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

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Abstract

In ammonites, the identification of mature shells is the logical but not naturally simple prerequisite to determine sexual dimorphism. Here, we provide elements suggesting sexual dimorphism in the upper Albian *Mariella bergeri* species (Turrilitidae), based on three specimens with preserved adult peristome from the Clansayes locality (southeastern France). We compare the morphology of the terminal peristomes observed in *M. bergeri* with that of the few other known examples in Turrilitidae. In turn, we hypothesize 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. The observed similarities seem to support the close relationships between these three genera inferred from the most recent phylogeny of the family Turrilitidae. Conversely, the

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

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

1. Introduction

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

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

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

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

2. Materials and methods

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

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

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

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

3. Results

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

3.1. *Mariella bergeri* (upper Albian)

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

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

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

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

3.2. *Turrilitoides hugardianus* (upper Albian)

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

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

3.3. *Mariella nobilis* (upper Albian)

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

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

3.4. *Mariella oehlerti* (lower Cenomanian)

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

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

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

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

One mature specimen of *M. cenomanensis* (Schlüter, 1876) with adult peristome from South Africa was documented by Wright and Kennedy (1996, pl. 102, fig. 14; refigured here as Fig. 6H). Additionally, one mature *M. circumtaeniata* with terminal peristome was documented from England by Klinger and Kennedy (1978, pl. 5C; refigured here as Fig. 6I). According to Wright and Kennedy (1996, p. 344), the peristome of the latter specimen ‘is marked by a constriction and lip’.

For both specimens discussed here, although only one view is available in the literature, the observed features of their peristome (perhaps slightly incomplete) suggest that their initial morphology was very similar – if not identical – to that of *M. bergeri* specimens from Clansayes and *M. oehlerti* specimens from Japan (see Figs 2V–AG, Fig. 5A–C and Fig. 6A–F).

3.6. *Hypoturritilites gravesianus* (lower Cenomanian)

According to Wright and Kennedy (1996, p. 363), ‘*Hypoturritilites* includes some of the largest turritid taxa, exceeded only by *Mariella* [...]’ and ‘adults of any given species fall into two size classes, as in other turritidids’. They documented (pl. 109, fig. 4; here refigured as Fig. 7F) a mature *H. gravesianus* specimen from England (Lower Chalk) and described its clearly complete adult peristome as ‘marked by a constriction and flare around the outer, exposed whorl face, and marked contraction at the lower side of the aperture’ (p. 363). Although we do not fully concur with the terminology used in the original description of this peristome, it is fully identical to that of *M. bergeri* specimens from Clansayes, as well as that of the *M. oehlerti* specimen GS. G168 from Japan (Matsumoto et al. 1999), in particular (compare Fig. 7F with Fig. 2X, AB and Fig. 5C).

3.7. *Turritilites costatus* (middle Cenomanian)

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

3.8. *Turrilites scheuchzerianus* (lower Cenomanian)

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

3.9. *Ostlingoceras puzosianum* (upper Albian)

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

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.

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

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

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

5. Conclusions

In our opinion, many criteria supporting the hypothesis of dimorphism are met in the upper Albian species *Mariella bergeri*. Based on the three specimens from the Clansayes locality, and on a literature review of available adult peristomes within the family Turrilitidae, it can be hypothesized that 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. This interpretation supports the proposed phylogeny for the family Turrilitidae by Cooper (1999). To further increase our knowledge on the distribution of different peristome

morphologies among Turrilitidae, additional complete and remarkably preserved specimens from various genera (e.g., *Eohypoturrilites*, *Klingerella*, *Mesoturrilites*, *Pseudhelicoceras*) are needed.

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Data availability

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

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Figure captions

Fig. 1. Geographic situation of the Clansayes locality from where the studied material was retrieved (modified after Jattiot et al., 2022). UTM coordinates: 44°22'05.90"N; 4°48'03.25"E

Fig. 2. Upper Albian *Turrilitoides* and *Mariella* specimens with adult peristome. Scale bar = 10 mm.

A. *Turrilitoides hugardianus* d'Orbigny, 1842; specimen BMNH C38201 from South Africa (original figure from Kennedy and Klinger, 1978, pl. 9, fig. M); microconch; X2. **B–E.** *Turrilitoides hugardianus*; specimen UBGD 032447 from Salazac, France (Latutrie collection); microconch. **F–I.** *Turrilitoides hugardianus*; specimen UBGD 032448 from Salazac, France (Latutrie collection); microconch. **J.** *Turrilitoides hugardianus*; specimen UBGD 32952 from Salazac, France (original figure from Jattiot et al., 2021, fig. 22Z); microconch. **K–L.** *Turrilitoides hugardianus*; specimen 32953 from Salazac, France (original figure from Jattiot et al., 2021, fig. 22AA, AB); microconch. **M–N.** *Turrilitoides hugardianus*; specimen 32954 from Salazac, France (original figure from Jattiot et al., 2021, fig. 22AE, AF); microconch. **O–P.** *Turrilitoides hugardianus*; specimen 32948 from Salazac, France (original figure from Jattiot et al., 2021, fig. 22W, X); microconch. **Q.** *Turrilitoides hugardianus*; specimen 32949 from Salazac, France (original figure from Jattiot et al., 2021, fig. 22Y); microconch. **R–U.** *Mariella nobilis* (Jukes-Browne, 1877); specimen UBGD 032449 from Salazac, France (Latutrie collection); microconch. **V–Y.** *Mariella bergeri* (Brongniart, 1822); specimen UBGD 293215 from Clansayes, France; microconch (see also Jattiot et al. 2022, pl. 16, figs. 5–8). **Z–AC.** *Mariella bergeri* (Brongniart, 1822); specimen UBGD 293255 from Clansayes, France; microconch (see also Jattiot et al. 2022, pl. 16, figs. 9–12). **AD–AG.** *Mariella bergeri* (Brongniart, 1822); specimen UBGD 293295 from Clansayes, France; macroconch.

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

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

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

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