



HAL
open science

Mature modifications and sexual dimorphism in Turrilitidae (heteromorph ammonites): contribution of remarkable *Mariella bergeri* specimens (upper Albian, southeastern France)

Romain Jattiot, Jens Lehmann, Isabelle Kruta, Isabelle Rouget

► **To cite this version:**

Romain Jattiot, Jens Lehmann, Isabelle Kruta, Isabelle Rouget. Mature modifications and sexual dimorphism in Turrilitidae (heteromorph ammonites): contribution of remarkable *Mariella bergeri* specimens (upper Albian, southeastern France). *Cretaceous Research*, 2023, 151, pp.105651. 10.1016/j.cretres.2023.105651 . hal-04206739

HAL Id: hal-04206739

<https://hal.science/hal-04206739v1>

Submitted on 15 Sep 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Mature modifications and sexual dimorphism in Turrilitidae (heteromorph**
2 **ammonites): contribution of remarkable *Mariella bergeri* specimens (upper**
3 **Albian, southeastern France).**

4

5 Romain Jattiot ^{a*}, Jens Lehmann ^b, Isabelle Kruta ^a and Isabelle Rouget ^a

6

7 ^a UMR 7207 Centre de Recherche en Paléontologie – Paris MNHN, CNRS, Sorbonne Université, 8
8 rue Buffon, CP 38, F-75005, Paris, France9 ^b Fachbereich 5 Geowissenschaften, Universität Bremen, Klagenfurter Strasse 4, 28357, Bremen,
10 Germany

11

12 * Corresponding author.

13 E-mail addresses: romain.jattiot@sorbonne-universite.fr (R. Jattiot), jens.lehmann@uni-bremen.de (J.
14 Lehmann), isabelle.kruta@sorbonne-universite.fr (I. Kruta), isabelle.rouget@mnhn.fr (I. Rouget)

15

16 **Abstract**

17

18 In ammonites, the identification of mature shells is the logical but not naturally simple prerequisite to
19 determine sexual dimorphism. Here, we provide elements suggesting sexual dimorphism in the upper
20 Albian *Mariella bergeri* species (Turrilitidae), based on three specimens with preserved adult
21 peristome from the Clansayes locality (southeastern France). We compare the morphology of the
22 terminal peristomes observed in *M. bergeri* with that of the few other known examples in Turrilitidae.
23 In turn, we hypothesize that upper Albian *Mariella* (e.g., *M. bergeri*), lower Cenomanian *Mariella*
24 (e.g., *M. oehlerti*) and lower Cenomanian *Hypoturrilites* (e.g., *H. gravesianus*) share the same
25 peristome morphology. The observed similarities seem to support the close relationships between
26 these three genera inferred from the most recent phylogeny of the family Turrilitidae. Conversely, the

27 peristome morphology of upper Albian *Turrilitoides* appears markedly different. Finally, it is unclear
28 how the shape of the adult peristome of upper Albian *Ostlingoceras* (e.g., *O. puzosianum*) and middle
29 Cenomanian *Turrilites* (e.g., *T. costatus*) can be related to the evolutionary lineages among
30 Turrilitidae. To further increase our knowledge on the differences in peristome morphologies among
31 Turrilitidae, more complete and remarkably preserved specimens of various genera are needed.

32

33 *Keywords:* Ammonite, Turrilitidae, sexual dimorphism, adult peristome, upper Albian.

34

35 **1. Introduction**

36

37 In most ammonoid specimens, the adult peristome is not preserved, mainly due to damage by
38 taphonomical processes or due to death prior to maturity. Consequently, complete ontogenesis is only
39 known from a few ammonoid taxa. In the past decades, numerous studies have documented mature
40 modifications (e.g., Makowski, 1962, 1971, 1991; Callomon, 1963; Brochwicz-Lewiński and Różak,
41 1976; Bucher and Guex, 1990; Bucher et al., 1996; Davis et al., 1996; Schweigert and Dietze, 1998;
42 Parent, 1997; Klug, 2004; Parent et al., 2008; Zatoń, 2008; Keupp and Riedel, 2010; Landman et al.,
43 2012; Tajika et al., 2015; Klug et al., 2015). Regarding the Cretaceous, the most renowned mature
44 modifications are certainly those of the Cretaceous heteromorphic ammonites of the superfamilies
45 Ancyloceratoidea and Turrilitoidea (see examples in Klug et al., 2015).

46 The unequivocal identification of mature shells is the logical prerequisite to determine sexual
47 dimorphism. Following Klug et al. (2015), the subsequent criteria (see also Makowski, 1962;
48 Callomon, 1963, 1981; Westermann, 1964; Davis, 1972; Davis et al., 1996) might support
49 dimorphism or even polymorphism: 1) the antidimorphs show differences in mature shell - it should
50 be noted that this may include a significant difference in adult size, as seen in many cases in Jurassic
51 ammonites (e.g., Makowski, 1962; Dommergues, 1993; Parent, 1997), 2) their early ontogenetic
52 stages, their stratigraphic ranges, and their palaeobiogeographic patterns are mostly identical, 3) there
53 is one common progenitor, 4) microconchs should not outnumber macroconchs within the
54 stratigraphic range, and vice versa.

55 Within the Turrilitoidea, the main difference between the antidimorphs is often size (e.g.,
56 *Didymoceras*, *Bostrychoceras*, *Nipponites*, *Oxybeloceras*, *Sciponoceras*; Kennedy, 1988; Cobban and
57 Kennedy, 1994), as underlined by Klug et al. (2015). Focusing on the family Turrilitidae, whose
58 representatives occur in the mid-Cretaceous (Albian–Cenomanian), inferred dimorphism rely as well,
59 in most cases, on size difference (e.g., Wright and Kennedy, 1996, p. 351, for *Turrilites*
60 *scheuchzerianus* Bosc, 1801). However, in some cases of assumed dimorphism in size, there actually
61 seem to be a continuous variation in size at which individuals develop features interpreted as
62 characteristic of mature shells (Lehmann, 1998, p. 37). Therefore, a dimorphism in size often cannot
63 be confirmed among representatives of the family Turrilitidae.

64 Here, based on three specimens from the Clansayes locality (Fig. 1; Jattiot et al., 2022), we describe
65 the adult peristome morphology of the upper Albian species *Mariella bergeri* (Brongniart, 1822) for
66 the first time. We consequently explore potential dimorphism in this species. Then, we compare the
67 peristome morphology of *M. bergeri* to that of peristomes seen in a few other Turrilitidae
68 representatives. Subsequently, we discuss the different peristome morphologies observed within the
69 family Turrilitidae in the frame of phylogeny.

70

71 **2. Materials and methods**

72

73 The material at hand consists of three incomplete mature *Mariella* specimens with adult peristome
74 (UBGD 293215, UBGD 293255 and UBGD 293295; Fig. 2V–Y, Z–AC and AD–AG, respectively)
75 from the Clansayes locality (Fig. 1, Jattiot et al., 2022), which were retrieved from a single level
76 representing the Rostratum Zone (upper Albian). Both UBGD 293215 and UBGD 293255 were
77 previously described and assigned to *M. bergeri* by Jattiot et al. (2022). The features observed in
78 UBGD 293295 (i.e., four rows of conical tubercles 22 tubercles per whorl in each row at a whorl
79 height of approximately 40 mm) also conform very well with the revised definition of the species *M.*
80 *bergeri* (Jattiot et al., 2022). Noteworthy, the body chamber section with preserved peristome (Fig.
81 2AF, AG) undoubtedly belongs to specimen UBGD 293295. It was found *in situ* slightly dislocated
82 from the main part (Fig. 2AD, AE). This is most likely due to post-mortem taphonomical processes

83 that induced slight shell disruptions and created a few millimeters gap (subsequently filled by
84 sediment) between the section with peristome and the main part. In all three specimens,
85 ornamentation prior to maturity consists of four rows of conical tubercles. The tubercles of the upper
86 row are placed some way above mid-flank and each is connected to the inter-whorl suture by a more
87 or less pronounced rib, while the lower two rows are slightly closer together than the rest. The
88 tubercles of the fourth, lowest row are partially concealed in the inter-whorl suture. Exceptionally
89 well-preserved (i.e., when the outer shell layer is preserved) tubercles give rise to short spines (Figs
90 2V–AG, 3A, 4; Appendices A, B). Where exposed, the base of the whorl shows that the tubercles of
91 the lowest row are linked to radial ribs progressively weakening towards the umbilicus. Specimen
92 UBGD 293215, dextral in coiling, bears on its last whorl 28 tubercles in each row; at maturity, its
93 whorl height is 10.3 mm. Specimen UBGD 293255, sinistral in coiling, bears on its last whorl 24
94 tubercles in each row; at maturity, its whorl height is 15.3 mm. Specimen UBGD 293295, sinistral in
95 coiling, bears on its last whorl approximately 22 tubercles in each row; at maturity, its whorl height is
96 approximately 40 mm.

97 For comparisons, additional material was included in the study; it comprises one *M. nobilis* specimen
98 from the Salazac locality (southeastern France, Fallax Zone; see Jattiot et al., 2021) and five
99 *Turrilitoides hugardianus* specimens from the same locality and zone (of which three were already
100 briefly described and figured by Jattiot et al., 2021). All studied specimens are deposited in the
101 collections of the Université de Bourgogne, Géologie Dijon (UBGD), France.

102 Specimens UBGD 293215 and UBGD 293255 were scanned using high-resolution computed
103 tomography at the AST-RX platform of the Muséum national d'Histoire naturelle, Paris (UMS 2700;
104 GE phoenix|X-ray v|tome|x 240). For UBGD 293215, the scan has been performed with 0.32 mm
105 Cu filter, an isotropic voxel size of 16 μm , using a voltage of 104 kV and a current of 160 μA with
106 2700 projections over 360°. For UBGD 293255, 0.41 Cu filter has been used. The voxel size is 23
107 μm , the voltage is 102 kV and the current 230 μA with 2700 projections over 360°. Images were
108 reconstructed using the Phoenix datos|x 2.0 rec software and the segmentation of the shell with its
109 peristome was done using Mimics software (Materialise NV, Belgium, Version 21.0).

110

111 3. Results

112

113 Here, we first thoroughly describe the adult peristome morphology of the upper Albian species
114 *Mariella bergeri*, based on the three specimens from Clansayes. Then, mainly on the basis of original
115 descriptions and illustrations of specimens in which the terminal peristome is partly or fully
116 preserved, we briefly review the peristome morphology of other taxa belonging to the family
117 Turrilitidae. We compare these peristome morphologies with that of *M. bergeri* specimens from
118 Clansayes (Figs 2V–AG, 3A, 4; Appendices A, B).

119

120 3.1. *Mariella bergeri* (upper Albian)

121

122 The exceptional preservation of the complete adult peristome in specimens UBGD 293215 and
123 UBGD 293255 (Figs. 2V–AC, 3A, but see also Appendices A, B for high-resolution 3D models in
124 which the details of the peristome of the two specimens are well-visible) allows for a thorough
125 description of the peristome morphology in *Mariella bergeri*. Although the peristome of specimen
126 UBGD 293295 is not fully preserved, its features suggest that the peristome morphology of this very
127 large specimen was originally very similar - if not identical - to the two smaller specimens.

128 In all three specimens, two or three strong flared ribs link the four tubercle rows and precede the adult
129 peristome. The latter is characterized by a distinct ventral extension, called ‘flared lip’ in the
130 following, which has a narrow pocket-like shape. The ventral extension of the final sector of the body
131 chamber deviates the coiling from the trochospiral direction up to this point. Interestingly, tubercles
132 develop on both sides of the flared lip’s terminal end (see Fig. 3A, Appendices A, B).

133 Regarding the whorl height at maturity, differences in size at maturity between specimen UBGD
134 293215 and specimen UBGD 293255 are most likely related to intraspecific variability in adult size.
135 By contrast, based on the measurements of whorl height at maturity (see ‘Material and methods’
136 section), the adult size of UBGD 293295 is nearly three and four times greater than that of specimen
137 UBGD 293215 and specimen UBGD 293255, respectively. In our opinion, this significant adult size
138 gap, as well the absence of known *M. bergeri* adults intermediate in size, suggests sexual dimorphism

139 in *M. bergeri*. Several additional criteria support the hypothesis of dimorphism in this case (e.g., the
140 specimens have identical early developmental stages and they occur in strata of the same stratigraphic
141 range; see ‘Introduction’ section). In turn, this would imply that the peristome morphology is overall
142 the same for *M. bergeri* microconchs and macroconchs. Another alternative interpretation would be
143 that the two smaller specimens (UBGD 293215 and specimen UBGD 293255) represent mesoconchs
144 (i.e., “microsomic macroconchs”, Chandler et al., 2019, p. 323; see also Parent et al., 2008, 2019,
145 Schweigert and Kuschel, 2017). More adult material of *Mariella bergeri* are greatly needed for further
146 discussion.

147

148 3.2. *Turrilitoides hugardianus* (upper Albian)

149

150 Klinger and Kennedy (1978, pl. 9, fig. M) documented a specimen from South Africa with its adult
151 peristome, which they assigned to *Turrilitoides densicostatus* (Passendorfer, 1930), a species recently
152 synonymized with *T. hugardianus* (d’Orbigny, 1842) by Jattiot et al. (2021). This specimen is
153 refigured here (Fig. 2A), as well as adult *T. hugardianus* specimens from the Salazac locality
154 (southeastern France, Fallax Zone) that were recently described by Jattiot et al. (2021, figs. 22W–AD;
155 refigured here as Fig. 2J–Q). Finally, two additional adult *T. hugardianus* specimens from the same
156 locality were recently sampled and are figured here for the first time (Fig. 2B–I).

157 On the ultimate part before the peristome, all of these specimens show a more or less progressive
158 smoothing of the body chamber. Then, maturity is characterized by a somewhat loosely coiled
159 peristome area, which successively exhibits a constriction, one or two flared ribs and finally a very
160 short smooth segment of shell (Figs 2B–I, 3B). These specimens seem to represent a fundamentally
161 complete peristome, with absence of a flared lip.

162

163 3.3. *Mariella nobilis* (upper Albian)

164

165 A possibly adult specimen of *M. nobilis* (Jukes-Browne, 1877) was recently sampled from the Salazac
166 locality (southeastern France, Fallax Zone; see Jattiot et al., 2021) and is figured here for the first time

167 (Fig. 2R–U). In this specimen, a smoothing of the body chamber is noted. The ultimate segment of
168 body chamber shows a flared rib followed by a very short smooth segment of shell. These features are
169 somewhat reminiscent of what is seen in adult *T. hugardianus* (see Fig. 2A–Q). However, in the
170 absence of further material, and because the position of the last suture line cannot be determined, it
171 remains unclear if this specimen represents maturity or is pathological. Thus, a potential
172 correspondence in peristome morphology between the contemporary species *T. hugardianus* and *M.*
173 *nobilis* remains open to question.

174

175 3.4. *Mariella oehlerti* (lower Cenomanian)

176

177 Several mature specimens of *M. oehlerti* (Pervinquière, 1910) from Japan have been documented by
178 Matsumoto et al. (1999), a species considered by Cooper (1999) as type species of a separate genus,
179 named *Cenomariella*. Among them, specimen GS. G168 shows a complete and very well-preserved
180 adult peristome (Matsumoto et al. 1999, fig. 4-1; refigured here as Fig. 5A–C). Specimen TKD
181 30086B (Matsumoto et al. 1999, fig. 3-3; refigured here as Fig. 6A–C) also preserves its terminal
182 peristome, but the overall shape of this specimen indicates heavy distortion, which may have altered
183 the morphology of the peristome. Finally, a mature specimen with partially preserved peristome is
184 figured by Matsumoto et al. (1999, fig. 3-1; refigured here as Fig. 6D–F). According to Matsumoto et
185 al. (1999, p. 109), the peristome of *M. oehlerti* is ‘provided with a rostrum that extends at first
186 downward and then recurves obliquely upward’. Although we do not concur with using ‘rostrum’ to
187 describe the feature seen, the peristome of these *M. oehlerti* specimens from Japan strongly recall that
188 of the *M. bergeri* specimens from Clansayes. In particular, the peristome of specimen GS. G168
189 (Matsumoto et al. 1999, fig. 4-1; refigured here as Fig. 5A–C) is nearly identical to that of specimen
190 UBGD 293255 (Fig. 2Z–AC).

191 Additionally, one mature specimen assigned to ‘*M. (Mariella) oehlerti oehlerti*’ is documented from
192 South Africa by Klinger and Kennedy (1978, pl. 6, fig. K; refigured here as Fig. 6G). Although most
193 likely incomplete, the observed features of the peristome suggest that its initial morphology was very

194 similar – if not identical – to that of the *M. bergeri* specimens from Clansayes and *M. oehlerti*
195 specimens from Japan (see Figs 2V–AG, Fig. 5A–C and Fig. 6A–F).

196

197 3.5. *Mariella cenomanensis* and *Mariella circumtaeniata* (*lower Cenomanian*)

198

199 One mature specimen of *M. cenomanensis* (Schlüter, 1876) with adult peristome from South Africa
200 was documented by Wright and Kennedy (1996, pl. 102, fig. 14; refigured here as Fig. 6H).

201 Additionally, one mature *M. circumtaeniata* with terminal peristome was documented from England

202 by Klinger and Kennedy (1978, pl. 5C; refigured here as Fig. 6I). According to Wright and Kennedy

203 (1996, p. 344), the peristome of the latter specimen ‘is marked by a constriction and lip’.

204 For both specimens discussed here, although only one view is available in the literature, the observed

205 features of their peristome (perhaps slightly incomplete) suggest that their initial morphology was

206 very similar – if not identical – to that of *M. bergeri* specimens from Clansayes and *M. oehlerti*

207 specimens from Japan (see Figs 2V–AG, Fig. 5A–C and Fig. 6A–F).

208

209 3.6. *Hypoturrilites gravesianus* (*lower Cenomanian*)

210

211 According to Wright and Kennedy (1996, p. 363), ‘*Hypoturrilites* includes some of the largest

212 turrilitid taxa, exceeded only by *Mariella* [...]’ and ‘adults of any given species fall into two size

213 classes, as in other turrilitids’. They documented (pl. 109, fig. 4; here refigured as Fig. 7F) a mature

214 *H. gravesianus* specimen from England (Lower Chalk) and described its clearly complete adult

215 peristome as ‘marked by a constriction and flare around the outer, exposed whorl face, and marked

216 contraction at the lower side of the aperture’ (p. 363). Although we do not fully concur with the

217 terminology used in the original description of this peristome, it is fully identical to that of *M. bergeri*

218 specimens from Clansayes, as well as that of the *M. oehlerti* specimen GS. G168 from Japan

219 (Matsumoto et al. 1999), in particular (compare Fig. 7F with Fig. 2X, AB and Fig. 5C).

220

221 3.7. *Turrilites costatus* (*middle Cenomanian*)

222

223 Several mature specimens of *T. costatus* Lamarck, 1801 from England (Lower Chalk) were
224 documented by Wright and Kennedy (1996, pl. 105, figs 1, 5, pl. 106, figs 2, 3, 6; refigured here as
225 Fig. 7A–E). The adult peristomes of these specimens were summarily described as ‘markedly
226 contracted’ (Wright and Kennedy 1996, p. 357). This would suggest the absence of a distinctive flared
227 lip compared to representatives of *Mariella* and *Hypoturrilites*. However, although only one view is
228 available in the literature, their supposedly nearly complete terminal peristome (Fig. 7A–E) is
229 somewhat reminiscent to that of *M. bergeri* specimens from Clansayes, *M. oehlerti* specimens from
230 Japan, as well as that of the *Hypoturrilites gravesianus* specimen from England (see Figs 2V–AG,
231 Fig. 5A–C, Fig. 6A–F and Fig. 7F).

232

233 3.8. *Turrilites scheuchzerianus* (lower Cenomanian)

234

235 Three mature specimens of *T. scheuchzerianus* Bosc, 1801 were documented from England by Wright
236 and Kennedy (1996, pl. 107, figs. 5–7; refigured here as Fig. 7G–I). Unfortunately, none of these
237 seem to preserve a complete adult peristome, precluding to get a full portrayal of the peristome.
238 However, it may be reasonably hypothesized that *T. scheuchzerianus* has a similar peristome to that of
239 other representatives of the genus *Turrilites*, such as *T. costatus* (see above).

240

241 3.9. *Ostlingoceras puzosianum* (upper Albian)

242

243 Two mature specimens of *O. puzosianum* (d’Orbigny, 1842) with well-preserved adult peristome
244 were documented from France (see Wright and Kennedy 1996, text-fig. 140H; Kennedy and Latil
245 2007, pl. 11, figs. 11, 12). Both specimens are refigured herein (Fig. 7J–L). According to Kennedy
246 and Latil (2007, p. 474), ‘single flared rib precedes the strongly constricted adult aperture’ in
247 specimen UJF-ID.10701 (Fig. 7K, L). In our opinion, these two specimens give us a nearly complete
248 (only one view is available in the literature) portrayal of the terminal peristome in this species,
249 indicating the absence of a flared lip.

250
251
252
253
254
255
256
257
258
259
260
261
262
263
264
265
266
267
268
269
270
271
272
273
274
275
276
277

4. Discussion

4.1. Relationships within Turrilitidae representatives with regard to peristome morphology

In our opinion, based on all mature Turrilitidae specimens with adult peristome reviewed above, it can be hypothesized that upper Albian *Mariella* (e.g., *M. bergeri*), lower Cenomanian *Mariella* (e.g., *M. oehlerti*) and lower Cenomanian *Hypoturrilites* (e.g., *H. gravesianus*) share the same peristome morphology, being mainly characterized by a distinctive flared lip significantly extending ventrally, with a narrow pocket-like shape. Conversely, the peristome morphology of upper Albian *Turrilitoides* appears markedly different, in being characterized mainly by a marked constriction followed by one or two flared ribs, as well as by the absence of a flared lip. Finally, the position of lower Cenomanian *Turrilites* (e.g., *T. costatus*) and *Ostlingoceras* (e.g., *O. puzosianum*) with regard to peristome morphology remains unclear. Regarding *Ostlingoceras*, it appears that the peristome morphology of the *O. puzosianum* specimens restudied herein is rather different compared to that of the *M. bergeri* specimens from Clansayes, *M. oehlerti* specimens from Japan, as well as that of the *Hypoturrilites gravesianus* specimen from England. Instead, it may be hypothesized that adult peristomes of *Turrilitoides* and *Ostlingoceras* are alike (in exhibiting the association of a constriction and flared ribs; compare Fig. 2A–Q with Fig. 7J–L). However, in the absence of additional complete and remarkably preserved adult *Ostlingoceras* specimens, the hypothesis of a similar peristome morphology shared between *Turrilitoides* and *Ostlingoceras* must remain uncorroborated for the time being. Regarding *Turrilites*, the peristome morphology of *Turrilites costatus* (see Fig. 7A–E) is somewhat reminiscent with that of *Mariella* and *Hypoturrilites*. However, because only one view is available in the literature for the *Turrilites costatus* adult specimens restudied herein, it is uncertain whether these specimens originally exhibited a flared lip as in *Mariella*. Consequently, the idea of a similar peristome morphology shared between *Turrilites* and *Mariella/Hypoturrilites* must remain uncorroborated for the time being.

278 4.2. Peristome morphologies in Turrilitidae in the frame of phylogeny and palaeobiology

279

280 Noteworthy, the similar peristome morphology observed in *Hypoturrilites* and *Mariella* seem to
281 support the phylogeny of Cooper (1999, Fig. 8), in which *Hypoturrilites* and *Mariella* belong to the
282 same clade. In turn, a comparable peristome morphology can be hypothesized for all representatives
283 of this clade (i.e., *Hypoturrilites*, *Eohypoturrilites*, *Klingerella*, *Mesoturrilites*, *Cenomariella* and
284 *Mariella*, Fig. 8). Unfortunately, completely preserved adult peristomes appear to be unknown for
285 some of these genera. Uncertainties around the peristome morphology of *Ostlingoceras* and *Turrilites*
286 preclude any further discussion with regard to Cooper's (1999) phylogenetic reconstruction.

287 Regarding palaeobiology, it has been often considered that the various shell morphologies of
288 ammonites would have constrained their life habits (see, e.g., Peterman and Ritterbush, 2022). Based
289 on its turriliticone shell, it is probable that *Mariella* was a poor swimmer (Reboulet et al. 2005;
290 Lukeneder, 2015). Indeed, its shell shape would have caused considerable hydrodynamic drag, and
291 the cumbersome orientation of the flared lip may have further hindered rapid movement and
292 migration over long distances. In turn, we here hypothesize that *Mariella* typically hovered above the
293 seafloor. Finally, the flared lip in *Mariella* may have acted as physical protection against attempts of
294 predators to reach the soft parts.

295

296 5. Conclusions

297

298 In our opinion, many criteria supporting the hypothesis of dimorphism are met in the upper Albian
299 species *Mariella bergeri*. Based on the three specimens from the Clansayes locality, and on a
300 literature review of available adult peristomes within the family Turrilitidae, it can be hypothesized
301 that that upper Albian *Mariella* (e.g., *M. bergeri*), lower Cenomanian *Mariella* (e.g., *M. oehlerti*) and
302 lower Cenomanian *Hypoturrilites* (e.g., *H. gravesianus*) share the same peristome morphology, being
303 mainly characterized by a distinctive flared lip significantly extending ventrally, with a narrow
304 pocket-like shape. This interpretation supports the proposed phylogeny for the family Turrilitidae by
305 Cooper (1999). To further increase our knowledge on the distribution of different peristome

306 morphologies among Turritidae, additional complete and remarkably preserved specimens from
307 various genera (e.g., *Eohypoturritites*, *Klingerella*, *Mesoturritites*, *Pseudhelicoceras*) are needed.

308

309 **Acknowledgments**

310 The authors are indebted to Horacio Parent who made valuable suggestions to improve the
311 manuscript. We thank Alexandre Lethiers for the hypothesized reconstruction of *Mariella bergeri*, as
312 well as Claude Monnet for fruitful discussions. Benjamin Latutrie is warmly thanked for providing
313 three specimens for study.

314

315 **Data availability**

316 CT Scan images and 3D segmented models (UBGD 293215 and UBGD 293255) are available on
317 <https://www.morphosource.org/>.

318

319 **References**

320

321 Bosc, L.A.G. 1801. In: Roissy, F. de (Ed.), Histoire naturelle, générale et particulière des
322 Mollusques, animaux sans vertèbres et à sang blanc. Ouvrage faisant suit aux Oeuvres de Leclerc de
323 Buffon, et partie du Cours complet d'Histoire naturelle, rédigé par C.S. Sonnini, membre de plusieurs
324 Sociétés savantes. Viii+448+3pp. Deterville, Paris.

325 Brochwicz-Lewiński, W. and Różak, Z. 1976. Some difficulties in recognition of sexual
326 dimorphism in Jurassic perisphinctids (Ammonoidea). Acta Palaeontologica Polonica, **21**, 115–124.

327 Brongniart, A. 1822. Sur quelques terrains de Craie hors du Bassin de Paris, pp. 80–101. In:
328 Cuvier, G. and Brongniart, A. (Eds.), Description géologique des environs de Paris. 3rd edn., 428 pp.
329 G. Dufour et E. d'Ocagne; Paris.

330 Bucher, H. and Guex, J. 1990. Rythmes de croissance chez les ammonites triasiques. Bulletin de
331 Géologie de Lausanne, **80** (2), 191–209.

332 Bucher, H., Landman, N.H., Klofak, S.M. and Guex, J. 1996. Mode and rate of shell growth. In:
333 Landman, N.H., Tanabe, K. and Davis, R.A. (eds). Ammonoid paleobiology. Plenum, New York.

- 334 Callomon, J.H. 1963. Sexual dimorphism in Jurassic ammonites. Leicester Literary and
335 Philosophical Society Transactions, **57**, 21–56.
- 336 Callomon, J.H. 1981. Dimorphism in ammonoids. In: House, M.R., Senior, J.R. (eds) The
337 Ammonoidea, vol 18. Systematics Association by Academic Press, London, 257–273.
- 338 Chandler, R.B. 2019. Two new stephanoceratid ammonites from the Aalenian-lower Bajocian
339 (Middle Jurassic, Dorset, UK) and their phylogenetic significance. Proceedings of the Geologists
340 Association, **130**, 307–325.
- 341 Cobban, W.A. and Kennedy, W.J. 1994. Upper Cretaceous ammonites from the Coon Creek
342 Tongue of the Ripley Formation at its type locality in McNairy County, Tennessee. US Geological
343 Survey Bulletin, **2073**, BI–B12.
- 344 Cooper, M.R., 1999. Towards a phylogenetic classification of the Cretaceous ammonites VII.
345 Turrititidae. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **213** (1), 1–18.
- 346 Davis, R.A. 1972. Mature modification and dimorphism in selected late Paleozoic ammonoids.
347 Bulletins of American Paleontology, **62** (272), 23–130.
- 348 Davis, R.A., Landman, N.H., Dommergues, J-L., Marchand, D. and Bucher, H. 1996. Mature
349 modifications and dimorphism in ammonoid cephalopods. In: Landman, N.H., Tanabe, K. and Davis,
350 R.A. (eds). Ammonoid paleobiology. Plenum, New York.
- 351 Dommergues, J-L. 1993. The Jurassic ammonite *Coeloceras*: an atypical example of dimorphic
352 progenesis elucidated by cladistics. Lethaia, **27**, 143–152.
- 353 Jattiot, R., Lehmann, J., Latutrie, B., Vuarin, P., Tajika, A. and Vennin, E. 2021. Reappraisal of
354 the latest Albian (*Mortoniceras fallax* Zone) cephalopod fauna from the classical Salzac locality
355 (Gard, southeastern France). Geobios, **64**, 1–46.
- 356 Jattiot, R., Lehmann, J., Latutrie, B., Tajika, A., Vennin, E., Vuarin, P., Brayard, A., Fara, E. and
357 Trincal, V. 2022. Upper upper Albian (*Mortoniceras rostratum* Zone) cephalopods from Clansayes
358 (Drôme, south-eastern France). Acta Geologica Polonica, **72** (2), 187–233.
- 359 Jukes-Browne, A.J. 1877. Supplementary notes on the fauna of the Cambridge Greensand.
360 Quarterly Journal of the Geological Society, London 33, 485–504.

- 361 Kennedy, W.J. 1988. Late Cenomanian and Turonian ammonite faunas from north-east and central
362 Texas. *Special Papers in Palaeontology*, **39**, 1–131.
- 363 Kennedy, W.J. and Latil, J.L. 2007. The Upper Albian ammonite succession in the Montloux
364 section, Hautes-Alpes, France. *Acta Geologica Polonica*, **57** (4), 453–478.
- 365 Keupp, H. and Riedel, F. 2010. Remarks on the possible function of the apophyses of the Middle
366 Jurassic microconch ammonite *Ebrayiceras sulcatum* (Zieten, 1830), with a discussion on the
367 palaeobiology of Aptychophora in general. *Neues Jahrbuch für Geologie und Paläontologie*,
368 *Abhandlungen*, **255** (3), 301–314.
- 369 Klinger, H.C. and Kennedy, W.J. 1978. Turrilitidae (Cretaceous Ammonoidea) from South Africa,
370 with a discussion of the evolution and limits of the family. *Journal of Molluscan Studies*, **4**, 1–48.
- 371 Klug, C. 2004. Mature modifications, the black band, the black aperture, the black stripe, and the
372 periostracum in cephalopods from the Upper Muschelkalk (Middle Triassic, Germany). *Mitteilungen*
373 *aus dem Geologisch-Paläontologischen Institut der Universität Hamburg*, **88**, 63–78.
- 374 Klug, C., M. Zatoń, H. Parent, B. Hostettler, and A. Tajika. 2015. Mature modifications and sexual
375 dimorphism. In: Klug, C., Korn, D., De Baets, K., Kruta, I. and Mapes, R.H. (eds). *Ammonoid*
376 *paleobiology: From anatomy to ecology*, 261–328. *Topics in geobiology*, **43**. Springer, Dordrecht,
377 Netherlands.
- 378 Lamarck, J.B.P. 1801. *Système des animaux sans vertèbres*. Deterville, Paris, 432 p.
- 379 Landman, N.H., Cobban, W.A. and Larson, N.L. 2012. Mode of life and habitat of scaphitid
380 ammonites. *Geobios*, **45**, 87–98.
- 381 Lehmann, J. 1998. Systematic palaeontology of the ammonites of the Cenomanian-Lower
382 Turonian (Upper Cretaceous) of northern Westphalia, north Germany. *Tiibinger Geowissenschaftliche*
383 *Arbeiten, Reihe A*, **37**, 1–58.
- 384 Lukeneder, A. 2015. Ammonoid habitats and life history. In: Klug, C., Korn, D., De Baets, K.,
385 Kruta, I. and Mapes, R.H. (eds.), *Ammonoid Paleobiology: From anatomy to ecology*, *Topics in*
386 *Geobiology*. Springer, Dordrecht, **43**, 689–791.
- 387 Makowski, H. 1962. Problem of sexual dimorphism in ammonites. *Palaeontologica Polonica*, **12**,
388 1–92.

- 389 Makowski, H. 1971. Some remarks on the ontogenetic development and sexual dimorphism in the
390 Ammonoidea. *Acta Geologica Polonica*, **21**, 321–340.
- 391 Makowski, H. 1991. Dimorphism and evolution of the goniatite *Tornoceras* in the Famennian of
392 the Holy Cross Mountains. *Acta Palaeontologica Polonica*, **36**, 241–254.
- 393 Matsumoto, T., Inoma, A. and Kawashita, Y. 1999. The turrilitid ammonoid *Mariella* from
394 Hokkaido-Part 1 (Studies of the Cretaceous ammonites from Hokkaido and Sakhalin-LXXXV).
395 *Paleontological research*, **3** (2), 106–120.
- 396 d’Orbigny, A. 1840–1842. *Paléontologie française. Terrains Crétacés. I: Céphalopodes*. Masson,
397 Paris, 662 p., 148 pls.
- 398 Parent, H. 1997. Ontogeny and sexual dimorphism of *Eurycephalites gottschei* (Tornquist)
399 (Ammonoidea) of the Andean Lower Callovian (Argentina-Chile). *Geobios*, **30**, 407–419.
- 400 Parent, H., Scherzinger, H. and Schweigert, G. 2008. Sexual phenomena in Late Jurassic
401 Aspidoceratidae (Ammonoidea). Dimorphic correspondence between *Physdoceras hermanni*
402 (Berckhemer) and *Sutneria subeumela* Schneid, and first record of possible hermaphroditism.
403 *Palaeodiversity*, **1**, 181–187.
- 404 Parent, H., Garrido, A.C., Scherzinger, A., Schweigert, G. and Brambilla L. 2019. Ammonites of
405 the subfamily Zapaliinae from the Lower Tithonian of Estancia María Juana, Vaca Muerta Formation
406 (Portada Covunco Member), Neuquén Basin, Argentina. *Rivista Italiana di Paleontologia e*
407 *Stratigrafia*, **125**, 473–488.
- 408 Passendorfer, E. 1930. Studjum stratygraficzne i paleontologiczne i paleontologiczne nad Kreda
409 serji wierchowej w Tatrach [Étude stratigraphique et paléontologique du Crétacé de la série
410 hauttatrique dans les Tatras]. *Prace Polskiego Instytutu Geologicznego*, **2**, 439–677 (for 1929) (in
411 Polish and French).
- 412 Pervinquière, L. 1910. Sur quelques ammonites du Crétacé algérien. *Mémoire de la Société*
413 *Géologique de France, Paléontologie*, **17**, mémoire 42, 1–86.
- 414 Peterman, D.J. and Ritterbush, K.A. 2022. Resurrecting extinct cephalopods with biomimetic
415 robots to explore hydrodynamic stability, maneuverability, and physical constraints on life habits.
416 *Scientific Reports*, **12** (1), 11287.

- 417 Reboulet, S., Giraud, F. and Proux, O. 2005. Ammonoid abundance variations related to changes
418 in trophic conditions across the Oceanic Anoxic Event 1d (Latest Albian, SE France). *Palaios*, **20**,
419 121–141.
- 420 Schlüter, C. 1876. Verbreitung der Cephalopoden in der oberen Kreide Norddeutschlands.
421 *Zeitschrift der Deutschen Geologischen Gesellschaft*, **28**, 475–518.
- 422 Schweigert, G. and Dietze, V. 1998. Revision der dimorphen Ammonitengattungen *Phlycticeras*
423 *Hyatt-Oecoptychius* Neumayr (Strigoceratidae, Mitteljura). *Stuttgarter Beiträge Naturkunde B*, **269**,
424 1–59.
- 425 Schweigert, G. and Kuschel, H. 2017. Comments on the identification of *Ammonites planula* Hehl
426 in Zieten, 1830 (Upper Jurassic, SW Germany). *Volumina Jurassica*, **15** (1), 1–15.
- 427 Tajika, A., Naglik, C., Morimoto, N., Pascual-Cebrian, E., Hennhöfer, D. and Klug, C. 2015.
428 Empirical 3D model of the conch of the Middle Jurassic ammonite microconch *Normannites*: its
429 buoyancy, the physical effects of its mature modifications and speculations on their function.
430 *Historical Biology*, **27** (2), 181–191.
- 431 Westermann, G.E.G. 1964. Sexual-Dimorphismus bei Ammonoideen und seine Bedeutung für
432 Taxionomie der Otoitidae (einschliesslich Sphaeroceratinae; Ammonitina, M. Jura).
433 *Palaeontographica Abteilung A*, **124** (1–3), 33–73.
- 434 Wright, C.W. and Kennedy, W.J. 1996. The Ammonoidea of the Lower Chalk, part 5, 320–403.
435 *Palaeontographical Society*; London.
- 436 Zatoń, M. 2008. Taxonomy and palaeobiology of the Bathonian (Middle Jurassic) tulitid ammonite
437 *Morrisiceras*. *Geobios*, **41**, 699–717.
- 438
- 439 **Figure captions**
- 440
- 441 **Fig. 1. Geographic situation of the Clansayes locality from where the studied material was**
442 **retrieved (modified after Jattiot et al., 2022). UTM coordinates: 44°22'05.90"N; 4°48'03.25"E**
443

444 **Fig. 2.** Upper Albian *Turrilitoides* and *Mariella* specimens with adult peristome. Scale bar = 10 mm.
445 **A.** *Turrilitoides hugardianus* d'Orbigny, 1842; specimen BMNH C38201 from South Africa (original
446 figure from Kennedy and Klinger, 1978, pl. 9, fig. M); microconch; X2. **B–E.** *Turrilitoides*
447 *hugardianus*; specimen UBGD 032447 from Salazac, France (Latutrie collection); microconch. **F–I.**
448 *Turrilitoides hugardianus*; specimen UBGD 032448 from Salazac, France (Latutrie collection);
449 microconch. **J.** *Turrilitoides hugardianus*; specimen UBGD 32952 from Salazac, France (original
450 figure from Jattiot et al., 2021, fig. 22Z); microconch. **K–L.** *Turrilitoides hugardianus*; specimen
451 32953 from Salazac, France (original figure from Jattiot et al., 2021, fig. 22AA, AB); microconch.
452 **M–N.** *Turrilitoides hugardianus*; specimen 32954 from Salazac, France (original figure from Jattiot et
453 al., 2021, fig. 22AE, AF); microconch. **O–P.** *Turrilitoides hugardianus*; specimen 32948 from
454 Salazac, France (original figure from Jattiot et al., 2021, fig. 22W, X); microconch. **Q.** *Turrilitoides*
455 *hugardianus*; specimen 32949 from Salazac, France (original figure from Jattiot et al., 2021, fig.
456 22Y); microconch. **R–U.** *Mariella nobilis* (Jukes-Browne, 1877); specimen UBGD 032449 from
457 Salazac, France (Latutrie collection); microconch. **V–Y.** *Mariella bergeri* (Brongniart, 1822);
458 specimen UBGD 293215 from Clansayes, France; microconch (see also Jattiot et al. 2022, pl. 16, figs.
459 5–8). **Z–AC.** *Mariella bergeri* (Brongniart, 1822); specimen UBGD 293255 from Clansayes, France;
460 microconch (see also Jattiot et al. 2022, pl. 16, figs. 9–12). **AD–AG.** *Mariella bergeri* (Brongniart,
461 1822); specimen UBGD 293295 from Clansayes, France; macroconch.

462

463 **Fig. 3.** Characteristics of the adult peristome in **A.** *Mariella bergeri* (specimen UBGD 293255, see
464 also Fig. 2Z–AC) and **B.** *Turrilitoides hugardianus* (specimen UBGD 032447, see also Fig. 2B–E).
465 Not to scale.

466

467 **Fig. 4.** **A.** Hypothesized reconstruction of an antidimorphic pair of the late Albian *Mariella bergeri*.
468 Naturally, many aspects of this reconstruction are speculative. The macroconch and the microconch
469 are represented with a sinistral coiling, since 93% of the *Mariella* specimens from Clansayes are
470 sinistral (Jattiot et al., 2022). **B.** Conceptual reconstructed shell mainly based on the features observed
471 in specimens UBGD 293215 and UBGD 293255.

472

473 **Fig. 5.** Lower Cenomanian *Mariella oehlerti* (Pervinquière, 1910) with adult peristome from
474 Hokkaido, Japan, specimen GS. G168 (original figure from Matsumoto et al., 1999, fig. 4);
475 macroconch. Scale bar = 10 mm.

476

477 **Fig. 6.** Upper Albian and lower Cenomanian *Mariella* specimens with adult peristome. Scale bar = 10
478 mm. **A–C.** *Mariella oehlerti*; specimen TKD 30086B from Hokkaido, Japan, lower Cenomanian
479 (original figure from Matsumoto et al., 1999, fig. 3–3); microconch. **D–F.** *Mariella oehlerti*; specimen
480 GS. G167 from Hokkaido, Japan, lower Cenomanian (original figure from Matsumoto et al., 1999,
481 fig. 3–1); microconch. **G.** *Mariella oehlerti* (Pervinquière, 1910); specimen BMNH C79806 from
482 South Africa, lower Cenomanian (original figure from Kennedy and Klinger, 1978, pl. 6, fig. K);
483 microconch. **H.** *Mariella cenomanensis* (Schlüter, 1876); specimen BMNH 88724 from the Lower
484 Chalk, England, lower Cenomanian (original figure from Wright and Kennedy, 1996, pl. 102, fig. 14);
485 microconch. **I.** *Mariella circumtaeniata* (Kossmat, 1895); specimen SAS A3137 from South Africa,
486 upper Albian (original figure from Kennedy and Klinger, 1978, pl. 5, fig. C); microconch.

487

488 **Fig. 7.** Lower Cenomanian *Turrilites*, *Hypoturrilites* and upper Albian *Ostlingoceras* specimens with
489 adult peristome. Scale bar = 10 mm. **A.** *Turrilites costatus* Lamarck, 1801; specimen BGS GSM 7785
490 from the Lower Chalk, England (original figure from Wright and Kennedy, 1996, pl. 106, fig. 6);
491 microconch. **B.** *Turrilites costatus*; specimen BMNH 10790 from the Lower Chalk, England (original
492 figure from Wright and Kennedy, 1996, pl. 105, fig. 1); microconch. **C.** *Turrilites costatus*; specimen
493 BMNH C77730 from the Lower Chalk, England (original figure from Wright and Kennedy, 1996, pl.
494 106, fig. 3); macroconch. **D.** *Turrilites costatus*; specimen SMC B35885 from the Lower Chalk,
495 England (original figure from Wright and Kennedy, 1996, pl. 106, fig. 2); macroconch. **E.** *Turrilites*
496 *costatus*; specimen SMC B35882 from the Lower Chalk, England (original figure from Wright and
497 Kennedy, 1996, pl. 105, fig. 5); macroconch. **F.** *Hypoturrilites gravesianus* (d'Orbigny, 1842);
498 specimen SMC B218 from the Lower Chalk, England (original figure from Wright and Kennedy,
499 1996, pl. 109, fig. 4); microconch. **G.** *Turrilites scheuchzerianus* Bosc, 1801; specimen BMNH 30210

500 from the Lower Chalk, England (original figure from Wright and Kennedy, 1996, pl. 107, fig. 7);
501 macroconch. **H.** *Turrilites scheuchzerianus*; specimen SMC B35809 from the Lower Chalk, England
502 (original figure from Wright and Kennedy, 1996, pl. 107, fig. 5); macroconch. **I.** *Turrilites*
503 *scheuchzerianus*; specimen BGS GSM 7772 from the Lower Chalk, England (original figure from
504 Wright and Kennedy, 1996, pl. 107, fig. 6); microconch. **J.** *Ostlingoceras puzosianum* (d'Orbigny,
505 1842) from La Fague, France (specimen number unknown, original figure from Wright and Kennedy,
506 1996, text-fig. 140H); macroconch. **K, L.** *Ostlingoceras puzosianum*; specimen UJF-ID.10701 from
507 Montlaux, France (original figure from Kennedy and Latil, 2007, pl. 11, figs. 11, 12); macroconch;
508 X0.5.

509

510 **Fig. 8.** Suggested phylogeny of the family Turrilitidae by Cooper (1999). Specimens of *T.*
511 *hugardianus*, *Mariella bergeri*, *Turrilites costatus*, *Hypoturrilites gravesianus* and *Ostlingoceras*
512 *puzosianum* figured herein (Figs 2B–E, 2Z–AC, 7E, 7F, 7J, respectively) are used as representatives
513 of the adult peristome of the genera *Turrilitoides*, *Mariella*, *Turrilites*, *Hypoturrilites* and
514 *Ostlingoceras*, respectively. The triangle highlights the genera that may share a peristome
515 morphology characterized by a flared lip extending ventrally, with a narrow pocket-like shape.

516

517

518

519