1999) as nomina oblita. If applicable, the precedence may be reserved.

As originally defined, *Emys hugi* is a chimera based on a syntype series that includes at least two taxa. The first, represented notably by specimen NMS 8693 (the lectotype of *Plesiochelys solodurensis*), corresponds to *Plesiochelys etalloni*, the second, represented by two typical neurals (Cuvier 1824, pl. 15.8, 9), corresponds to *Tropidemys langii*. Gray (1831) did not designate a type specimen, but his description of *Emys hugi* matches the description of NMS 8693 by Cuvier (1824). NMS 8693 is therefore designated herein as the lectotype of *Emys hugi*, which means that *Emys hugi* can be considered as the objective senior synonym of *Plesiochelys solodurensis* and, by extension, the subjective senior synonym of *Plesiochelys etalloni*. To our knowledge, *Emys hugi* was not used as a valid name since Gray (1831). In contrast, both *Plesiochelys solodurensis* and *Plesiochelys etalloni* have been used as valid names on multiple occasions since Rütimeyer (1873a). Following Article 23.9 of the ICZN (1999), *Emys hugi* must be considered a nomen oblitum, and we here therefore disregard its objective synonymy with *Plesiochelys solodurensis* and senior synonymy with *Plesiochelys etalloni*.

Emys hugii Gray, 1831

nomen oblitum

(senior synonym of *Plesiochelys etalloni* [Pictet and Humbert, 1857])

Taxonomic history. *Emys hugii* Gray, 1831 (new species); *Clemmys*? *hugii* = *Emys jurensis* (pro parte) Fitzinger 1835 (new combination and partial objective synonymy).

Type material. A lateral fragment of carapace (holotype; Cuvier 1824, pl. 15.6), whereabouts uncertain (see below).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Cuvier 1824; Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. *Emys hugii* is based on a single specimen described and figured by Cuvier (1824), who noted its large size (estimated carapace length of 22 French inches, about 60 cm) and flatness (see *Emys hugi* above for additional background information). However, the morphology of this specimen does not significantly depart from what is known in *Plesiochelys etalloni*, but is otherwise distinct from all other species present in Solothurn, Switzerland (Anquetin, Püntener and Billon-Bruyat 2014). To our knowledge, *Emys hugii* was not used as a valid name since Giebel (1847), in contrast to *Plesiochelys etalloni*, which has repeatedly been used as a valid name since Pictet and Humbert (1857). Following Article 23.9 of the ICZN (1999), we therefore consider *Emys hugii* to be a nomen oblitum and disregard its senior synonymy with *Plesiochelys etalloni*.

We have not located this specimen in the NMS collections, but we did not specifically look for it either. The type is similar to NMS 8512 (formerly NMS 125), but that appears to be superficial as the latter was only found in 1876 (Bräm 1965:123).

Emys jurensis Keferstein, 1834

nomen oblitum [lectotype designation]

(senior synonym of *Plesiochelys etalloni* [Pictet and Humbert, 1857])

Taxonomic history. *Emys jurensis* Keferstein 1834 (new species); *Clemmys*? *grayi*, *Clemmys*? *hugii*, *Clemmys*? *trionychoides* = *Emys jurensis* (pro parte, respectively) Fitzinger 1835 (partial objective synonymy).

Type material. NMS 8693 (lectotype; formerly NMS 59), a distorted, near-complete shell (Cuvier 1824, pl. 15.4, 5; Rütimeyer 1873a, pl. 12.1, 2; Anquetin, Püntener and Billon-Bruyat 2014, fig. 2); NMS 8738 (paralectotype; formerly NMS 134), a disarticulated, partial skull with associated mandible, hyoid elements, and shell fragment (Cuvier 1824, pl. 15.7; Rütimeyer 1873a, pl. 14.5; Gaffney 1975a, fig. 6; Gaffney 1976, figs. 14, 35–37, 41–43, 48); NMS 8547 (paralectotype; formerly NMS 61), a fragment of the pygal region of a carapace in visceral view (Cuvier 1824, pl. 21.1; Rütimeyer 1873a, pl. 4.2). Keferstein (1834) also designated the following specimens as parts of the type series: a lateral fragment of carapace (Cuvier 1824, pl. 15.6); two neurals clearly assignable to *Tropidemys langii* (Cuvier 1824, pl. 15.8, 9); a pelvis (Cuvier 1824, pl. 15.10); a plastron fragment (Cuvier 1824, pl. 15.11).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Cuvier 1824; Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. Keferstein (1834) was undoubtedly unaware of the work of Gray (1831) when he proposed the name *Emys jurensis* for all the specimens from Solothurn, Switzerland described and figured by Cuvier (1824; see *Emys hugi* above). We herein designate NMS 8693 as the lectotype of *Emys jurensis*, thereby rendering this species a junior objective synonym of *Emys hugi* and a senior objective synonym of *Plesiochelys solodurensis*. *Emys jurensis* is also a senior synonym of *Plesiochelys etalloni*, but, as it has not been used as a valid name since Keferstein (1834), we here follow Article 23.9 of the ICZN (1999) by considering *Emys jurensis* a nomen oblitum and by ignoring its senior synonymy with *Plesiochelys etalloni* (see *Emys hugi* above for additional background information).

Emys trionychoides Gray, 1831

nomen oblitum

(senior synonym of *Plesiochelys etalloni* [Pictet and Humbert, 1857])

Taxonomic history. *Emys trionychoides* Gray, 1831 (new species); *Clemmys*? *trionychoides* = *Emys jurensis* (pro parte) Fitzinger 1835 (new combination and partial objective synonymy); [*Emys trionychoides*] Giebel 1847 (improper use of name).

Type material. NMS 8547 (holotype; formerly NMS 61), a fragment of the pygal region of a carapace in visceral view (Cuvier 1824, pl. 21.1; Rütimeyer 1873a, pl. 4.2).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Cuvier 1824; Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. *Emys trionychoides* is based on a posterior carapacial fragment depicted in visceral view consisting of the last pair of costals, the last two pairs of peripherals, the two suprapygals, the pygal, and, anteriorly, a single median element that may correspond to the "intermediate element" of Anquetin, Püntener and Billon-Bruyat (2014). As noted by Cuvier (1824), the last costals contact one another medially, a character that is known to vary intraspecifically at least in *Plesiochelys etalloni*, *Plesiochelys bigleri*, and *Craspedochelys jaccardi* (Anquetin, Püntener and Billon-Bruyat 2014; Püntener et al. 2017). Rütimeyer (1873a) referred this specimen to *Plesiochelys solodurensis*, but he was apparently unaware of the name *Emys trionychoides*. Bräm (1965) hesitated between a referral to *Plesiochelys solodurensis* or *Plesiochelys etalloni*. According to our own experience of the Solothurn material, NMS 8547 can be safely referred to *Plesiochelys etalloni*. To our knowledge, *Emys trionychoides* was not used as a valid name since Giebel (1847). In contrast, *Plesiochelys etalloni* has been used as a valid name repeatedly since Pictet and Humbert (1857). Following Article 23.9 of the ICZN (1999), *Emys trionychoides* must be considered a nomen oblitum and its senior synonymy with *Plesiochelys etalloni* can be disregarded (see *Emys hugi* above for additional background information).

Giebel (1847) listed *Emys trionychoides* as a valid species but modified its circumscription. In particular, he referred the holotype of *Emys trionychoides* to *Emys* indet. but assigned the skull NMS 8738 (formerly NMS 134, and currently referred to *Plesiochelys etalloni*) to *Emys trionychoides*. This is nomenclaturally incorrect, and *Emys trionychoides* cannot be a valid name for NMS 8738 if the holotype of this species is simultaneously referred to *Emys* indet.

Euryaspis radians Wagner, 1861a

nomen dubium

Taxonomic history. *Euryaspis radians* Wagner, 1859 (nomen nudum); *Euryaspis radians* Wagner, 1861a (new species); *Eurysternum crassipes* = *Achelonia formosa* = *Acichelys redtenbacheri* [sic] = *Euryaspis radians* = *Eurysternum wagleri* = *Palaeomedusa testa* Rütimeyer 1873b (synonymy); *Eurysternum wagleri* = *Aplax oberndorferi* = *Achelonia formosa* = *Acichelys redenbacheri* = *Euryaspis radians* = *Eurysternum crassipes* = *Palaeomedusa testa* = *Parachelys eichstaettensis* Zittel 1877a (junior synonym); *Acichelys redenbacheri* = *Achelonia formosa* (?) = *Euryaspis radians* (?) = *Eurysternum crassipes* = *Palaeomedusa testa* Lydekker 1889b (junior synonym).

Type material. BSPG uncat. (holotype), a partial carapace in dorsal view (Wagner 1861a, pl. 2), now considered lost (see below).

Type locality. Locality unknown, Germany (Wagner 1861a); lithographic limestone, Tithonian, Late Jurassic (Wagner 1861a).

Comments. The discovery of a new taxon, *Euryaspis radians*, was first announced by Wagner (1859), but no description, definition, or indication was given, leaving the new name unavailable for nomenclatural considerations. The formal designation of *Euryaspis radians* as a new taxon was undertaken two years later and accompanied by a well-executed illustration (Wagner 1861a). According to Wagner (1861a), the holotype of *Euryaspis radians* was originally part of the collection of Dr Häberlein. Maack (1869) later mentioned that the specimen had been transferred to Munich, where it was studied by Rütimeyer (1873a) and Zittel (1877a). However, this specimen is now missing from the collections of the BSPG and must be considered lost. A surviving cast of the holotype housed in London (NHMUK OR49157) confirms most of the characters illustrated and described by Wagner (1861a). However, some additional details are apparent that must have been uncovered from the rock after Wagner's original description. In particular, the outlines of vertebrals I and V are more visible, as are parts of the pleurals. No bony sutures are visible. Unfortunately, none of the observed characters are diagnostic for a species level taxon, which is probably why *Euryaspis radians* was ignored by most workers during the last century. Therefore, we consider *Euryaspis radians* to be a nomen dubium.

Eurysternum crassipes **Wagner, 1861a**

nomen invalidum

(objective junior synonym of *Palaeomedusa testa* Meyer, 1860)

Taxonomic history. *Eurysternum crassipes* Wagner, 1859 (nomen nudum); *Eurysternum crassipes* = *Palaeomedusa testa* Wagner, 1861a (new species and proposed objective junior synonym); *Eurysternum crassipes* = *Acichelys redenbacheri* = *Palaeomedusa testa* Wagner 1861b (subjective and objective synonym, respectively); *Palaeomedusa testa* = *Eurysternum crassipes* Meyer 1861 (junior objective synonym); *Eurysternum crassipes* = *Achelonia formosa* = *Acichelys redtenbacheri* [sic] = *Euryaspis radians* = *Eurysternum wagleri* = *Palaeomedusa testa* Rütimeyer 1873b (synonymy); *Eurysternum wagleri* = *Aplax oberndorferi* = *Achelonia formosa* = *Acichelys redenbacheri* = *Euryaspis radians* = *Eurysternum crassipes* = *Palaeomedusa testa* = *Parachelys eichstaettensis* Zittel 1877a (junior synonym); *Acichelys redenbacheri* = *Achelonia formosa* (?) = *Euryaspis radians* (?) = *Eurysternum crassipes* = *Palaeomedusa testa* Lydekker 1889b (junior synonym); *Eurysternum wagleri* = *Eurysternum crassipes* = *Hydropelta meyeri* = *Parachelys eichstättensis* Oertel 1915 (junior synonym); *Palaeomedusa testa* = *Eurysternum crassipes* = *Thalassemys marina* Joyce 2003 (junior synonym).

Type material. BSPG AS I 818 (holotype), partial anterior half of a carapace with skull, articulated cervical series, and complete right and partial left forelimbs (Meyer 1860, pl. 20.1).

Type locality. Kelheim, Bavaria, Germany (Meyer 1860; Wagner 1861a; Figure 4); Solnhofen Formation, early Tithonian, Late Jurassic (Schweigert 2007).

Comments. The name *Eurysternum crassipes* was first mentioned by Wagner (1859), but only became available two years later with the description of the holotype specimen (Wagner 1861a). In the meantime, the same specimen was described as the basis for the taxon *Palaeomedusa testa* Meyer, 1860. Consequently, *Eurysternum crassipes* and *Palaeomedusa testa* are objective synonyms. Because Wagner (1859) coined his name before Meyer (1860), Wagner (1861a, 1861b) concluded that his name should be given priority, as did most following authors (e.g., Maack 1869; Rütimeyer 1873a; Lortet 1892). However, using the current rules of zoological nomenclature, Wagner's (1859) original contribution is nomenclaturally irrelevant because a description, definition, or indication is lacking in this work (ICZN 1999, art. 12). *Eurysternum crassipes* Wagner, 1861a is therefore a junior objective synonym of *Palaeomedusa testa* Meyer, 1860.

Eurysternum ignoratum **Bräm, 1965**

nomen invalidum

(junior synonym of *Thalassemys hugii* Rütimeyer, 1873a)

Taxonomic history. *Eurysternum ignoratum* Bräm, 1965 (new species); *Thalassemys hugii* = *Thalassemys gresslyi* = *Eurysternum ignoratum* Anquetin, Püntener and Billon-Bruyat 2014 (junior synonym).

Type material. NMS 8612 to NMS 8627 (holotype; formerly NMS 5), disarticulated and fragmentary remains of the shell and postcranium, including three costals, the hyoplastra, the scapulae, a humerus, and the pubes (Rütimeyer 1873a, pl. 6.4; Bräm 1965, pl. 8.6; Anquetin, Püntener and Billon-Bruyat 2014, fig. 6).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Bräm 1965; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. *Eurysternum ignoratum* is based on an assemblage of fragmentary remains from the shell (three costals, hyoplastra) and postcranium (scapulae, humerus, pubes) of the same individual from the Kimmeridgian of Solothurn, Switzerland (Bräm 1965). Rütimeyer (1873a) originally identified this specimen as a young *Thalassemys hugii*, but Bräm (1965) concluded that this material represented a new species, which he referred to the genus *Eurysternum*. His main argument for this referral was the presence of lateral plastral fontanelles, a feature he supposed to be absent in *Thalassemys hugii* but considered diagnostic of "Eurysternidae." *Eurysternum ignoratum* was mostly overlooked by subsequent workers, with the exception of Broin (1994) and Lapparent de Broin et al. (1996), who tentatively suggested a possible synonymy between *Eurysternum ignoratum* and *Solnhofia parsonsi*. However, Anquetin, Püntener and Billon-Bruyat

(2014) recently revealed that lateral plastral fontanelles were also present in *Thalassemys hugii* and concluded that *Eurysternum ignoratum* was a junior synonym of this species. We follow that assessment herein.

Hispaniachelys prebetica **Slater et al., 2011**

nomen dubium

Taxonomic history. *Hispaniachelys prebetica* Slater et al., 2011 (new species).

Type material. MPUG RGCHSP-62-52 (holotype), an incomplete and poorly preserved shell (Slater et al. 2011, figs. 2–8, pl. 1; Pérez-García 2014, fig. 1).

Type locality. Sierra de Cazorla, Andalusia, Spain (Figure 4); Riogazas-Chorro section, Lorente Formation, late Oxfordian, Late Jurassic (Slater et al. 2011).

Comments. *Hispaniachelys prebetica* is based on an imperfect shell from the Oxfordian of the Sierra de Cazorla area in southeastern Spain (Slater et al. 2011). The preservation of this specimen is rather poor, which led to contrasting interpretations of its morphology. Although Slater et al. (2011) noted some similarities with *Plesiochelys solodurensis* as defined by Bräm (1965), they concluded that this specimen was not a “plesiochelyid,” as it presumably possesses only one cervical scute, and probably represented a more basal taxon, as highlighted by the purported presence of epiplastral processes. The proposed reconstruction of the shell (Slater et al. 2011, fig. 3) exhibits several surprising characteristics: the vertebrals are much narrower than in the actual specimen, the epiplastron-hyoplastron suture is strongly oblique, the xiphiplastron is very short, and the inframarginals are restricted to the anterior half of the plastron and do not extend posteriorly beyond the pectoral-abdominal sulcus. Pérez-García (2014) reviewed the specimen and proposed a different interpretation of its morphology. According to this author, the nuchal is too poorly preserved to conclude upon the number of cervical scutes and the vertebrals are wider than depicted by Slater et al. (2011). According to Pérez-García (2014), the morphology of the plastron is quite different from that initially interpreted. For example, the epiplastron-hyoplastron suture is subperpendicular to the axial plane, the purported epiplastal process is lacking, and the inframarginal series is complete. Based on these new observations, Pérez-García (2014) concluded that this material represents an indeterminate “plesiochelyid” turtle and we follow this conclusion herein.

Idiochelys wagneri **Meyer, 1840b**

nomen invalidum

(junior synonym of *Idiochelys fitzingeri* Meyer, 1839b)

Taxonomic history. *Idiochelys wagneri* Meyer 1840a (nomen nudum); *Idiochelys wagneri* Meyer, 1840b (new species); *Idiochelys wagnerorum* Meyer in Bronn 1848 (unjustified emendation); *Idiochelys fitzingeri* = *Idiochelys wagneri* Wagner 1853 (junior synonym); *Idiochelys fitzingeri* = *Idiochelys wagnerorum* = *Chelonemys plana* = *Chelonemys ovata* Rütimeyer 1873b (junior synonym).

Type material. BSPG uncat. (holotype), the posterior portion of a shell with fragments of the right hind limb and a few articulated caudal vertebrae (Meyer 1840b, pl. 7.1; Meyer 1860, pl. 18.1), now considered lost (see below).

Type locality. Kelheim, Bavaria, Germany (Meyer 1840a, 1840b; Figure 4); Solnhofen Formation, early Tithonian, Late Jurassic (Schweigert 2007).

Comments. Meyer (1839b) described *Idiochelys fitzingeri* based on a relatively complete skeleton from the lithographic limestone quarries of Kelheim, Germany. Soon after, Meyer (1840b) described yet another specimen from the same locality that appeared to be different enough that he felt justified in erecting a new species, *Idiochelys wagneri*. The pygal region of the new specimen appeared unique: two pairs of ribs insert into peripheral XI, and the position of the vertebral sulci appear to be positioned one costal farther anterior relative to *Idiochelys fitzingeri*. In the following years, Wagner (1853, 1861b) argued that both taxa should be united into one, because he considered all differences either to be preservational artifacts or not to be significant enough to justify two taxa. In return, Meyer (1854, 1860) defended his position, but did not offer any additional evidence to support his arguments. As both sides did not retreat from their positions, no consensus was reached and the discussion finally subsided. A reanalysis of the type illustrations reveals intriguing details that give partial credit to both positions. Most of the anatomical characters observed by Meyer (1839b, 1840b) can be confirmed as far as the illustrations permit, but many of the observed differences are due to an anomaly of the shell developed in the holotype of *Idiochelys wagneri*. The shell of turtles is typically composed of eight pairs of costal elements, but, unknown to many early authors, this number can vary on an individual basis. As the anterior part of the carapace is missing in both holotypes, Meyer (1839b, 1840b) assumed that both individuals possessed eight pairs of costals and, consequently, counted the costal elements starting with the posteriormost pair, thus offsetting the relative position of the sulci by one costal element in *Idiochelys wagneri* relative to most turtles. Like many supernumerary elements, this ninth pair of costals is significantly smaller than all other costals, but it appears to have only slightly misplaced the costals VIII, as can be seen by the relative position of the fourth intervertebral sulcus. In conclusion, all the differences observed by Meyer (1840b) are due to a supernumerary pair of costals, thus supporting the synonymy of I*diochelys fitzingeri* and *Idiochelys wagneri*.

Idiochelys wagneri was commonly referred to as *Idiochelys wagnerorum* during the mid-19th century. Surprisingly, this alteration of the name was first proposed by Meyer himself (in Bronn 1848), but no reasons were given for it. Most likely, this alteration was intended as a grammatical correction: *Idiochelys wagneri* was named in honor of two people named Wagner (Andreas Wagner from Munich, Germany and Rudolph Wagner from Erlangen, Germany) and the correct grammatical declension (genitive plural) of their name is *wagnerorum*. Following the current nomenclatural rules, incorrect Latinization is not an acceptable justification for the correction of an original spelling (ICZN 1999, art. 32.5.1). The modification proposed by Meyer (in Bronn 1848) is therefore an unjustified emendation. Such emendation may be maintained as the correct spelling only if it is in prevailing use (ICZN 1999, art. 33.2.3.1), which is difficult to argue in the present case. Hence, *Idiochelys wagnerorum* Meyer in Bronn, 1848 is available and a junior objective synonym of *Idiochelys wagneri*.

According to Meyer (1840a), the holotype of *Idiochelys wagneri* was originally part of the fossil collection of George Graf zu Münster of Bayreuth, Germany. This collection was later transferred to Munich, Germany (Wagner 1853), where the holotype was studied by several paleontologists (Maack 1869; Rütimeyer 1873a; Zittel 1877a; Oertel 1915). The holotype is currently missing from the collections of the BSPG and it must be inferred to have been destroyed during World War II together with much of the remaining collection (Wellnhofer 1967).

Plesiochelys choffati Sauvage, 1898

nomen invalidum

(junior synonym of *Craspedochelys jaccardi* [Pictet, 1860])

Taxonomic history. *Plesiochelys choffati* Sauvage, 1898 (new species); *Craspedochelys choffati* Antunes et al. 1988 (new combination).

Type material. MG-LNEG 28 (holotype), a shell missing most of its posterior rim and associated limb elements (Sauvage 1898, pls. 5.9, 6).

Type locality. Vila Franca do Rosário, Lisbon District, Portugal (Figure 4); Freixial Formation, Tithonian, Late Jurassic (Sauvage 1898; Antunes et al. 1988; Pérez-García et al. 2008).

Comments. *Plesiochelys choffati* is based on a relatively complete shell that lacks most of its posterior rim, from the Tithonian of Vila Franca do Rosário, Portugal (Sauvage 1898). The holotype specimen is relatively small (total carapace length estimated at 24 cm). Sauvage (1898) already noted that this turtle shares some similarities with *Craspedochelys jaccardi*, in particular, the carapace is low and broad, the hyoplastron is as wide as long, and the posterior lobe of the plastron is reduced. Antunes et al. (1988) reached similar a conclusion and provisionally proposed the new combination *Craspedochelys choffati*.

The type specimen of *Plesiochelys choffati* is incompletely prepared and has not been reassessed since Sauvage (Antunes et al. 1988; Pérez-García et al. 2008). As a matter of fact, Sauvage (1898) described this material based on photographs and drawings only. However, based on recent photographs of the specimen, we were able to make several additional observations. First, the shell is very similar in morphology to several Solothurn specimens (notably NMS 8713 to NMS 8718 and NMS 9174; see Anquetin, Püntener and Billon-Bruyat 2014) referred to *Craspedochelys jaccardi*. Second, several characters we consider diagnostic for *Craspedochelys jaccardi* are also present in the holotype of *Plesiochelys choffati*, in particular the presence of a broad, rounded carapace with a high length/width ratio of the costal bones (around 4.4–4.7 for costal IV) and a wider than long hyoplastron and xiphiplastron. Based on these characters, *Plesiochelys choffati* is herein considered to be a junior subjective synonym of *Craspedochelys jaccardi*, thereby extending the presence of this taxon to the Iberian Peninsula. MG-LNEG 28 is the smallest known individual referred to this taxon, being about half the length of the other known specimens. It is therefore interesting to note that this specimen retains small costo-peripheral fontanelles (at least from peripherals III–IX), but lacks a central plastral fontanelle.

Plesiochelys langii Rütimeyer, 1873a

nomen invalidum

(junior synonym of *Plesiochelys etalloni* [Pictet and Humbert, 1857])

Taxonomic history. *Plesiochelys langii* Rütimeyer, 1873a (new species); *Plesiochelys solodurensis* = *Plesiochelys langii* (pro parte) Bräm 1965 (junior synonym); *Plesiochelys solodurensis* = *Chelonides robusta* = *Chelonides wittei* = *Emys etalloni* = *Plesiochelys langii* = *Plesiochelys minor* = *Stylemys hannoverana* = *Stylonides* [sic] *lindensis* [sic] Karl et al. 2007 (junior synonym); *Plesiochelys etalloni* = *Plesiochelys solodurensis* = *Plesiochelys sanctaeverenae* = *Plesiochelys langii* Anquetin, Deschamps and Claude 2014 (junior synonym); *Plesiochelys langii* Anquetin 2015 (lectotype designation).

Type material. NMS 8515 (lectotype, see Anquetin 2015; formerly NMS 123), a subcomplete carapace missing the right and posterior margins (Rütimeyer 1873a, pl. 6.1, 2; Anquetin, Püntener and Billon-Bruyat 2014, fig. 2); NMS 8511 (paralectotype; formerly NMS 126), a shell heavily encrusted with pyritic mineralizations, not figured (Anquetin, Püntener and Billon-Bruyat 2014); NMS 8733 (paralectotype; formerly NMS 124), some partly articulated costals and two peripherals (Rütimeyer 1873a, pl. 6.3; Bräm 1965, pl. 8.4; Anquetin, Püntener and Billon-Bruyat 2014, fig. 6), now referred to *Thalassemys hugii* (see Anquetin, Püntener and Billon-Bruyat 2014).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. Rütimeyer (1873a) originally erected *Plesiochelys langii* based on three specimens from Solothurn, Switzerland, which together form the syntype series. Bräm (1965) revealed that this syntype series was a composite and concluded that two of these specimens (NMS 8511 and NMS 8515) should be referred to *Plesiochelys solodurensis*, whereas the third (NMS 8733) belonged to a different taxon (probably *Eurysternum ignoratum*). Anquetin, Püntener and Billon-Bruyat (2014) partly confirmed these conclusions and designated NMS 8515 as the lectotype of *Plesiochelys langii* in order to avoid potential future issues with the taxonomic status of this species (see Anquetin 2015). These authors furthermore concluded that *Plesiochelys langii* is a junior synonym of *Plesiochelys etalloni* and referred NMS 8733 to *Thalassemys hugii*, the senior synonym of *Eurysternum ignoratum*.

Plesiochelys minima Oertel, 1915

nomen dubium

Taxonomic history. *Plesiochelys minima* Oertel, 1915 (new species).

Type material. BSPG uncat. (holotype), a partial carapace (Oertel 1915, fig. 1), now considered lost.

Type locality. Kelheim, Bavaria, Germany (Oertel 1915); Late Jurassic (Oertel 1915).

Comments. *Plesiochelys minima* is based on a partial carapace from the region of Kelheim (Oertel 1915). The precise locality is unknown and this fossil must therefore be assumed to be Late Jurassic in age. The holotype was originally housed at the BSPG, but is now considered lost (Karl et al. 2007). Any conclusion regarding this taxon must therefore be based solely on the original description and illustration (Oertel 1915, fig. 1). According to Oertel (1915), the holotype resembles that of *Plesiochelys* species from Solothurn and Hannover. However, Oertel (1915) noted some differences, such as the loose contact of the middle peripherals with the costals (though without costo-peripheral fontanelles) and the relatively wide vertebrals. Based on the original illustration, the vertebrals clearly cover more than half of the costals laterally and there seems to be fontanelles between costals VII and VIII and adjoining peripherals. These features could suggest a referral to "eurysternids" instead of "plesiochelyids." Based on current knowledge, *Plesiochelys minima* can neither be synonymized with any other Late Jurassic taxon, nor be diagnosed properly without revising the holotype. This taxon is therefore considered as a nomen dubium herein.

Plesiochelys minor Portis, 1878

nomen dubium

Taxonomic history. *Plesiochelys minor* Portis, 1878 (new species); *Plesiochelys solodurensis* = *Chelonides robusta* = *Chelonides wittei* = *Emys etalloni* = *Plesiochelys langii* = *Plesiochelys minor* = *Stylemys hannoverana* = *Stylonides* [sic] *lindensis* [sic] Karl et al. 2007 (junior synonym).

Type material. GZG 769-7 (syntype), a small hyo- and hypoplastron, probably of two distinct specimens (Portis 1878, pl. 16.8); GZG 769-8 (syntype), a small hypoplastron (Portis 1878, not figured); GZG 769-9 (syntype), a small hyoplastron (Portis 1878, not figured).

Type locality. Hannover, Lower Saxony, Germany; *Pteroceras* layer (= *Aporrhais* layer), Kimmeridgian, Late Jurassic (Portis 1878; Karl et al. 2007).

Comments. *Plesiochelys minor* is based on isolated plastral elements from the Kimmeridgian of Hannover (Portis 1878). These elements are mainly characterized by their relatively small size. Portis (1878) provided some measurements for the main specimen (GZG 769-7, probably a composite), but deemed the material too incomplete to warrant a proper description. Oertel (1924) proposed a close relationship of *Plesiochelys minor* with *Stylemys hannoverana* (not *Plesiochelys solodurensis* contra Karl et al. 2007), but refrained from synonymizing these two taxa. Karl et al. (2007) synonymized *Plesiochelys minor* with *Plesiochelys solodurensis*. However, the material is too incomplete to allow any conclusive determination. *Plesiochelys minor* is therefore considered a nomen dubium in the present study.

Plesiochelys normandica **Bergounioux, 1937**

nomen invalidum

(objective junior synonym of *Emys dollfusii* Lennier, 1870)

Taxonomic history. *Plesiochelys normandicus* Bergounioux, 1937 (new species); *Emys dollfussi* [sic] = *Plesiochelys normandicus* Bigot 1939 (objective junior synonym); *Plesiochelys normandica* Kuhn 1964b (justified correction).

Type material. MHNH uncat. (holotype), a fragmentary shell (Lennier 1870, pl. 7.1, 2; Lennier 1887, pl. 22.1, 2; Bergounioux 1937, pl. 1); destroyed during World War II (Lapparent de Broin, pers. comm., 2014).

Type locality. Cap de la Hève, near Le Havre, Department of Seine-Maritime, France (Figure 4); Formation unknown, Kimmeridgian, Late Jurassic (Bergounioux 1937).

Comments. As revealed by Bigot (1939), Bergounioux (1937) erected *Plesiochelys normandica* based on the specimen that Lennier (1870) had previously described as *Emys dollfusii*. *Plesiochelys normandica* is therefore an objective junior synonym of *Emys dollfusii* (herein considered a nomen dubium, see above).

Plesiochelys oblonga **Oertel, 1924**

nomen dubium

Taxonomic history. *Plesiochelys oblonga* Oertel, 1924 (new species).

Type material. A partial carapace (holotype; Oertel 1924, fig. 15), now considered lost (see below).

Type locality. Holzen, Lower Saxony, Germany (Figure 4); Kimmeridgian or Tithonian, Late Jurassic (Oertel 1924).

Comments. *Plesiochelys oblonga* is based on a partial carapace that was, at the time, the most complete turtle specimen known from the Portlandian of Holzen (Oertel 1924). This specimen was originally housed at the TUB (Oertel 1924), but our investigation revealed that it is now missing from this institution, as well as from the SNHM where part of the TUB collections was transferred in the late 1990s. *Plesiochelys oblonga* was originally compared exclusively with *Plesiochelys sanctaeverenae* from Solothurn, a species now synonymized with *Plesiochelys etalloni* (Oertel 1924; Bräm 1965; Anquetin, Deschamps and Claude 2014; Anquetin, Püntener and Billon-Bruyat 2014). Given that the original description and illustration are insufficient to confirm Oertel's (1924) observations and that the type specimen now must be considered lost, we conclude that *Plesiochelys oblonga* should be considered a nomen dubium.

Plesiochelys pumilio **Oertel, 1924**

nomen dubium

Taxonomic history. *Plesiochelys pumilio* Oertel, 1924 (new species).

Type material. A partial carapace and plastron (holotype; Oertel 1924, figs. 16, 17), now considered lost (Karl et al. 2007).

Type locality. Holzen, Lower Saxony, Germany (Figure 4); Kimmeridgian or Tithonian, Late Jurassic (Oertel 1924).

Comments. *Plesiochelys pumilio* is based on a single specimen that was collected in Kimmeridgian or Tithonian (= Portlandian) sediments exposed at Holzen, Germany (Oertel 1924). The specimen was originally held in a private collection but appears to have been lost since (Karl et al. 2007). Oertel (1924) distinguished *Plesiochelys pumilio* from other species of the genus based on carapace shape (widely elliptic) and size (carapace length of about 28 cm), and by the geometry of the neurals, costals, and suprapygals. However, since the original material is lost, we are unable to confirm Oertel's (1924) observations based solely on his description and illustrations. *Plesiochelys pumilio* must therefore be considered a nomen dubium.

Plesiochelys sanctaeverenae **Rütimeyer, 1873a**

nomen invalidum

(junior synonym of *Plesiochelys etalloni* [Pictet and Humbert, 1857])

Taxonomic history. *Plesiochelys sanctaeverenae* Rütimeyer, 1873a (new species); *Plesiochelys sanctaeverenae* Bräm 1965 (lectotype designation); *Plesiochelys etalloni* = *Plesiochelys jaccardi* = *Stylemys lindensis* [sic] = *Plesiochelys solodurensis* = *Plesiochelys sanctaeverenae* = *Craspedochelys picteti* = *Craspedochelys crassa* Gaffney 1975a (junior synonym); *Plesiochelys etalloni* = *Plesiochelys solodurensis* = *Plesiochelys sanctaeverena*e = *Plesiochelys langii* Anquetin, Deschamps and Claude 2014 (junior synonym).

Type material. NMS 8514 (lectotype; formerly NMS 118), a large carapace missing its lateral aspects (Rütimeyer 1873a, pl. 13; Anquetin, Püntener and Billon-Bruyat 2014, fig. 2); NMS uncat. (paralectotypes), two isolated neurals (Rütimeyer 1873a, pl. 10.8, 10). Additional paralectotypes possibly exist but are impossible to identify with certainty based on the original publication.

Type locality. Solothurn, Canton of Solothurn, Switzerland (Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. *Plesiochelys sanctaeverenae* was originally based at least on three syntypes from the Kimmeridgian of Solothurn, Switzerland (Rütimeyer 1873a; Bräm 1965). Bräm (1965) nevertheless addressed the best-preserved specimen, a near complete carapace, as the "holotypus," which, according to ICZN (1999) regulations, should be considered as a lectotype designation. With the exception of two figured neurals (Rütimeyer 1873a), paralectotypes are difficult to identify since no specimen numbers where used in the original publication. According to Rütimeyer (1873a) and Bräm (1965), *Plesiochelys sanctaeverenae* is distinguished by its slightly greater size, more elongate carapace, and well-developed nuchal notch and sulci. Subsequent authors all agreed that these features were not diagnostic (Gaffney 1975a; Lapparent de Broin et al. 1996; Anquetin, Deschamps and Claude 2014). *Plesiochelys sanctaeverenae* is therefore considered a junior synonym of *Plesiochelys etalloni*.

Plesiochelys solodurensis **Rütimeyer, 1873a**

nomen invalidum

(junior synonym of *Plesiochelys etalloni* [Pictet and Humbert, 1857])

Taxonomic history. *Plesiochelys solodurensis* Rütimeyer, 1873a (new species); *Plesiochelys solodurensis* = *Plesiochelys langii* (pro parte) Bräm 1965 (senior synonym; lectotype designation); *Plesiochelys etalloni* = *Plesiochelys jaccardi* = *Stylemys lindensis* [sic] = *Plesiochelys solodurensis* = *Plesiochelys sanctaeverenae* = *Craspedochelys picteti* = *Craspedochelys crassa* Gaffney 1975a (junior synonym); *Plesiochelys solodurensis* = *Chelonides robusta* = *Chelonides wittei* = *Emys etalloni* = *Plesiochelys langii* = *Plesiochelys minor* = *Stylemys hannoverana* = *Stylonides* [sic] *lindensis* [sic] Karl et al. 2007 (synonymy); *Plesiochelys etalloni* = *Plesiochelys solodurensis* = *Plesiochelys sanctaeverenae* = *Plesiochelys langii* Anquetin, Deschamps and Claude 2014 (junior synonym).

Type material. NMS 8693 (lectotype; formerly NMS 59), a distorted, subcomplete shell (Cuvier 1824, pl. 15.4, 5; Rütimeyer 1873a, pl. 12.1, 2; Anquetin, Püntener and Billon-Bruyat 2014, fig. 2); NMS 8547 (formerly NMS 61), NMS 8696 (formerly NMS 63a), and five uncatalogued NMS specimens (paralectotypes), fragments of carapaces and plastra, and a partial steinkern (Rütimeyer 1873a, pls. 4.2, 7.6, 7, 8.7, 10.2, 5, 7). Additional paralectotypes possibly exist but are impossible to identify with certainty based on the original publication.

Type locality. Solothurn, Canton of Solothurn, Switzerland (Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. *Plesiochelys solodurensis* is based on a series of shell remains from the Kimmeridgian of Solothurn, Switzerland (Rütimeyer 1873a; Bräm 1965). Apart from the specimens that were illustrated (see above), the complete syntype series is impossible to identify. The main specimen (NMS 8693, formerly NMS 59) consists of a distorted shell, which was designated as the lectotype by Bräm (1965). As defined by Rütimeyer (1873a) and Bräm (1965), this is the most abundant turtle species in Solothurn, Switzerland. It is mainly differentiated from *Plesiochelys etalloni* by the absence of a central plastral fontanelle. Gaffney (1975a) and Lapparent de Broin et al. (1996) subsequently considered the persistence of a central plastral fontanelle as an intraspecific variation. Gaffney (1975a) synonymized *Plesiochelys solodurensis*, as well as several other taxa, with *Plesiochelys etalloni*. In contrast, Lapparent de Broin et al. (1996) considered *Plesiochelys solodurensis* to be the only valid *Plesiochelys* species in Solothurn, and they restricted *Plesiochelys etalloni* to its holotype from the French Jura. The recent rediscovery and redescription of the holotype of *Plesiochelys etalloni* (MAJ 2005-11-1) led to the conclusion that *Plesiochelys solodurensis* was indistinguishable from *Plesiochelys etalloni*, and that the persistence of a central plastral fontanelle in some individuals was best interpreted as an intraspecific variation (Anquetin, Deschamps and Claude 2014). We therefore agree that *Plesiochelys solodurensis* is a junior synonym of *Plesiochelys etalloni*.

Plesiochelys solodurensis langenbergensis **Oertel, 1924**

nomen invalidum

(junior synonym of *Plesiochelys etalloni* [Pictet and Humbert, 1857])

Taxonomic history. *Plesiochelys solodurensis langenbergensis* Oertel, 1924 (new subspecies); *Craspedochelys jaccardi = Plesiochelys solodurensis langenbergensis* Karl et al. 2007 (junior synonym).

Type material. GZG 763-4 (holotype), posterior part of an articulated carapace and plastron (Oertel 1924, figs. 6, 7).

Type locality. Langenberg, near Oker, Lower Saxony, Germany (Figure 4); Langenberg Formation, middle Kimmeridgian, Late Jurassic (Oertel 1924; Karl et al. 2007).

Comments. *Plesiochelys solodurensis langenbergensis* is based on a single specimen from the middle Kimmeridgian of Oker, Germany. It was initially named as a variety, but, following the rules of the ICZN (1999), it is here discussed as a subspecies. According to Oertel (1924), this taxon differs from *Plesiochelys solodurensis* (now *Plesiochelys etalloni*) mainly by the shape of suprapygal II. However, the size and shape of suprapygals is relatively variable in this species (Anquetin, Püntener and Billon-Bruyat 2014) and we therefore see little reason to use this character to maintain a distinct taxon. Karl et al. (2007) explicitly synonymized a part of *Plesiochelys solodurensis langenbergensis* with *Plesiochelys solodurensis* and another part with *Craspedochelys jaccardi*. As mentioned above, however, the type material of *Plesiochelys solodurensis langenbergensis* only consists of a single specimen, which Karl et al. (2007) incidentally referred to *Craspedochelys jaccardi*. We therefore retain only this synonymy herein. Observation of the holotype (GZG 763-4) suggests that this specimen is consistent with the diagnosis of *Plesiochelys etalloni* proposed by Anquetin, Deschamps and Claude (2014) and Anquetin, Püntener and Billon-Bruyat (2014). We therefore consider *Plesiochelys solodurensis langenbergensis* Oertel, 1924 to be a junior subjective synonym of *Plesiochelys etalloni* (Pictet and Humbert, 1857).

Stylemys hannoverana Maack, 1869

nomen invalidum, designation of lectotype

(junior synonym of *Plesiochelys etalloni* [Pictet and Humbert, 1857])

Taxonomic history. *Stylemys hannoverana* Maack, 1869 (new species); *Plesiochelys hannoverana = Stylemys lindenensis* (pro parte) Portis 1878 (new combination and synonymy); *Plesiochelys solodurensis = Chelonides robusta = Chelonides wittei = Emys etalloni = Plesiochelys langii = Plesiochelys minor = Stylemys hannoverana = Stylonides* [sic] *lindensis* [sic] Karl et al. 2007 (synonymy).

Type material. GZG 773-35 (lectotype), an almost complete plastron, now lost (Maack 1869, pl. 35.36; Portis 1878, pl. 16.7); GZG 773-36 to GZG 773-49 (paralectotypes), carapacial and plastral fragments (Maack 1869, pls. 35.37–37.51; Karl et al. 2007, pl. 2.1, 2).

Type locality. Region of Hannover, Lower Saxony, Germany (Figure 4); *Pteroceras* layer (= *Aporrhais* layer), Kimmeridgian, Late Jurassic (Maack 1869; Karl et al. 2007).

Comments. *Stylemys hannoverana* is based on a large series of shell remains from the Kimmeridgian of the region of Hannover, Germany (Maack 1869). Numerous specimens (GZG 773-35 to GZG 773-49) were illustrated by Maack (1869) and are therefore part of the syntype series (see above), but only a few of these were specifically mentioned in the original description (GZG 773-35, GZG 773-39, GZG 773-40/41, GZG 773-47, GZG 773-49). To the exception of GZG 773-35 (a near-complete plastron), most of this series consists of poorly diagnosable shell fragments. For this reason, we designate the plastron GZG 773-35 as the lectotype of *Stylemys hannoverana*. This specimen is considered lost since the 1990s, but a good drawing was published by Portis (1878). The morphological characteristics of this plastron, notably the presence of epiplastral bulbs and the longer than wide hyoplastron, are consistent with the concept of *Plesiochelys etalloni* as revised by Anquetin, Deschamps and Claude (2014), Anquetin, Püntener and Billon-Bruyat (2014), and Püntener et al. (2017). Therefore, *Stylemys hannoverana* Maack, 1869 is considered as a junior synonym of *Plesiochelys etalloni* (Pictet and Humbert, 1857).

Maack (1869) initially referred *Stylemys hannoverana* and *Stylemys lindenensis* (see below) to *Stylemys*, a genus that has already been established by Leidy (1851) for the Eocene North American tortoise (*Testudinidae*) *Stylemys nebrascensis* Leidy, 1851. Although Maack (1869) was fully aware of Leidy's (1851) work and that his newly named species have no relationships with the North American material, he felt justified in using the name *Stylemys*, as Leidy (1852) has "withdrawn" this name from usage by referring his species to the genus *Testudo* Linnaeus, 1758. This line of reasoning is, of course, not permissible using the more recently established rules of zoological nomenclature (ICZN 1999).

Stylemys lindenensis Maack, 1869

nomen dubium

Taxonomic history. *Stylemys lindenensis* Maack, 1869 (new species); *Tropidemys seebachi = Stylemys lindenensis* (pro parte) Portis 1878 (synonymy); *Plesiochelys hannoverana =*

Stylemys lindenensis (pro parte) Portis 1878 (synonymy); *Chelonides wittei* = *Stylemys lindenensis* (pro parte) Portis 1878 (junior synonym); *Plesiochelys etalloni* = *Stylemys lindensis* [sic] Bräm 1965 (junior synonym); *Plesiochelys etalloni* = *Plesiochelys jaccardi* = *Stylemys lindensis* [sic] = *Plesiochelys solodurensis* = *Plesiochelys sanctaeverenae* = *Craspedochelys picteti* = *Craspedochelys crassa* Gaffney 1975a (junior synonym); *Plesiochelys solodurensis* = *Chelonides robusta* = *Chelonides wittei* = *Emys etalloni* = *Plesiochelys langii* = *Plesiochelys minor* = *Stylemys hannoverana* = *Stylonides* [sic] *lindensis* [sic] Karl et al. 2007 (synonymy).

Type material. GZG 773-18 to GZG 773-34 (syntypes), a series of fragmentary and disarticulated shell elements (Maack 1869, pls. 34.19–35.35; Portis 1878, pl. 15.4).

Type locality. Tönniesberg (= Tönjesberg), Hannover, Lower Saxony, Germany (Figure 4); *Pteroceras* layer (= *Aporrhais* layer), middle Kimmeridgian, Late Jurassic (Maack 1869; Karl et al. 2007).

Comments. *Stylemys lindenensis* is based on a series of fragmentary and disarticulated shell elements from the middle Kimmeridgian of Tönniesberg in Hannover, Germany (Maack 1869; Karl et al. 2007). Maack (1869) designated GZG 773-18 and GZG 773-19 as “Hauptvertreter” (main representatives). These were apparently found within a single block with several other syntypes: GZG 773-22, GZG 773-23, GZG 773-24, and GZG 773-25. However, this material is too fragmentary to allow any conclusive determination. Therefore, *Stylemys lindenensis* is considered as a nomen dubium herein.

According to Oertel (1924), Rütimeyer (1873b) first proposed that *Stylemys lindenensis* and *Stylemys hannoverana* should be referred to the genus *Plesiochelys* and represented a single species, *Plesiochelys hannoverana*. That is, however, incorrect, as Rütimeyer (1873b) simply noted that the material described by Maack (1869) was fragmentary, but that more complete material would probably lead to the conclusion that this material should be referred to one or several of the *Plesiochelys* species known from Solothurn, Switzerland. A few years later, Portis (1878) recognized *Stylemys hannoverana* as a valid taxon, but split the syntype material of *Stylemys lindenensis* between three different taxa: *Tropidemys seebachi*, *Stylemys hannoverana*, and *Chelonides wittei*. Oertel (1924) mostly followed the conclusions of Portis (1878).

Thalassemys gresslyi **Rütimeyer, 1873a**

nomen invalidum

(junior synonym of *Thalassemys hugii* Rütimeyer, 1873a)

Taxonomic history. *Thalassemys gresslyi* Rütimeyer, 1873a (new species); *Thalassemys hugii* = *Thalassemys gresslyi* Bräm 1965 (junior synonym); *Thalassemys hugii* = *Thalassemys gresslyi* = *Eurysternum ignoratum* Anquetin, Püntener and Billon-Bruyat 2014 (junior synonym).

Type material. NMS 8555 (holotype), anterior part of a large, partly disarticulated carapace (Anquetin, Püntener and Billon-Bruyat 2014, fig. 6).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. *Thalassemys gresslyi* is based on a single, poorly preserved carapace fragment from the Solothurn Turtle Limestone. Rütimeyer (1873a) argued that this taxon could be differentiated from *Thalassemys hugii* by larger size, differences in proportions of neural I and costal I, and a different sculpturing of the bone surface. However, Bräm (1965) much later concluded that *Thalassemys gresslyi* is a junior synonym of *Thalassemys hugii* and that all apparent differences are the result of individual variations or postmortem deformation, an opinion more recently confirmed by Anquetin, Püntener and Billon-Bruyat (2014). We agree with this assessment.

Thalassemys heusseri **Oertel, 1924**

nomen dubium

Taxonomic history. *Thalassemys heuseri* Oertel 1915 (nomen nudum); *Thalassemys heusseri* Oertel, 1924 (new species with alternative spelling).

Type material. A partial carapace (holotype; Oertel 1924, fig. 14), now considered lost (see below).

Type locality. Holzen, Lower Saxony, Germany (Figure 4); Kimmeridgian or Tithonian, Late Jurassic (Oertel 1924).

Comments. *Thalassemys heusseri* is based on a partial carapace (about 30 cm in length) from the Kimmeridgian or Tithonian (= Portlandian) of Holzen, Germany (Oertel 1924). This specimen was originally housed at the TUB (Oertel 1924), but our investigation revealed that it is now missing from this institution, as well as from the SNHM, where part of the TUB collections was transferred in the late 1990s. *Thalassemys heusseri*, initially spelt *heuseri*, first appeared in the literature in Oertel (1915) as a name only, and only became available a few years later when Oertel (1924) described and illustrated the holotype. The flat carapace and retention of small costo-peripheral fontanelles is fairly consistent with the concept of *Thalassemys* (see above). However, the high length/width ratio of costal IV and the pattern of carapacial scutes recall what is known in *Craspedochelys*. With the type specimen lost, the original description and illustration are insufficient to provide clearly diagnostic characters. For this reason, Püntener et al. (2015) concluded that *Thalassemys heusseri* should be considered a nomen dubium and we agree with this assessment herein.

Trionyx primoevus Bergounioux, 1937

nomen dubium

Taxonomic history. *Trionyx primoevus* Bergounioux, 1937 (new species, also incorrectly spelt as *Trionyx primaevus*).

Type material. MHNH uncat. (holotype), a poorly preserved plastron (Bergounioux 1937, pl. 2), destroyed during World War II (Lapparent de Broin, pers. comm., 2014).

Type locality. Cap de la Hève, near Le Havre, Department of Seine-Maritime, France (Figure 4); formation unknown, Kimmeridgian, Late Jurassic (Bergounioux 1937).

Comments. *Trionyx primoevus* is based on a poorly preserved, but relatively complete, plastron from the Kimmeridgian of Cap de la Hève near Le Havre, France (Bergounioux 1937). The species name is consistently misspelt as *primaevus* (e.g., Kuhn 1964b; Lapparent de Broin 2001), likely because Bergounioux (1937) already misspelt the name in the type description. Bergounioux (1937) felt that the morphology of the plastron was peculiar and therefore referred this taxon to *Trionyx*. However, the characters he lists, in particular the absence of scutes and the purported presence of additional plates, do not withstand examination of the published photograph. Webb (1962) accordingly expressed doubts as to whether *Trionyx primoevus* was really a trionychid. More recently, Lapparent de Broin (2001) suggested that *Trionyx primoevus* was possibly a synonym of *Chelonides wittei*. However, *Chelonides wittei* is a much smaller form with less extensive plastral fenestration. Instead, we find that *Trionyx primoevus* shares more similarities with "thalassemydids." The shape of the hyo- and hypoplastron recalls that of *Thalassemys marina*, whereas the wide inguinal passage and the slender xiphiplastron are reminiscent of the condition in *Thalassemys hugii*. The size of the specimen is also more congruent with "thalassemydids." Sadly, the specimen was destroyed during World War II. It is therefore preferable to consider *Trionyx primoevus* as an indeterminate thalassemydid and a nomen dubium.

Tropidemys expansa Rütimeyer, 1873a

nomen invalidum

(junior synonym of *Tropidemys langii* Rütimeyer, 1873a)

Taxonomic history. *Tropidemys expansa* Rütimeyer, 1873a (new species); *Tropidemys langii* = *Tropidemys expansa* = *Tropidemys gibba* = *Craspedochelys plana* Bräm 1965 (junior synonym); *Tropidemys langii* = *Chelone valanginiensis* = *Stylemys lindensis* [sic] (pro parte) = *Tropidemys expansa* = *Tropidemys gibba* = *Tropidemys seebachi* Karl et al. 2007 (junior synonym).

Type material. NMS 8553 (syntype; formerly NMS 33), two costals and three articulated peripherals (Rütimeyer 1873a, pl. 9.4). NMS 8556 (syntype; formerly NMS 32), carapace fragment consisting of two partial neurals and the medial part of three adjoining left costals (Rütimeyer 1873a, pl. 9.3).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. Rütimeyer (1873a) did not explicitly refer to any specimens in his original description of *Tropidemys expansa*. However, he figured specimens NMS 8553 and NMS 8556 from the Kimmeridgian of Solothurn, Switzerland, and we here interpret these two as forming the syntype series. Both specimens were revised by Bräm (1965) and Püntener et al. (2014), who concluded that they are referable to *Tropidemys langii* from the same locality. We therefore agree that *Tropidemys expansa* is a junior synonym of *Tropidemys langii*.

Tropidemys gibba Rütimeyer, 1873a

nomen invalidum

(junior synonym of *Tropidemys langii* Rütimeyer, 1873a)

Taxonomic history. *Tropidemys gibba* Rütimeyer, 1873a (new species); *Tropidemys langii* = *Tropidemys expansa* = *Tropidemys gibba* = *Craspedochelys plana* Bräm 1965 (junior synonym); *Tropidemys langii* = *Chelone valanginiensis* = *Stylemys lindensis* [sic] (pro parte) = *Tropidemys expansa* = *Tropidemys gibba* = *Tropidemys seebachi* Karl et al. 2007 (junior synonym).

Type material. NMS 8665 (holotype; formerly NMS 38), carapace fragment including neurals III–VI and medial parts of the associated costals (Rütimeyer 1873a, pl. 4.1; Bräm 1965, pl. 8.5).

Type locality. Solothurn, Canton of Solothurn, Switzerland (Rütimeyer 1873a; Figure 4); Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation, late Kimmeridgian, Late Jurassic (Meyer 1994).

Comments. *Tropidemys gibba* is based on a carapace fragment from the Kimmeridgian of Solothurn, Switzerland (Rütimeyer 1873a). The holotype specimen was revised by Bräm (1965) and Püntener et al. (2014), who concluded that *Tropidemys gibba* was a junior synonym of *Tropidemys langii* from the same locality. We agree with this straightforward assessment.

Tropidemys morinica **Sauvage, 1880**

nomen dubium

Taxonomic history. *Tropidemys morinica* Sauvage, 1880 (new species).

Type material. MHNB uncat. (syntype), the posterior portion of a carapace (Sauvage 1880, pl. 20.2, 3); MHNB uncat. (syntype), a large bone interpreted as a pubis (Sauvage 1880, pl. 20.1). This material is now considered lost (Vadet and Rose 1986).

Type locality. Boulogne-sur-Mer, Department of Pas-de-Calais, France (Figure 4); formation unknown, Kimmeridgian (= Portlandian), Late Jurassic (Sauvage 1880).

Comments. *Tropidemys morinica* is based on the posterior portion of a carapace and a supposedly associated large bone interpreted as a pubis, which were collected from Kimmeridgian (= Portlandian) deposits near Boulogne-sur-Mer, France (Sauvage 1880). This material was initially housed in the Natural History Museum of Boulogne-sur-Mer, which has since closed. What remains of Sauvage’s turtle collection is currently under study (F. de Lapparent de Broin, pers. comm., 2014), but the type material of *Tropidemys morinica* is apparently lacking and therefore appears to be lost, as had previously been established by Vadet and Rose (1986). Sauvage (1880) described the main carapacial element as a 19 cm long fragment with five neurals (his vertebrals). Sauvage (1880) described these neurals as elongate elements, shortened posteriorly, and lacking the hexagonal outline seen in *Tropidemys seebachi* (also present in *Tropidemys langii*). However, he stated that the neurals were keeled. Sauvage (1880, pl. 20.2, 3) illustrated a neural, but it is difficult to reproduce the author’s observations. If correct, Sauvage’s description excludes this species from *Tropidemys*, as diagnosed herein, but does not offer adequate diagnostic characters. The second element is, according to Sauvage (1880), a 20 cm long pubis. This interpretation is difficult to confirm based on the illustration, especially as this element resembles a plastron fragment. If it is really a pubis, its size clearly does not fit with that of the carapace fragment discussed above. Except for a few rapid mentions from Sauvage himself (Sauvage 1900, 1912), this taxon was never subsequently discussed in the literature. Based on the aforementioned considerations, *Tropidemys morinica* is best interpreted as a nomen dubium.

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Appendix 1

Institutional Abbreviations

BSPG	Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany
CAMSM	Sedgwick Museum, Department of Geology, University of Cambridge, Cambridge, United Kingdom
GZG	Geowissenschaftliches Zentrum der Universität Göttingen, Göttingen, Germany
JM	Jura-Museum Eichstätt, Eichstätt, Germany
MAJ	Musée d'archéologie du Jura, Lons-le-Saunier, France
MCG	Musée cantonale de géologie, Lausanne, Switzerland
MG-LNEG	Museu Geológico, Laboratório Nacional de Energia e Geologia, Lisbon, Portugal
MHNB	Muséum d'histoire naturelle, Boulogne-sur-Mer, France
MHNH	Muséum d'histoire naturelle, Le Havre, France
MHNL	Musée des confluences, Lyon, France

MHNN	Muséum d'histoire naturelle, Neuchâtel, Switzerland
MJSN	JURASSICA Museum, Porrentruy, Switzerland
MLP	Museo de La Plata, La Plata, Argentina
MNB	Museum für Naturkunde, Berlin, Germany
MNHN	Muséum national d'histoire naturelle, Paris, France
MOZ	Museo Profesor Olsacher, Zapala, Provincia de Neuquén, Argentina
MPUG	Museo de Paleontología, Universidad de Granada, Granada, Spain
NHMUK	Natural History Museum, London, United Kingdom
NMAG	Naturmuseum Augsburg, Augsburg, Germany
NMS	Naturmuseum Solothurn, Solothurn, Switzerland
OUMNH	Oxford University Museum of Natural History, Oxford, United Kingdom
PIMUZ	Paläontologisches Institut und Museum, Universität Zürich, Zürich, Switzerland
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany
SNHM	Staatliches Naturhistorisches Museum, Braunschweig, Germany
TM	Teyler Museum, Haarlem, Netherlands
TUB	Technische Universität, Braunschweig, Germany
ZPAL	Institute of Paleobiology, Polish Academy of sciences, Warsaw, Poland

Appendix 2

Named Genera of *Thalassochelydia*

Achelonia Meyer, 1860 (type species: *Achelonia formosa* Meyer, 1860)

Acichelys Meyer, 1854 (type species: *Acichelys redenbacheri* Meyer, 1854)

Anaphotidemys Hay, 1905 (type species: *Chelonides wittei* Maack, 1869)

Aplax Meyer, 1843 (type species: *Aplax oberndorferi* Meyer, 1843)

Chelonemys Jourdan, 1862 (type species: *Chelonemys plana* Jourdan, 1862)

Chelonides Maack, 1869 (type species: *Chelonides wittei* Maack, 1869)

Craspedochelys Rütimeyer, 1873a (type species: *Craspedochelys picteti* Rütimeyer, 1873a)

Cyrtura Jaekel, 1904 (type species: *Cyrtura temnospondyla* Jaekel, 1904)

Enaliochelys Seeley, 1869 (type species: *Enaliochelys chelonia* Seeley, 1869)

Euryaspis Wagner, 1861a (type species: *Euryaspis radians* Wagner, 1861a)

Eurysternum Meyer, 1839c (type species: *Eurysternum wagleri* Meyer, 1839c)

Hispaniachelys Slater et al., 2011 (type species: *Hispaniachelys prebetica* Slater et al., 2011)

Hydropelta Meyer, 1860 (type species: *Chelone*? *meyeri* Thiollière, 1851)

Idiochelys Meyer, 1839b (type species: *Idiochelys fitzingeri* Meyer, 1839b)

Jurassichelon Pérez-García, 2015b (type species: *Jurassichelon oleronensis* Pérez-García, 2015b)

Neusticemys Fernández and de la Fuente, 1993 (type species: *Eurysternum*? *neuquinum* Fernández and de la Fuente, 1988)

Owadowia Szczygielski et al., 2017(type species: *Owadowia borsukbialynickae* Szczygielski et al., 2017)

Palaeomedusa Meyer, 1860 (type species: *Palaeomedusa testa* Meyer, 1860)

Parachelys Meyer, 1864 (type species: *Parachelys eichstaettensis* Meyer, 1864)

Pelobatochelys Seeley, 1875 (type species: *Pelobatochelys blakii* Seeley, 1875)

Plesiochelys Rütimeyer, 1873a (type species: *Plesiochelys solodurensis* Rütimeyer, 1873a)

Portlandemys Gaffney, 1975a (type species: *Portlandemys mcdowelli* Gaffney, 1975a)

Solnhofia Gaffney, 1975b (type species: *Solnhofia parsonsi* Gaffney, 1975b)

Stegochelys Lydekker, 1889a (type species: *Chelone planiceps* Owen, 1842)

Stylemys Maack, 1869 (type species: *Stylemys lindenensis* Maack, 1869 [junior homonym of *Stylemys* Leidy, 1851 (*Testudinidae*)])

Thalassemys Rütimeyer, 1873a (type species: *Thalassemys hugii* Rütimeyer, 1873a)

Tropidemys Rütimeyer, 1873a (type species: *Tropidemys langii* Rütimeyer, 1873a)

Appendix 3

Biogeographical Summary of *Thalassochelydia*

Numbers in brackets reference Figure 4

Abbreviation: TL, type locality

Argentina

[1] Late Jurassic, early to late Tithonian; Neuquén Province; *Neusticemys neuquina* (TL) (Fernández and de la Fuente 1988, 1993; Gasparini et al. 1997, 2015; de la Fuente and Fernández 2011; de la Fuente 2007)

France

[2] Late Jurassic, Kimmeridgian; Le Havre, Department of Seine-Maritime; *Craspedochelys* sp. (= *Emys dollfusii* of Lennier 1870, = *Plesiochelys normandica* of Bergounioux 1937), "Thalassemydidae" indet. (= *Trionyx primoevus* of Bergounioux 1937)

[3] Late Jurassic, Kimmeridgian; Boulogne-sur-Mer, Department of Pas-de-Calais; "Plesiochelyidae" indet. (= *Emys dutertrei* of Sauvage 1872), "Thalassemydidae" indet. (= *Emys beaugrandi* of Sauvage 1872)

[4] Late Jurassic, late Kimmeridgian; Fumel, Department of Lot-et-Garonne; *Tropidemys* sp., *Thalassochelydia* indet. (Sauvage 1902; Lapparent de Broin et al. 1996)

[5] Late Jurassic, late Kimmeridgian; Cerin, Department of Ain; *Achelonia formosa* (TL) (Meyer 1860; Rütimeyer 1873a; Lortet 1892), *Hydropelta meyeri* (TL) (Thiollière 1851; Meyer 1860; Lortet 1892; Oertel 1915; Karl, Tichy, and Valdiserri 2012), *Idiochelys fitzingeri* (Jourdan 1862; Rütimeyer 1873a; Lortet 1892)

[6] Late Jurassic, Kimmeridgian and Tithonian; several localities north of Cahors, Department of Lot; *Solnhofia* sp., *Craspedochelys jaccardi*, *Craspedochelys* sp. (Lapparent de Broin et al. 1996)

[7] Late Jurassic, late Kimmeridgian or early Tithonian; Moirans-en-Montagne, Department of Jura; *Plesiochelys etalloni* (TL) (Pictet and Humbert 1857; Rütimeyer 1873a; Bräm 1965; Lapparent de Broin et al. 1996; Anquetin, Deschamps, and Claude 2014)

[8] Late Jurassic, Tithonian; Canjuers, Department of Var; *Solnhofia* sp., *Eurysternum* sp. (Broin 1994)

[9] Late Jurassic, Tithonian; Isle of Oléron, Department of Charente-Maritime; *Jurassichelon oleronensis* (TL) (Rieppel 1980; Pérez-García 2015b)

Germany

[10] Late Jurassic, Oxfordian; Drügendorf, Bavaria; "Plesiochelyidae" indet. (Kuhn 1949)

[11] Late Jurassic, early Kimmeridgian; Hildesheim, Lower Saxony; *Tropidemys* sp. (pers. obs. SMNS)

[12] Late Jurassic, middle Kimmeridgian; Oker, Lower Saxony; *Plesiochelys etalloni* (= *Plesiochelys solodurensis langenbergensis* of Oertel 1924; Karl et al. 2007)

[13] Late Jurassic, middle Kimmeridgian; Hannover, Lower Saxony; *Chelonides wittei* (TL) (Maack 1869; Karl et al. 2007), *Tropidemys seebachi* (TL) (Portis 1878; Karl, Gröning, and Brauckmann 2012), *Plesiochelys etalloni* (= *Stylemys hannoverana* of Maack 1869), "Plesiochelyidae" indet. (= *Chelonides robusta* of Portis 1878)

[14] Late Jurassic, Kimmeridgian or Tithonian; Holzen, Lower Saxony; *Thalassochelydia* indet. (= *Plesiochelys oblonga*, *Plesiochelys pumilio*, and *Thalassemys heusseri* of Oertel 1924)

[15] Late Jurassic, late Kimmeridgian; Wattendorf, Bavaria; *Tropidemys seebachi* (Mäuser 2014; Joyce 2015)

[16] Late Jurassic, late Kimmeridgian; Nusplingen, Baden-Württemberg; "Eurysternidae" indet. (Klein et al. 2016), *Thalassochelydia* indet. (Maisch 1999)

[17] Late Jurassic, Kimmeridgian/Tithonian; Ettling and Neuburg an der Donau, Bavaria; Eurysternidae indet. (Ebert et al. 2015); *Thalassochelydia* indet. (*Acichelys approximata* of Wagner 1856)

[18] Late Jurassic, Kimmeridgian/Tithonian; Schamhaupten and Denkendorf/Zandt, Bavaria; *Eurysternum wagleri* (Zittel 1877a; Anquetin and Joyce 2014), *Solnhofia parsonsi* (Joyce 2000)

[19] Late Jurassic, early Tithonian; Eichstätt and Solnhofen, Bavaria; *Eurysternum wagleri* (TL) (H. von Meyer 1839a, 1839c, 1854; Anquetin and Joyce 2014), *Parachelys eichstaettensis* (TL) (H. von Meyer 1864; Lydekker 1889b), *Solnhofia parsonsi* (TL) (Parsons and Williams 1961; Gaffney 1975b); *Thalassochelydia* indet. (Wellnhofer 1967)

[20] Late Jurassic, Tithonian; Kelheim, Bavaria; *Idiochelys fitzingeri* (TL) (Meyer 1839a, 1839b, 1840a, 1840b, 1854, 1860; Wagner 1853, 1861b), *Palaeomedusa testa* (TL) (Meyer 1860; Wagner 1861a; Joyce 2003)

[21] Late Jurassic, Tithonian; Schnaitheim, Baden-Württemberg; *Thalassemys marina* (TL) (Fraas 1903)

Poland

[22] Late Jurassic, late Kimmeridgian; Krzyżanowice, Iłża District, Silesian Voivodeship; "Plesiochelyidae" indet. (Borsuk-Białynicka and Młynarski 1968)

[23] Late Jurassic, Tithonian; Tomaszów Mazowiecki, Łódź Voivodeship; *Thalassochelydia* indet. (Szczygielski et al. 2017)

Portugal

[24] Late Jurassic, Kimmeridgian; Romão, Leiria District; *Craspedochelys* sp. (*Craspedochelys* cf. *jaccardi* of Antunes et al. 1988)

[25] Late Jurassic, late Kimmeridgian to Tithonian; Torres Vedras and Vila Franca do Rosário, Lisbon District; *Craspedochelys jaccardi* (= *Plesiochelys choffati* of Sauvage 1898), *Plesiochelys* sp. (Pérez-García et al. 2008), *Tropidemys* sp. (Pérez-García 2015a)

Spain

[26] Late Jurassic, late Oxfordian; Sierra de Cazorla, Andalusia; "Plesiochelyidae" indet. (= *Hispaniachelys prebetica* of Slater et al. 2011; Pérez-García 2014)

[27] Late Jurassic, Kimmeridgian (?); area of Gijón-Ribadesella, Asturias; "Plesiochelyidae" indet. (Pérez-García 2009)

[28] Late Jurassic, late Tithonian; Galve, Aragon; *Tropidemys* sp., *Plesiochelys* sp., "Plesiochelyidae" indet. (Pérez-García et al. 2013)

Switzerland

[29] Late Jurassic, Kimmeridgian; Glovelier, Courtedoux, and Porrentruy, Canton of Jura; *Plesiochelys bigleri* (TL) (Püntener et al. 2017); *Plesiochelys etalloni* (Gaffney 1975a), *Portlandemys gracilis* (TL) (Anquetin et al. 2015), *Tropidemys langii* (Püntener et al. 2014), *Thalassemys bruntrutana* (TL) (Püntener et al. 2015), *Thalassemys hugii* (Püntener et al. 2015)

[30] Late Jurassic, late Kimmeridgian; Solothurn, Canton of Solothurn; *Craspedochelys jaccardi*, *Craspedochelys picteti* (TL), *Plesiochelys etalloni*, *Tropidemys langii* (TL), *Thalassemys hugii* (TL), *Jurassichelon moseri* (TL) (Rütimeyer 1873a; Bräm 1965; Anquetin, Püntener, and Billon-Bruyat 2014), *Solnhofia parsonsi* (Gaffney 1975b), *Thalassemys bruntrutana* (Püntener et al. 2015)

[31] Late Jurassic, late Kimmeridgian or early Tithonian; Les Hauts-Geneveys, Canton of Neuchâtel; *Craspedochelys jaccardi* (TL) (Pictet 1860; Rütimeyer 1873a; Bräm 1965; Anquetin, Püntener, and Billon-Bruyat 2014)

[32] Early Cretaceous, Valanginian (dubious, see text); Sainte-Croix (uncertain locality and horizon), Canton of Vaud; *Tropidemys* sp. (Pictet and Campiche 1858–1860; Püntener et al. 2014)

United Kingdom

[33] Late Jurassic, (early?) Kimmeridgian; Ely, Cambridgeshire; *Enaliochelys chelonia* (TL) (Seeley 1869; Pérez-García 2015b)

[34] Late Jurassic, Kimmeridgian; Abington, Oxfordshire; *Thalassemys hugii* (Pérez-García 2015c; Püntener et al. 2015)

[35] Late Jurassic, Kimmeridgian; Swindon, Wiltshire; *Craspedochelys passmorei* (TL) (Andrews 1921)

[36] Late Jurassic, Kimmeridgian; Weymouth and Isle of Purbeck, Dorset; *Pelobatochelys blakii* (TL) (Seeley 1875; Pérez-García 2015a), *Plesiochelys etalloni* and *Tropidemys langii* (Anquetin and Chapman 2016), *Thalassemys bruntrutana* (Püntener et al. 2015)

[37] Late Jurassic, Tithonian; Isle of Portland, Dorset; *Plesiochelys planiceps* (TL) (Owen 1842; Gaffney 1975a), *Portlandemys mcdowelli* (TL) (Parsons and Williams 1961; Gaffney 1975a)

Appendix 4

Hierarchical Taxonomy of *Thalassochelydia*

"Eurysternidae" Dollo, 1886

- *Achelonia formosa* Meyer, 1860
- *Chelonides wittei* Maack, 1869
- *Eurysternum wagleri* Meyer, 1839c
- *Hydropelta meyeri* (Thiollière, 1851)
- *Idiochelys fitzingeri* Meyer, 1839b
- *Palaeomedusa testa* Meyer, 1860
- *Parachelys eichstaettensis* Meyer, 1864
- *Solnhofia parsonsi* Gaffney, 1975b

"Plesiochelyidae" Baur, 1888

- *Craspedochelys* Rütimeyer, 1873a
  - *Craspedochelys jaccardi* (Pictet, 1860)
  - *Craspedochelys passmorei* (Andrews, 1921)
  - *Craspedochelys picteti* Rütimeyer, 1873a
- *Plesiochelys* Rütimeyer, 1873a
  - *Plesiochelys bigleri* Püntener et al., 2017
  - *Plesiochelys etalloni* (Pictet and Humbert, 1857)
  - *Plesiochelys planiceps* (Owen, 1842)
- *Portlandemys* Gaffney, 1975a
  - *Portlandemys mcdowelli* Gaffney, 1975a
  - *Portlandemys gracilis* Anquetin et al., 2015
- *Tropidemys* Rütimeyer, 1873a
  - *Tropidemys langii* Rütimeyer, 1873a
  - *Tropidemys seebachi* Portis, 1878

"Thalassemydidae" Zittel, 1889

Thalassemys Rütimeyer, 1873a

Thalassemys bruntrutana Püntener et al. 2015

Thalassemys hugii Rütimeyer, 1873a

Thalassemys marina Fraas, 1903

Incertae sedis

Enaliochelys chelonia Seeley, 1869

Jurassichelon Pérez-García, 2015b

Jurassichelon moseri (Bräm, 1965)

Jurassichelon oleronensis Pérez-García, 2015b

Neusticemys neuquina (Fernández and de la Fuente, 1988)

Owadowia borsukbialynickae Szczygielski et al., 2017

Pelobatochelys blakii Seeley, 1875

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