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1 The rediscovery and redescription of the holotype of the Late Jurassic turtle *Plesiochelys*  
2 *etalloni*

3

4 Jérémy Anquetin<sup>1,2</sup>, Sylvie Deschamps<sup>3</sup> and Julien Claude<sup>4</sup>

5

6 <sup>1</sup>Section d'archéologie et paléontologie, Office de la culture, République et Canton du Jura,

7 Hôtel des Halles, 2900 Porrentruy, Switzerland

8 <sup>2</sup>UMR CNRS 7207 MNHN UPMC, Muséum national d'Histoire naturelle, CP38, 8 rue

9 Buffon, 75231 Paris cedex 05, France

10 <sup>3</sup>Musée d'Archéologie du Jura, CCE René Rémond, 133 rue René Maire, 39000 Lons-le-

11 Saunier, France

12 <sup>4</sup>Institut des Sciences de l'Evolution de Montpellier, UMR 5554 CNRS, 2 Place Eugène

13 Bataillon, 34095 Montpellier cedex 5, France

14

15 Corresponding author:

16 Jérémy Anquetin

17 Section d'archéologie et paléontologie

18 Office de la culture, République et Canton du Jura

19 Hôtel des Halles

20 2900 Porrentruy

21 Switzerland

22 [j.anquetin@gmail.com](mailto:j.anquetin@gmail.com)

23 Phone: +41 32 420 8463

24

25 **ABSTRACT**

26 Plesiochelyidae are a major component of Late Jurassic shallow marine environments  
27 throughout Europe. However, the taxonomy of the plesiochelyid turtles is rather confused.  
28 Over the years, many taxa have been synonymized with *Plesiochelys etalloni*, one of the first  
29 described species. However, the holotype of *P. etalloni* (and only specimen known from the  
30 type locality) was lost for more than 150 years. This specimen has been recently rediscovered  
31 in the collections of the Musée d'archéologie du Jura in Lons-le-Saunier, France. For the first  
32 time since its original description in 1857, the holotype of *P. etalloni* is redescribed and  
33 compared to relevant material. The taxonomical status of this taxon is revised accordingly.  
34 Based on the morphology of the newly rediscovered holotype, the species *P. solodurensis*, *P.*  
35 *sanctaeverenae* and *P. langii* are synonymized with *P. etalloni*. Known skull-shell  
36 associations for *P. etalloni* are re-evaluated in light of the new morphological information  
37 available since the rediscovery of this holotype specimen. Finally, we confirm that  
38 *Plesiochelys* is represented by a single species in Solothurn, Switzerland.

39

## INTRODUCTION

40

41 Despite numerous historical discoveries dating from as early as the beginning of the  
42 nineteenth century (e.g., Cuvier, 1824; Pictet & Humbert, 1857; Meyer, 1860; Pictet, 1860;  
43 Wagner, 1861; Maack, 1869; Rüttimeyer, 1873), the diversity of Late Jurassic European  
44 turtles still eludes our understanding. Traditionally referred to the families Plesiochelyidae,  
45 Thalassemydidae and Eurysternidae, these forms are generally considered to be basal  
46 eucryptodires, but their exact relationships with one another and with other turtle groups  
47 remain largely unclear and usually vary among authors (e.g., Gaffney & Meylan, 1988;  
48 Hirayama, Brinkman & Danilov, 2000; Gaffney et al., 2007; Joyce, 2007; Sterli, 2010; Rabi  
49 et al., 2013). A number of reasons may be invoked to explain this situation, but at least two of  
50 these are the much needed revision of the rich historical material and the limited number of  
51 skull-shell associations. Cranial characters are important for turtle systematics, yet many Late  
52 Jurassic turtles from Europe are known only from postcranial material. There are few  
53 exceptions however, for which both the skull and the shell are known: notably *Solnhofia*  
54 *parsonsi* Gaffney, 1975b and *Plesiochelys etalloni* (Pictet & Humbert, 1857).

55 *Emys etalloni* Pictet & Humbert, 1857 was described based on a single shell found in the  
56 French Jura Mountains (see below). A few years later, Rüttimeyer (1873) correctly reassigned  
57 this species to his newly created genus *Plesiochelys*. The type species of *Plesiochelys* is *P.*  
58 *solodurensis* Rüttimeyer, 1873, a species typified based on material from the prolific quarries  
59 near Solothurn in the Swiss Jura Mountains. Rüttimeyer (1873) and Bräm (1965) afterwards  
60 both recognized the presence of *P. solodurensis* and *P. etalloni* in the Solothurn deposits.  
61 Although turtle skulls were known in Solothurn since as early as the 1820s (Cuvier, 1824; see  
62 Bräm, 1965 for an historical account), they were not fully prepared until the 1970s (Gaffney,  
63 1975a). Based on this material, Gaffney (1975a) concluded that *Emys etalloni* Pictet &  
64 Humbert, 1857, *Emys jaccardi* Pictet, 1860, *Styemys lindenensis* Maack, 1869, *Plesiochelys*

65 *solodurensis* Rüttimeyer, 1873, *Plesiochelys sanctaeverenae* Rüttimeyer, 1873,  
66 *Craspedochelys picteti* Rüttimeyer, 1873, and *Craspedochelys crassa* Rüttimeyer, 1873  
67 represented a single species, which should be named *Plesiochelys etalloni* (Pictet & Humbert,  
68 1857) in application of the Principle of Priority. The immediate effect was that *P. etalloni* was  
69 henceforth included into phylogenetic analyses, which helped to improve our understanding  
70 of the systematics and relationships of Late Jurassic and Early Cretaceous turtles from Europe  
71 and Asia (e.g., Gaffney & Meylan, 1988; Hirayama, Brinkman & Danilov, 2000; Joyce,  
72 2007). However, this relatively inclusive synonymy list was not generally accepted among  
73 specialists (including ourselves), at least at the alpha level. For example, several subsequent  
74 authors still considered *Craspedochelys* as a distinct form, and *P. etalloni* and *P. solodurensis*  
75 as different species (e.g., Antunes, Becquart & de Broin, 1988; Lapparent de Broin, Lange-  
76 Badré & Dutrieux, 1996).

77 This extremely confusing situation is in part due to the fact that the holotype of  
78 *Plesiochelys etalloni* was considered to be lost since the 1860s and was therefore unavailable  
79 notably to Rüttimeyer (1873), Bräm (1965), Gaffney (1975a), and Lapparent de Broin, Lange-  
80 Badré & Dutrieux (1996). These authors based their conclusions on the original description  
81 (Pictet & Humbert, 1857) and on plaster casts of the type specimen, which are available in  
82 several European museums, notably in Paris and Geneva. We have been fortunate to locate  
83 this historical specimen in the collections of the Musée d'archéologie du Jura in Lons-le-  
84 Saunier, France. We have also been able to retrace the history of this specimen as it passed  
85 from one owner to the other. This material is redescribed herein and the taxonomic status of  
86 *Plesiochelys etalloni* is revised accordingly. Finally, this rediscovery allow us to re-evaluate  
87 the known skull-shell associations for *P. etalloni*.

88 **Institutional Abbreviations: MAJ**, Musée d'archéologie du Jura, Lons-le-Saunier, France;  
89 **MH**, Naturhistorisches Museum, Basel, Switzerland; **NMS**, Naturmuseum Solothurn,  
90 Switzerland.

91

92

## HISTORICAL BACKGROUND

93 Pictet and Humbert (1857) explained that the holotype of *Plesiochelys etalloni* was  
94 collected by a local priest in the forest close to the village of Lect, near Moirans-en-Montagne  
95 (Jura, France). When they studied the specimen, it was in possession of Joseph Célestin  
96 Girod, vicar general of the Saint-Claude diocese (France). Neither Rüttimeyer (1873) nor  
97 Bräm (1965) gave indication relative to the repository of this specimen. Gaffney (1975a)  
98 indicated that H. Bräm told him the specimen was lost. Lapparent de Broin, Lange-Badré &  
99 Dutrieux (1996) explained that they actively looked for the type but were unable to locate it,  
100 but they figured the plaster cast housed in the Natural History Museum in Geneva,  
101 Switzerland. Finally, without further explanation, Lapparent de Broin (2001) stated that the  
102 holotype of *P. etalloni* had been located in the Natural History Museum of Besançon, France.  
103 After verification, it appears that this information is incorrect.

104 One of us (SD) rediscovered the original specimen a few years ago in the collections of the  
105 Musée d'archéologie du Jura in Lons-le-Saunier, France. Examination leaves no doubt  
106 whatsoever on the identity of this specimen (Figs 1 and 2). This specimen (MAJ 2005-11-1)  
107 was not always housed at the MAJ: it was donated to the museum by a private owner in 1994.  
108 The MAJ also houses a plaster copy of the fossil, which was offered by C-A Etallon, the  
109 renowned geologist, on March 30th, 1857. After a careful investigation, we were able to  
110 uncover most of the history of the fossil shell before it was finally donated to the MAJ.

111 The claim that the holotype of *P. etalloni* was housed in the Natural History Museum of  
112 Besançon (Lapparent de Broin, 2001) is not entirely incorrect. We have found evidences that

113 the specimen was actually part of the Besançon Museum collection, if only for a short time.  
114 This part of the story can be followed in the *Mémoires de la Société d'émulation du*  
115 *département du Doubs* dated from 1859 and 1860. Bishop Mabile, Vicar Girod's superior,  
116 offered the specimen to Mr Thiébaud, a member of the Société d'émulation du Doubs (a  
117 French scientific society), who gave it to the Besançon Museum. The exact date is unclear,  
118 but it was somewhere between 1857 and 1859. In 1859, Vicar Girod wrote to the French  
119 Minister of Public Education and Cults, who turned him down, then to the Rector explaining  
120 that he had never agreed for the fossil to be given for free to the Besançon Museum and  
121 claimed property on the specimen. The Rector abided and the holotype of *P. etalloni* was sent  
122 back to Saint-Claude (Jura, France). Joseph Célestin Girod died in 1863 and the track of the  
123 specimen was lost.

124 The last piece of the puzzle was revealed when Mr and Mrs Lacroix donated the specimen  
125 to the MAJ in 1994. After claiming the fossil as his own, the Vicar sold it to a private party,  
126 the ancestor of Mr and Mrs Lacroix, in order to finance the renovation of his church. The  
127 transaction must have occurred between 1859 and 1863. Until 1994, the holotype of *P.*  
128 *etalloni* remained in this family and was passed from one generation to another (Fig. 1).

129

## 130 SYSTEMATIC PALEONTOLOGY

131

TESTUDINES Batsch, 1788

132

EUCRYPTODIRA Gaffney, 1975c

133

PLESIOCHELYIDAE Rüttimeyer, 1873

134

*Plesiochelys* Rüttimeyer, 1873

135

*Plesiochelys etalloni* (Pictet & Humbert, 1857)

136

*Emys Etalloni* Pictet & Humbert, 1857 (original description)

137

*Plesiochelys solodurensis* Rüttimeyer, 1873 (subjective synonymy)

138 *Plesiochelys sanctaeverenae* Rüttimeyer, 1873 (subjective synonymy)

139 *Plesiochelys langii* Rüttimeyer, 1873 (subjective synonymy)

140 Type material.—MAJ 2005-11-1, a shell missing a large part of the carapace medially.

141 Holotype by monotypy.

142 Type horizon and locality.—"Forêt de Lect" (Lect is a small village) near Moirans-en-

143 Montagne (Department of Jura, France), Late Jurassic. The exact horizon is uncertain, but

144 most outcrops in the vicinity of Lect are either Kimmeridgian or early Tithonian. According

145 to Etallon (1857), the specimen was found in the "calcaires portlandiens". *Gravesia gigas* was

146 also found in these limestones (Etallon, 1857), which led Lapparent de Broin, Lange-Badré &

147 Dutrieux (1996) to conclude that MAJ 2005-11-1 was from the early Tithonian.

148 Illustrations of type.—Pictet & Humbert (1857:plates I-III); Figs 1 and 2.

149 Referred specimens.—See Bräm (1965): specimens referred to *P. etalloni*, *P. solodurensis*,

150 *P. sanctaeverenae* and *P. langii* (except NMS 124). For cranial material, see Gaffney (1975a).

151 Revised diagnosis.—Based on shell only (see Gaffney, 1975a for a diagnosis based on

152 cranial characters): relatively large (up to 550 mm in carapace length) turtle with completely

153 ossified carapace; shell bones relatively thick; carapace oval in outline; wide and shallow

154 nuchal notch; nuchal wide and trapezoidal; additional trapezoidal element often present

155 between the neural series and first suprapygal; three cervical scales; wide vertebral scales,

156 usually extending approximately half the length of the costals; anterior marginal scales very

157 short and not extending onto costals; relatively long plastron (85-90% of carapace length)

158 sutured to the carapace along a long osseous bridge; entoplastron variable in size, usually

159 diamond-shaped with a more or less extended posterior part; hyoplastron and xiphiplastron

160 longer than wide; central plastral fontanelle retained in some adults; short gular and extragular

161 scales; long humeral scale; four inframarginal scales mostly covering the plastral elements.



162       Remarks.—The synonymy list is intentionally restricted to the *Plesiochelys* species  
163 described by Rütimeyer (1873) and later revised by Bräm (1965). The synonymy list  
164 proposed by Gaffney (1975a) is more inclusive, but testing it would require an extensive  
165 revision of historical material at the European scale, something that was done neither by  
166 Gaffney (1975a, 1976) nor any subsequent author (see Discussion).

167

168

## DESCRIPTION

### 169 **General Description**

170       The holotype of *Plesiochelys etalloni* (MAJ 2005-11-1) is a large, oval shell with carapace  
171 and plastron still articulated (Fig. 2 and Video S1). The specimen may have been slightly  
172 flattened during fossilization, but there are no indications of severe deformation. The  
173 specimen is fairly complete, although part of the left bridge and central part of the carapace  
174 are missing. The part of the carapace that is missing reveals the steinkern, which probably  
175 explains why the locals regarded this specimen as the imprint of a human torso (Pictet &  
176 Humbert, 1857). The shell is filled with matrix. There are some indications in the right  
177 axillary and inguinal notches that some elements of the appendicular skeleton are preserved  
178 within the matrix, but as it stands these elements are undetermined.

179

### 180 **Carapace**

181       As preserved, the length of the carapace is 471 mm, but most of the pygal is missing (Figs  
182 2A–C and S2). The carapace is evenly oval in outline, except anteriorly where there is a  
183 broad, shallow nuchal notch. A large part of the carapace is missing centrally. As a result, the  
184 neural series and the medial half of most costals are only visible as imprints on the steinkern.

185       The nuchal is a wide and trapezoidal element. The nuchal notch is shallow, but it extends  
186 laterally on the medial part of the first peripheral. Only the anterior part of the first neural is

187 preserved. This element was apparently longer than wide and rectangular. Neural 2–6 are  
188 preserved as imprints on the steinkern. They are elongate, hexagonal elements with their  
189 shorter sides facing anteriorly. The sixth neural is shorter than the previous elements in the  
190 series. Behind the sixth neural, the imprint of the anterior part of the seventh neural is also  
191 preserved. Posteriorly, the steinkern is covered by the bony carapace, but the sutures in this  
192 area are hardly visible and it is uncertain whether or not there are additional elements to the  
193 neural series. Although it is impossible to be certain, the eighth costals may contact one  
194 another in the midline. Most specimens from Solothurn referred to *P. etalloni* (sensu this  
195 study) have an eighth neural and an additional trapezoidal element of uncertain identity  
196 between the seventh neural and the first suprapygal. This area is however relatively variable  
197 in plesiochelyids and neurals 7 and or 8 may be reduced or lost allowing a medial contact of  
198 costals 7 and/or 8 (Bräm, 1965; JA, unpublished data). There are eight costals. The first  
199 costals is relatively short compared to the following ones. Anteriorly, it contacts the nuchal  
200 and the three first peripherals. Costals 2–4 are wider and longer elements, with costal 3 being  
201 notably wide distally. Costals 5–8 decrease progressively in length and width. There were  
202 certainly 11 peripherals, even if they cannot be clearly all observed on the fossil. The sutures  
203 between peripherals 4, 5 and 6 are not preserved dorsally, but they are visible ventrally.  
204 Posteromedially, the suture between the tenth and eleventh peripherals is also not preserved,  
205 but it must have been there. Peripherals are longer than wide, rectangular elements. Most of  
206 peripheral 11 is missing on both sides. The posteromedial region of the carapace is rather  
207 poorly preserved. There are two large suprapygals. The first suprapygal is a broad element  
208 that contacts the costals 8 anteriorly along a long, anteriorly concave suture, the peripherals  
209 11 (probably) laterally, and the second suprapygal posteriorly along a more or less straight  
210 suture (poorly preserved). The exact outline of the second suprapygal is uncertain, because

211 most of its sutures with surrounding elements are effaced. Posteriorly, just in front of the  
212 broken margin of the carapace, the suture with the pygal is barely discernible.

213 Three cervical scales are clearly visible on the nuchal. Plesiochelyids have long been  
214 thought to be characterized by this character, but its distribution is actually wider. For  
215 example, several eury sternids are known to have three cervical scales (Bräm, 1965; Joyce,  
216 2003; Anquetin & Joyce, unpublished data). Scale sulci are clearly apparent on the carapace,  
217 but very little can be said about the vertebral scales because a large part of the carapace is  
218 missing. The first vertebral scale is a broad element, wider anteriorly than posteriorly. Its  
219 lateral margins extends on the first costal and first peripheral, but not on the nuchal. Laterally,  
220 the first vertebral scale reaches the lateral part of the first marginal. Nothing can be said about  
221 the second and third vertebral scales. The fourth vertebral scale is a broad element extending  
222 laterally about two-thirds of the length of the sixth and seventh costals. The outline of the  
223 fourth vertebral scale is somewhat unusual. Posterolaterally, its lateral margin extends  
224 abruptly onto the tenth peripheral. This unusual shape is symmetrical, but, based on our  
225 experience of the intraspecific variability in plesiochelyids, we grant it no systematic value.  
226 The fifth vertebral scale is a wide, pentagonal element extending onto costals 8, suprapygal 1  
227 and 2, and peripherals 10 and 11. There are four pleural scales. The outlines of pleurals 1–3  
228 are uncertain. The first pleural scale contacts marginals 1–4 and maybe also the fifth marginal  
229 scale. The first pleural scale is slightly shorter than pleurals 2 and 3. The second pleural scale  
230 reaches the seventh marginal scale posteriorly on the sixth peripheral. The fourth pleural scale  
231 is a reduced element covering only a small portion of the sixth and seventh costals and the  
232 medial part of the ninth and tenth peripherals. Marginals are only partly preserved. Marginals  
233 1–6 are still partly visible on the right anterolateral part of the carapace. When preserved, the  
234 pleuro-marginal sulci are always on the peripherals and never extend onto the costals. It

235 should also be noted that the last marginal scales (probably the twelfth pair, although it is  
236 impossible to be sure) extend anteriorly onto the second suprapygal.

237

### 238 **Plastron**

239 The plastron of MAJ 2005-11-1 is mostly complete (Figs 2D–F and S3). The anterior  
240 margin of the left epiplastron, the bridge area on the left hand side, and posterior tip of the  
241 xiphiplastra are broken. The matrix preserved the imprints of the broken parts of the bridge  
242 and xiphiplastra. The total length of the plastron is 431 mm, measuring from the epiplastra  
243 anteriorly to the imprint of the xiphiplastra posteriorly. As such, the plastron represents 91.5%  
244 of the length of the carapace (the true ratio would be slightly lower if the pygal had been  
245 preserved). The plastron is strongly sutured to the carapace. The bridge extends from the  
246 posterior part of the third peripheral to the anterior part of the eighth. The axillary and  
247 inguinal notches are deep. A small central fontanelle is present between the hyo- and  
248 hypoplastra. The anterior lobe is shorter than the posterior lobe, which is itself shorter than  
249 the bridge measured between the axillary and inguinal notches. The anterior lobe is  
250 trapezoidal in outline with a nearly straight anterior margin. The posterior lobe has a  
251 triangular outline with a slightly rounded posterior tip. The central part of the plastron is  
252 slightly concave. This concavity may have been natural.

253 None of the two epiplastra is complete. The left one is missing its anterior margin, whereas  
254 the lateral part of the right one is partly covered by matrix. As preserved, the epiplastra are  
255 relatively short, wider than long elements. They contact one another medially, the hyoplastra  
256 posteriorly, and the entoplastron medially. The epi-hyoplastron suture is straight and  
257 transverse. The entoplastron is a diamond-shaped, slightly longer than wide element with its  
258 posterior faces slightly more elongated than the anterior. The hyoplastron is a large, longer  
259 than wide element. Posteromedially, the hyoplastra form the anterior third of the central

260 plastral fontanelle. The hyo-hyoplastral suture is slightly concave anteriorly, more so  
261 medially. The hypoplastra are shorter than the hyoplastra. They form the remaining two-thirds  
262 of the central fontanelle. The suture between the hypoplastron and the xiphiplastron is mostly  
263 straight and transverse medially. Laterally, it bends suddenly backwards, as it is so often  
264 seen in turtles. The xiphiplastra are triangular, longer than wide elements with a slight  
265 broadening where the femoro-anal sulcus meets their lateral margin, as correctly noted by  
266 Pictet & Humbert (1857). The midline contacts between the different plastral elements are  
267 partly disarticulated (Fig. S3), so that the exact position of the sutures is difficult to assess.  
268 Probably as a result, Pictet & Humbert (1857) erroneously described and depicted a very  
269 small fontanelle between the hypo- and xiphiplastra. Direct examination of the specimen and  
270 observation of the 3D surface reconstruction (Video S1 and Fig. S3) both suggest that there is  
271 no such fontanelle in MAJ 2005-11-1.

272 Gular and extragular scales are relatively small. The gular scales extend only a little onto  
273 the anteromedial part of the entoplastron. The extragular scales are restricted to the epiplastra.  
274 The long humeral scales cover the rest of the anterior plastral lobe. The pectoral scale is  
275 nearly as long as the abdominal scale on the midline, but both are shorter than the humeral  
276 scale. The abdominal-femoral sulcus is oblique and extends from the inguinal notch to the  
277 posterior third of the central plastral fontanelle. The femoral is the longest scale of the  
278 plastron. The femoral-anal sulcus is deeply concave posteriorly in its medial part. The anal  
279 scales are restricted to the xiphiplastra. The medial sulcus between paired scales is unusually  
280 irregular. The median sulcus diverges strongly from the midline between the humeral and  
281 pectoral scales, being notably sinusoidal between the latter. The median sulcus is more poorly  
282 preserved between the femoral and anal scales, but observation of the 3D surface  
283 reconstruction (Video S1) suggests that it might also have been slightly sinusoidal, at least in  
284 the posterior part of the femoral scales. The bridge area is covered by four inframarginal

285 scales increasing in length posteriorly. The two first and the last are restricted to the  
286 hyoplastron and hypoplastron, respectively. The third inframarginal scale covers the  
287 hyoplastron anteriorly, the hypoplastron posteriorly, and a small portion of the fifth peripheral  
288 laterally.

289

290

## DISCUSSION

### 291 **Skull-Shell Associations**

292 Despite a profusion of material collected from the Late Jurassic of Europe, relatively few  
293 species are known from both skull and shell material. European lithographic limestone  
294 localities (especially Solnhofen, Kelheim, and Cerin) have produced a fair number of  
295 relatively complete, articulated specimens with shell, skull, and various elements of the  
296 skeleton (e.g., Meyer, 1860), but the cranial material is always badly crushed and very  
297 difficult to interpret. Hence, the skull is 'known' in species such as *Eurysternum wagleri*,  
298 *Idiochelys fitzingeri*, and *Palaeomedusa testa* (e.g., Jourdan, 1862; Joyce, 2003; Anquetin &  
299 Joyce, unpublished data), but only scarce information can be gathered from these examples.

300 Among European Late Jurassic turtles, only *Solnhofia parsonsi* and *Plesiochelys etalloni*  
301 are sufficiently known from both skull and shell material. Additional skull and associated  
302 fragmentary shell remains were described by Rieppel (1980) and assigned to *Thalassemys*  
303 *moseri* Bräm, 1965, but the validity of both this taxon and this referral was questioned by  
304 subsequent authors (e.g., Gaffney & Meylan, 1988; Lapparent de Broin, Lange-Badré &  
305 Dutrieux, 1996). This material should therefore be revised. *Solnhofia parsonsi* was described  
306 by Gaffney (1975b) based on two isolated skulls, one from the Solnhofen region (Germany),  
307 one from Solothurn (Switzerland). Later, Joyce (2000) described a nearly complete skeleton  
308 that can be confidently referred to *S. parsonsi*.

309 Skulls of *P. etalloni* are known since the early nineteenth century (e.g., Cuvier, 1824;  
310 Rüttimeyer, 1873; Bräm, 1965), although they were not necessarily assigned to this species in  
311 those times. The Solothurn Turtle Limestone has produced four *Plesiochelys* skulls, which  
312 Gaffney (1975a) prepared and identified as belonging to a single species. Among these four  
313 skulls, only one (NMS 594) is associated with significant shell material (few disarticulated  
314 costals and peripherals and partial posterior half of a plastron). Bräm (1965) identified this  
315 specimen as *P. etalloni* based on the probable presence of a central plastral fontanelle.  
316 However, this material is too fragmentary to allow a definitive specific identification. Only  
317 one other skull-shell association exists for *P. etalloni*. It is a specimen (MH 435) that was  
318 found in the Kimmeridgian near Glovelier (Canton of Jura, Switzerland). Bräm (1965)  
319 referred this material to *P. etalloni* without further description and depicted the skull and a  
320 humerus (ibid.:plate 4, figs 1–4). The skull, one of the best for *P. etalloni*, was prepared by  
321 Gaffney (1975a), who followed the identification of Bräm (1965). Gaffney (1975a:7)  
322 examined the associated, incompletely prepared shell material and concluded that "the shell  
323 features as determinable at this time are consistent with [his] concept of *Plesiochelys*  
324 *etalloni*". Because Gaffney's (1975a) concept of *P. etalloni* is inclusive and not necessarily  
325 accepted among fossil turtle specialists, it was important to reassess the shell material of MH  
326 435 and compare it with the newly rediscovered holotype specimen of *P. etalloni*.

327 If the skull of MH 435 has been extensively studied (Gaffney, 1975a, 1976; Sterli et al.,  
328 2010; Carabajal et al., 2013), the associated shell material has never been described or  
329 illustrated. This material (Fig. 3) consists of the anterior half of a shell with carapace and  
330 plastron still in articulation. Everything posterior to the fifth costal on the carapace and  
331 inguinal notch on the plastron is missing. Both the carapace and the plastron are greatly  
332 fractured. Many fragments of the costals are missing. The carapace is oval in outline with a  
333 broad, shallow nuchal notch (Fig. 3A–B). The nuchal is a wide and trapezoidal element. The

334 first neural is rectangular, whereas neurals 2–4 are hexagonal with their shorter sides  
335 anteriorly. Cervical scale sulci are not preserved. The first vertebral scale is a broad,  
336 trapezoidal element that extends laterally onto the first peripheral and contacts the lateral  
337 border of the first marginal scale. The second and third vertebral scales are wide and  
338 hexagonal. Their sulci are moderately sinuous, as it is common in Solothurn specimens  
339 referred to *P. etalloni* (Bräm, 1965). The anterior margin of the anterior lobe of the plastron is  
340 rounded (Fig. 3C–D). The epiplastron is separated from the hyoplastron by a straight,  
341 transverse suture. The hyoplastron is longer than wide. There is an oval central fontanelle  
342 between the hyo- and hypoplastron. The hyo-hyoplastral suture is relatively straight and  
343 slightly oblique defining a small concavity toward the anterior. The bridge is long and  
344 osseous. It extends from the posterior half of the third peripheral to the anterior part of the  
345 eighth peripheral. The scale arrangement on the plastron is similar to that of MAJ 2005-11-1.  
346 The median sulcus between the humeral and pectoral scales diverges strongly from the  
347 midline, although it is not sinusoidal as in the holotype of *P. etalloni*. There are four  
348 inframarginal scales increasing in length posteriorly. Based on this description, MH 435 can  
349 be confidently referred to *P. etalloni* (sensu this study, not Gaffney, 1975a). This confirms the  
350 importance of this specimen, especially for phylogenetic reconstructions.

351

### 352 **Alpha Taxonomy**

353 As mentioned above, comparisons for the present study are restricted to the *Plesiochelys*  
354 species described by Rüttimeyer (1873) and later revised by Bräm (1965), i.e. forms first  
355 described from the Late Jurassic of the Swiss and French Jura Mountains. Many specimens  
356 from the Late Jurassic of France, Germany, England, Spain and Portugal have afterwards  
357 been either referred to *P. etalloni* and *P. solodurensis* or assigned to new species, but these  
358 need to be revised thoroughly. Kuhn (1964) listed 22 species of *Plesiochelys* typified based



359 on European material. It is far beyond the scope of the present study to revise the taxonomy of  
360 the genus *Plesiochelys*.

361 Another issue is the relatively inclusive synonymy list proposed by Gaffney (1975a), who  
362 synonymized the following species with *P. etalloni*: *Emys jaccardi*, *Stylemys lindenensis*, *P.*  
363 *solodurensis*, *P. sanctaeverenae*, *Craspedochelys picteti*, and *C. crassa*. *Stylemys lindenensis*  
364 is a form from the Late Jurassic of Hannover, Germany, and, along with many other  
365 specimens from the same region, it has never been properly revised since Oertel (1924). All  
366 other species but *E. jaccardi* were described based on material from Solothurn, Switzerland.  
367 *Emys jaccardi* was referred to *Plesiochelys* by Rütimeyer (1873) and Bräm (1965). In  
368 contrast, Antunes, Becquart & de Broin (1988) and Lapparent de Broin, Lange-Badré &  
369 Dutrieux (1996) referred this species to the genus *Craspedochelys* Rütimeyer, 1873, which  
370 they distinguished from *Plesiochelys* by a shell as wide as long and a shortened plastron.  
371 Gaffney (1975a) argued that variation in shell shape, especially relative width (as used to  
372 differentiate *E. jaccardi* and *C. picteti* from *P. etalloni*), was probably the result of  
373 postmortem deformation and should not be considered for systematic purposes. The objective  
374 of the present paper is not to settle this argument. The fact is that Bräm (1965) is the last  
375 author to have thoroughly reassessed the shell morphology of these forms. Gaffney (1975a)  
376 focussed essentially on skull description and did not describe shell morphology in detail.  
377 Lapparent de Broin, Lange-Badré & Dutrieux (1996) studied some of the Solothurn material,  
378 but they did not clearly formalized their views, instead proposing a general discussion as part  
379 of the description of new material from France. In contrast to these authors, we have  
380 thoroughly revised the Solothurn material. Our conclusions, which concern several additional  
381 species besides *P. etalloni*, will be presented elsewhere. For the purpose of the present paper,  
382 we restrict our comparisons to *P. solodurensis*, *P. sanctaeverenae* and *P. langii*.

383 According to Rüttimeyer (1873) and Bräm (1965), both *P. etalloni* and *P. solodurensis* are  
384 present in Solothurn, the type locality of *P. solodurensis*. However, Bräm (1965) himself  
385 admitted that differentiating the two species was not easy. *Plesiochelys etalloni* was supposed  
386 to produce slightly larger individuals than *P. solodurensis* and to retain a small central plastral  
387 fontanelle in the adults (Bräm, 1965). The proposed difference in size is minor (about 10%)  
388 and is not interpreted as being significant. We have scrutinized all fairly complete  
389 specimens from Solothurn referred to both *P. etalloni* and *P. solodurensis*, representing about  
390 30 individuals. We have extensively looked for additional characters that would confirm the  
391 presence of two species (one with a central plastral fontanelle and one without), but have  
392 found none. For example, a close comparison between MAJ 2005-11-1 (holotype of *P.*  
393 *etalloni*) and NMS 59 (lectotype of *P. solodurensis*) reveals only little differences: the shape  
394 of the posterolateral sulcus of the fourth vertebral (probably anomalous in MAJ 2005-11-1);  
395 the very minute extension of the fourth marginal onto costal 2 in NMS 59; the central plastral  
396 fontanelle in MAJ 2005-11-1; and the extension of the anal scale onto the hypoplastron in  
397 NMS 59. Anomalous scale shape is relatively common among Solothurn turtles, especially  
398 for vertebral scales. Similarly, both the extension of the fourth marginal onto costals and the  
399 extension of the anal scale onto the hypoplastron, characters that are otherwise diagnostic for  
400 Xinjiangchelyidae (e.g., Tong et al., 2012; Rabi et al., 2013; Pérez-García, Gasulla & Ortega,  
401 in press), are variable in *P. etalloni*. Hence, the retention of a central plastral fontanelle in  
402 adults is interpreted as an intraspecific variation of *P. etalloni*, and *P. solodurensis* is  
403 considered a subjective junior synonym of this species.

404 Bräm (1965) found no significant difference between NMS 123 and NMS 126, two  
405 carapaces referred to *P. langii*, and NMS 59, and therefore synonymized *P. langii* with *P.*  
406 *solodurensis*. We agree and similarly find no significant difference between these specimens  
407 and MAJ 2005-11-1. Consequently, *P. langii* is synonymized with *P. etalloni*. *Plesiochelys*

408 *sanctaeverenae* was defined by Rüttimeyer (1873) mainly based on NMS 118, a large,  
409 incomplete carapace. Bräm (1965) designated this specimen as the lectotype and considered  
410 this species as valid based on its larger size (carapace length = 565 mm) and elongate outline.  
411 However, observable characteristics do not allow to differentiate NMS 118 from others  
412 specimens we refer here to *P. etalloni*, especially neither from MAJ 2005-11-1 nor NMS 59.  
413 Concerning the outline of this specimen, Bräm (1965) was probably misled by the fact that  
414 the lateral parts of the carapace are largely missing. Consequently, *P. sanctaeverenae* is also  
415 considered a subjective synonym of *P. etalloni*.

416 From the above, we recognize only one species of *Plesiochelys* in Solothurn: *Plesiochelys*  
417 *etalloni*. Although this conclusion may appear superficially similar to that of Gaffney  
418 (1975a), we reached it through an extensive re-evaluation of the Solothurn material and a  
419 redescription of the type material of *P. etalloni*, which was unavailable for these past 150  
420 years. Since Gaffney (1975a, 1976), we have an excellent knowledge of the cranial  
421 morphology of *P. etalloni*. Thanks to the present study, we now have a better understanding  
422 of the shell morphology and intraspecific variability of this species.

423

424

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433

434

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#### 518 **FIGURE CAPTIONS**

519 FIGURE 1—MAJ 2005-11-1, holotype of *Plesiochelys etalloni* (Pictet & Humbert, 1857).  
520 Specimen mounted on a wooden socle with the old label "*Emys Etalloni*, (Pictet et Humbert) -  
521 Portland - Moirans (Jura)". (A) carapace; (B) plastron. Note that the specimen is upside  
522 down.

523

524 FIGURE 2—MAJ 2005-11-1, holotype of *Plesiochelys etalloni* (Pictet & Humbert, 1857).  
525 (A) photograph of the carapace; (B) interpretative drawing of the carapace; (C) 3D surface  
526 reconstruction of the carapace; (D) photograph of the plastron; (E) interpretative drawing of  
527 the plastron; (F) 3D surface reconstruction of the plastron. Bones are white; stripped lines  
528 indicate internal bone layers; green solid lines indicate scale sulci; matrix is gray.

529 Abbreviations: *ab*, abdominal scale; *an*, anal scale; *ce*, cervical scale; *co*, costal; *eg*, extragular  
530 scale; *epi*, epiplastron; *ento*, entoplastron; *fem*, femoral scale; *gu*, gular scale; *hyo*,  
531 hyoplastron; *hypo*, hypoplastron; *hum*, humeral scale; *m*, marginal scale; *n*, neural; *nu*,

532 nuchal; p, peripheral; *pect*, pectoral scale; *pl*; pleural scale; py, pygal; sp, suprapygal; v,  
533 vertebral scale; xi, xiphiplastron.

534

535 FIGURE 3—MH 435, *Plesiochelys etalloni* (Pictet & Humbert, 1857). (A) photograph of the  
536 carapace; (B) interpretative drawing of the carapace; (C) photograph of the plastron; (D)

537 interpretative drawing of the plastron. Bones are white; stripped lines indicate internal bone

538 layers; green solid lines indicate scale sulci; dotted areas indicate reconstructed parts; matrix

539 is gray. Abbreviations: *ab*, abdominal scale; *co*, costal; *eg*, extragular scale; *epi*, epiplastron;

540 *ento*, entoplastron; *fem*, femoral scale; *gu*, gular scale; *hyo*, hyoplastron; *hypo*, hypoplastron;

541 *hum*, humeral scale; *n*, neural; *nu*, nuchal; *p*, peripheral; *pect*, pectoral scale; *pl*; pleural scale;

542 *v*, vertebral scale.

543



544 FIGURE 1

545





