A taxonomic review of the Late Jurassic turtles from the Jura Mountains (Switzerland and France)

Background. Turtles from the Late Jurassic (mainly Kimmeridgian) deposits of the Jura Mountains (Switzerland and France) are among the earliest named species traditionally referred to the Plesiochelyidae, Thalassemydidae, and Eurysternidae. As such, they are a reference for the study of Late Jurassic turtles at the European scale. Fifteen species and four genera have been typified based on material from the Late Jurassic of the Jura Mountains. In the past 50 years, diverging taxonomic reassessments have been proposed for these turtles with little agreement in sight. In addition, there has been a shift of focus from shell to cranial anatomy in the past forty years, although most of these species are only represented by shell material. As a result, the taxonomic status of many of these 15 species remains ambiguous, which prevents comprehensive comparison of Late Jurassic turtle assemblages throughout Europe and hinders description of new discoveries, such as the new assemblage recently unearthed in the vicinity of Porrentruy, Switzerland.

Methods. An exhaustive reassessment of the available material provides new insights into the comparative anatomy of these turtles. The taxonomical status of each of the 15 species typified based on material from the Late Jurassic of the Jura Mountains is evaluated. A new diagnosis and a general description are proposed for each valid taxon.

Results. Six out of the 15 original species are recognized as valid: *Plesiochelys etalloni*, *Craspedochelys picteti*, *Craspedochelys jaccardi*, *Tropidemys langii*, *Thalassemys hugii*, and *'Thalassemys' moseri*. The intraspecific variability of the shell of *P. etalloni* is discussed based on a sample of about 30 relatively complete specimens. New characters are proposed to differentiate *P. etalloni* on the one hand, and *C. picteti* and *C. jaccardi* on the other hand, therefore rejecting the previously proposed synonymy of these forms. Based partly on previously undescribed specimens, the plastral morphology of *Th. hugii* is redescribed. The presence of lateral plastral fontanelles is notably revealed in this species, which calls into question the traditional definitions of the Thalassemydidae and Eurysternidae. Based on

these new data, *Eurysternum ignoratum* is considered a junior synonym of *Th. hugii.* The Eurysternidae are therefore only represented by *Solnhofia parsonsi* in the Late Jurassic of the Jura Mountains. Finally, *'Th.' moseri* is recognized as a valid species, although a referral to the genus *Thalassemys* is refuted.

1 A taxonomic review of the Late Jurassic turtles from the Jura Mountains (Switzerland and

2 France)

3 Jérémy Anquetin[1, 2], Christian Püntener[1] and Jean-Paul Billon-Bruyat[1]

4 [1]Section d'archéologie et paléontologie, Office de la culture, République et Canton du Jura, Hôtel

5 des Halles, 2900 Porrentruy, Switzerland, j.anquetin@gmail.com

6 [2]UMR CNRS 7207 MNHN UPMC, Muséum national d'histoire naturelle, CP38, 8 rue Buffon,

7 75231 Paris cedex 05, France.

8 Corresponding author:

9 Jérémy Anquetin

10 Section d'archéologie et paléontologie

11 Office de la culture, République et Canton du Jura

12 Hôtel des Halles

13 2900 Porrentruy

14 Switzerland

15 j.anquetin@gmail.com

16 Phone: +41 32 420 8463

INTRODUCTION

From 2000 to 2011, controlled excavations along the future course of the A16 Transjurane

highway have opened an unprecedented window into the late Kimmeridgian of the Jura

Mountains, in the vicinity of Porrentruy (Canton of Jura, NW Switzerland; Fig. 1). The mission

of the PAL A16 team (Section d'archéologie et paléontologie, Office de la culture, République et

Canton du Jura, Switzerland) was first to document the geology and paleontology of intersected

sedimentary rocks. This notably led to the discovery of a rich and diverse Mesozoic coastal

marine vertebrate fauna, including fishes, turtles, crocodilians, and pterosaurs, and several

extensive dinosaur track-bearing sites (e.g., Marty & Hug, 2003; Billon-Bruyat, 2005; Marty et

al., 2007; Marty & Billon-Bruyat, 2009). The PAL A16 team is now entering the second phase of

its mission: the scientific study of this rich material. Turtles are among the most abundant

vertebrates discovered during the excavations. Up to now, the PAL A16 Mesozoic turtle

collection includes about 80 shells (more than 50 of which are already prepared), five crania,

four mandibles and thousands of isolated remains. Preliminary investigations reveal that this

turtle assemblage is taxonomically diverse. A recent study focussed on the species *Tropidemys*

langii Rütimeyer, 1873 and described new, articulated material collected by the PAL A16 team

that considerably improved our knowledge of this characteristic Late Jurassic plesiochelyid turtle

(Püntener et al., 2014). The PAL A16 turtle assemblage also includes several taxa that can be

provisionally referred to the traditional families Plesiochelyidae Baur, 1888, Thalassemydidae

Zittel, 1889, and Eurysternidae Dollo, 1886. The definition of these families is however rather

confused (Joyce, 2003, 2007; Anquetin, Deschamps & Claude, 2014; Anquetin & Joyce, in

press).

Numerous turtles have been collected from the Kimmeridgian of the Jura Mountains since the

early nineteenth century, notably from the famous Solothurn Turtle Limestone (Canton of

41 Solothurn, Switzerland; e.g., Bräm, 1965; Meyer & Thüring, 2009) and from the vicinity of

42 Porrentruy (e.g. Marty & Billon-Bruyat, 2009; Püntener et al., 2014). A total of five localities

43 have produced significant turtle material (Fig. 1). Fifteen species, including *Plesiochelys etalloni*

44 (Pictet & Humbert, 1857), *P. solodurensis* Rütimeyer, 1873, *Craspedochelys picteti* Rütimeyer,

45 1873, *C. jaccardi* (Pictet, 1860), *Tropidemys langii*, *Thalassemys hugii* Rütimeyer, 1873, and *Th.*

46 *moseri* Bräm, 1965, have been typified based on specimens from the Late Jurassic of the Jura

47 Mountains. The PAL A16 Mesozoic turtle collection must therefore be directly compared to

48 these early finds, but there is currently no proper agreement upon their taxonomy. In particular,

49 previous authors disagreed on the number of species represented in Solothurn (see Previous

50 Work, below). This situation prevents a detailed interpretation of the PAL A16 turtle assemblage.

51   *Plesiochelys solodurensis*, *C. picteti*, *Tr. langii*, and *Th. hugii* are the type species of their

52 respective genus. Similarly, *Plesiochelys* Rütimeyer, 1873 and *Thalassemys* Rütimeyer, 1859 are

53 the type genera of plesiochelyids and thalassemydids, respectively. Late Jurassic turtles from the

54 Jura Mountains are therefore of major importance for the taxonomy of basal eucryptodires.

55 However, since Bräm (1965), no author has properly reassessed the shell morphology of these

56 forms. The purpose of the present contribution is to review the taxonomy of the 15 turtle species

57 typified based on fossil specimens from the Late Jurassic of the Jura Mountains. This study is

58 tightly linked to a recent paper in which we announced the rediscovery of the holotype material

59 of *P. etalloni* (Anquetin, Dechamps & Claude, 2014). The type material of each of these 15

60 species has been carefully scrutinized in order to evaluate the taxonomies proposed by recent

61 authors (e.g., Gaffney, 1975a; Lapparent de Broin, Lange-Badré & Dutrieux, 1996). Many

62 additional specimens from Solothurn have also been studied first-hand as part of the present

63 work (Table S1). This reassessment is an essential first step toward a broader revision of the

64 plesiochelyids and thalassemydids at the European scale and will serve as a solid reference for

65 the interpretation of new discoveries, most notably the rich material recently unearthed by the

66 PAL A16 team in the vicinity of Porrentruy.

67 **Institutional abbreviations.**—**MAJ**, Musée d'archéologie du Jura, Lons-le-Saunier, France;

68 **MH**, Naturhistorisches Museum, Basel, Switzerland; **MHNN**, Muséum d'histoire naturelle,

69 Neuchâtel, Switzerland; **MJSN**, Musée jurassien des sciences naturelles, Porrentruy,

70 Switzerland; **NMS**, Naturmuseum Solothurn, Switzerland; **PMZH**, Paläontologisches Institut

71 und Museum, Universität Zürich, Switzerland.

72 **PREVIOUS WORK**

73 Bräm (1965) related the history of the Solothurn turtle collection in details. This collection,

74 whose origins go back to the years 1820 and 1830, is tied to the fate of Professor F. J. Hugi, keen

75 naturalist and alpinist, who established the "Naturforschenden Gesellschaft Solothurn" (Society

76 of Natural History of Solothurn) in 1823 (Lienhard, 2008). Being the first to recognize the

77 presence of turtle remains in the Solothurn quarries, he gave a lecture on his fossil turtle

78 collection in 1824 during a meeting of the "Naturforschenden Gesellschaft Solothurn" and even

79 sent informations and specimens to G. Cuvier, who figured a turtle skull (NMS 134) and other

80 specimens from Solothurn in the second edition of his *Recherches sur les ossemens fossiles*

81 (Cuvier, 1824: 227-232; Bräm, 1965; Gaffney, 1975a). In 1825, F. J. Hugi sold his private

82 collection to the city and was appointed as first director of the newly created city museum

83 (Meyer & Thüring, 2009). A few decades later, Professor F. Lang, the successor of F. J. Hugi at

84 the head of the Solothurn museum, appointed Dr L. Rütimeyer to study the huge turtle collection

85 in question. Lang & Rütimeyer (1867) published a first account on the geology of the Solothurn

86 quarries that contained a monograph on the specimens referable to *Platychelys oberndorferi*

87 Wagner, 1853, a species originally defined based on a specimen from the Tithonian of Kelheim,

88 Germany. All the other turtles from Solothurn were described in Rütimeyer (1873).

89   At the time when Rütimeyer was starting to work on the Solothurn material, the Swiss

90 paleontologist F.-J. Pictet described two new turtles from the Late Jurassic of the Jura

91 Mountains: *Emys etalloni* Pictet and Humbert, 1857 from the vicinity of Moirans-en-Montagne

92 (French Jura) and *Emys jaccardi* Pictet, 1860 from Les Hauts-Geneveys (Canton of Neuchâtel,

93 Swiss Jura; Fig. 1). Rütimeyer (1873) subsequently referred these two species to his newly

94 created genus *Plesiochelys*. Surprisingly, despite being the reference for the application of the

95 species names *etalloni* and *jaccardi*, this material received relatively little attention since Pictet's

96 time.

97   Bräm (1965) proposed a detailed reassessment of the Solothurn turtle fauna, including

98 specimens discovered after the work of Rütimeyer. This contribution remains a major reference

99 today. Each of the 13 species recognized by Rütimeyer (1873) was evaluated; this count

100 excludes *Platychelys oberndorferi*, which is both non-controversial and not typified based on

101 material from the Jura Mountains. Eight were confirmed and two new species were created.

102 Table 1 summarizes the taxonomy proposed by the different authors discussed herein. According

103 to Bräm (1965), there is only one species of *Craspedochelys* and *Tropidemys* in Solothurn,

104 instead of three in each genus as proposed by Rütimeyer (1873). Bräm (1965) still recognized

105 two species of *Thalassemys* in Solothurn. The first is the type species *Th. hugii*, but the second is

106 different from the one proposed earlier by Rütimeyer (1873) and was referred to a new species,

107 *Th. moseri*. In addition, Bräm (1965) erected a new species, *Eurysternum ignoratum*, for some of

108 the remains previously assigned to *Thalassemys* by Rütimeyer (1873). The two authors were

109 more or less on the same line concerning the genus *Plesiochelys*: Bräm (1965) still recognized

the presence of four species out of the five originally described in Solothurn (*P. etalloni*, *P. jaccardi*, *P. solodurensis* and *P. sanctaeverenae*).

Ten years later, E. S. Gaffney developed an interest for Late Jurassic turtles from Europe. In contrast to previous workers, he focussed more specifically on cranial material, often considering that the turtle shell was subject to too much individual variations to be heavily relied upon for systematic purposes. In the Late Jurassic of the Jura Mountains, only plesiochelyids have produced significant cranial material. Studying the material from Solothurn and Glovelier (Canton of Jura, Switzerland; Fig. 1), Gaffney (1975a) reached the conclusion that all available skulls should be assigned to a unique species. In parallel, he rejected all the shell-based arguments proposed by Bräm (1965) to support the distinction between the various *Plesiochelys* and *Craspedochelys* species. He notably synonymized *P. solodurensis*, *P. jaccardi*, *P. sanctaeverenae* and *C. picteti* with *P. etalloni* (Pictet & Humbert, 1857).

In contrast to previous authors, Antunes, Becquart & Broin (1988) assigned *Emys jaccardi* Pictet, 1860 to the genus *Craspedochelys* Rütimeyer, 1873, creating the new combination *Craspedochelys jaccardi* (Pictet, 1860). They also suggested that European plesiochelyids and thalassemydids should be revised, as neither Bräm's (1965) nor Gaffney's (1975a) taxonomies were satisfactory. Although they did not propose an extensive revision of these groups, Lapparent de Broin, Lange-Badré & Dutrieux (1996) exposed a certain number of considerations regarding their taxonomy and possible relationships (Table 1). They recognized two valid species in the genus *Plesiochelys*, *P. etalloni* and *P. solodurensis*. They considered that only one species of *Plesiochelys* was present in Solothurn, *P. solodurensis*, and that *P. etalloni* was closely related but different. *Craspedochelys jaccardi* and *C. picteti* were also considered as valid. Finally, thalassemydids were restricted to *Thalassemys hugii*, and *Th. moseri* was synonymized with *P. solodurensis*.

SYSTEMATIC PALEONTOLOGY

TESTUDINES Batsch, 1788

EUCRYPTODIRA Gaffney, 1975c

PLESIOCHELYIDAE Baur, 1888

Plesiochelys Rütimeyer, 1873

1873   *Plesiochelys* — Rütimeyer [new genus]

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

Revised diagnosis.—Form traditionally referred to the Plesiochelyidae based on the presence of three cervical scales and a completely ossified carapace. Differing from *Craspedochelys* in: carapace more elongated and oval; deeper nuchal notch usually extending laterally up to the middle of peripheral 1; lower length/width ratio of costal bones (3.1–3.6, as opposed to 4.3–4.8 or more for the fourth costal in *Craspedochelys*); relatively long plastron (about 85–90% of carapace length); hyoplastron longer than wide. Differing from *Tropidemys* in: absence of neural keel; elongated neurals; wider vertebral scales.

Remarks.—Closely following the original definition of Rütimeyer (1873), Bräm (1965) mainly diagnosed *Plesiochelys* based on the following characters: carapace oval in outline, usually longer than wide; nuchal notch extending laterally up to the middle of the first peripheral; plastron large and oval in outline; anterior lobe with bulbous epiplastral processes; posterior lobe rounded, occasionally slightly notched; entoplastron wide and often shield-shaped; hyoplastra longer than hypoplastra; central plastral fontanelle present or absent; pelvic girdle connected to plastron by means of the prepubic process. Gaffney (1975a: 6) proposed a slightly updated diagnosis, which by his own opinion "does not serve as a satisfactory set of identifying criteria."

157   Proposing a complete diagnosis for the genus *Plesiochelys* is indeed relatively complicated as

158 several Late Jurassic forms from Europe, notably from Germany, France and Portugal (e.g.,

159 Antunes, Becquart & Broin, 1988; Lapparent de Broin, 2001; Karl et al., 2007), are in need of

160 serious reconsideration. Considering only *Plesiochelys* and not other potentially synonymous

161 genera, a score of species are typified based on European material (Kuhn, 1964). As it stands,

162 only two of these species are currently sufficiently known: *P. etalloni* (sensu Anquetin,

163 Deschamps & Claude, 2014) and *P. planiceps* (Owen, 1842) from the Tithonian of southern

164 England (Gaffney, 1975a). The latter is known by a single, isolated cranium with associated

165 mandible. The above revised diagnosis is a first step, which will be refined in the future as the

166 understanding of the taxonomy of Late Jurassic European turtles improves.

167   *Plesiochelys solodurensis* Rütimeyer, 1873

168   1873   *Plesiochelys solodurensis* — Rütimeyer [new species]

169   1975a *Plesiochelys etalloni* — Gaffney [subjective synonymy]

170   2014   *Plesiochelys etalloni* — Anquetin, Deschamps & Claude [subjective

171   synonymy]

172   Taxonomic assessment.—Invalid name, subjective synonym of *Plesiochelys etalloni* (Pictet &

173 Humbert, 1857).

174   Synonymy.—None.

175   Type material.—NMS 59, a distorted sub-complete shell. Lectotype designated by Bräm

176 (1965: 81).

177   Type horizon and locality.—Solothurn Turtle Limestone, uppermost member of the

178 Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of

179 Solothurn, Switzerland (Fig. 1).

180   Illustrations of type.—Rütimeyer (1873: plate XII, figs. 1 and 2); Fig. 2E–H.

181   Referred specimens.—See Bräm (1965).

182   Remarks.—Rütimeyer (1873) and Bräm (1965) referred most of the *Plesiochelys* material

183 from Solothurn either to *P. solodurensis* or *P. etalloni*. The main difference they recognized

184 between the two species was the presence of a central plastral fontanelle in *P. etalloni*. Bräm

185 (1965: 60–62) even concluded that the two species were very similar, to the point of being hardly

186 differentiable if hyo- and hypoplastron were not preserved. Considering the fact that the

187 retention of a small plastral fontanelle is variable in some extant species (i.e., some adults have

188 one and some do not; see Pritchard, 2008), Gaffney (1975a) assumed this was also the case in

189 *Plesiochelys* and referred *P. solodurensis*, *P. jaccardi* and *P. etalloni* to the same species.

190 Lapparent de Broin, Lange-Badré & Dutrieux (1996) also considered the persistence of a small

191 central plastral fontanelle in adults as an intraspecific variation of *P. solodurensis*, which they

192 considered as a distinct species. Based on an extensive review of the relevant material, we

193 reached a conclusion similar to that of Gaffney (1975a) and Lapparent de Broin, Lange-Badré &

194 Dutrieux (1996), although we ultimately disagree on the delimitation and inclusiveness of

195 *Plesiochelys* species (Anquetin, Deschamps & Claude, 2014; see also Table 1 and Discussion).

196   *Plesiochelys etalloni* (Pictet & Humbert, 1857)

197   1857   *Emys etalloni* — Pictet & Humbert [new species]

198   1873   *Plesiochelys Etalloni* — Rütimeyer [new combination]

199   Taxonomic assessment.—Valid name.

200   Synonymy.—*Plesiochelys solodurensis* Rütimeyer, 1873, *Plesiochelys sanctaeverenae*

201 Rütimeyer, 1873, and *Plesiochelys langii* Rütimeyer, 1873.

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

203 Holotype by monotypy.

204   Type horizon and locality.—"Forêt de Lect" near Moirans-en-Montagne (Department of Jura,

205 France; Fig. 1), possibly early Tithonian (but see Anquetin, Deschamps & Claude, 2014), Late

206 Jurassic.

207   Illustrations of type.—Pictet & Humbert (1857: plates I-III); Anquetin, Deschamps & Claude

208 (2014: figs. 1, 2, S2 and S3); Fig. 2A–D.

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

210 and *P. sanctaeverenae*. For cranial material, see Gaffney (1975a).

211   Revised diagnosis.—See Anquetin, Deschamps & Claude (2014).

212   Remarks.—Lost for more than 150 years, the holotype of *P. etalloni* has been recently

213 relocated. Thanks to this rediscovery, the taxonomy of this species was revised (Anquetin,

214 Deschamps & Claude, 2014). For the purpose of the present study, we have reassessed a great

215 number of specimens from the Late Jurassic of the Jura Mountains. In contrast to Gaffney

216 (1975a), we reached the conclusion that *Craspedochelys picteti* and *C. jaccardi* are not

217 synonyms of *P. etalloni* (see below).

218   *Plesiochelys sanctaeverenae* Rütimeyer, 1873

219   1873   *Plesiochelys Sanctae Verenae* — Rütimeyer [new species]

220   1975a *Plesiochelys etalloni* — Gaffney [subjective synonymy]

221   2014   *Plesiochelys etalloni* — Anquetin, Deschamps & Claude [subjective

222   synonymy]

223   Taxonomic assessment.—Invalid name, subjective synonym of *Plesiochelys etalloni* (Pictet &

224 Humbert, 1857).

225 Synonymy.—None.

226 Type material.—NMS 118, a large carapace missing both sides. Lectotype designated by

227 Bräm (1965: 126).

228 Type horizon and locality.— Solothurn Turtle Limestone, uppermost member of the

229 Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of

230 Solothurn, Switzerland (Fig. 1).

231 Illustrations of type.—Rütimeyer (1873: plate XIII); Fig. 2I–J.

232 Referred specimens.—None.

233 Remarks.—According to Bräm (1965), *P. sanctaeverenae* differs from *P. solodurensis* and *P.*

234 *etalloni* by a greater size (up to 550 mm), a more elongate carapace, a well-developed nuchal

235 notch, and well-developed sulci. However, Bräm (1965: 127) himself admitted that the

236 morphology of NMS 118 (lectotype of *P. sanctaeverenae*) was in fact very similar to that of the

237 largest specimens he otherwise referred to *P. etalloni* or *P. solodurensis*. Gaffney (1975a)

238 attributed these minor differences to individual variations and synonymized *P. sanctaeverenae*

239 with *P. etalloni*. According to Lapparent de Broin, Lange-Badré & Dutrieux (1996), only one

240 species of *Plesiochelys* (*P. solodurensis*, not *P. etalloni*) is present in Solothurn, which implies

241 that they considered *P. sanctaeverenae* as a synonym of *P. solodurensis*, although they did not

242 make that clear in their paper. A recent review of the relevant material confirmed that it is

243 impossible to differentiate NMS 118 from other specimens referred to *P. etalloni* (Anquetin,

244 Deschamps & Claude, 2014).

245 *Plesiochelys langii* Rütimeyer, 1873

246 1873 *Plesiochelys Langii* — Rütimeyer [new species]

247 1965 *Plesiochelys solodurensis* — Bräm [subjective synonymy]

248   2014   *Plesiochelys etalloni* — Anquetin, Deschamps & Claude [subjective

249   synonymy]

250   Taxonomic assessment.—Invalid name, subjective synonym of *Plesiochelys etalloni* (Pictet &

251 Humbert, 1857).

252   Synonymy.—None.

253   Type material.—NMS 123, a sub-complete carapace missing the right and posterior margins.

254 Herein designated as lectotype (see Remarks, below).

255   Type horizon and locality.— Solothurn Turtle Limestone, uppermost member of the

256 Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of

257 Solothurn, Switzerland (Fig. 1).

258   Illustrations of type.—Rütimeyer (1873: plate VI, figs. 1 and 2); Fig. 2K–L.

259   Referred specimens.—NMS 126, a shell heavily encrusted with pyritic mineralizations

260 (paralectotype).

261   Remarks.—Rütimeyer (1873) erected *Plesiochelys langii* based on three specimens, which

262 together form the original syntype series: NMS 123, NMS 124 and NMS 126. He primarily

263 differentiated *P. langii* based on a circular carapace outline and unusually wide peripherals

264 forming alternating projections with costals. Bräm (1965) attributed these features to individual

265 variation or postmortem deformation and synonymized *P. langii* with *P. solodurensis*. A recent

266 review of the available material confirmed that NMS 123 and NMS 126 do not significantly

267 differ from other specimens referred to *P. etalloni*, notably NMS 59 (lectotype of *P. solodurensis*)

268 and MAJ 2005-11-1 (holotype of *P. etalloni*). Therefore, *P. langii* was synonymized with *P.*

269 *etalloni* (Anquetin, Deschamps & Claude, 2014). As pointed out by Bräm (1965), NMS 124

270 clearly belongs to a different genus (see below). In order to avoid potential future issues with the

271 taxonomic status of *P. langii*, NMS 123, the main specimen described by Rütimeyer (1873), is

272 herein designated as the lectotype of this species.

273 　NMS 124 was initially described by Rütimeyer (1873) as a juvenile individual of *P. langii*.

274 Bräm (1965) first recognized that this specimen does not belong to *Plesiochelys*: the vertebrals

275 are reduced in width and costo-peripheral fontanelles are present. However, the exact opinion of

276 Bräm (1965) upon the correct attribution of this specimen remains somewhat confused. At first,

277 he declared that the specimen should be attributed to *Thalassemys* (ibid.: 29). Then, he seemed to

278 hesitate between a referral to *Thalassemys* and one to *Eurysternum ignoratum*, finally

279 concluding that, given the great correspondence between NMS 124 and NMS 5 (the type of *E.*

280 *ignoratum*), the latter identification was more likely (ibid.: 168). NMS 124 is herein referred to

281 *Thalassemys hugii* (see below).

282 　　　　　　　　　　　　　　　*Craspedochelys* Rütimeyer, 1873

283 　　　1873　*Craspedochelys* — Rütimeyer [new genus]

284 　　　1975a　*Plesiochelys* — Gaffney [subjective synonymy]

285 　Type species.—*Craspedochelys Picteti* Rütimeyer, 1873.

286 　Revised diagnosis.—Form traditionally referred to the Plesiochelyidae based on the presence

287 of three cervical scales and a completely ossified carapace. Differing from *Plesiochelys* in:

288 broad, more rounded carapace, usually as wide as long (as preserved); shallower nuchal notch

289 usually restricted to nuchal plate; higher length/width ratio of costal bones (4.3–4.8 or more, as

290 opposed to 3.1–3.6 for the fourth costal in *Plesiochelys*); plastron reduced in length (less than

291 80% of carapace length; at least in *C. jaccardi*); hyoplastron proprotionally wider (even wider

than long in *C. jaccardi*). Differing from *Tropidemys* in: absence of neural keel; elongated neurals; wider vertebral scales.

Remarks.—According to Bräm (1965), *Craspedochelys* is monospecific and his diagnosis of the genus is therefore restricted to *C. picteti*: carapace as wide as long and shaped like a heraldic shield; anterior carapace rim almost straight up to third peripheral, then bending almost at right angle toward the rear; weak nuchal notch; free first thoracic rib, articulated neither to first costal nor to second thoracic rib; second thoracic rib stronger than following ones and connected only to second thoracic vertebra. Gaffney (1975a) tentatively synonymized *Craspedochelys* with *Plesiochelys*, explaining differences in shell outline and development of the nuchal notch by postmortem compression and individual variation, respectively. However, he concluded that the condition of the first and second thoracic ribs may prove to be consistent when more specimens are known. Subsequent studies tended to re-establish a distinction between *Craspedochelys* and *Plesiochelys*, based mostly on shell shape criteria (Antunes, Becquart & Broin, 1988; Lapparent de Broin, Lange-Badré & Dutrieux, 1996).

Morphologically, *Craspedochelys* and *Plesiochelys* are relatively close. However, as already noted by Lapparent de Broin, Lange-Badré & Dutrieux (1996), the available material from the Jura Mountains clearly reveals two morphotypes: *Plesiochelys* has a more elongate carapace and a relatively long plastron, whereas *Craspedochelys* has a broader, more rounded carapace (more or less as wide as long, as preserved) and a shorter plastron (only known in *C. jaccardi*). These differences cannot be explained by postmortem deformation alone (see Discussion). In the course of the present study, we have also identified a set of characters related to the proportions of various shell elements that differentiate *Craspedochelys* from *Plesiochelys* (see Discussion).

Craspedochelys picteti Rütimeyer, 1873

315   1873 *Craspedochelys Picteti* — Rütimeyer [new species]

316   1975a *Plesiochelys etalloni* — Gaffney [subjective synonymy]

317   1988 *Craspedochelys jaccardi* — Antunes, Becquart & Broin [subjective synonymy]

318 Taxonomic assessment.—Valid name.

319 Synonymy.—*Craspedochelys crassa* Rütimeyer, 1873.

320 Type material.—NMS 129, anterior half of a shell with plastron poorly preserved and right

321 part of the carapace missing. Holotype by monotypy (Bräm, 1965: 137).

322 Type horizon and locality.— Solothurn Turtle Limestone, uppermost member of the

323 Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of

324 Solothurn, Switzerland (Fig. 1).

325 Illustrations of type.—Rütimeyer (1873: plate V, fig. 1); Fig. 3A–D.

326 Referred specimens.—Specimens listed in Bräm (1965); NMS 130 (holotype of

327 *Crapedochelys crassa* Rütimeyer, 1873).

328 Revised diagnosis.—*Craspedochelys picteti* can be diagnosed as a representative of

329 *Craspedochelys* by a broad carapace, about as wide as long (as preserved), a weak nuchal notch,

330 a high length/width ratio of costal bones, and a hyoplastron only slightly longer than wide.

331 Differing from *C. jaccardi* in: greater size (carapace length up to 550 mm); carapace heraldic

332 shield-shaped and more quadrangular anteriorly; slightly lower length/width ratio of costal bones

333 (4.3 as opposed to 4.8 or more for the fourth costal in *C. jaccardi*); relatively small pygal;

334 contact between peripheral 11 and costal 8 limited or absent; hyoplastron slightly longer than

335 wide.

336 Remarks.—Bräm (1965) notably characterized *C. picteti* by the following suite of features:

337 carapace as wide as long and shaped like a heraldic shield, with anterior rim extending only

338 slightly convex up to the third peripheral then bending almost at right angle toward the rear;

339 nuchal notch weak; vertebral scales moderately broad extending only about one third of the

340 length of costals; free first thoracic rib; second thoracic rib contacting only the second thoracic

341 vertebra. Gaffney (1975a) tentatively synonymized *C. picteti* with *P. etalloni*, considering the

342 features proposed by Bräm (1965) as resulting either from postmortem deformation (carapace

343 shape and width) or from biological variation (degree of nuchal emargination, width of vertebral

344 scales). Furthermore, Gaffney (1975a) argued that the first and second thoracic ribs are only

345 visible in NMS 608, and that their condition is ambiguous due to incomplete preparation and

346 postmortem damage. NMS 608 is currently mounted on a wall in the NMS exhibition, and we

347 were therefore unable to confirm Bräm's (1965) observations. Antunes, Becquart & Broin (1988)

348 rejected Gaffney's (1975a) conclusions and synonymized *C. picteti* with *C. jaccardi*, though

349 without directly studying the Swiss material. Finally, Lapparent de Broin, Lange-Badré &

350 Dutrieux (1996) re-established *C. jaccardi* and *C. picteti* as distinct species, considering the first

351 as a smaller form with thinner shell plates.

352   NMS 129, NMS 608, and NMS 130 (holotype of *C. crassa*) share a number of features that

353 clearly distinguish them from other species from the Jura Mountains: anterior part of the

354 carapace broad with anterior rim almost straight up to the level of the p3–p4 suture; reduced

355 nuchal notch restricted to the nuchal plate; second and third vertebral scales extending about one

356 third of the length of the costals (Fig. 3). These are the same characters Gaffney (1975a)

357 dismissed as resulting from postmortem deformation or biological variation. However, our

358 review of the Solothurn material indicates that these features are never found in any other

359 specimen, no matter how deformed or variable it may be (see Discussion). Therefore, we

360 consider Bräm's (1965) conclusions on *C. picteti* as valid. However, this species is relatively

361 poorly known and more material is needed.

<center>*Craspedochelys crassa* Rütimeyer, 1873</center>

1873   *Craspedochelys crassa* — Rütimeyer [new species]

1965   *Craspedochelys picteti* — Bräm [subjective synonymy]

Taxonomic assessment.—Invalid name, subjective synonym of *Craspedochelys picteti*

Rütimeyer, 1873.

Synonymy.—None.

Type material.—NMS 130, a poorly preserved carapace fragment. Holotype by monotypy

(Bräm, 1965: 139).

Type horizon and locality.— Solothurn Turtle Limestone, uppermost member of the

Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of

Solothurn, Switzerland (Fig 1).

Illustrations of type.—Rütimeyer (1873 :plate IX, figs. 5 and 5b).

Referred specimens.—None.

Remarks.—The illustration published by Rütimeyer (1873) greatly improves on the actual

specimen (NMS 130), whose state of preservation is rather poor. However, the anterior outline of

the carapace and the vertebral covering less than half of the length of the costals correspond to

what is known in *C. picteti*. Rütimeyer (1873) distinguished *C. picteti* and *C. crassa* based on the

greater thickness of the costal bones in the latter, which is, as pointed out by Bräm (1965: 137), a

feature subject to a certain level of individual variations. We see no reason to separate the two

species based on the available material and agree with Bräm (1965) in synonymizing *C. crassa*

with *C. picteti*.

<center>*Craspedochelys plana* Rütimeyer, 1873</center>

1873   *Craspedochelys plana* — Rütimeyer [new species]

385   1965   *Tropidemys langii* — Bräm [subjective synonymy]

386   Taxonomic assessment.—Invalid name, subjective synonym of *Tropidemys langii* Rütimeyer,

387 1873.

388   Synonymy.—None.

389   Type material.—NMS 132, anterolateral (left) portion of a carapace. Holotype by monotypy

390 (Bräm, 1965: 183).

391   Type horizon and locality.— Solothurn Turtle Limestone, uppermost member of the

392 Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of

393 Solothurn, Switzerland (Fig. 1).

394   Illustrations of type.—Rütimeyer (1873: plate IX, figs. 1 and 2).

395   Referred specimens.—None.

396   Remarks.—Bräm (1965: 184) concluded that NMS 132 should in fact be assigned to

397 *Tropidemys langii*. What is preserved of the dorsal surface of the carapace does not allow a

398 definitive attribution to either *C. picteti* or *Tr. langii*. However, the visceral surface of costal 1

399 clearly shows a crest-like axillary buttress, a feature characteristic of *Tr. langii* (Püntener et al.,

400 2014). We therefore follow Bräm (1965) and Püntener et al. (2014) in referring this specimen to

401 *Tr. langii*.

402   *Craspedochelys jaccardi* (Pictet, 1860)

403   1860   *Emys jaccardi* — Pictet [new species]

404   1873   *Plesiochelys Jaccardi* — Rütimeyer [new combination]

405   1975a *Plesiochelys etalloni* — Gaffney [subjective synonymy]

406   1988   *Craspedochelys jaccardi* — Antunes, Becquart & Broin [new combination]

407   Taxonomic assessment.—Valid name.

408   Synonymy.—None.

409   Type material.—MHNN FOS 977, a complete shell. Holotype by monotypy.

410   Type horizon and locality.—Les Hauts-Geneveys, Canton of Neuchâtel, Switzerland (Fig. 1),

411   "Virgulien supérieur", possibly corresponding to the early Tithonian (see Lapparent de Broin,

412   Lange-Badré & Dutrieux, 1996: 552). According to Pictet (1860), the specimen was collected

413   from a quarry near Les Brenets, whereas for Jaccard (1860) the specimen came from a different

414   quarry near Les Hauts-Geneveys. Jaccard (1870) confirmed the locality as being Les Hauts-

415   Geneveys (Ayer, 1997).

416   Illustrations of type.—Pictet (1860: plates I-III); Lapparent de Broin, Lange-Badré &

417   Dutrieux (1996: plate IV); Fig. 4A–D.

418   Referred specimens.—See Bräm (1965).

419   Revised diagnosis.—*Craspedochelys jaccardi* can be diagnosed as a representative of

420   *Craspedochelys* by a broad carapace, about as wide as long (as preserved), a weak nuchal notch,

421   a high length/width ratio of costal bones, a plastron reduced in length (less than 80% of carapace

422   length), and a hyoplastron wider than long. Differing from *C. picteti* in: smaller size (carapace

423   length up to 420 mm); carapace more evenly rounded anteriorly; higher length/width ratio of

424   costal bones (4.8 or more, as opposed to 4.3 for the fourth costal); hyoplastron wider than long

425   (slightly longer than wide in *C. picteti*).

426   Remarks.—*Emys jaccardi* Pictet, 1860 was referred to the genus *Plesiochelys* by Rütimeyer

427   (1873). A conclusion followed by Bräm (1965), who differentiated this species based mainly on

428   the following features: carapace about as wide as long; nuchal notch evenly rounded; plastron

429   oval in outline; small xiphiplastral notch; plastron length about 73% that of the carapace; small

430   central plastral fontanelle, mainly formed by hypoplastron; vertebrals relatively narrow. Gaffney

431   (1975a) synonymized *P. jaccardi* with *P. etalloni*, notably explaining the broad shell of the

former by postmortem compression. Antunes, Becquart & Broin (1988) were the first to refer the species *jaccardi* to the genus *Craspedochelys* based on the following characters: broad carapace (width/length ratio exceeding 90%); pentagonal outline with anterior part quadrangular; small central plastral fontanelle; and vertebral scales reduced in width. This position was later confirmed by Lapparent de Broin, Lange-Badré & Dutrieux (1996), although, in contrast to Antunes, Becquart & Broin (1988), they recognized *C. picteti* and *C. jaccardi* as two distinct forms, based primarily on size difference and variation in the thickness of the shell bones.

The characteristics exhibited by the holotype of *C. jaccardi* (MHNN FOS 977) are inconsistent with a referral to *P. etalloni*, as suggested by Gaffney (1975a). For example, postmortem compression or individual variation cannot explain the significant reduction of the plastron length in *C. jaccardi* (Table 2). The proportions of costals, hyoplastron, and xiphiplastron are also markedly different in the two species (see Discussion). Therefore, *C. jaccardi* is considered as a valid species. However, this species is only known by a limited number of specimens and some interrogation remains regarding the attribution of the Solothurn specimens to this species (see Discussion).

Tropidemys Rütimeyer, 1873

1873   *Tropidemys* — Rütimeyer [new genus]

Type species.— *Tropidemys Langii* Rütimeyer, 1873.

Revised diagnosis.—See Püntener et al. (2014)

Remarks.—*Tropidemys* is mainly characterized by wide, hexagonal and often keeled neurals. The validity of this genus has never been questioned. A recent review is available in Püntener et al. (2014).

454   *Tropidemys langii* Rütimeyer, 1873

455   1873   *Tropidemys Langii* — Rütimeyer [new species]

456   Taxonomic assessment.—Valid name.

457   Synonymy.—*Tropidemys expansa* Rütimeyer, 1873, *Tropidemys gibba* Rütimeyer, 1873, and

458 *Craspedochelys plana* Rütimeyer, 1873.

459   Type material.—NMS 16, posterior part of a carapace. Lectotype designated by Bräm (1965:

460 176).

461   Type horizon and locality.— Solothurn Turtle Limestone, uppermost member of the

462 Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of

463 Solothurn, Switzerland (Fig. 1).

464   Illustrations of type.—Rütimeyer (1873: plate VII, fig. 1); Fig. 5A–B.

465   Referred specimens.—See Püntener et al. (2014).

466   Revised diagnosis.—See Püntener et al. (2014).

467   Remarks.— Rütimeyer (1873) initially described three species of *Tropidemys* in Solothurn:

468 *Tr. langii*, *Tr. expansa* and *Tr. gibba*. Bräm (1965), who had access to a sub-complete carapace

469 (NMS 15; Fig. 5C–D), concluded that there was no reason to differentiate three species based on

470 the available material. Püntener et al. (2014) recently revised the Solothurn material and

471 described new specimens from the Kimmeridgian in the vicinity of Porrentruy, Switzerland (Fig.

472 1). They confirmed Bräm's (1965) conclusions.

473   *Tropidemys expansa* Rütimeyer, 1873

474   1873   *Tropidemys expansa* — Rütimeyer [new species]

475   1965   *Tropidemys langii* — Bräm [subjective synonymy]

2014   *Tropidemys langii* — Püntener et al. [subjective synonymy]

Taxonomic assessment.—Invalid name, subjective synonym of *Tropidemys langii* Rütimeyer, 1873.

Synonymy.—None.

Type material.—Rütimeyer (1873) did not explicitly refer to a type specimen in his description of *Tr. expansa*. However, he figured specimens NMS 32 and NMS 33 (Rütimeyer, 1873: plate IX, figs. 3–4), and they, at least, form part of the syntype series.

Type horizon and locality.— Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of Solothurn, Switzerland (Fig. 1).

Illustrations of type.—Rütimeyer (1873: plate IX, figs. 3–4).

Referred specimens.—None.

Remarks.—Püntener et al. (2014) revised this material and concluded that *Tr. expansa* was a junior subjective synonym of *Tr. langii*.

Tropidemys gibba Rütimeyer, 1873

1873   *Tropidemys gibba* — Rütimeyer [new species]

1965   *Tropidemys langii* — Bräm [subjective synonymy]

2014   *Tropidemys langii* — Püntener et al. [subjective synonymy]

Taxonomic assessment.—Invalid name, subjective synonym of *Tropidemys langii* Rütimeyer, 1873.

Synonymy.—None.

Type material.—NMS 38, a fragment of carapace with neurals 3–6 and medial parts of associated costals. Holotype designated by Rütimeyer (1873).

499   Type horizon and locality.— Solothurn Turtle Limestone, uppermost member of the

500 Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of

501 Solothurn, Switzerland (Fig. 1).

502   Illustrations of type.—Rütimeyer (1873: plate IV, fig. 1) and Bräm (1965: plate VIII, fig. 5).

503   Referred specimens.—NMS 38a.

504   Remarks.—Püntener et al. (2014) studied this material and concluded that *Tr. gibba* was a

505 junior subjective synonym of *Tr. langii*.

506   THALASSEMYDIDAE Zittel, 1889

507   *Thalassemys* Rütimeyer, 1859

508   1859   *Thalassemys* — Rütimeyer [new genus]

509   Type species.—*Thalassemys Hugii* Rütimeyer, 1873.

510   Revised diagnosis.—Form traditionally referred to the Thalassemydidae, a monotypic family.

511 Differing from *Plesiochelys*, *Craspedochelys*, and *Tropidemys* in: great anterior widening of first

512 neural; presence of small costo-peripheral fontanelles in the adults; presence of clearly visible

513 linear striations perpendicular to sutures between most shell elements; presence of a lateral

514 plastral fontanelle; non-sutural connection of the epiplastron and entoplastron with the

515 hyoplastron; presence of a small xiphiplastral fontanelle.

516   Remarks.—Bräm (1965) diagnosed *Thalassemys* mainly based on the following combination

517 of features: carapace relatively flat and more or less heart-shaped in outline; shell moderately

518 high, the height being mostly the result of the ascending processes of the hyo- and hypoplastra;

519 costo-peripheral fontanelles retained in adult individuals; one cervical scale; large central plastral

520 fontanelle (extending over most of the length of the plastron in *Th. hugii*); lateral plastral

521 fontanelle absent. According to Bräm (1965), *Thalassemys* includes *Th. hugii* and *Th. moseri*,

522 but not *Th. marina* Fraas, 1903 from the Tithonian of Schnaitheim, Germany (a form he referred

523 to *Eurysternum* on the account of the presence of a lateral plastral fontanelle).

524 Our review of the Solothurn material indubitably establishes that a lateral plastral fontanelle

525 was indeed present in *Th. hugii*, the type species of *Thalassemys*. Additionally, we were able to

526 reassess the plastral morphology of *Th. hugii* (see Discussion). Based notably on these new data,

527 *'Th.' moseri* is excluded from *Thalassemys* (see below), whereas *Th. marina* is consistent with

528 our concept of *Thalassemys*.

529 *Thalassemys hugii* Rütimeyer, 1873

530 1873 *Thalassemys Hugii* — Rütimeyer [new species]

531 Taxonomic assessment.—Valid name.

532 Synonymy.—*Thalassemys Gresslyi* Rütimeyer, 1873 and *Eurysternum ignoratum* Bräm,

533 1965.

534 Type material.—NMS 1, a large carapace plus associated plastron fragments and postcranial

535 remains. Lectotype designated by Bräm (1965: 143).

536 Type horizon and locality.— Solothurn Turtle Limestone, uppermost member of the

537 Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of

538 Solothurn, Switzerland (Fig. 1).

539 Illustrations of type.—Rütimeyer (1873: plate I); Bräm (1965: plate 7); Fig. 6A–D.

540 Referred specimens.—Specimens listed in Bräm (1965); NMS 5 (holotype of *Eurysternum*

541 *ignoratum* Bräm, 1965), NMS 12 (holotype of *Th. gresslyi* Rütimeyer, 1873), NMS 124, NMS

542 412, NMS 20981, NMS 22325-22327 (and associated remains), NMS 37251.

Revised diagnosis.—*Thalassemys hugii* can be diagnosed as a representative of *Thalassemys* by the great widening of neural 1, the retention of costo-peripheral fontanelles, the presence of clearly visible linear striations perpendicular to sutures between most shell elements, the presence of a lateral plastral fontanelle, the absence of sutural connection of the epi- and entoplastron with the hyoplastron, and the presence of a small xiphiplastral fontanelle. Differing from *Th. marina* in: narrower vertebral scales with anterolateral and posterolateral margins of equal length (as opposed to posterolateral margin shorter in *Th. marina*); smaller lateral plastral fontanelle.

Remarks.—Because *Thalassemys hugii* was typified based on a relatively completed shell and partial associated post-cranial remains, its validity has never been questioned. This turtle is nonetheless not very well known and remains are relatively rare in contemporaneous deposits. This is the biggest turtle in Solothurn reaching more than 630 mm (the pygal is missing in NMS 1). Bräm (1965) diagnosed *Th. hugii* by the following features: presence of a large longitudinal central plastral fontanelle, sometimes closed anteriorly by the hyoplastra and posteriorly by the xiphiplastra; vertebral scales relatively narrow (as opposed to wide in *'Th.' moseri*); very large size.

During our review of the Solothurn material, we were able to identify a set of characters that prompted a revision of the traditional concept of *Th. hugii* (see Discussion). Perhaps the most important of these characters is the presence of a lateral plastral fontanelle, the purported absence of which was used by Bräm (1965) to differentiate *Thalassemys* from *Eurysternum*. Based on this review of the material, *E. ignoratum* is synonymized with *Th. hugii* (see below).

Thalassemys gresslyi Rütimeyer, 1873

1873   *Thalassemys Gresslyi* — Rütimeyer [new species]

566   1965   *Thalassemys hugii* — Bräm [subjective synonymy]

567   Taxonomic assessment.—Invalid name, subjective synonym of *Thalassemys hugii* Rütimeyer,

568 1873.

569   Synonymy.—None.

570   Type material.—NMS 12, anterior half of a large carapace partly disarticulated. Holotype by

571 monotypy (see Bräm, 1965: 152).

572   Type horizon and locality.— Solothurn Turtle Limestone, uppermost member of the

573 Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of

574 Solothurn, Switzerland (Fig. 1).

575   Illustrations of type.—Fig. 6I–J.

576   Referred specimens.—None.

577   Remarks.—Rütimeyer (1873) considered NMS 12 should be assigned to a separate species

578 because of differences in proportions of the first neural and first costal, a larger size and a

579 different sculpturing of the bone surface compared to *Th. hugii*. However, Bräm (1965: 152)

580 concluded that these differences could be explained either by individual variations or

581 postmortem deformation and synonymized *Th. gresslyi* with *Th. hugii*. The state of preservation

582 of this specimen is rather poor and the sculpturing of the bone surface is undoubtedly of

583 postmortem origin. The size of the specimen and the shape of the vertebral scales are consistent

584 with our concept of *Th. hugii*. Therefore, we follow Bräm's (1965) conclusion.

585   *'Thalassemys' moseri* (Bräm, 1965)

586   1965   *Thalassemys moseri* — Bräm [new species]

587   1996   *Plesiochelys solodurensis* — Lapparent de Broin, Lange-Badré & Dutrieux

588 [subjective synonymy]

589　　　Taxonomic assessment.—Valid name.

590　　　Synonymy.—None.

591　　　Type material.—NMS 618, partial carapace and plastron. Holotype (Bräm, 1965: 155).

592　　　Type horizon and locality.— Solothurn Turtle Limestone, uppermost member of the

593　Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of

594　Solothurn, Switzerland (Fig. 1).

595　　　Illustrations of type.—Bräm (1965: plate 8, figs. 2 and 3); Fig. 7A–D.

596　　　Referred specimens.—Specimens listed in Bräm (1965); PMZH A/III 514, a nearly complete

597　skull and partial shell from the early Tithonian of La Morelière (Isle of Oléron, Department of

598　Charente-Maritime, France) referred by Rieppel (1980).

599　　　Revised diagnosis.— Species of dubious affinity characterized by the combination of the

600　following features: medium-sized shell (carapace length about 350 mm); three cervical scales;

601　wide vertebrals covering about half of the costals laterally; pattern of carapacial scales recalling

602　that of *Plesiochelys* and *Craspedochelys*; presence of costo-peripheral fontanelles; costal bones

603　relatively thin distally; rib tips easily disarticulated from peripherals; large central plastral

604　fontanelle, oval in outline; absence of lateral plastral fontanelle; epi- and entoplastron not sutured

605　to hyoplastron; xiphiplastron possibly forming a small xiphiplastral notch. See Rieppel (1980)

606　for cranial characters. Differing from *Plesiochelys etalloni*, *Craspedochelys picteti*, *C. jaccardi*,

607　and *Tropidemys langii* in: retention of costo-peripheral fontanelles; epi- and entoplastron not

608　sutured to hyoplastron. Differing from *Thalassemys hugii* in: smaller size; wide vertebrals

609　covering about half of the costals laterally; absence of lateral plastral fontanelle.

610　　　Remarks.—Bräm (1965) originally diagnosed *'Thalassemys' moseri* as a representative of

611　*Thalassemys* by the retention of costo-peripheral fontanelles and the absence of lateral plastral

612　fontanelles. *'Thalassemys' moseri* was furthermore differentiated from *Th. hugii* by a smaller

613 size, the presence of broad vertebral scales, and the presence of a large central plastral fontanelle

614 closed anteriorly by the hyoplastra and posteriorly by the hypoplastra (as opposed to the very

615 extensive central fontanelle he considered to be present in *Th. hugii*; but see Discussion).

616 Lapparent de Broin, Lange-Badré & Dutrieux (1996) argued that the holotype of *'Th.' moseri*

617 (NMS 618) with its three cervicals, wide vertebrals and oval central plastral fontanelle was

618 probably a young individual of *P. solodurensis*, the only *Plesiochelys* species they recognized in

619 Solothurn. According to them, this specimen could not be referred to *Thalassemys* because the

620 type species of this genus is a very large form with only one cervical scale. Bräm (1965: 155)

621 himself was aware of the apparent similarities between *'Th.' moseri* and what he described as *P.*

622 *etalloni* (i.e., *Plesiochelys* specimens with a central plastral fontanelle). This is especially true for

623 the pattern of carapacial scales. However, *'Th.' moseri* and *P. etalloni* diverge on characters that

624 are traditionally used to differentiate plesiochelyids from thalassemydids, such as the presence of

625 carapacial fontanelles between costals and peripherals.

626　　Our review of the material clearly indicates that *'Th.' moseri* is unique among Solothurn

627 turtles. The presence of costo-peripheral fontanelles and the absence of sutural contact between

628 the hyoplastron and the epiplastron and entoplastron are inconsistent with an attribution to *P.*

629 *etalloni*, *C. picteti*, or *C. jaccardi*. The elongated neurals, the absence of a neural keel, and the

630 broad vertebral scales clearly differentiate *'Th.' moseri* from *Tr. langii*. Finally, the smaller size,

631 the broad vertebrals, and the absence of a lateral plastral fontanelle distinguish *'Th.' moseri* from

632 *Th. hugii*. Therefore, we confirm the conclusions of Bräm (1965) and consider *'Th.' moseri* as a

633 distinct species. However, the generic attribution to *Thalassemys* is rejected. The pattern of

634 carapacial scales and the absence of lateral plastral fontanelle suggest that this species is more

635 closely related to *Plesiochelys* than to *Thalassemys*. Rieppel (1980) reached a similar conclusion

636 (see Discussion).

EURYSTERNIDAE Dollo, 1886

Eurysternum Meyer, 1839

Type species.—*Eurysternum Wagleri* Meyer, 1839.

Revised diagnosis.—See Anquetin & Joyce (in press).

Remarks.—A discussion on the genus *Eurysternum* and a reevaluation of its type species *E. wagleri* are available in Anquetin & Joyce (in press).

Eurysternum ignoratum Bräm, 1965

1965   *Eurysternum ignoratum* — Bräm [new species]

Taxonomic assessment.—Invalid name, subjective synonym of *Thalassemys hugii* Rütimeyer, 1873.

Synonymy.—None.

Type material.—NMS 5, disarticulated and fragmentary remains (three costals, hyoplastra, scapulae, humerus, pubes). Holotype (Bräm, 1965: 166).

Type horizon and locality.— Solothurn Turtle Limestone, uppermost member of the Reuchenette Formation (Kimmeridgian, Late Jurassic), vicinity of Solothurn, Canton of Solothurn, Switzerland (Fig. 1).

Illustrations of type.—Rütimeyer (1873: plate VI, fig. 4); Bräm (1965: plate 8, fig. 6); Fig. 6E–H.

Referred specimens.—NMS 124 and NMS 412 (see Bräm, 1965). The NMS catalogue also assigns four additional specimens to *E. ignoratum*. NMS 20981 and NMS 37251 are herein referred to *Th. hugii*. NMS 21908 and NMS 21922 consist of isolated bones that have been

658 included in resin and sampled for histological analysis prior to the present study, which prevents

659 proper examination.

660   Remarks.—Bräm (1965) identified *Eurysternum ignoratum* as a representative of

661 *Eurysternum* based on the presence of a lateral plastral fontanelle. He differentiated *E.*

662 *ignoratum* from *E. wagleri* by the presence of narrow vertebral scales. Broin (1994) and

663 Lapparent de Broin, Lange-Badré & Dutrieux (1996) tentatively suggested a possible synonymy

664 between *E. ignoratum* and *Solnhofia parsonsi* Gaffney, 1975b, but the material referred to *E.*

665 *ignoratum* was never actually revised in detail since Bräm (1965).

666   Our review of the concerned material leads us to the conclusion that there is not a single

667 character that differentiates *E. ignoratum* from *Th. hugii* (see Discussion). *Eurysternum*

668 *ignoratum* is therefore interpreted as a subjective junior synonym of *Th. hugii*.

669 **DISCUSSION**

670 *Plesiochelys etalloni*

671 *Plesiochelys etalloni* is known from about 30 relatively complete shells and uncountable shell

672 fragments, most of which from the quarries in the vicinity of Solothurn, Switzerland (Fig. 1).

673 This material provides a good opportunity to grasp the level of intraspecific variability in this

674 fossil species. A general description of the shell morphology of *P. etalloni* can be found in

675 Anquetin, Deschamps & Claude (2014).

676   The carapace of *P. etalloni* is usually evenly oval, but some specimens have a more

677 quadrangular anterior rim (e.g., NMS 78 and NMS 116; Fig. 8). Carapaces that have been

678 flattened during fossilization tend to be characterized by a more pronounced angulation of their

679 anterior margin, resulting from the partial disarticulation of some peripherals. In *P. etalloni* and

680 *Craspedochelys jaccardi* (MHNN FOS 977; Fig. 4), this angulation is always located at the level

681 of the p2–p3 suture, whereas *C. picteti* (NMS 129 and NMS 608; Fig. 3) is unique in showing an

682 angulation at the level of the p3–p4 suture (see below).

683   The posteromedial region of the carapace is relatively variable in *P. etalloni*, as generally

684 common in turtles (Zangerl, 1969). The seventh and eighth neurals are usually shorter and more

685 variable in shape than the preceding ones. These two neurals even fuse in some specimens (e.g.,

686 NMS 79 and NMS 669; Fig. 8). The eighth neural might even be much reduced or absent in

687 certain individuals allowing a midline contact of the eighth costals (e.g., MAJ 2005-11-1; Fig. 2;

688 see Anquetin, Deschamps & Claude, 2014). In most specimens, there is an intermediate element

689 of varying size and shape between the eighth neural and the first suprapygal (Figs. 2 and 8). We

690 are uncertain of the identity of this additional element (ninth neural, additional suprapygal, or

691 neomorphic bone). Its shape and size are quite variable, from a small quadrangular element

692 about the size of preceding neurals to a large triangular or trapezoidal element about the size of

693 the following suprapygal. This extreme variation of size and shape is probably inconsistent with

694 an identification as a ninth neural, but this intermediate element is also articulated with the

695 vertebral series (at least partially), which is incongruent with an identification as a suprapygal.

696 For the time being, we prefer to simply refer to this element as the 'intermediate' element. It is

697 particularly interesting to note that a similar element in known in *C. picteti* (Fig. 3), *C. jaccardi*

698 (Fig. 4), *Tropidemys langii* (Fig. 5), and *Thalassemys hugii* (Fig. 6). The fourth intervertebral

699 sulcus always runs on this intermediate element, or on the first suprapygal if the intermediate

700 element is absent. Posterior to the intermediate element, there are usually two suprapygals,

701 which sometimes fuse into one single element. The first suprapygal is generally larger and wider

702 than the second, preventing a contact between the latter and the eighth pair of costals, but the

703 actual size of each suprapygal is relatively variable from one individual to another (Fig. 8).

704   The three cervical scales are visible in all specimens in which this area is sufficiently

705   preserved, but it should be noted that the cervical sulci are lost relatively quickly once the area is

706   slightly damaged. The presence of three cervicals have long been though to represent a unifying

707   character of Plesiochelyidae sensu stricto, including *Plesiochelys*, *Craspedochelys*, and

708   *Tropidemys* (e.g., Bräm, 1965; Lapparent de Broin, Lange-Badré & Dutrieux, 1996; Slater et al.,

709   2011; Püntener et al., 2014; Pérez-García, in press). However, the presence of three cervicals has

710   been reported in some Eurysternidae (Joyce, 2003; Anquetin & Joyce, in press), and three

711   cervicals may also have been present in *Th. hugii* (see below).

712   *Plesiochelys etalloni* shares a common pattern of carapacial scales with *C. picteti*, *C. jaccardi*,

713   and *'Th.' moseri*. In *P. etalloni*, this pattern is subject to a certain degree of variability. This

714   informs us on the variability that may be expected in the other aforementioned species, which are

715   currently represented by considerably less specimens. The vertebral sulci are generally sinuous,

716   but to a variable extent from one individual to another. Vertebrals 2–4 are wide, hexagonal

717   scales. However, if the second and third vertebrals consistently cover about half of the costal

718   length laterally, the lateral extent of the fourth vertebral is more variable. In some specimens

719   (e.g., NMS 79 and NMS 118; Figs. 2 and 8), the fourth vertebral extends as far as the peripherals

720   laterally, significantly reducing the width of the fourth pleural in the process. The marginals are

721   generally restricted to the peripherals, but in some specimens the fourth and/or seventh marginals

722   extend very slightly on the costals (e.g., NMS 59, NMS 60, and NMS 669; Figs. 2 and 8).

723   Finally, it is interesting to note that, in all specimens in which this area is known, the twelfth pair

724   of marginals extends anteriorly on the second suprapygal, whereas it is restricted to the pygal in

725   *C. picteti* and *C. jaccardi* (not known in *'Th.' moseri*).

726   Bräm (1965) mentioned the presence of epiplastral bulbs in *P. etalloni*. We confirm that two

727   pairs of epiplastral bulbs are present in specimens with undamaged epiplastra (e.g., NMS 59,

728 NMS 94, NMS 629, NMS 669; Figs. 2 and 8). The entoplastron is usually diamond-shaped, but

729 in some specimens its posterior half is more or less elongated. Finally, the presence/absence of a

730 central plastral fontanelle is interpreted as an intraspecific variation of *P. etalloni* (Gaffney,

731 1975a; Lapparent de Broin, Lange-Badré & Dutrieux, 1996; Anquetin, Deschamps & Claude,

732 2014). Like their carapacial counterparts, the plastral scales exhibit a certain degree of variability

733 in their shape and relations with underlying bony elements. In some specimens (e.g., MAJ 2005-

734 11-1 and NMS 94; Figs. 2 and 8), the plastral midline sulcus is irregularly sinuous. The length of

735 the pectoral compared to that of the humeral is quite variable in *P. etalloni*. The pectoral may be

736 shorter (e.g., MAJ 2005-11-1, NMS 59, NMS 94), about equal (e.g., NMS 66, NMS 669), or

737 longer than the humeral (e.g., NMS 629, NMS 675). Most commonly, there are four pairs of

738 inframarginals, except in NMS 78 where there are five pairs (Fig. 8). These inframarginals are

739 either entirely restricted to plastral elements (e.g., NMS 59, NMS 79), or some of them, usually

740 the third and/or fourth, may extend slightly laterally on the peripherals (e.g., MAJ 2005-11-1,

741 NMS 94). Finally, the anal scales very rarely extend anteriorly on the hypoplastra (e.g., NMS 59,

742 NMS 79), otherwise the anals are restricted to the xiphiplastra (Figs. 2 and 8).

743 *Craspedochelys picteti*

744 *Craspedochelys picteti* is known mainly from two specimens from Solothurn (Fig. 1). The

745 holotype (NMS 129) is relatively incomplete, consisting only of the anterior left quarter of the

746 carapace and associated hyoplastra, but NMS 608 consists of a large, sub-complete carapace

747 (Fig. 3). *Craspedochelys picteti* is mainly characterized by a heraldic shield-shaped carapace.

748 Anteriorly, the carapace rim is almost straight transversally from the nuchal to the third

749 peripheral. The carapace margin then bends abruptly posteriorly at the level of the p3–p4 suture.

750 As discussed above for *P. etalloni*, variations in the degree of angulation of the anterior part of

751 the carapace are probably the result of postmortem compression in these turtles, but the shift in

752 the location of this angulation in *C. picteti* indicates that the anterior outline of the carapace was

753 truly broader in this taxon. From peripherals 4 to 7, the margin is almost straight and parallel to

754 the anteroposterior axis of the carapace. At the level of the p7–p8 suture, the margin bends

755 abruptly medially and continues obliquely toward the pygal. The width of the carapace decreases

756 rapidly from the eighth peripheral to the pygal.

757   The nuchal is a wide, trapezoidal element with a shallow nuchal notch, which does not extend

758 on the first peripheral. Specimens referred to *P. etalloni* usually have a more pronounced and

759 more laterally extended nuchal notch. There are eight neurals. The first neural is more

760 rectangular. Neurals 2–6 are elongate, hexagonal elements with shorter sides facing anteriorly.

761 As in *P. etalloni*, there was probably a certain amount of intraspecific variability in the

762 morphology of the seventh and eighth neurals. In NMS 608, neural 7 is a short hexagonal

763 element, whereas neural 8 is an irregularly shaped, wider than long element. Posterior to neural

764 8, there is a large trapezoidal element that corresponds to the intermediate element described in

765 *P. etalloni* (see above). In NMS 608, the two suprapygals may have been fused together, but poor

766 preservation prevents a definitive conclusion on the matter. The pygal is a relatively small,

767 almost square-shaped element. In *P. etalloni* and *C. jaccardi*, the pygal is usually much wider

768 (Figs. 2 and 4). Probably as a result of the reduced size of the pygal, the eleventh peripheral does

769 not contact the eighth costal in NMS 608. It is uncertain whether this unique configuration of the

770 pygal area is a true characteristic of *C. picteti* or an individual variation of NMS 608, but NMS

771 61 (an indeterminate carapace fragment) exhibits the exact same arrangement. There are eight

772 pairs of costals. The length of costals 6–8 decreases rapidly posteriorly. Proportionally to their

773 length the costals of *C. picteti* are thinner than those of *P. etalloni*, but not as much as those of *C.*

774 *jaccardi* (Table 3). The arrangement and shape of carapacial scales remind that of *P. etalloni*, to

775 the notable exception that vertebral scales are narrower and cover about a third to half of the

776 costal length. However, this character appears to be subject to a significant amount of variation

777 in *P. etalloni*. There are three cervical scales. The twelve pairs of marginals never extend on the

778 costals. In contrast to *P. etalloni*, the twelfth marginals do not extend anteriorly on the second

779 suprapygal.

780   Our knowledge of the plastron of *C. picteti* is limited to the hyoplastron of NMS 129 (Fig.

781 3C–D). This element is slightly longer than wide, which contrasts with the condition in *C.

782 jaccardi* (see below). Based on the shape of its sutural contact with the hyoplastron, the

783 entoplastron was probably a small element. A central plastral fontanelle was present in NMS

784 129. There are no further indications on the shape and size of the plastron in this species, which

785 prevents comparison with other taxa from the Jura Mountains, notably *P. etalloni* and *C.

786 jaccardi*.

787 ***Craspedochelys jaccardi***

788 *Craspedochelys jaccardi* was originally described based on a single shell (MHNN FOS 977)

789 from the vicinity of Neuchâtel, Switzerland (Fig. 1). Subsequently, additional specimens from

790 Solothurn were referred to this species (Rütimeyer, 1873; Bräm, 1965), but they are

791 characterized by a slightly divergent morphology. Therefore, the following discussion is

792 primarily based on the morphology of the holotype (Fig. 4A–D). *Craspedochelys jaccardi* is a

793 moderately sized turtle (carapace length up to 420 mm) characterized notably by a shortened

794 plastron representing less than 80% of the carapace length (as opposed to 85–90% in

795 *Plesiochelys etalloni*; see Table 2). As preserved, the shell is broad, even as wide as long in some

796 specimens. Postmortem compression may affect our perception of shell width, but none of the

797 many Solothurn specimens referred to *P. etalloni* has a shell as wide as long, no matter how

flattened it is. In contrast to what Gaffney (1975a) suggested, the specimens referred to *C. jaccardi* are not more dorsoventrally flattened than specimens referred to *P. etalloni*. Anteriorly, the carapace is evenly rounded with only a weak nuchal notch mostly restricted to the nuchal bone. The carapace is slightly pentagonal in outline. The nuchal is a broad, trapezoidal element. The first neural is rectangular, whereas following neurals tend to be elongate and hexagonal with shorter sides anteriorly. There are up to eight neurals, but several specimens exhibit a reduction or loss of the seventh and/or eighth neurals allowing a midline contact of the seventh and/or eighth costals. As in *P. etalloni* and *C. picteti* notably, there is usually an intermediate element between the last neural and the first suprapygal (see above). As in other species, this element is relatively variable in shape and size. There are usually two suprapygals, the first larger than the second. The pygal is a wider than long element, larger than the same bone in *C. picteti*. There are eight pairs of costals, which are proportionally thinner and longer (higher length/width ratio; see Table 3) than those of *P. etalloni* and *C. picteti*. There are 11 pairs of longer than wide peripherals greatly increasing in width posteriorly. The posteriormost peripherals may have been slightly wider than long. The arrangement and shape of carapacial scales remind that of *P. etalloni*, but there seems to be a greater variability in the outline of vertebral scales in *C. jaccardi* (see below). There are three cervical scales. The twelve pairs of marginals never extend on the costals. In contrast to *P. etalloni*, the twelfth marginals do not extend anteriorly on the second suprapygal.

As noted above, the plastron of *C. jaccardi* is greatly reduced in length compared to that of *P. etalloni*. This reduction seems to result mainly from the shortening of the posterior lobe, which is apparent from the long post-xiphiplastral space (Lapparent de Broin, Lange-Badré & Dutrieux, 1996). The exact outline of the anterior plastral lobe is uncertain because the epiplastra are damaged in all known specimens. The posterior lobe is broad and rounded. There is a small

central plastral fontanelle. The epi-hyoplastral suture is mostly transversal. Similarly to *P. etalloni*, the entoplastron is a diamond-shaped, longer than wide element with its anterior sides shorter than the posterior ones, but there appears to be a great variation in the size of this element between individuals (Fig. 4). The hyoplastron is remarkable in being wider than long (see Table 4), which probably reflects both the increased width of the shell and the reduced length of the plastron. Similarly, the xiphiplastron is as wide as long, which contrast with the longer than wide element found in most other turtles. There is a weak xiphiplastral notch, barely visible in some specimens. The extragular scales are restricted to the epiplastra. It is uncertain whether or not the gulars extended onto the anteromedial part of the entoplastron. The pectoral is reduced in length compared to the humeral. The anal scales are restricted to the xiphiplastra. There are four inframarginals increasing in length posteriorly. All inframarginals but the first extend slightly over the peripheral laterally (only visible in NMS 673).

As mentioned above, there is a certain number of differences between the holotype of *C. jaccardi* (MHNN FOS 977) and specimens from Solothurn referred to this species (notably NMS 101 and NMS 673). On the carapace, the most obvious differences concern the vertebral scales. The vertebral pattern of MHNN FOS 977 is somewhat unusual (Fig. 4A–B). The first vertebral is narrower than the nuchal bone posteriorly and it widens greatly anteriorly to reach the sulcus between the first and second marginal. The second vertebral is similarly narrow anteriorly and its anterolateral margin curves greatly toward the midline. The second and third intervertebral sulci are displaced anteriorly lying just anterior to the middle of neural 3 and neural 5, respectively (instead of just posterior to the middle of neural 3 and over the posterior part of neural 5 in most other turtles). Consequently, the third vertebral is shorter, whereas the fourth vertebral is significantly longer (Fig. 4). An unusually long fourth vertebral is also known in a referred specimen from the Kimmeridgian of Murat (Lot, France; Lapparent de Boin, Lange-Badré &

846 Dutrieux, 1996: figs. 3–4). As a result of this unusual arrangement of the vertebrals, the second

847 pleural of MHNN FOS 977 is shortened, whereas the third pleural is greatly lengthened. The

848 vertebral pattern of NMS 101 is also relatively unusual (Fig. 4E–F). Vertebral sulci are

849 irregularly sinuous. The outline of vertebrals 2–4 is particularly odd, with notably a narrower,

850 sub-quadrangular third vertebral. The fifth vertebral is significantly shorter than in other

851 specimens referred to *C. jaccardi*. The vertebral pattern of NMS 673 is less unusual (Fig. 4I–J).

852 The first vertebral is wide and trapezoidal. Vertebrals 2–4 are wide, hexagonal elements.

853 Laterally, vertebrals 2–3 extend slightly less than the mid-length of the costals, which is slightly

854 less than in MHNN FOS 977. In NMS 101 and NMS 673, the sulcus between the fifth vertebral

855 and the twelfth marginals is located just posterior to the suture between the second suprapygal

856 and the pygal, whereas the sulcus is positioned around the mid-length of the pygal in MHNN

857 FOS 977. Finally, the two Solothurn specimens are unique in having a first interpleural sulcus

858 reaching the fourth marginal on the third peripheral, instead of the fourth as in most turtle,

859 including the holotype of *C. jaccardi* (Fig. 4).

860   MHNN FOS 977, NMS 101, and NMS 673 also exhibit differences regarding their plastral

861 morphology. The plastron is proportionally shorter in the Solothurn specimens (about 70% of the

862 carapace length, as opposed to 78% in MHNN FOS 977; see Table 2). Their entoplastron is

863 larger. In the holotype, the central plastral fontanelle is formed equally by the hyo- and

864 hypoplastra, whereas in the Solothurn specimens it is formed mostly or entirely by the

865 hypoplastra. The central plastral fontanelle is rounded in MHNN FOS 977 and NMS 101, but it

866 is oval and narrow in NMS 673.

867   The aforementioned differences can be diversely interpreted and may ultimately warrant the

868 placement of the Solothurn specimens in a different species. However, intraspecific variability

869 (notably sexual dimorphism in the case of the variation of the relative plastral length),

870 ontogenetic development (NMS 101 and NMS 673 are about 15% larger than the holotype

871 specimen), and stratigraphical age (MHNN FOS 977 is possibly slightly younger than the

872 Solothurn specimens) may also explain at least part of these differences. In order to avoid the

873 unnecessary creation of a new species, we still tentatively refer NMS 101 and NMS 673 to *C.*

874 *jaccardi*. Hopefully, new discoveries will eventually shed light on this particular question. In the

875 meantime, comparisons should be made primarily with MHNN FOS 977, the holotype of *C.*

876 *jaccardi*.

877　　Lapparent de Boin, Lange-Badré & Dutrieux (1996) proposed a number of relative

878 proportions of various shell measurements in order notably to discriminate between the different

879 *Plesiochelys* and *Craspedochelys* species (carapace length/width ratio, ratio between the length

880 of the second intercostal sulcus and the width of the third vertebral, ratio between the length of

881 the posterior plastral lobe and the length of the bridge, posterior plastral lobe length/width ratio,

882 ratio between the length of the bridge and the length of the carapace, ratio between the length of

883 the post-xiphiplastral space and the length of the carapace). However, many of these proportions

884 are not discriminative and the others are too much influenced by postmortem deformation. In the

885 course of the present study, we have also been looking for ratios that would allow to discriminate

886 between the species at hand. As discussed above the ratio between the length of the plastron and

887 the length of the carapace clearly differentiate *C. jaccardi* from *P. etalloni* (Table 2). For the

888 other ratios, we have focussed on individual bones whose measurements are not extensively

889 affected by postmortem deformation. The length/width ratios of the hyoplastron and

890 xiphiplastron discriminate between *C. jaccardi* and *P. etalloni* (Tables 4 and 5). In *C. jaccardi*,

891 the hyoplastron is wider than long and the xiphiplastron about as wide as long, whereas the

892 hyoplastron and xiphiplastron are both longer than wide in *P. etalloni*. The ratio between the

893 length of the carapace and the length of the fourth costal reveals that the shell is proportionally

894 wider in *C. jaccardi* than in *P. etalloni* and *C. picteti* (Table 6). Finally, the length/width ratio of

895 the fourth costal is probably the most interesting feature, because it clearly allows to discriminate

896 between the three aforementioned species. This ratio is high in *C. jaccardi*, slightly lower in *C.*

897 *picteti*, and much lower in *P. etalloni* (Table 3). This is also clearly visible directly on the

898 specimens where costals 2–6 seem thinner and elongate in *C. jaccardi* (Fig. 4), whereas they are

899 wider and shorter in *P. etalloni* (Figs. 2 and 8). It is also interesting to note that measurements

900 taken from MHNN FOS 977, NMS 101, and NMS 673 are generally congruent, which suggests

901 that these specimens truly belong to a single species.

902 ***Tropidemys langii***

903 In the Jura Mountains, the shell of *Tropidemys langii* is known from 19 specimens (out of which

904 five are relatively complete) from the localities of Solothurn and Porrentruy, Switzerland (Fig.

905 1). In addition to this material, a partial carapace is also known from the site of Sainte-Croix

906 (Canton of Vaud, Switzerland), but this specimen is supposed to have been found in Valanginian

907 (Early Cretaceous) deposits. The material from Porrentruy is particularly important because it

908 provides additional information regarding the plastron and limb bones (humerus and femur) of

909 this species. All this material has been recently revised and described by Püntener et al. (2014).

910   The carapace of *Tr. langii* is tectiform in the posterior part. Its outline varies from oval to

911 roundish. The nuchal is relatively variable in *Tr. langii*. The nuchal notch can be more or less

912 pronounced, and is even absent in some individuals. MJSN VTT006-563 exhibits a pair of small

913 supernumerary bones on the anterolateral edges of the nuchal, which changes its usually

914 trapezoidal outline (Püntener et al., 2014: fig. 8). *Tropidemys langii* is mainly characterized by

915 the presence of thick, wide, hexagonal, and keeled neurals. Although the angle formed by the

916 keel and the geometry of the neurals are subjected to some intraspecific variation (see Püntener

917 et al., 2014: table 1), these characters clearly distinguish *Tr. langii* from other Late Jurassic

918 turtles, including *Plesiochelys etalloni*, *Craspedochelys picteti*, *Craspedochelys jaccardi*,

919 *Thalassemys hugii*, and *'Thalassemys' moseri*. The midline keel is barely noticeable on the

920 anterior neurals, then it becomes progressively more pronounced posteriorly before subsiding on

921 the suprapygals. It nevertheless reaches as far as the pygal posteriorly. The pygal region itself is

922 relatively poorly known. There are usually two suprapygals that vary in shape among specimens.

923 In some specimens, there seems to be an intermediate element between the eighth neural and the

924 first suprapygal (Fig. 5), as in *P. etalloni*, *C. picteti*, *C. jaccardi*, and *Th. hugii*. The pygal is a

925 wide and rectangular element. There are eight pairs of costals. It is remarkable that costals 1 and

926 2 curve strongly anteriorly in their distal parts, whereas costals 4–8 curve posteriorly. The third

927 costal is straight and widens distally, compensating for the diverging curvature of costals 2 and 4.

928   All sufficiently preserved specimens of *Tr. langii* have three cervical scales, but they vary in

929 shape and proportion. *Tropidemys langii* is characterized by its very narrow vertebral scales. The

930 intervertebral sulci are usually convex anteriorly in the midline. The third intervertebral sulcus is

931 variably located on the fifth or the sixth neural (Püntener et al., 2014: table 1). In contrast to *P.*

932 *etalloni*, *C. picteti*, *C. jaccardi*, and *Th. hugii* in which the fourth intervertebral sulcus is usually

933 located posterior to the eighth neural on the intermediate element, if present, or on the first

934 suprapygal, this sulcus extends medially on the eighth neural in *Tr. langii*. Furthermore, the

935 arrangement of vertebral scales distinguishes *Tr. langii* from *Tr. seebachi* Portis, 1878, the only

936 other valid species in this genus. This species is only known from the Kimmeridgian of Hanover,

937 Germany, and is characterized by the presence of up to eight vertebral scales and an additional

938 row of paired scales intercalated between the vertebrals and pleurals (Karl, Gröning &

939 Brauckmann, 2012). The pleural scales are very wide in *Tr. langii*. The interpleural sulci are

940 usually located on the posterior part of costals 2, 4, and 6, but the first intercostal sulcus may

extend onto the third costal (e.g., MJSN VTT006-253 and NMS 15; see Fig. 5). MJSN VTT006-176 exhibits paired supernumerary pleural scales immediately lateral to the first vertebral (Püntener et al., 2014: fig. 4B). The marginals of *Tr. langii* are generally rectangular in outline and about twice as long as wide. The fourth and fifth marginals may extend slightly onto the costals in some specimens (e.g., MJSN VTT006-253 and MJSN VTT006-563).

The plastral anatomy of *Tr. langii* was poorly known until Püntener et al (2014) described some articulated material from Porrentruy. The connexion between the carapace and plastron is relatively strong, as indicated by the extensive attachment sites for the plastral buttresses on the ventral surface of the first and fifth costals. The epi-, ento-, and xiphiplastron of *Tr. langii* are unknown. Similar to the condition observed in *C. jaccardi* (see Table 4), the hyoplastron of *Tr. langii* varies in proportion from about as wide as long (MJSN VTT006-290) to wider than long (MJSN VTT006-563). There is a central plastral fontanelle mainly formed by the hyoplastra (e.g., MJSN VTT006-290 and MJSN VTT006-563), but is is possible that the central plastral fontanelle was reduced or absent in some individual, as suggested by MJSN VTT006-52 (Püntener et al., 2014).

As in *C. jaccardi*, the humeral scale is significantly longer than the pectoral scale. Similar to the condition observed on the carapace, the arrangement of plastral scales exhibits a certain amount of variability, such as the presence of supernumerary scales. For example, in MJSN VTT006-563, a small triangular scale is intercalated between the hyoplastra (Püntener et al., 2014: fig. 12B). A similar supernumerary scale is known in MAJ 2005-11-1, the holotype of *Plesiochelys etalloni* (Fig. 2). Based on the available material, the anal scale was probably restricted to the xiphiplastron. There were apparently four inframarginals on each side, the second inframarginal being the longest in the series.

Thalassemys hugii

Bräm (1965) listed 15 specimens of *Thalassemys hugii* in the historical Solothurn collection. At

the beginning of the 1990's, the Geological Institute of Bern, Switzerland, collected additional

turtle remains from the locality of St Niklaus (Meyer & Thüring, 2009; and references therein).

This rich material is now housed in the NMS. If most of this material remains undetermined up

until today, we have been able to identify a few specimens as *Th. hugii*. However, a detailed

review of all the Solothurn material assignable to *Th. hugii* goes beyond the scope of the present

study, and we will simply provide important additional information on the plastral morphology

of this species.

Bräm (1965) described the carapace of *Th. hugii* as heart-shaped, but most peripherals are

missing in the holotype (NMS 1; Fig. 6A–D). Lapparent de Broin, Lange-Badré & Dutrieux

(1996) revealed that posterior peripherals were actually relatively wide and that the carapace was

oval. The nuchal is a broad, trapezoidal element, much similar to that of *Plesiochelys* and

Craspedochelys, but without nuchal notch. There are eight neurals. The first neural is

quadrangular and notably broadened anteriorly. Neural 2–6 are elongate, hexagonal elements

with shorter sides facing anteriorly. In NMS 1, the sixth neural is subdivided into two elements,

but this is not interpreted as having any systematic value. The seventh and eighth neurals are

shorter, hexagonal elements. Historically, authors have described three suprapygals in *Th. hugii*

(Rütimeyer, 1873; Bräm, 1965; Lapparent de Broin, Lange-Badré & Dutrieux, 1996).

Comparisons suggest that the arrow-shaped element located directly posterior to the eighth

neural in NMS 1 may actually correspond to the 'intermediate' element described in *Plesiochelys*

etalloni, *Craspedochelys picteti*, and *Craspedochelys jaccardi* (see above). The ventral aspect of

this element indicates that it was articulated to the vertebral series, but only for the anterior half

of its length. As discussed above for *P. etalloni*, identifying this element is rather difficult.

988 Posterior to this arrowhead-shaped element, there are two suprapygals. The pygal is not

989 preserved in NMS 1. There are eight pairs of costals. Costals 1 and 2 are sutured to peripherals

990 1–3 in adult individuals. Small costo-peripheral fontanelles are retained between remaining

991 costals and peripherals.

992 Bräm (1965) and Lapparent de Broin, Lange-Badré & Dutrieux (1996) described only one

993 cervical scale in *Th. hugii*, but examination of the type specimen suggests that three may have

994 been present. A more detailed review of the available material would be necessary in order to

995 determinate the number of cervical scales in this species. The first vertebral is trapezoidal and

996 greatly enlarged anteriorly. Posteriorly, its width is similar to that of the nuchal, but the first

997 vertebral reaches the middle of the second marginal scale anterolaterally. Vertebrals 2–4 are

998 significantly narrower than the same elements in *P. etalloni*, *C. picteti*, and *C. jaccardi*. Vertebral

999 2 is the narrowest and shortest of these three scales, whereas vertebral 4 is the widest and

1000 longest. The outlines of vertebrals 2–4 are characteristic. Their anterior and posterior borders are

1001 mostly straight and transverse. Their anterolateral borders are always slightly concave laterally,

1002 whereas their posterolateral borders are usually straight. These anterolateral and posterolateral

1003 borders are usually of about the same length for a given vertebral scale. As a consequence of the

1004 reduced width of the vertebrals, pleurals 1–3 are clearly wider than long.

1005 The reconstruction of the plastron proposed by Bräm (1965: fig. 30) is mainly based on the

1006 plastron of the holotype (NMS 1), which is poorly preserved and gives a misleading image of the

1007 true plastral morphology of *Th. hugii* (Fig. 6C–D). Referred specimens, such as NMS 20, NMS

1008 593, and NMS 22325, provide important indications (Fig. 9). The central plastral fontanelle is

1009 not as extensive as to prevent a median contact of the hypoplatra, as suggested by Bräm's (1965)

1010 reconstruction. In contrast, the hypoplastra do meet posteriorly for about half of their length

1011 along a strongly interdigitating contact. Behind this contact there is a small xiphiplastral

1012 fontanelle that prevents the xiphiplastra from meeting anteriorly. More posteriorly, the

1013 xiphiplastra meet along an interdigitating contact. However, the most important characteristic

1014 revealed by specimens NMS 20, NMS 593, and NMS 22325 is the definitive presence of a

1015 lateral plastral fontanelle in *Th. hugii* (Fig. 9). Based mainly on NMS 1, Bräm (1965) concluded

1016 that a lateral plastral fontanelle was absent in *Th. hugii*, which allowed to differentiate this taxon

1017 from eurysternids like *Eurysternum* (see *Eurysternum ignoratum*, above). However, Bräm (1965)

1018 overlooked the fact that a lateral plastral fontanelle is clearly present notably in NMS 20 and

1019 NMS 593. NMS 22325, a large right hyoplastron from St Niklaus (collected during the 1990s

1020 excavations by the Geological Institute of Bern, Switzerland) pertaining to a specimen that was

1021 only slightly smaller than the holotype, also indubitably shows a lateral plastral fontanelle. The

1022 presence of a lateral plastral fontanelle in *Th. hugii* calls into question the traditional diagnoses

1023 of the Thalassemydidae and Eurysternidae.

1024   During our review of the material, we have also identified two additional characters that allow

1025 to differentiate *Th. hugii* from other Solothurn turtles. The first of these characters is the presence

1026 of well-developed linear striations perpendicular to sutures between most shell elements,

1027 somewhat recalling the condition known in the Early Cretaceous *Pleurosternon bullockii* (e.g.,

1028 Milner, 2004). These striations are clearly visible notably in NMS 1 (see Rütimeyer, 1873: plate

1029 1; Bräm, 1965: plate 7, fig. 4; Fig. 6), NMS 9, and NMS 22326-22327 (costals associated with

1030 the hyoplastron NMS 22325). They are also present in several specimens previously referred to

1031 *E. ignoratum* (see above): NMS 5, NMS 124, and NMS 412. The second character is the

1032 presence of a strong axillary buttress that is articulated over a large area on the ventral surface of

1033 the distal part of the first costal, as seen in NMS 1, NMS 412, and NMS 37251. The inguinal

1034 buttress is also relatively massive, although less so than the axillary buttress.

1035   Bräm (1965) designated NMS 5 as the holotype of *Eurysternum ignoratum* and further

1036 referred NMS 124 (but see *Plesiochelys langii*, above) and NMS 412 to this species. However,

1037 these specimens are indiscernible from other specimens referred to *Th. hugii* (Fig. 6): e.g.,

1038 vertebral scales with similar outlines and proportions (e.g., second vertebral length/width ratio of

1039 about 69% and 72% in NMS 1 and NMS 412, respectively); presence of clearly visible linear

1040 striations perpendicular to sutures between most shell elements (present in NMS 5, NMS 124,

1041 and NMS 412); presence of a strong attachment site for a large axillary buttress on the ventral

1042 surface of the distal part of the first costal (visible only in NMS 412). As in *Th. hugii* (see above;

1043 not Bräm, 1965), the plastron of NMS 5 has lateral plastral fontanelles and a central plastral

1044 fontanelle closed anteriorly by a median, interdigitating contact of the hyoplastra. A preliminary

1045 comparison of the girdle elements (notably the scapula and pubis) of NMS 5 (holotype of *E.*

1046 *ignoratum*), NMS 1 (holotype of *Th. hugii*), and NMS 9 (a specimen referred to *Th. hugii*) also

1047 reveals a very close morphology. Therefore, *E. ignoratum* is interpreted herein as a subjective

1048 synonym of *Th. hugii*.

1049 ***'Thalassemys' moseri***

1050 Bräm (1965) typified *'Thalassemys' moseri* based on a partial carapace and plastron (NMS 618;

1051 Fig. 7A–D). He also referred three additional specimens to this species: a partial carapace (NMS

1052 62; Fig. 7E–F), an isolated right hyoplastron (NMS 64), and an isolated left hyoplastron (NMS

1053 111). As already noted by Bräm (1965) and Lapparent de Broin, Lange-Badré & Dutrieux

1054 (1996), the carapace of *'Th.' moseri* is superficially similar to that of *Plesiochelys etalloni*: large

1055 trapezoidal nuchal with a broad and shallow nuchal notch; neurals elongated; three cervical

1056 scales; vertebrals wide and hexogonal with slightly sinuous sulci. However, *'Th.' moseri* is

1057 characterized by the retention of costo-peripheral fontanelles in adults. NMS 618 and NMS 62

would have had an approximative carapace length of 400 mm. Specimens of similar size referred to *P. etalloni* are common in Solothurn (e.g., NMS 78 and NMS 107), but all have a completely ossified carapace. Furthermore, NMS 606, a juvenile *P. etalloni* with a carapace length of about 200 mm, also have an entirely ossified carapace. The retention of costo-peripheral fontanelles in adults is therefore a diagnostic feature of *'Th.' moseri*. Close examination of NMS 618 and NMS 62 also reveals that their costals are very thin distally. This is clearly different from the condition known in *Th. hugii*, in which the costals remain relatively thick distally. Hence, the costals taper progressively distally in *'Th.' moseri*, whereas their distal end is proportionally thicker and blunt in *Th. hugii*.

The plastron of *'Th.' moseri* is best known from the holotype specimen (NMS 618). It is characterized by the presence of a central plastral fontanelle that is proportionally larger than that of *P. etalloni* or *C. jaccardi*. In contrast to *Th. hugii* (see above; not Bräm, 1965), the central plastral fontanelle is closed anteriorly and posteriorly by tight sutural contacts of the hyo- and hypoplastra, respectively. There is no lateral plastral fontanelle. Bräm (1965) noted that the epi- and entoplastron were not suturally connected to the hyoplastron. This reminds the condition in *Th. hugii*, but clearly departs from the strong sutural contact observed in *P. etalloni* and *C. jaccardi*. Finally, as suggested by Bräm (1965), there may have been a small xiphiplastral notch posteriorly.

Rieppel (1980) described a skull and associated, fragmentary shell remains (PMZH A/III 514) from the early Tithonian of La Morelière (Isle of Oléron, France) that he referred to *'Th.' moseri*. Subsequent authors disagreed with this referral, considering that the specimen from La Morelière was a different taxon (Lapparent de Broin, Lange Badré & Dutrieux, 1996; A. Pérez-García, pers. comm., 2014) According to Rieppel's (1980) conclusions, *'Th.' moseri* is more closely related to *Plesiochelys* than to *Thalassemys*, but many features in the skull of *'Th.' moseri* are

1082 plesiomorphic compared to the same features in *P. etalloni*. In the present study, we furthermore

1083 reveal that *Th. hugii* has a lateral plastral fontanelle, a feature absent in *'Th.' moseri*. The referral

1084 of *'Th.' moseri* to the genus *Thalassemys* is therefore highly improbable. However, in the current

1085 state of knowledge, the generic assignment of this species remains uncertain. A revision of the

1086 specimen described by Rieppel (1980) would certainly be an essential step toward a better

1087 understanding of this species, but ultimately more material is needed first to confirm or refute

1088 Rieppel's (1980) identification, and second to gain insight into the morphology and relationships

1089 of this turtle.

1090   **CONCLUSIONS**

1091 Fifteen species have historically been typified based on material from the Late Jurassic of the

1092 Jura Mountains. Bräm (1965) proposed the last systematic review of all the available material

1093 from Solothurn and still recognized nine out of these 15 species. Subsequent studies focussed

1094 their attention mainly on the genera *Plesiochelys* and *Craspedochelys*, representing a total of five

1095 species according to Bräm's (1965) taxonomy. Gaffney (1975a) united these five species into a

1096 single one (*P. etalloni*), whereas Lapparent de Broin, Lange-Badré & Dutrieux (1996)

1097 recognized four out of five species as valid (*P. etalloni*, *P. solodurensis*, *C. picteti*, and *C.

1098 jaccardi)*.

1099   The present study is the most complete taxonomic review of the Late Jurassic turtles from the

1100 Jura Mountains since Bräm (1965). Its purpose was not only to reassess the taxonomy of these

1101 turtles, but also to reevaluate the available material in light of recent knowledge. We have not

1102 only considered the type specimens, but have also directly observed numerous referred

1103 specimens notably from the Solothurn collection (see Table S1). Out of the original 15 species,

1104 we recognize six as valid: *Plesiochelys etalloni*, *Craspedochelys picteti*, *Craspedochelys*

1105 *jaccardi*, *Tropidemys langii*, *Thalassemys hugii*, and *'Thalassemys' moseri*. These species are

1106 temporarily assigned to the traditional families Plesiochelyidae (*P. etalloni*, *C. picteti*, *C.*

1107 *jaccardi*, and *Tr. langii*) and Thalassemydidae (*Th. hugii*), although the proper definition of these

1108 taxa needs to be reconsidered in a phylogenetic context. The generic and suprageneric

1109 assignment of *'Th.' moseri* remains conjectural. The presence of lateral plastral fontanelles in *Th.*

1110 *hugii* calls into question the traditional distinction between the Thalassemydidae and the

1111 Eurysternidae. Since *Eurysternum ignoratum* is considered a junior synonym of *Th. hugii*,

1112 eurysternids should be regarded as relatively rare in the Late Jurassic of the Jura Mountains.

1113 Indeed, they are now only represented by a single skull of *Solnhofia parsonsi* from Solothurn

1114 (Gaffney, 1975b).

1115   If the present taxonomic review represents a dramatic reduction in terms of number of

1116 species, the presence of six more or less closely related, relatively large coastal marine turtles in

1117 the same paleoenvironment is still remarkable. In order to extend comparisons and interpret

1118 these results in terms of paleoecology and paleobiogeography, future studies should apply a

1119 similar methodology to other Late Jurassic turtle assemblages throughout Europe, notably in

1120 Germany, UK, France, Spain, and Portugal. The present paper will serve as a base for future

1121 work on Late Jurassic European turtles, notably for the study of the rich Kimmeridgian material

1122 unearthed by the PAL A16 team in the vicinity of Porrentruy, Switzerland.

REFERENCES

Anquetin J, Joyce WG. In press. A reassessment of the Late Jurassic turtle *Eurysternum wagleri* (Eucryptodira, Eurysternidae). *Journal of Vertebrate Paleontology*.

Anquetin J, Deschamps S, Claude J. 2014. The rediscovery and redescription of the holotype of the Late Jurassic turtle *Plesiochelys etalloni*. *PeerJ* 2:e258.

Antunes MT, Becquart D, Broin F de. 1988. Découverte de "*Plesiochelys*", chélonien marin-littoral, dans le Kimméridgien d'Alcobaça, Portugal. *Ciências Da Terra (UNL)* 9:141–152.

Ayer J. 1997. Les collections géologiques du Muséum d'histoire naturelle de Neuchâtel : tradition, nouvelle gestion et perspectives. *Bulletin de La Société Neuchâteloise Des Sciences Naturelles* 120:5–17.

Batsch AJGC. 1788. *Versuch einer Anleitung, zur Kenntniß und Geschichte der Thiere und Mineralien*. Jena: Akademische Buchhandlung.

Baur G. 1888. Osteologische Notizen über Reptilien (Fortsetzung II). *Zoologischer Anzeiger* 11:417–424.

Billon-Bruyat J-P. 2005. A "turtle cemetery" from the Late Jurassic of Switzerland. *Abstracts, 3rd Swiss Geoscience Meeting, Zürich* 2005: 238.

Bräm H. 1965. Die Schildkröten aus dem oberen Jura (Malm) der Gegend von Solothurn. *Schweizerische Paläontologische Abhandlungen* 83:1–190.

Broin F de. 1994. Données préliminaires sur les chéloniens du Tithonien inférieur des calcaires lithographiques de Canjuers (Var, France). *Geobios* 16:167–175.

Cuvier G. 1824. *Recherches sur les ossemens fossiles, où l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces*. 2nd Edition, Tome 5, Part 2. Paris: Dufour et d'Ocagne.

Dollo L. 1886. Première note sur les Chéloniens du Bruxellien (Éocène moyen) de la Belgique. *Bulletin du Musée Royal d'Histoire Naturelle de Belgique* 4:75–100.

Fraas E. 1903. *Thalassemys marina* E. Fraas aus dem oberen weissen Jura von Schnaitheim nebst Bemerkungen über die Stammesgeschichte der Schildkröten. *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg* 59:72–104.

Gaffney ES. 1975a. A taxonomic revision of the Jurassic turtles *Portlandemys* and *Plesiochelys*. *American Museum Novitates* 2574:1–19.

Gaffney ES. 1975b. *Solnhofia parsonsi*, a new cryptodiran turtle from the Late Jurassic of Europe. *American Museum Novitates* 2576:1–22.

Gaffney ES. 1975c. A phylogeny and classification of the higher categories of turtles. *Bulletin of the American Museum of Natural History* 155:387–436.

Jaccard A. 1860. Première partie. Aperçu géologique sur les étages supérieurs du terrain jurassique du Jura neuchâtelois. In: Pictet F-J, ed. *Matériaux pour la paléontologie suisse*. Troisième série. Genève: J. Kessmann & H. Georg, 3–15.

Jaccard A. 1870. Les fossiles du Jura II: La tortue de la carrière des Hauts-Geneveys. *Rameau de Sapin* 5:39–40.

Joyce WG. 2003. A new Late Jurassic turtle specimen and the taxonomy of *Palaeomedusa testa* and *Eurysternum wagleri*. *PaleoBios* 23:1–8.

Joyce WG. 2007. Phylogenetic relationships of Mesozoic turtles. *Bulletin of the Peabody Museum of Natural History* 48:3–102.

Karl H-V, Gröning E, Brauckmann C. 2012. Revision of *Tropidemys seebachi* Portis, 1878 (Testudines: Eucryptodira) from the Kimmeridgian (Late Jurassic) of Hannover (northwestern Germany). *Studia Palaeocheloniologica* 4:11–24.

Karl H-V, Staesche U, Tichy G, Lehmann J, Peitz S. 2007. Systematik der Schildkröten

    (Anapsida: Chelonii) aus Oberjura und Unterkreide von Nordwestdeutschland. *Geologisches*

    Jahrbuch, Reihe B 98:5–89.

Kuhn O. 1964. Pt. 107, Testudines. In: Westphal F, ed. *Fossilium Catalogus*. Volume 1,

    Animalia. Den Haag: Dr W. Junk, 1–299.

Lang F, Rütimeyer L. 1867. Die fossilen Schildkröten von Solothurn. *Neue Denkschrift der*

    allgemeinen schweizerischen naturforschenden Gesellschaft 22:1–47.

Lapparent de Broin F de. 2001. The European turtle fauna from the Triassic to the Present.

    Dumerilia 4:155–217.

Lapparent de Broin F de, Lange-Badré B, Dutrieux M. 1996. Nouvelles découvertes de tortues

    dans le Jurassique supérieur du Lot (France) et examen du taxon Plesiochelyidae. *Revue de*

    Paléobiologie 15:533–570.

Lienhard L. 2008. Hugi, Franz Joseph. *Dictionnaire historique de la Suisse*. Available at

    http://www.hls-dhs-dss.ch/textes/f/F28857.php (Accessed 23 February 2014).

Marty D, Hug WA. 2003. Le Kimméridgien en Ajoie (Mésozoïque) : premiers résultats de

    fouilles et de recherches paléontologique sur le tracé de la Transjurane (A16). *Actes de la*

    Société jurassienne d'émulation 2003:27–44.

Marty D, Billon-Bruyat J-P. 2009. Field-trip to the excavations in the Late Jurassic along the

    future Transjurane highway near Porrentruy (Canton Jura, NW Switzerland): dinosaur tracks,

    marine vertebrates and invertebrates. In: Billon-Bruyat J-P, Marty D, Costeur L, Meyer CA,

    Thüring B, eds. *Abstracts and Field Guides, 5th International Symposium on Lithographic*

    Limestone and Plattenkalk, Actes 2009 bis de la Société jurassienne d'émulation. Porrentruy,

    Switzerland, 94–129.

1196   Marty D, Ayer J, Becker D, Berger J-P, Billon-Bruyat J-P, Braillard L, Hug WA, Meyer CA.

1197   2007. Late Jurassic dinosaur tracksites of the Transjurane highway (Canton Jura, NW

1198   Switzerland): overview and measures for their protection and valorization. *Bulletin for*

1199   *Applied Geology* 12:75–89.

1200   Meyer CA, Thüring S. 2009. Late Jurassic marginal marine ecosystem of the Southern Jura

1201   Mountains. In: Billon-Bruyat J-P, Marty D, Costeur L, Meyer CA, Thüring B, eds. *Abstracts*

1202   *and Field Guides, 5th International Symposium on Lithographic Limestone and Plattenkalk,*

1203   *Actes 2009 bis de la Société jurassienne d'émulation*. Porrentruy, Switzerland, 130–141.

1204   Meyer H von. 1839. *Eurysternum Wagleri*, Münster. Eine Schildkröte aus dem Kalkschiefer von

1205   Solnhofen. *Beiträge zur Petrefacten-Kunde* 1:75–82.

1206   Milner AR. 2004. The turtles of the Purbeck Limestone Group of Dorset, Southern England.

1207   *Palaeontology* 47:1441–1467.

1208   Owen R. 1842. Report on British fossil reptiles, part II. *Report for the British Association for the*

1209   *Advancement of Science, Plymouth 1841* 11:60–204.

1210   Pérez-García A. In press. Reinterpretation of the Spanish Late Jurassic "*Hispaniachelys*

1211   *prebetica*" as an indeterminate plesiochelyid turtle. *Acta Palaeontologica Polonica*.

1212   Pictet F-J. 1860. Deuxième partie. Description des fossiles. In: Pictet F-J, Jaccard A. Description

1213   de quelques débris de reptiles et de poissons fossiles trouvés dans l'étage jurassique supérieur

1214   (Virgulien) du Jura neuchâtelois. In: Pictet F-J, ed. *Matériaux pour la paléontologie suisse.*

1215   Troisième série. Genève: J. Kessmann & H. Georg, 15–88.

1216   Pictet F-J, Humbert A. 1857. Description d'une émyde nouvelle (*Emys Etalloni*) du terrain

1217   jurassique supérieur des environs de St-Claude. In: Pictet F-J, ed. *Matériaux pour la*

1218   *paléontologie suisse.* Première série. Genève: J. Kessmann, 1–10.

Portis A. 1878. Ueber fossile Schildkröten aus dem Kimmeridge von Hannover. *Palaeontographica* 25:125–140.

Pritchard PCH. 2008. Evolution and structure of the turtle shell. In: Wyneken J, Godfrey MH, Bels V, eds. *Biology of Turtles*. Boca Raton, FL: CRC Press, 45–83.

Püntener C, Billon-Bruyat J-P, Bocat L, Berger J-P, Joyce WG. 2014. Taxonomy and phylogeny of the turtle *Tropidemys langii* Rütimeyer, 1873 based on new specimens from the Kimmeridgian of the Swiss Jura Mountains. *Journal of Vertebrate Paleontology* 34:353–374.

Rieppel O. 1980. The skull of the Upper Jurassic cryptodire turtle *Thalassemys*, with a reconsideration of the chelonian braincase. *Palaeontographica, Abt. A* 171:105–140.

Rütimeyer L. 1859. Notiz über Schildkröten von Solothurn. *Verhandlungen der schweizerischen naturforschenden Gesellschaft* 43:57–59.

Rütimeyer L. 1873. Die fossilen Schildkröten von Solothurn und der übrigen Juraformation. *Neue Denkschrift der allgemeinen schweizerischen naturforschenden Gesellschaft* 25:1–185.

Slater BJ, Reolid M, Schouten R, Benton MJ. 2011. A new Late Jurassic turtle from Spain: phylogenetic implications, taphonomy and palaeoecology. *Palaeontology* 54:1393–1414.

Wagner A. 1853. Beschreibung einer fossilen Schildkröte und etlicher anderer Reptilien-Ueberreste aus den lithographischen Schiefern und dem Grünsandsteine von Kelheim. *Abhandlungen der königlich bayerischen Akademie der Wissenschaften, zweite Classe* 7:241–264.

Zangerl R. 1969. The turtle shell. In: Gans C, Bellairs AA, Parsons TS, eds. *Biology of the Reptilia*. Volume 1, Morphology A. London: Academic Press, 311–339.

Zittel KA. 1889. *Handbuch der Palaeontologie*. Section 1: Palaeozoologie, Volume 3, Vertebrata, Shipment 3: Reptilia. München: R. Oldenbourg.

Figure 1

Map showing the location of the Late Jurassic turtle sites throughout the Jura Mountains (Switzerland and France).
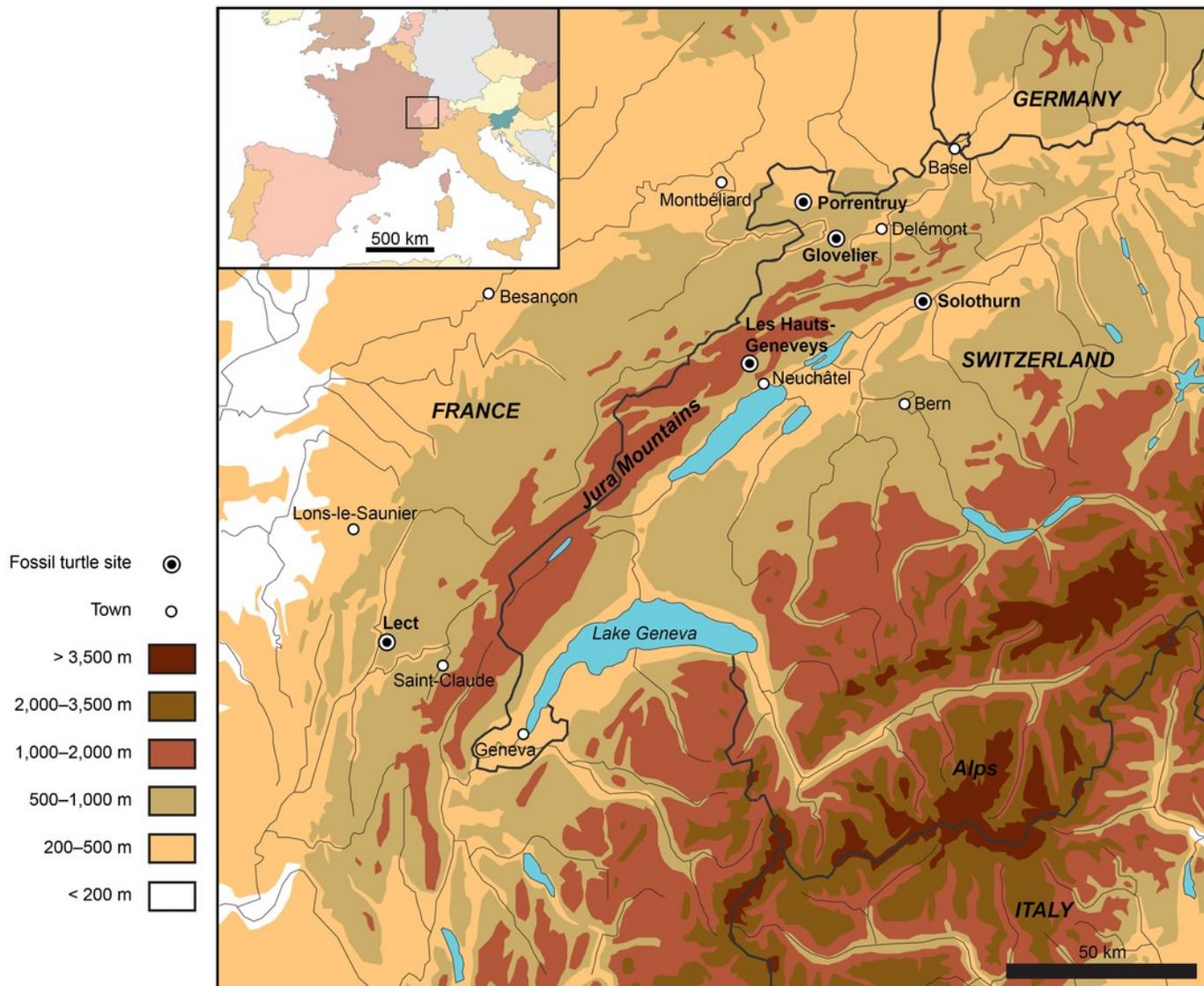
Figure 2

Plesiochelys etalloni.

Holotype of *P. etalloni*, MAJ 2005-11-1: (A) photograph of the carapace; (B) interpretative drawing of the carapace; (C) photograph of the plastron; (D) interpretative drawing of the plastron. Lectotype of *P. solodurensis*, NMS 59: (E) photograph of the carapace; (F) interpretative drawing of the carapace; (G) photograph of the plastron; (H) interpretative drawing of the plastron. Lectotype of *P. sanctaeverenae*, NMS 118: (I) photograph of the carapace; (J) interpretative drawing of the carapace. Lectotype of *P. langii*, NMS 123: (K) photograph of the carapace; (L) interpretative drawing of the carapace. Bones are white; stripped lines indicate internal bone layers; green solid lines indicate scales sulci; matrix is gray. Abbreviations: eb; epiplastral bulb; n, neural; *, intermediate element (see text).
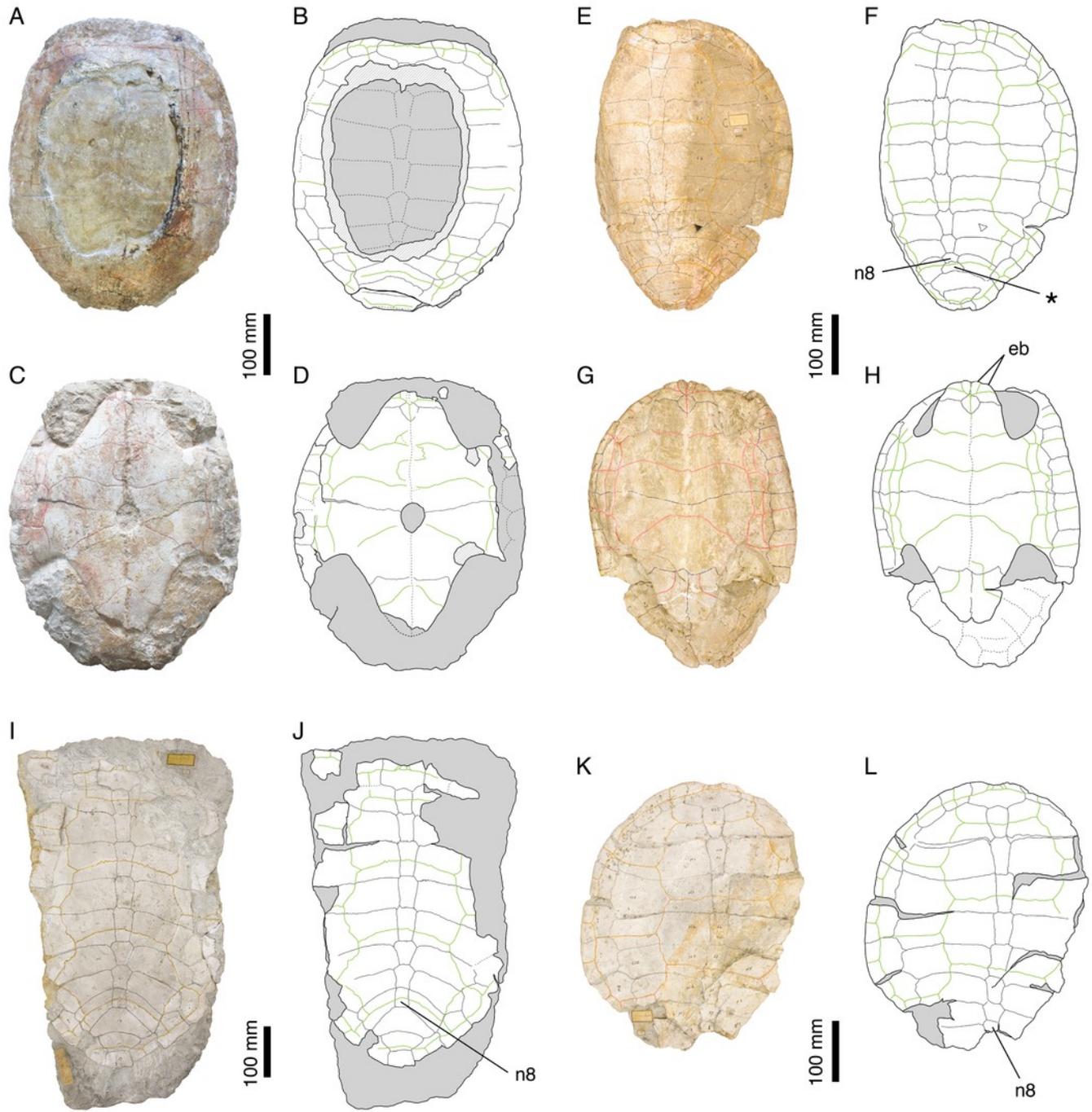
Figure 3

Craspedochelys picteti.

Holotype of *C. picteti*, NMS 129: (A) photograph of the carapace; (B) interpretative drawing of the carapace; (C) photograph of the plastron; (D) interpretative drawing of the plastron. Referred specimen, NMS 608: (E) photograph of the carapace; (F) interpretative drawing of the carapace. Bones are white; green solid lines indicate scales sulci; matrix is gray. Abbreviations: ca, carapace; cpf, central plastral fontanelle; hyo, hyoplastron; p, peripheral; pla, plastron; py, pygal; sp, suprapygal; *, intermediate element (see text).
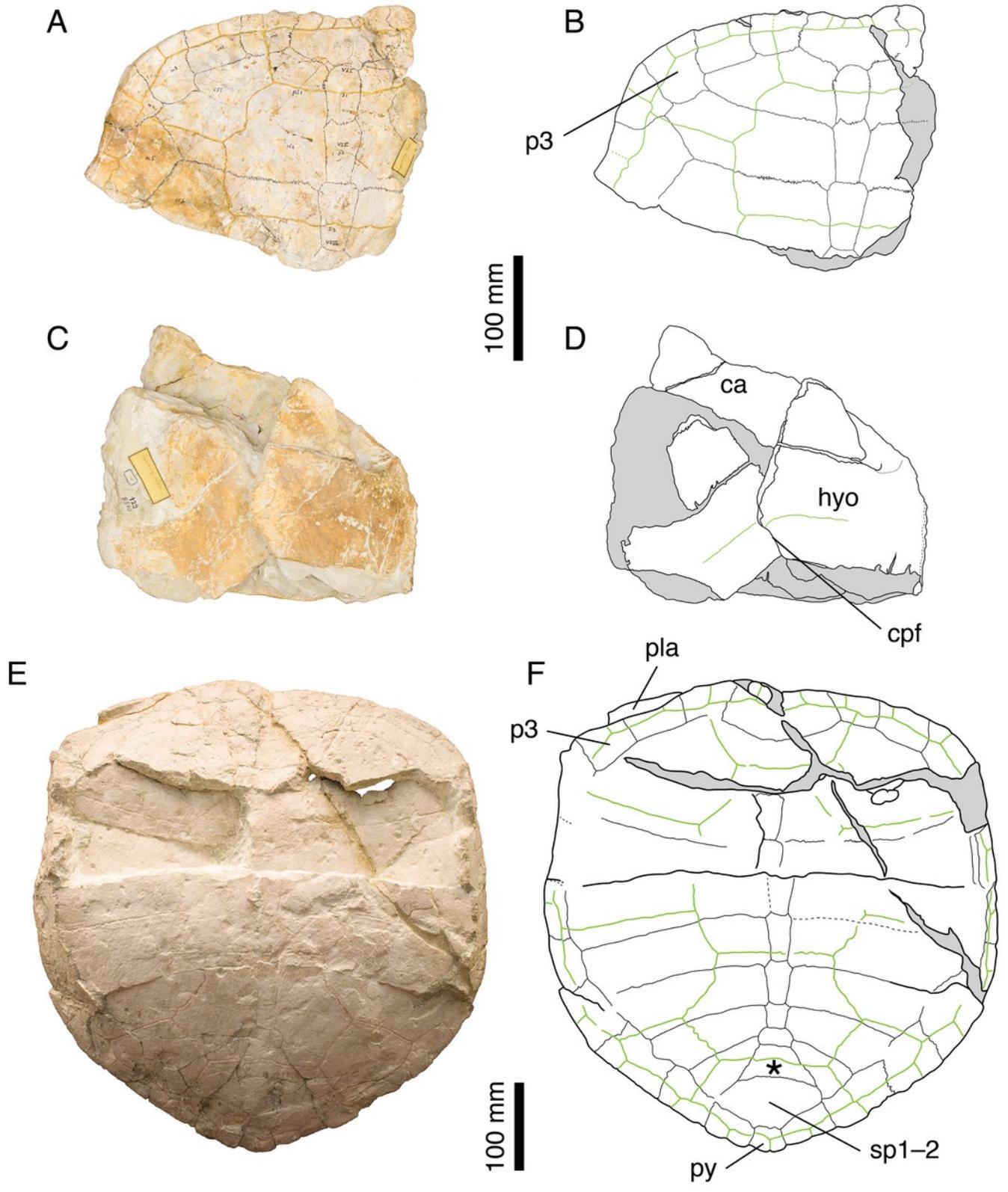
Figure 4

Craspedochelys jaccardi.

Holotype of *C. jaccardi*, MHNN FOS 977: (A) photograph of the carapace; (B) interpretative drawing of the carapace; (C) photograph of the plastron; (D) interpretative drawing of the plastron. Referred specimen, NMS 101: (E) photograph of the carapace; (F) interpretative drawing of the carapace; (G) photograph of the plastron; (H) interpretative drawing of the plastron. Referred specimen, NMS 673: (I) photograph of the carapace; (J) interpretative drawing of the carapace; (K) photograph of the plastron; (L) interpretative drawing of the plastron. Referred specimen, NMS 102a: (M) photograph of the carapace; (N) interpretative drawing of the carapace. Bones are white; green solid lines indicate scales sulci; matrix is gray. Abbreviations: co, costal; n, neural; p, peripheral; *, intermediate element (see text).

A

B
p2
n7
co8
*

C

D

E

F
p2
*

G

H

I

J
p2
*

K

L

M

N
p2
*

100 mm
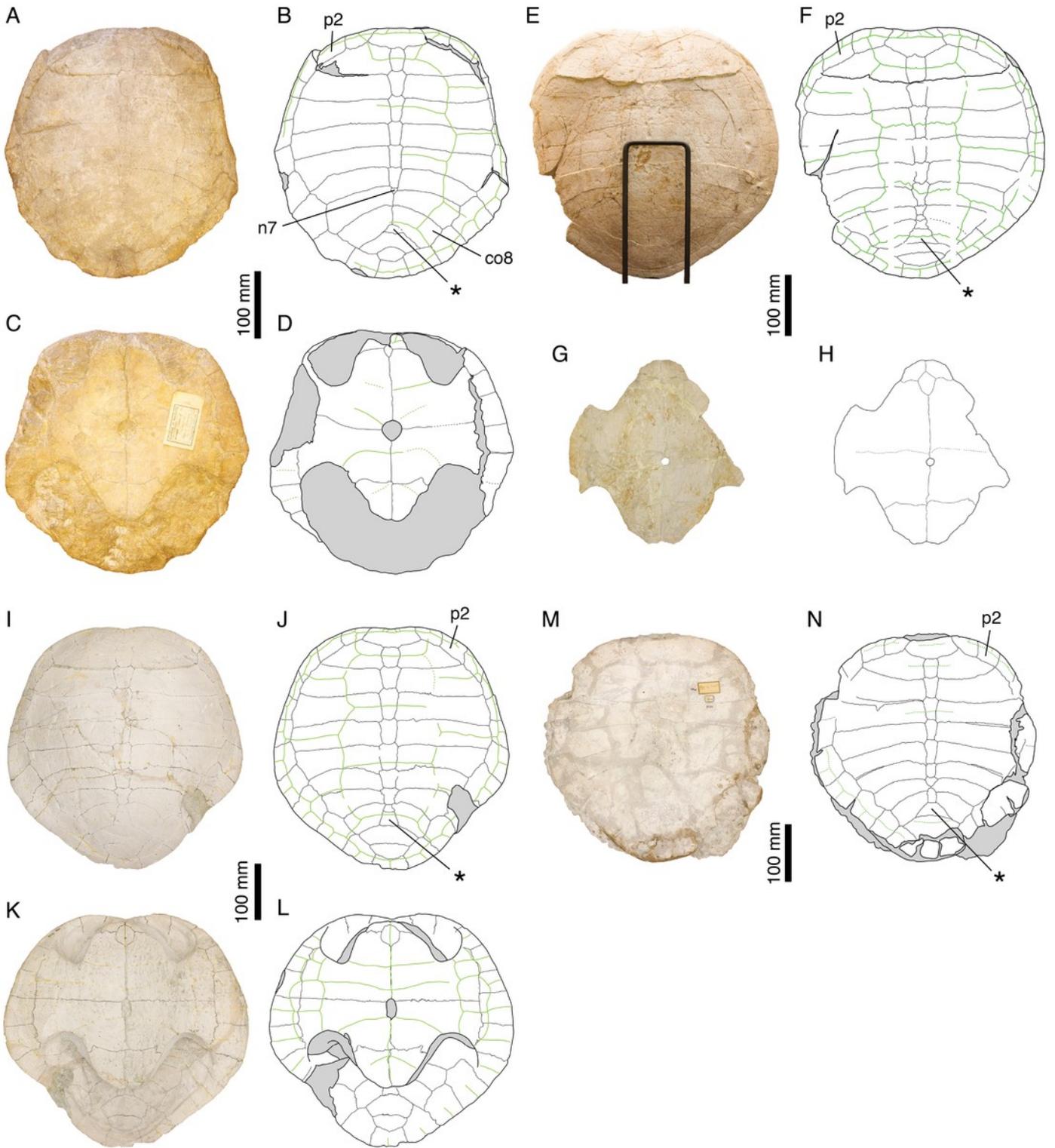
Figure 5

Tropidemys langii.

Lectotype of *Tr. langii*, NMS 16: (A) photograph of the carapace; (B) interpretative drawing of the carapace. Referred specimen, NMS 15: (C) photograph of the carapace; (D) interpretative drawing of the carapace. Bones are white; green solid lines indicate scales sulci; matrix is gray. Abbreviations: co, costal; n, neural; sp, suprapygal; *, intermediate element (see text).
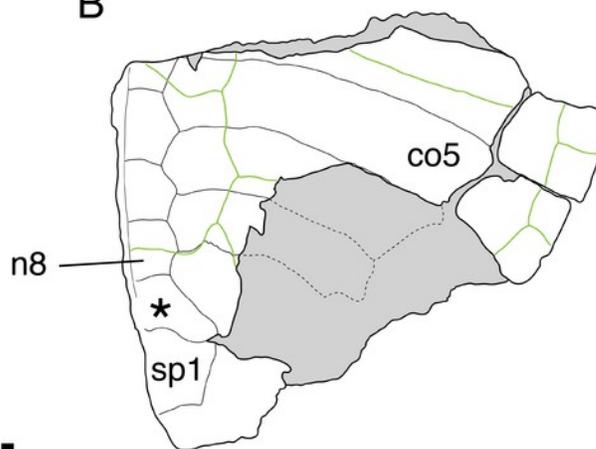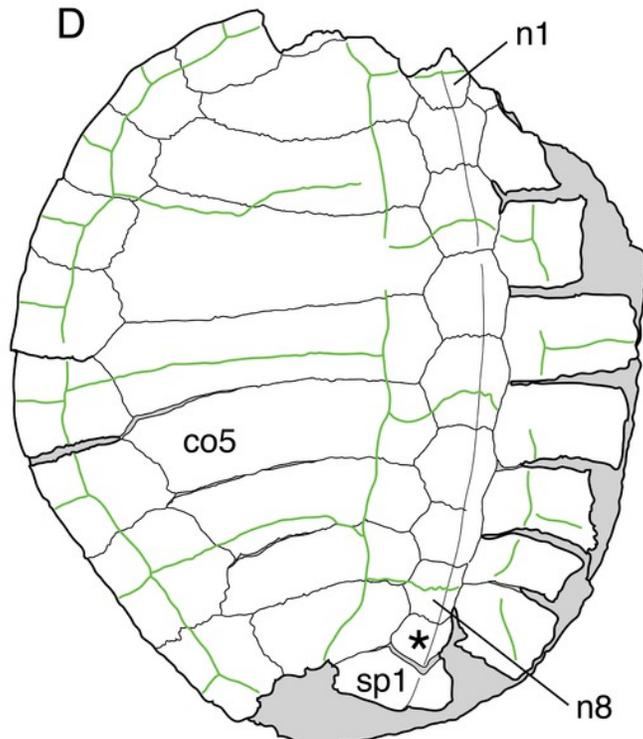
Figure 6

Thalassemys hugii.

Lectotype of *Th. hugii*, NMS 1: (A) photograph of the carapace; (B) interpretative drawing of the carapace; (C) photograph of the plastron; (D) interpretative drawing of the plastron. Holotype of *Eurysternum ignoratum*, NMS 5: (E) photograph of costals 4–6; (F) interpretative drawing of costals 4–6; (G) photograph of the hyoplastra; (H) interpretative drawing of the hyoplastra. Holotype of *Th. gresslyi*, NMS 12: (I) photograph of the carapace; (J) interpretative drawing of the carapace. Referred specimen, NMS 124: (K) photograph of the carapace; (L) interpretative drawing of the carapace. Referred specimen, NMS 412: (M) photograph of the carapace; (N) interpretative drawing of the carapace. Bones are white; green solid lines indicate scales sulci; matrix is gray. Abbreviations: co, costal; hyo, hyoplastron; hypo, hypoplastron; n, neural; sp, suprapygal; *v*, vertebral scale; xi, xiphiplastron; *, intermediate element (see text).
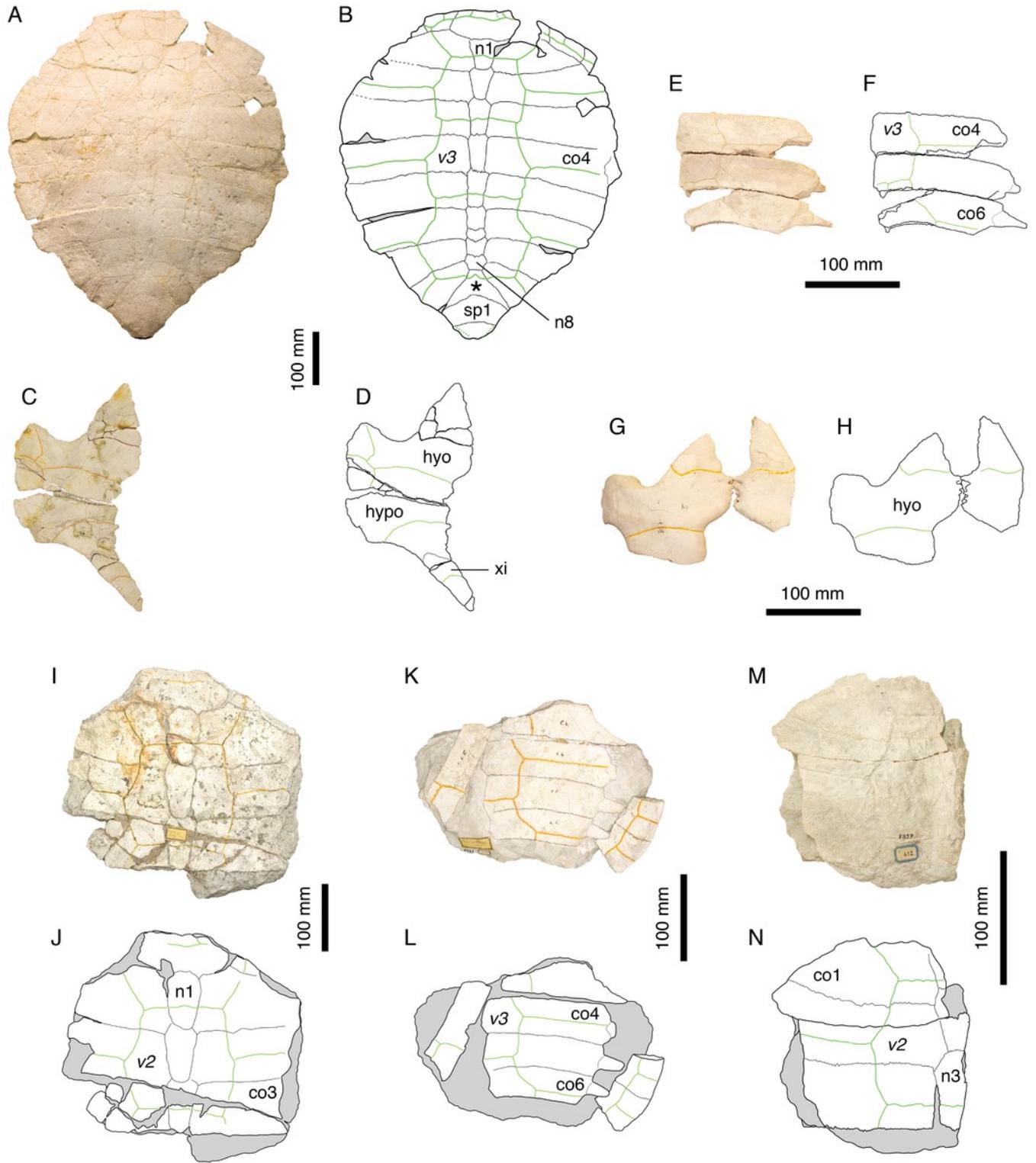
Figure 7

'*Thalassemys*' *moseri*.

Holotype of *'Th.' moseri*, NMS 618: (A) photograph of the carapace; (B) interpretative drawing of the carapace; (C) photograph of the plastron; (D) interpretative drawing of the plastron. Referred specimen, NMS 62: (E) photograph of the carapace; (F) interpretative drawing of the carapace. Bones are white; stripped lines indicate internal bone layers; green solid lines indicate scales sulci; matrix is gray. Abbreviations: *ce*, cervical scale; co, costal; hyo, hyoplastron; n, neural; nu, nuchal.
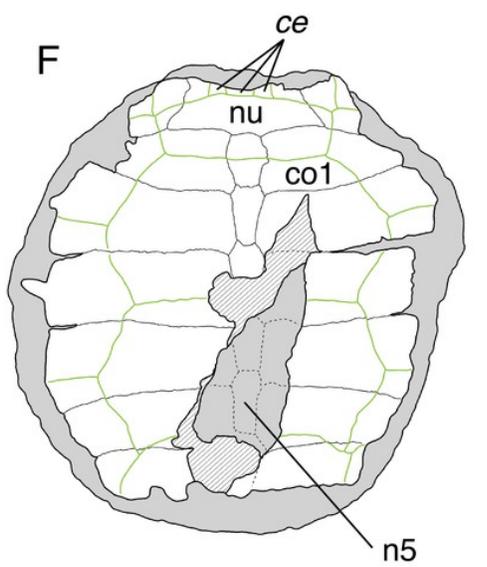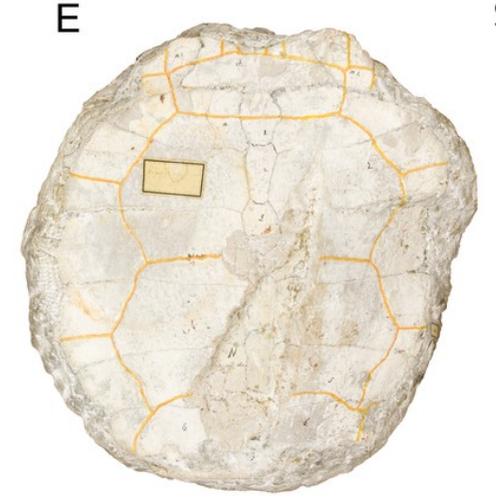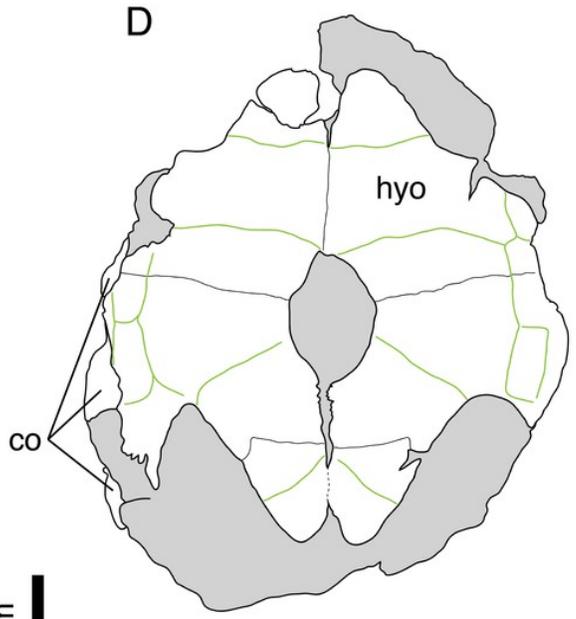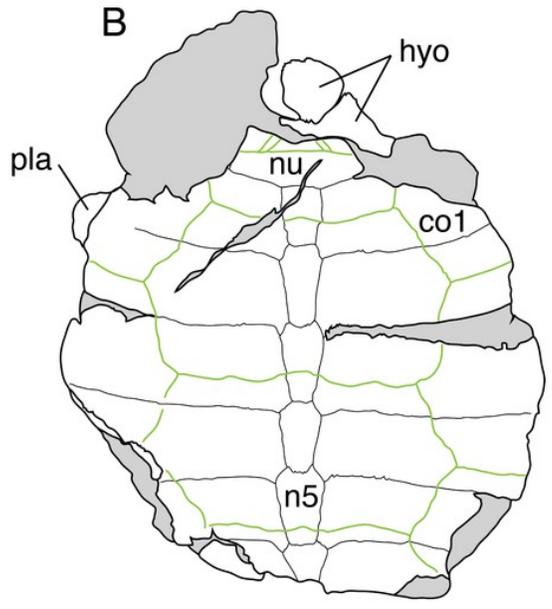
Figure 8

Intraspecific variability in *Plesiochelys etalloni*.

NMS 78: (A) photograph of the carapace; (B) interpretative drawing of the carapace; (C) photograph of the plastron; (D) interpretative drawing of the plastron. NMS 79: (E) photograph of the carapace; (F) interpretative drawing of the carapace; (G) photograph of the plastron; (H) interpretative drawing of the plastron. NMS 669: (I) photograph of the carapace; (J) interpretative drawing of the carapace; (K) photograph of the plastron; (L) interpretative drawing of the plastron. NMS 675: (M) photograph of the carapace; (N) interpretative drawing of the carapace; (O) photograph of the plastron; (P) interpretative drawing of the plastron. NMS 116: (Q) photograph of the carapace; (R) interpretative drawing of the carapace; (S) photograph of the plastron; (T) interpretative drawing of the plastron. NMS 94: (U) photograph of the plastron; (V) interpretative drawing of the plastron. NMS 629: (W) photograph of the plastron; (X) interpretative drawing of the plastron. Bones are white; stripped lines indicate internal bone layers; green solid lines indicate scales sulci; support material is brown; matrix is gray. Abbreviations: eb, epiplastral bulb; n, neural; sp, suprapygal; *, intermediate element (see text).
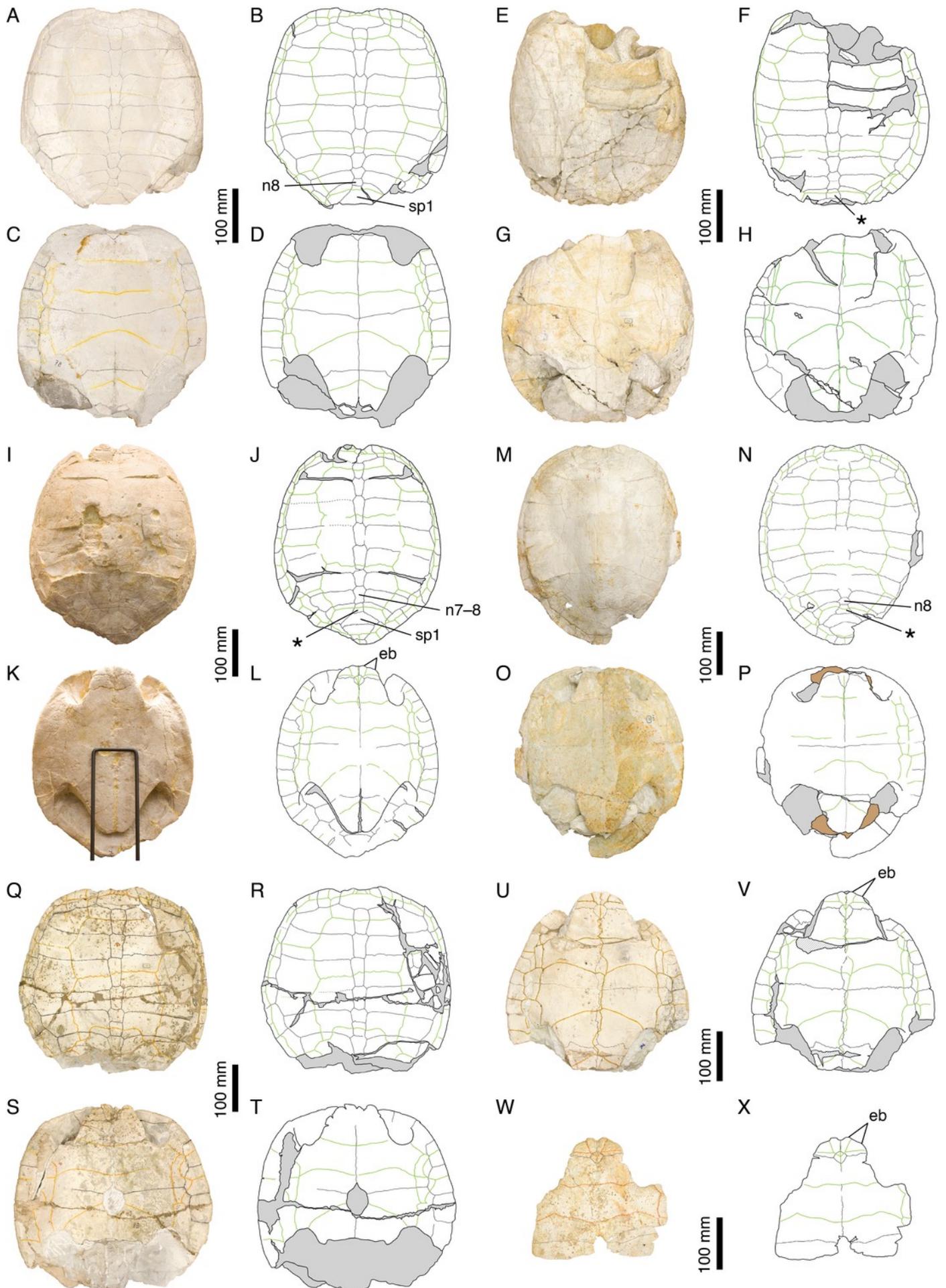
Figure 9

The plastral morphology of *Thalassemys hugii*.

NMS 593: (A) photograph of the right hyo- and hypoplastron in ventral view; (B) interpretative drawing of the right hyo- and hypoplastron in ventral view; (C) photograph of the right hyo- and hypoplastron in visceral view; (D) interpretative drawing of the right hyo- and hypoplastron in visceral view. NMS 22325: (E) photograph of the right hyoplastron in ventral view; (F) interpretative drawing of the right hyoplastron in ventral view; (G) photograph of the right hyoplastron in visceral view; (H) interpretative drawing of the right hyoplastron in visceral view. NMS 37251: (I) photograph of the shell in ventral view; (J) interpretative drawing of the shell in ventral view. Bones are white; stripped lines indicate internal bone layers; green solid lines indicate scales sulci; matrix is gray. Abbreviations: ax, axillary buttress; cax, contact for axillary buttress; co, costal; hyo, hyoplastron; hypo, hypoplastron; in, inguinal buttress; lpf, lateral plastral fontanelle; xi, xiphiplastron.
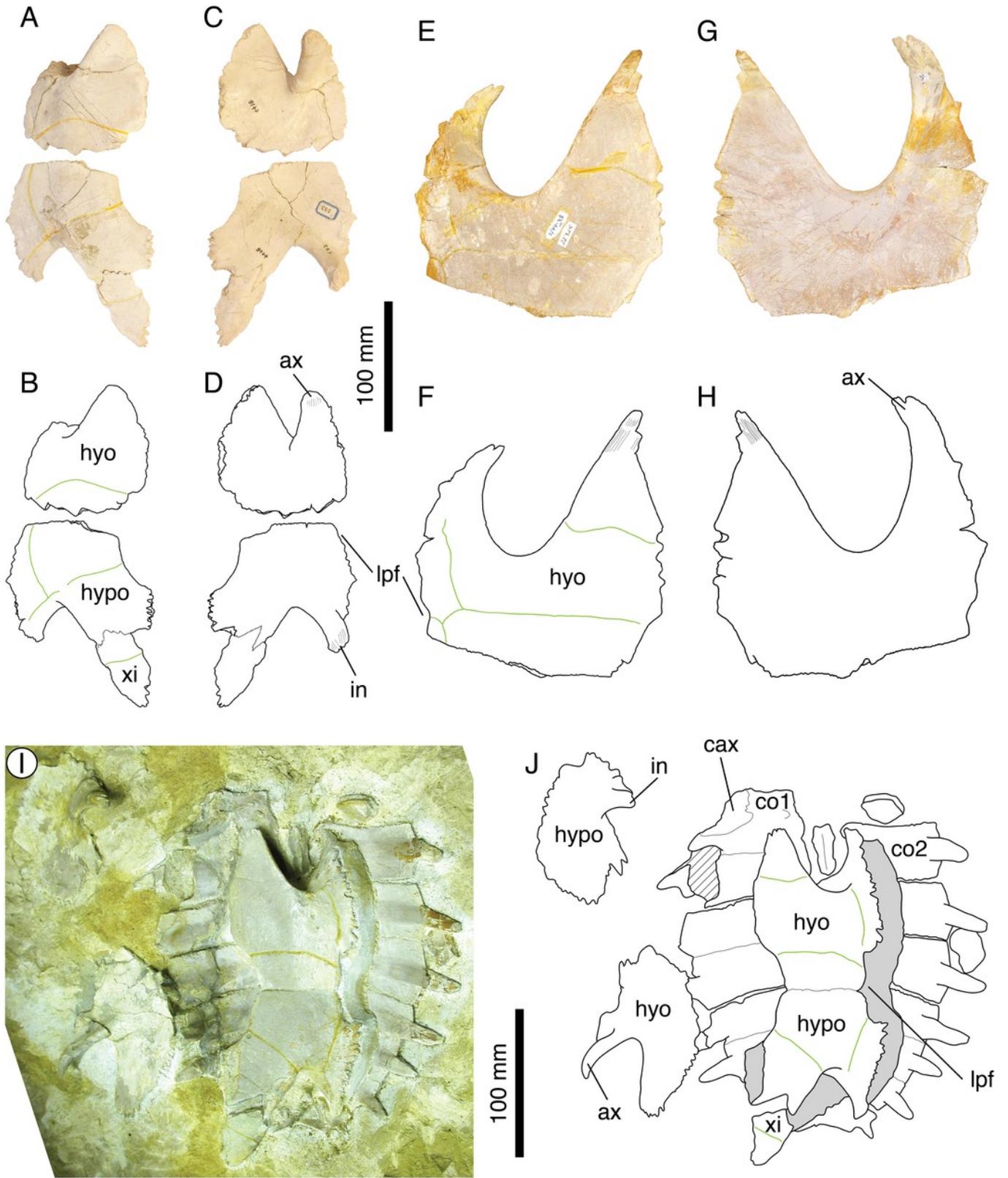
Table 1 (on next page)

Summary of the various taxonomies proposed for the turtles species typified based on material from the Late Jurassic of the Jura Mountains since Rütimeyer (1873).

Merged cells represent synonymies; n-dash indicates that the taxon was not considered in the concerned study. Abbreviations: *C.*, *Craspedochelys*; *E.*, *Eurysternum*; *P.*, *Plesiochelys*; *Th.*, *Thalassemys*; *Tr.*, *Tropidemys*.

Rütimeyer, 1873	Bräm, 1965	Gaffney, 1975	Lapparent de Broin, Lange-Badré & Dutrieux, 1996	This study
P. Etalloni	*P. etalloni*	*P. etalloni*	*P. etalloni*	*P. etalloni*
P. solodurensis	*P. solodurensis*		*P. solodurensis*	
P. Langii	(partial)		—	
P. Sanctae Verenae	*P. sanctaeverenae*		—	
P. Jaccardi	*P. jaccardi*		*C. jaccardi*	*C. jaccardi*
C. Picteti	*C. picteti*		*C. picteti*	*C. picteti*
C. crassa		—	—	
C. plana		—	—	
Tr. Langii	*Tr. langii*	—	*Tr. langii*	*Tr. langii*
Tr. expansa		—	—	
Tr. gibba		—	—	
Th. Hugii	*Th. hugii*	—	*Th. hugii*	*Th. hugii*
Th. Gresslyi		—	—	
—	*E. ignoratum*	—	—	
—	*Th. moseri*	—	Ref. to *P. solodurensis*	*'Th.' moseri*

Table 2 (on next page)

Comparison of the ratio between the length of the plastron and the length of the carapace in selected specimens referred to *P. etalloni*, *C. picteti*, and *C. jaccardi*.

[a], carapace missing about 20mm; [b], estimated plastron length.

	Plastron length (mm)	Carapace length (mm)	Ratio
Plesiochelys etalloni			
NMS 59	400	474	**0.84**
NMS 78	–	361[a]	–
NMS 79	–	–	–
NMS 116	–	–	–
NMS 669	363	410	**0.89**
NMS 675	369	445	**0.83**
MAJ 2005-11-1	431	471	**0.92**
Craspedochelys jaccardi			
NMS 101	300[b]	413	**0.73**
NMS 102a	–	363	–
NMS 612	–	–	–
NMS 673	292	411	**0.71**
MHNN FOS 977	283	365	**0.78**
Craspedochelys picteti			
NMS 608	–	540	–

Table 3(on next page)

Comparison of the length/width ratio of the fourth costal in selected specimens referred to *P. etalloni*, *C. picteti*, and *C. jaccardi*.

	Costal 4 length (mm)	Costal 4 width (mm)	Ratio
Plesiochelys etalloni			
NMS 59	176	56	**3.14**
NMS 78	152	46	**3.30**
NMS 79	163	45	**3.62**
NMS 116	–	–	–
NMS 669	160	47	**3.40**
NMS 675	178	49	**3.63**
MAJ 2005-11-1	–	–	–
Craspedochelys jaccardi			
NMS 101	188	38	**4.95**
NMS 102a	164	32	**5.13**
NMS 612	155	32	**4.84**
NMS 673	181	38	**4.76**
MHNN FOS 977	–	–	–
Craspedochelys picteti			
NMS 608	217	50	**4.34**

Table 4 (on next page)

Comparison of the length/with ratio of the hyoplastron in selected specimens referred to *P. etalloni*, *C. picteti*, and *C. jaccardi*.

[a], length incomplete; [b], incorrect measurement in Bräm (1965); [c], from 3D surface mesh (see Anquetin, Deschamps & Claude, 2014); [d], width incomplete.

	Hyoplastron length (mm)	Hyoplastron width (mm)	Ratio
Plesiochelys etalloni			
NMS 59	168	145	**1.16**
NMS 78	154	133	**1.16**
NMS 79	152[a]	138	**1.10**
NMS 116	166	147	**1.13**
NMS 669	156[b]	130[b]	**1.20**
NMS 675	168[b]	149	**1.13**
MAJ 2005-11-1	183[c]	156[c]	**1.17**
Craspedochelys jaccardi			
NMS 101	117	158[d]	**0.74**
NMS 102a	–	–	–
NMS 612	–	–	–
NMS 673	122	156	**0.78**
MHNN FOS 977	118	123	**0.96**
Craspedochelys picteti			
NMS 608	–	–	–

Table 5(on next page)

Comparison of the length/with ratio of the xiphiplastron in selected specimens referred to *P. etalloni*, *C. picteti*, and *C. jaccardi*.

[a], length incomplete; [b], width incomplete; [c], from 3D surface mesh (see Anquetin, Deschamps & Claude, 2014); [d], length missing about 10mm.

	Xiphiplastron length (mm)	Xiphiplastron width (mm)	Ratio
Plesiochelys etalloni			
NMS 59	89	66	**1.35**
NMS 78	84[a]	66	**1.27**
NMS 79	81	59	**1.37**
NMS 116	–	–	–
NMS 669	79	68	**1.16**
NMS 675	84	66[b]	**1.27**
MAJ 2005-11-1	90[c]	68[c]	**1.32**
Craspedochelys jaccardi			
NMS 101	62[d]	70	**0.89**
NMS 102a	–	–	–
NMS 612	–	–	–
NMS 673	66	64	**1.03**
MHNN FOS 977	55	55	**1.00**
Craspedochelys picteti			
NMS 608	–	–	–

Table 6(on next page)

Comparison of the ratio between the length of the carapace and the length of the fourth costal in selected specimens referred to *P. etalloni*, *C. picteti*, and *C. jaccardi*.

[a], carapace missing about 20mm.

	Carapace length (mm)	Costal 4 length (mm)	Ratio
Plesiochelys etalloni			
NMS 59	474	176	**2.69**
NMS 78	361[a]	152	**2.38**
NMS 79	–	163	–
NMS 116	–	–	–
NMS 669	410	160	**2.56**
NMS 675	445	178	**2.50**
MAJ 2005-11-1	471	–	–
Craspedochelys jaccardi			
NMS 101	413	188	**2.20**
NMS 102a	363	164	**2.21**
NMS 612	–	155	–
NMS 673	411	181	**2.27**
MHNN FOS 977	365	–	–
Craspedochelys picteti			
NMS 608	540	217	**2.49**