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Authors: Reboulet, Stéphane, and Rard, Anthony

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Double alignments of ammonoid aptychi from the Lower Cretaceous of Southeast France: Result of a post-mortem transport or bromalites?

STÉPHANE REBOULET and ANTHONY RARD

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A new preservation of aptychi is described from the Valanginian limestone-marl alternations of the Vergol section (Drôme), located in the Vocontian Basin (SE France). Aptychi are arranged into two parallel rows which are generally 50 mm in length and separated by 4 mm. The alignments are very often made by entire aptychi (around 10 mm in length), oriented following their harmonic margin. Aptychi show the outside of valve to the viewer: they are convex-up. This fossilization of aptychi is successively interpreted as the result of post-mortem transport by bottom currents (taphonomic-resedimentation process) or the residues (bromalites: fossilized regurgitation, gastric and intestinal contents, excrement) from the digestive tract of an ammonoid-eater (biological processes). Both the parallel rows of aptychi are more likely interpreted as a coprolite (fossil faeces) and they could be considered as both halves (hemi-cylindrical in shape) of the same cylindrical coprolite which would have been separated in two parts (following the long axis) just after the animal defecated. Considering this hypothesis, a discussion is proposed on the hypothetical ammonoid-eater responsible for them.

Key words: Ammonoidea, taphonomy, aptychus, coprolite, predation, Valanginian, Cretaceous, France.

Stéphane Reboulet [stephane.reboulet@univ-lyon1.fr], Université de Lyon, (UCBL1, La Doua), UFR des Sciences de la Terre, CNRS-UMR 5125 PEPS, Bâtiment Géode, 2 Rue Raphaël Dubois, 69622 Villeurbanne cedex, France;
Anthony Rard [anthony.rard@cc-thouarsais.fr], Centre d'interprétation géologique du Thouarsais, Réserve Naturelle Géologique du Toarcien, Les Ecuries du Château, 79100 Thouars, France.

Introduction

After numerous papers of Trauth (1927, 1928, 1935, 1936, 1938), most authors classically interpreted aptychi as protective opercula closing the aperture of ammonoids (Arkell 1957; Schindewolf 1958). The hypothesis of Meek and Hayden (1864) and Meek (1876), who were the first to correctly describe and interpret aptychi as ammonoid lower jaws, did not prevail (Landman and Waage 1993). The question of the function of aptychi was reopened as a result of the works of Lehmann (1970, 1972, 1978, 1979, 1981a, b) and Kaiser and Lehmann (1971) which have clearly demonstrated for several ammonoid genera that both anaptychi (single organic plate) and aptychi (pair of calcareous plates) are lower jaws. This interpretation has been well documented and almost universally accepted (Morton 1981; Morton and Nixon 1988; Landman and Waage 1993; Nixon 1996 and references therein), even if some authors such as Kennedy and Cobban (1976), Lehmann and Kulicki (1990), and Seilacher (1993) suggested that aptychi served as opercula (possible secondary function) in addition to functioning as jaws (primary function; see discussion in Tanabe and Fukuda 1999).

The preservation of aptychi within the body chamber is always very rare as much in involute/evolute planispiral ammonoids as in heteromorph ammonoids (Trauth 1928, 1935, 1936; Arkell 1957; Lehmann 1981a,b; Nixon 1996; Reboulet 1996; Tanabe and Fukuda 1999; Tanabe and Landman 2002), except for some uncoiled ammonoids (Barremian *Karsteniceras*, Lukeneder and Tanabe 2002) and U-shaped heteromorphs (Aptian *Tonohamites*, Monks and Palmer 2002; Turonian scaphitids, Tanabe 1979; Maastrichtian scaphitids (*Hoploscaphites* and *Jeletzkytes*, Landman and Waage 1993) for which this kind of fossil record seems slightly more frequent (see the recent compilation of occurrences of aptychi assigned to the Ancyloceratina in Wippich and Lehmann 2004). For example, among 48,700 ammonoids and 6,000 aptychi coming from ten Valanginian–Hauterivian sections (limestone-marls alternations) of the Vocontian basin (Southeast France), only two specimens of *Haploceras grasianum* (planispiral ammonoid, Haploceratidae) and one specimen of *Neocomites* sp. (planispiral ammonoid, Neocomitidae) are characterized by an aptychus in their body chamber (Reboulet 1996; Reboulet et al. 2003; this study). This can be explained by the quick separation of the body (and so the aptychi) from the shell after the death of the animal (Chamberlain et al. 1981; Chirat 2000; Reboulet et al. 2003, 2005, and references therein). In the Vocontian basin successions, aptychi frequently occur in isolation; sometimes their paired structure is preserved (bivalved aptychi) but more often they are single (one of the pair of plate; Reboulet 1996; Reboulet et al. 2003). This kind of fos-

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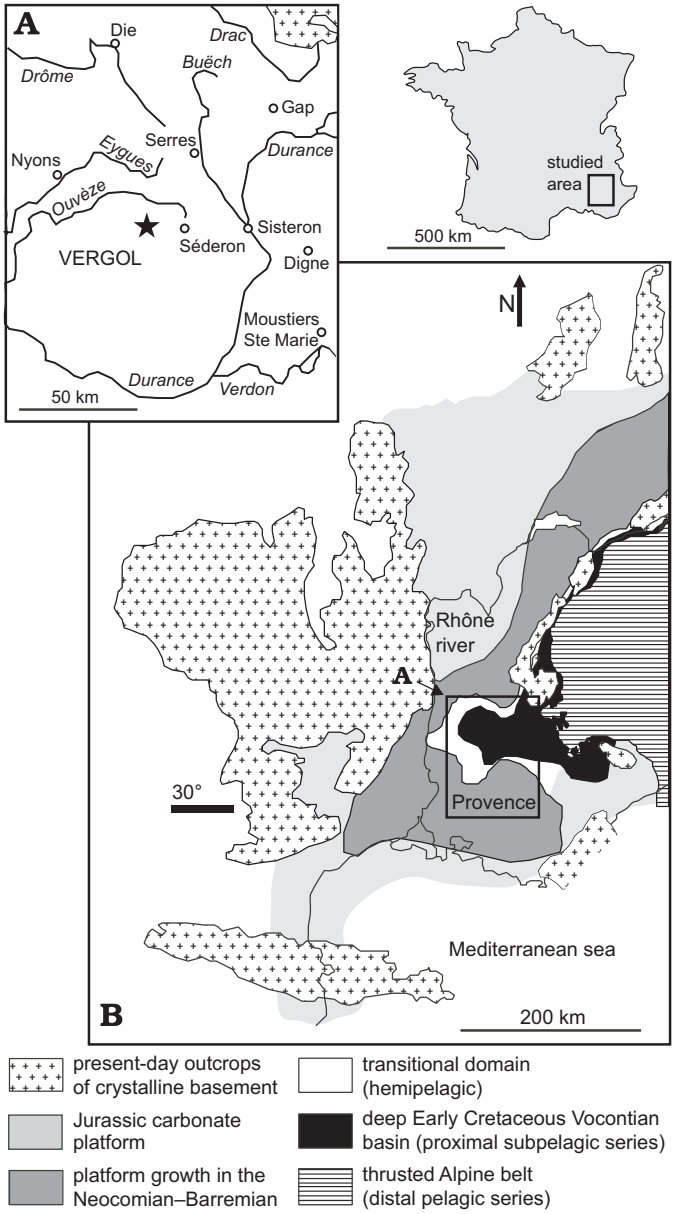

Fig. 1. **A**. Location map of the Vergol (Drôme) section. **B**. Palaeogeographical map of the Vocontian Basin (Southeast France; Lower Cretaceous), modified from Ferry (1991).

silization of aptychi is the norm for the Mesozoic successions (see references above). However, Mehl (1978a) has described a particular preservation characterized by one alignment of broken aptychi (a dozen pieces), found in the Solnhofen Limestone (Lower Tithonian). The author interpreted this fossilization as a coprolite (6 mm large, 40 mm long) attributed to predatory holostean fish.

A similar preservation but with two rows of aptychi has been found in the mid-Valanginian limestone-marl alternations of the Vergol section (Drôme, Fig. 1A) located in the epicontinental Vocontian basin (Fig. 1B). The aim of this study is to describe this new kind of occurrence of aptychi and to discuss some preservational aspects. This discovery has been made within a quantitative approach of the mid-Valanginian macrofauna; the results and interpretation of the quantification of ammonoid absolute abundance will be presented in another paper. We here focus only on a particular and unusual occurrence of aptychi.

Institutional abbreviation.—FSL, Faculté des Sciences de Lyon, Geology Department of Lyon University, France.

Geological setting: the Vergol section

The Vocontian basin (Southeast France) is a hemipelagic to pelagic intrashelf basin of the European Tethyan passive margin. During the Valanginian, this epicontinental basin was approximately located at a palaeolatitude of 30° North (Reboulet et al. 2003). It was partly isolated from the Western Tethys Ocean and surrounded by carbonate platforms (Fig. 1B). The Valanginian marl-limestone alternations are remarkably continuous within the Vocontian basin as demonstrated by Cotillon et al. (1980), Reboulet (1996), and Reboulet and Atrops (1999). Dilution cycles by carbonate mud exported from shallow platform environments to the basin were probably the main factor controlling the Valanginian marl-limestone formation (Reboulet et al. 2003).

The Vergol section, which is well dated by ammonoids (Reboulet 1996; Reboulet and Atrops 1999; Reboulet et al. 2003), is dominantly calcareous in its lower part (Lower Valanginian; *Tirnovella pertransiens* Zone, sensu Hoedemaeker et al. 2003; Reboulet et al. 2006), then gradually becomes more argillaceous from the uppermost part of the Lower Valanginian (*Busnardoites campylotoxus* Zone) to the lowermost part of the Upper Valanginian (*Saynoceras verrucosum* Zone) (Fig. 2A). From the *S. verrucosum* Zone up to the Valanginian–Hauterivian boundary, a gradual increase in carbonate content is observed. The marl-limestone alternation is stacked in bundles, becoming more calcareous towards their top. The Valanginian outcrops of the Vergol section are characterized by four 1 centimetre-thick organic carbon-rich layers (B1 to B4; *Busnardoites campylotoxus* Zone, *Karakaschiceras biassalense* Subzone, *Saynoceras fuhri* Horizon sensu Hoedemaeker et al. 2003; Fig. 2A),

Fig. 2. The Vergol section. **A**. Marl-limestone succession, levels after Reboulet (1996), location of the four organic carbon-rich layers (Barrande layers, B1 to B4; Reboulet 2001; Reboulet et al. 2003), stratigraphic ranges of Valanginian ammonoids with their relative abundance (Reboulet 1996), ammonoid biozonation (from Reboulet et al. 2003, slightly modified; abbreviated ABR) and correlation with the Valanginian standard zones (from the "Kilian Group", Hoedemaeker et al. 2003; Reboulet et al. 2006; abbreviated VSZ-KG). **B**. Detailed lithostratigraphic column of the interval studied in the Vergol section (levels 98 to 109 (column "a") in Reboulet (1996) are equivalent to layers 1 to 67 (column "b"), positions of the macrofauna sampling stations ("c") and layers where double alignments of aptychi were found (black squares); p., partly. →

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named "Barrande" layers (Reboulet 2001; Reboulet et al. 2003) which define the onset of the mid-Valanginian positive C-isotope excursion (through the *K. biassalense–S. verrucosum* subzones; McArthur et al. 2007) which is correlated with the Valanginian Weissert oceanic anoxic event (Erba et al. 2004). The major extinction event in the history of Valanginian ammonoids occurs simultaneously with a global perturbation of the carbon cycle which takes place across the Lower–Upper Valanginian boundary.

The studied interval is comprised between beds 98 to 109 (21.5 metres), on both parts of the Lower–Upper Valanginian boundary from the top of the *Neocomites platycostatus* Horizon (*B. campylotoxus* Zone, *K. biassalense* Subzone) to the middle part of the *S. verrucosum* Horizon (*S. verrucosum* Zone and Subzone) (Fig. 2B). The ammonoid biozonation of the Vergol section is based on the works of Reboulet (1996), Reboulet and Atrops (1999) and Reboulet et al. (2003). Correlation with the Valanginian standard zones (Hoedemaeker et al. 2003; Reboulet et al. 2006) is given (Fig. 2A). It is important to note that *S. verrucosum*, index species of its zone, subzone and horizon, appears just below bed 101 (layer 17a); previously, its appearance was located between beds 101 and 102 (Reboulet et al. 2003) (Fig. 2A, B).

Material and methods

In the studied interval, the ammonoid fauna of the Vergol section is very abundant and consists of eleven genera and subgenera grouped into six families for which a systematic revision was conducted recently (Fig. 2A; Reboulet 1996 and references therein; Reboulet and Atrops 1999). They are assigned to two morphologic units using the terminology proposed in the glossary of *Ammonoid Paleobiology* (Landman et al. 1996): involute/evolute planispirals (normal coiling including Neocomitidae, Olcostephanidae, Haploceratidae, Lytoceratidae, Phylloceratidae) and orthocones (Bochianitidae). The dissolution of shells is the norm and specimens are preserved as internal, generally calcareous moulds; pyritised ammonoids are only abundant in some layers.

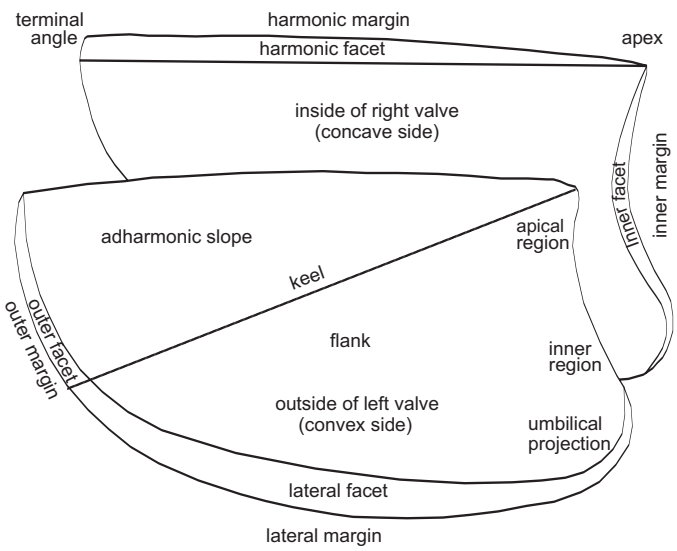

Fig. 3. Morphological nomenclature of aptychi. Redrawn and partially modified from Arkell (1957) and Farinacci et al. (1976).

Aptychi are *Lamellaptychus* Trauth, 1927 (Arkell 1957; Gąsiorowski 1962; Vašiček 1996; Vašiček and Hoedemaeker 1997). They are preserved with their calcitic shells or as internal moulds when a part of, or the entire, calcitic remain has been removed and lost during sampling. The morphological terminology of aptychi used here corresponds to Arkell (1957) and Farinacci et al.'s (1976) nomenclature (Fig. 3).

The macrofaunal quantification was carried out in sixty-one successive sampling stations covering layers 1 (in bed 98) to 67 (in bed 109), both in marls and limestones (Fig. 2B). The quantitative study enabled to find nearly 20,000 ammonoids (entire or more or less fragmented) and 4,800 aptychi (generally entire). Aptychi frequently occur in isolation, single (Fig. 4A) or bivalved (Fig. 4B). The paired structures are mainly located in the intervals 15 to 17, 27 to 37, and layers 41, 43, 47, 51, 53, and 55 (Fig. 2B). The new fossilization of aptychi is represented by ten examples found in layers 15, 16, 17, 41, 43, 47, and 51.

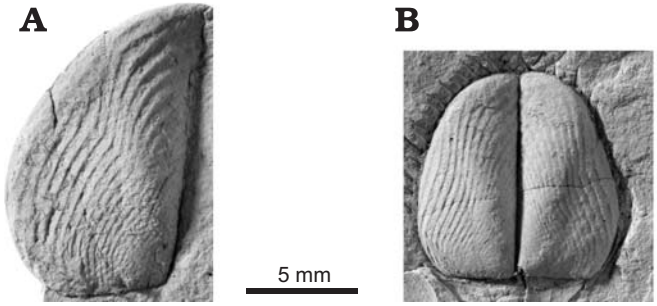

Fig. 4. Mid-Valanginian aptychi in isolation. **A**. Single aptychus (one of the pair of plate), FSL 710901, Vergol section, layer 22 (Fig. 2B), *Saynoceras verrucosum* Zone, Subzone, and Horizon. **B**. Bivalved aptychi (paired structure), FSL 710902, Vergol section, layer 55 (Fig. 2B), *S. verrucosum* Zone, Subzone, and Horizon.

Results

In six samples, aptychi are arranged into two parallel rows. Regarding complete structure, the length of alignment varies from 43 mm (FSL 710903, Fig. 5A) to 54 mm (FSL 710904, 5B; FSL 710905, Fig. 5C). For other samples, one of the two rows (FSL 710906, Fig. 5D) or both (FSL 710907, Fig. 6A; FSL 710911, Fig. 6E) reach the border of the rock and the measurements (53 mm; 44 mm; 19 mm, respectively) possibly do not correspond to the maximal length of the alignment of aptychi. The samples FSL 710906 (Fig. 5D) and FSL 710905 (Fig. 5C) do not show a symmetrical structure as one alignment is shorter. The rows of aptychi are generally separated by 4 mm; the width between two rows is larger (6 mm) for the sample FSL 710905 (Fig. 5C). The alignments are very often made by entire aptychi which are all oriented fol-

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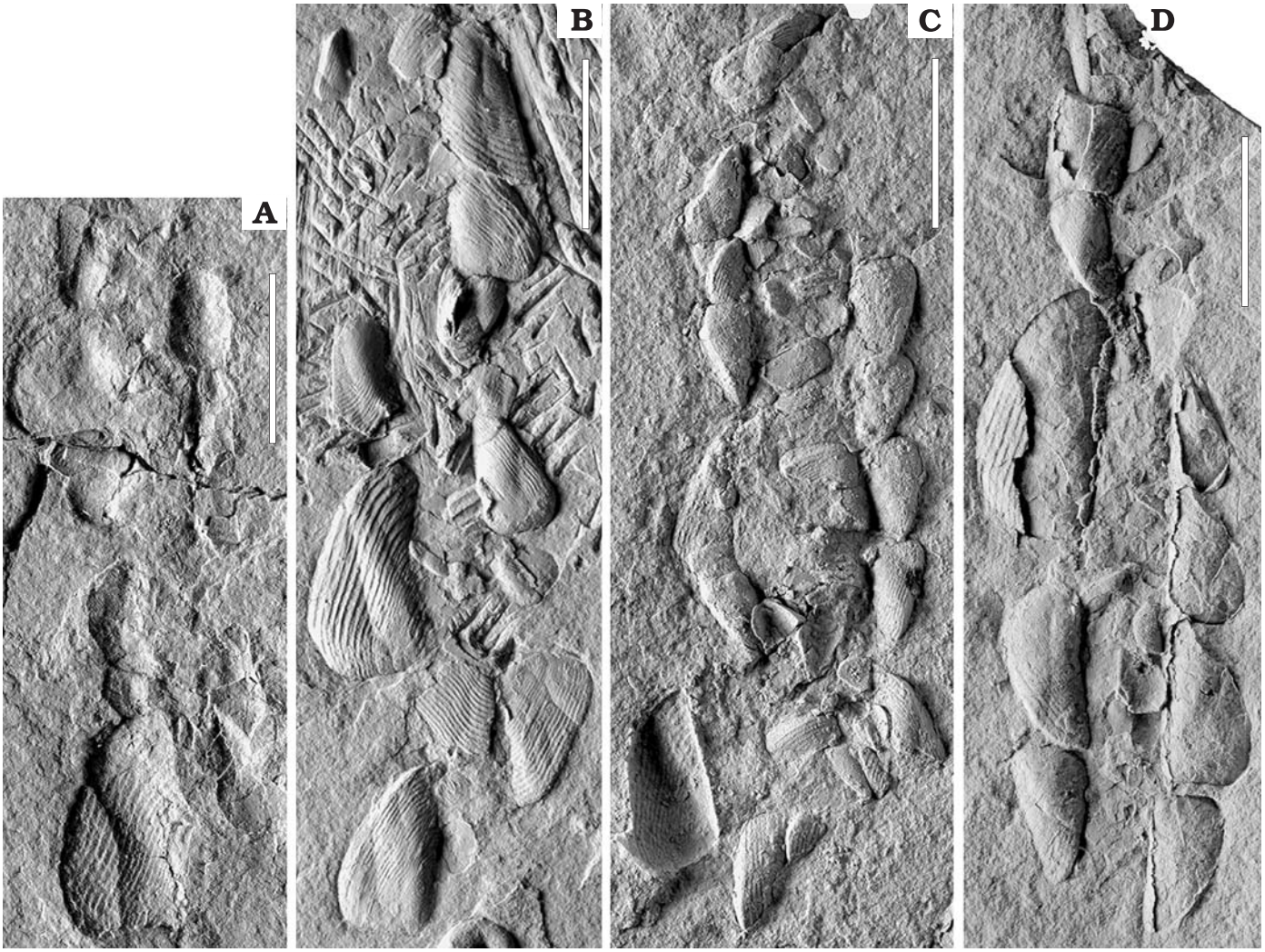

Fig. 5. Mid-Valanginian aptychi in alignments. **A**. FSL 710903, Vergol section, layer 17 (Fig. 2B), *Saynoceras verrucosum* Zone, Subzone, and Horizon. **B**. FSL 710904, Vergol section, layer 16 (Fig. 2B), *Busnardoites campylotoxus* Zone, *Karakaschiceras biassalense* Subzone, and *Neocomites platycostatus* Horizon. **C**. FSL 710905, Vergol section, layer 41 (Fig. 2B), *S. verrucosum* Zone, Subzone, and Horizon. **D**. FSL 710906, Vergol section, layer 43 (Fig. 2B), *S. verrucosum* Zone, Subzone, and Horizon. Scale bars 10 mm.

lowing their larger side (harmonic margin or symphysis; Figs. 3 and 7). The lateral margin of aptychi faces the outer side of the row. All aptychi show their convex side (outside of valve) to the viewer: they are convex-up except for one aptychus which is outside the alignment (FSL 710905, Fig. 5C, left row). Generally, aptychi are juxtaposed (FSL 710906, Fig. 5D) but an overlapping of their terminal (or ventral) angle can be observed (FSL 710904, Fig. 5B; FSL 710907, Fig. 6A). The terminal angle of aptychi is not oriented in a preferential direction (Fig. 7); opposite directions can be observed when two parallel rows are compared but also in the same row (for example in the left row of sample FSL 710906 (Fig. 5D); in the right row of sample FSL 710904 (Fig. 5B). The distribution of size seems also to be at random. The samples FSL 710905 (Fig. 5C) and FSL 710907 (Fig.6A) are characterized by small (around 5–7 mm in length) and large (around 10–15 mm in length) aptychi, respectively. But, small, medium and large aptychi occur in the same sample (FSL 710906, Figs. 5D and 7, the aptychi in the left row are larger than the ones in the right row) or in the same row (FSL 710906, Fig. 5D, left row with medium and large aptychi; FSL 710904, Fig. 5B; FSL 710903, Fig. 5A). Laterally, aptychi of the left and right rows do not correspond to the bivalved structure of the same individual as their size is often different and/or their terminal angle is in the opposite direction (Fig. 7). A few small entire aptychi can take place in the median part (space between two parallel rows) (FSL 710906, Fig. 5D), but more often, it is characterized by broken aptychi (FSL 710904, Fig. 5B; FSL 710905, Fig. 5C). When alignments can be observed in cross section (FSL 710906, Fig. 5D; FSL 710907, Fig. 6A), it does not seem that there are two superimposed rows of aptychi (one on the exposed surface and one in the rock). Radiographies (X-rays) have been made on samples FSL 710903 (Fig. 5A), FSL 710904 (Fig. 5B) and FSL 710906 (Fig. 5D). No row of aptychi inside the rock has been observed under the row exposed on the surface.

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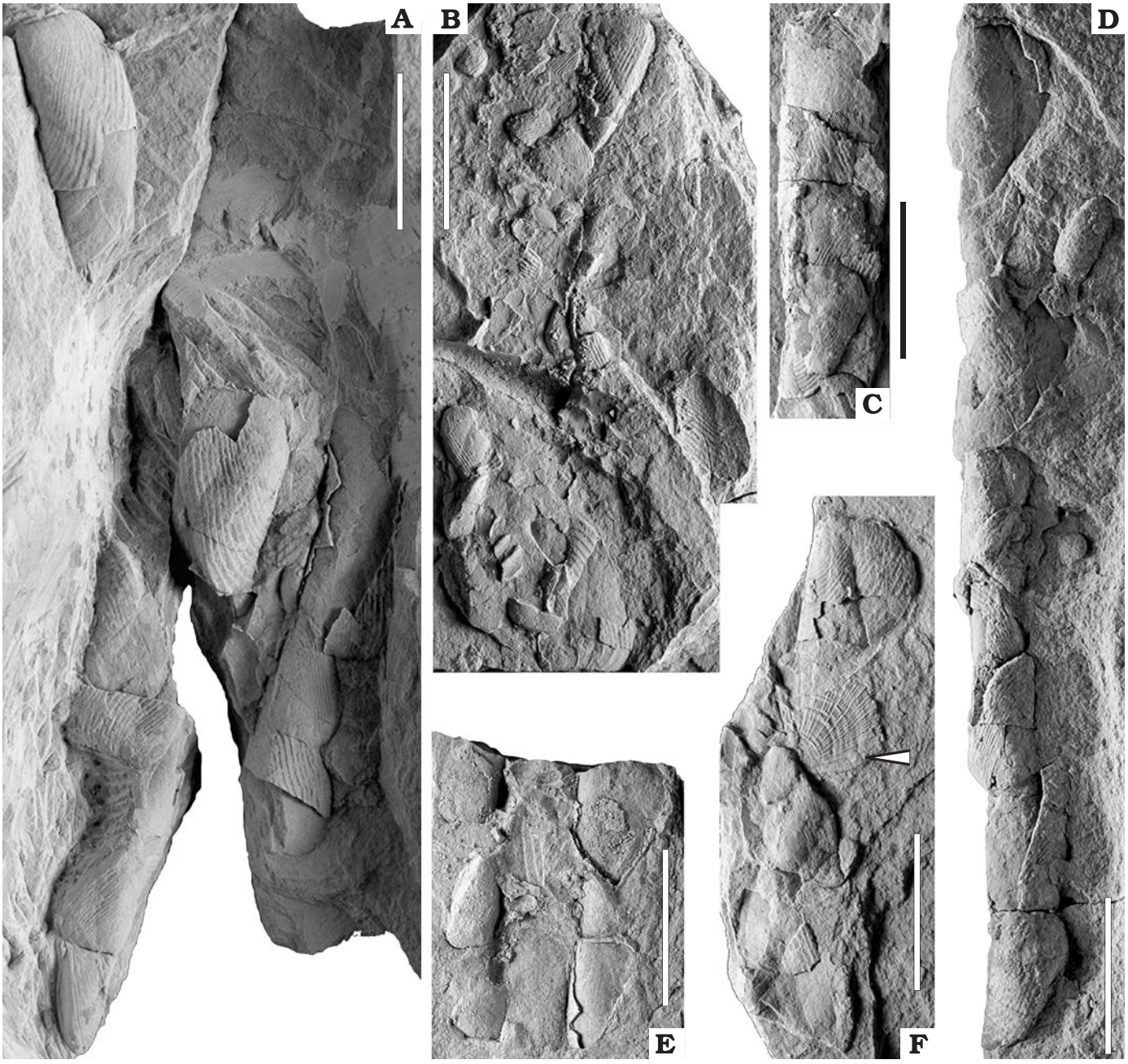

Fig. 6. Mid-Valanginian aptychi in alignments. **A**. FSL 710907, Vergol section, layer 51 (Fig. 2B), *Saynoceras verrucosum* Zone, Subzone, and Horizon. **B**. FSL 710908, Vergol section, layer 15 (Fig. 2B), *Busnardoites campylotoxus* Zone, *Karakaschiceras biassalense* Subzone and *Neocomites platycostatus* Horizon. **C**. FSL 710909, Vergol section, layer 17 (Fig. 2B), *S. verrucosum* Zone, Subzone, and Horizon. **D**. FSL 710912, Vergol section, layer 51 (Fig. 2B), *S. verrucosum* Zone, Subzone, and Horizon. **E**. FSL 710911, Vergol section, layer 47 (Fig. 2B), *S. verrucosum* Zone, Subzone, and Horizon. **F**. FSL 710910, Vergol section, layer 17 (Fig. 2B), *S. verrucosum* Zone, Subzone, and Horizon (the bivalve is indicated by an arrowhead). Scale bars 10 mm.

On one sample (FSL 710908, Fig. 6B), double alignment of aptychi (43 mm length) does not appear easily. The right and left rows are underlined by three and one aptychi, respectively. The structure is mainly characterized by the broken aptychi in the median part.

Samples FSL 710909 (Fig. 6C) and FSL 710910 (Fig. 6F) have been found in the same piece of rock. But it was impossible to restore the whole structure (double alignment) with certitude, so, they are described separately. Sample FSL 710909 (Fig. 6C) is 25 mm in length and shows an overlapping of aptychi. Sample FSL 710910 (Fig. 6F) is 32 mm in length and is characterized by the presence of one bivalve.

Sample FSL 710912 (Fig. 6D) is made of one row of aptychi which measures 67 mm in length. There is some overlapping of aptychi. The whole alignment can be observed in cross section and there is no superimposed row of aptychi in the sediment.

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Discussion

The double alignments of aptychi can be interpreted either as the result of transport by bottom currents before burial (see below "Result of physical processes") or as the residues (indigestible part) from the digestive tract of an ammonoid-eater (see below "Result of biological processes"). In the latter case, their assignment to a hypothetical producer can be considered (see below "Potential ammonoid-eaters").

Result of physical processes.—The first solution is to consider the double alignments of aptychi as the result of transport by bottom currents before burial ("transport model"). Once accumulated on the sea-floor, aptychi can be affected by a resedimentation process (sensu Fernández-López 1991); it does not necessarily imply significant lateral transport. The fact that the harmonic margin (Fig. 3) of aptychi always run parallel to the direction of the alignment could be due to a preferential orientation by bottom current (Fig. 7). In isolation (single or bivalved, Fig. 4) and in alignments (Figs. 5 and 6), aptychi are generally convex-up. This probably corresponds to the most stable position for transported bowl-shaped material. For instance, shells of brachiopods and bivalves deposited in areas with strong currents tend to rest convex-up, while those in unturbulent water tend to rest concave-up (Parsons and Brett 1991). However, Kidwell and Bosence (1991) note that "hydraulic reworking does not always result in convex-up orientations of bowl-shaped shells, and thus this is not a foolproof guide to water energy". The presence of an aptychus (FSL 710905, Fig. 5C, left row) with a convex-down orientation could be explained by a short lateral transport (rolling) or by a biological reworking. The broken aptychi found in the median part of the structure could be generated during the transport along the bottom. More generally, the weak fragmentation of ammonoid shells of the Vergol section seems related to a nearly in situ resedimentation by bottom-currents (Reboulet 1996; Reboulet et al. 2003; this study).

However, some data does not fit with the "transport model". The existence of several double alignments of aptychi seems to defy explanation by random processes. This pattern would be easier to explain if the aptychi were open but still hinged (Fig. 4B) during transport. But they are too far apart laterally (generally 4 mm) for this interpretation (Fig. 7). Moreover, it has never been possible to piece together aptychi of each alignment to recognize a paired structure; they do not correspond laterally to the paired structure of the same individual (see "Results'). If aptychi have been preferentially reoriented by bottom currents, the same direction or the more frequent direction of their terminal angle should be recorded; but it is not the case (see "Results"). The orthoconic shells of bochianitids are very abundant in the mid-Valanginian assemblages (Reboulet 1996; Reboulet et al. 2003) and around 8,500 specimens have been found in the studied interval. They are generally not oriented in a preferential direction when several specimens are found together, except in some cases where their shells are closely accumulated and more or less parallel

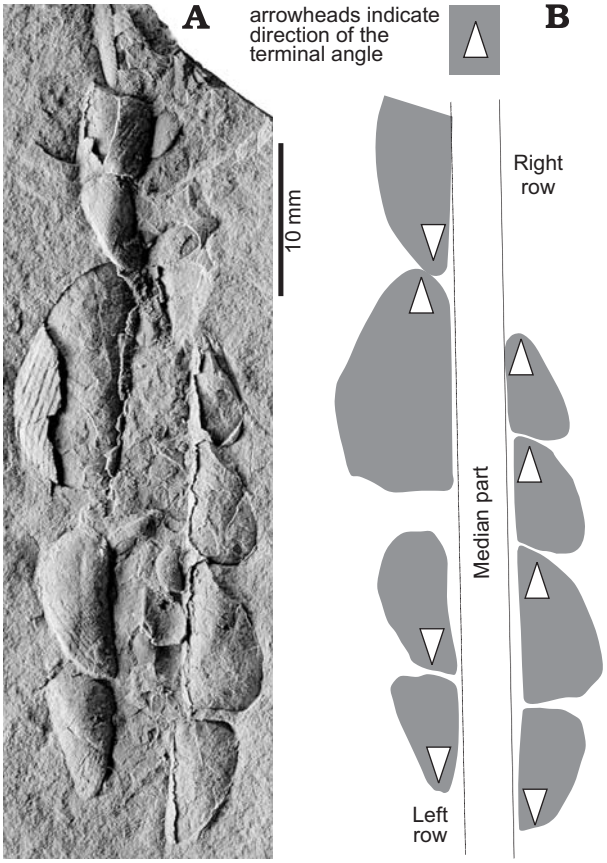

Fig. 7. **A**. FSL 710906, Vergol section, layer 43 (Fig. 2B), *Saynoceras verrucosum* Zone, Subzone, and Horizon. **B**. Schematic drawing of a double alignment of aptychi based on sample FSL 710906.

as was observed in the following layers (the number of cases is indicated in parenthesis): 10 (3); 13c (1); 14 (2); 21 (2); 22 (1); 27 (4); 28 (2); 36 (1); 65 (1) (Fig. 2B). In layers 51 and 67, thirty and five belemnites are closely accumulated and parallel, respectively. Except in layer 51, double alignments of aptychi have not been found in these layers.

Result of biological processes.—The second solution is to consider the double alignments of aptychi as the residues (indigestible part) from the digestive tract of an ammonoid-eater. This includes regurgitalites (fossilized vomit or regurgitation), gastric residues (fossilized stomach contents and stomach stones), cololites (fossilized intestinal contents) and coprolites (fossilized excrements). These different trace fossils can be grouped under the term "bromalites" defined by Hunt (1992; Hunt et al. 1994).

Regurgitations are produced by some predators (e.g., carnivorous birds, some reptiles, and some fishes) that remove indigestible components of the prey's body through their mouth because they are too large to pass through the digestive tract and could damage internal organs or be too hard to be digested. Fossil regurgitations have been recognized in different geologic ages, as well as in marine as in continental palaeoenvironments (Schäfer 1972; Bishop 1975; Pollard 1990; Walton 1990; Zatoń et al. 2007). Regurgitalites con-

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tain partially digested material and have a texture similar to coprolites but have a larger area and thinner profile (Hasiotis et al. 2007). A mass of juvenile belemnite rostra, dated to 160 Ma (Oxfordian) and found by Peter Doyle (University of Greenwich) in a quarry near Peterborough (UK), has been interpreted as the vomit of an ichthyosaur (BBC News 2002; National Geographic News 2002). Their study revealed "acid etching marks" caused by digestive fluids from the stomach. These belemnites are not preferentially arranged. More recently, a study of densely packed fossil aggregates from the Middle Jurassic of Poland suggests that these accumulations are probably the result of regurgitation (Zatoń et al. 2007). Even if the skeletal elements (ammonoids, belemnites, bivalves, echinoderms, and brachiopods) are spatially definable (round to elliptical aggregates, 60–200 mm in diameter), they are dispersed without distinctive features. Taking into account these observations and data on modern and fossil regurgitations of different animals (Bishop 1975; Pollard 1990; Walton 1990; Hasiotis et al. 2007; Zatoń et al. 2007), the position of Valanginian aptychi into two parallel rows cannot correspond to the regurgitation of an ammonoid-eater.

Fossilized stomach contents have also been well described in literature as the gastric contents of ichthyosaurs or sharks (Pollard 1968 and references therein; Bishop 1975; Pollard 1990; Hasiotis et al. 2007). Lower Jurassic ammonites have been found in saurian stomach contents (Frentzen in Kennedy and Cobban 1976). The gastric mass is generally oval in shape and composed of residues of the prey (such as bones, fish remains, belemnite rostra, cephalopod hooklets, stones, Pollard 1968, 1990; Bishop 1975; Hasiotis et al. 2007) in random orientation. Following these characteristics, the well arranged Valanginian aptychi in double alignments cannot correspond to the residues of stomach contents of a hypothetical ammonoid-eater.

Another possibility is to interpret the new preservation of Valanginian aptychi as a cololite. In this case, the double alignments of aptychi could correspond to a fold of the gut in which aptychi were arranged with their convex side towards the intestinal wall; this would explain the asymmetrical structure of some double alignments (one of both alignments shorter, see "Results") and that aptychi show their convex side on the same face of the alignments. However, it is also possible to consider that the fold of the intestinal gut could be at the origin of cololites characterized by non-parallel alignments composed by aptychi which could be convex-up on one row and convex-down on the other one. This has never been observed in the six well preserved Valanginian samples (see "Results"). So, they are probably not cololites. Moreover, the identification of cololites is not certain unless they are located in the ventral region of the body fossil of an animal (Hasiotis et al. 2007), and it is not the case in this study.

The double alignments of Valanginian aptychi could be more likely interpreted as coprolites ("coprolite model"). Among criteria allowing their recognition (Häntzschel et al. 1968; Sarjeant 1975; Pollard 1990; Hunt 1992; Hunt et al. 1994; Hasiotis et al. 2007), some of them can be used here: morphology similar to animal gut (see the section on cololites and the interpretation below), narrow range of linear dimensions in a population (alignments of aptychi are around 50 mm in length. See "Results"), and ordered internal structure (aptychi showing their convex-side, their lateral margin facing the outer side of the row. See "Results"). In the literature, there are only a few examples describing some samples interpreted as coprolites in which ammonoid shells or their mandibles are present. Kennedy and Cobban (1976) and Mapes et al. (1995) evoked the occurrence of masses of whole and fragmentary shells of ammonoids which could represent the faecal matter accumulation of carnivores like reptiles, fishes or cephalopods. Young ammonoids and adult *Baculites* have been found in coprolites derived from plesiosaurs (Wetzel 1960; Lehmann 1981b). Mapes (1987: 526, fig. 3.8) published a photo showing Palaeozoic cephalopod mandibles stacked like ice-cream cones in a phosphatic nodule. This arrangement has been interpreted by Boston and Mapes (1991) as the result of a biological digestive process of a cephalopod-eater, concentrating the indigestible parts (mandibles) in the middle of faecal material. It can be observed that these authors excluded an explanation by random processes. The fossilization of the Valanginian aptychi in double alignments is similar but they are not preserved in a phosphatic matrix. However, if coprolites are generally rich in organic matter and in calcium phosphate, their composition may be modified much by diagenetic processes (Häntzschel et al. 1968; Sarjeant 1975; Hunt et al. 1994). Barthel and Janicke (1970) interpreted an accumulation (25 mm in length) of broken and entire (around 4 mm in length) aptychi (*Lamellaptychus*) from Solnhofen as a digestion residue of predatory fishes. Mehl (1978a) described a single alignment of broken aptychi found in the Solnhofen limestones (Lower Tithonian). It measures around 40 mm length and 6 mm width. He interpreted this fossilization as a coprolite attributed to predatory holostean fishes. The double alignments of Valanginian aptychi could correspond to a cylindrical coprolite (using the terminology of Schäfer 1972) in which aptychi were arranged with their convex side towards the intestinal wall. In this model, a cross-section made on each row of the exposed surface would reveal the other half of the cylindrical coprolite in the rock. But no aptychus has been observed inside the rock under the alignments (see "Results"). However, both parallel rows of aptychi could be considered as both halves (hemi-cylindrical in shape) of the same cylindrical coprolite which would have been separated in two parts (following the long axis) just after the animal defecated. To have aptychi with their convex side to the viewer, the division of the cylindrical coprolite must be done by the base. Two cases can be evoked. Firstly, the division of the cylindrical coprolite is made when the excrements go down in the water column. As the aptychi are well-arranged in line, excretion probably occurred when the animal was close to the sea bottom. If excretion was made directly on the sea floor, the aptychi fell down on both sides of the median part and the di-

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vision of the faeces would give two rows of aptychi with their convex side to the bottom (and not to the viewer). Secondly, the division of the cylindrical coprolite could be related to the anatomy (morphology) of the anus or cloaca. A bulge at the ventral part of the anus or cloaca (as the presence of the penis in the modern crocodilians) or the presence of an anal scale (as in modern snakes; O'Malley 2005) could divide the cylindrical coprolite and give two rows of aptychi with their convex side to the viewer. As it is the case for some aquatic animals (Schäfer 1972), the faeces of a hypothetical ammonoid-eater could be enveloped by a mucus. This would make easier the preservation of alignments of the aptychi before burial but would not prevent its division.

The preservation of aptychi in double alignments suggests their rapid burial. More generally, taphonomic studies of the Valanginian macrofauna show that the residence time of the ammonoid shells on the sea-floor seems to have been relatively low (Reboulet 1996; Reboulet et al. 2003; this study). Although original volume and shape of the living chamber are quite often preserved in internal moulds, the phragmocones are usually compressed by diagenetic compaction. This is indicative of a rapid sedimentary infill of the living chamber and high accumulation rate (Fernández-López et al. 2000; see also Boston and Mapes (1991), Kidwell and Bosence (1991), Maeda and Seilacher (1996) for further information on ammonoid taphonomy).

Potential ammonoid-eaters.—The "coprolite model" appears as the most probable solution to explain the double alignments of Valanginian aptychi and their assignment to a hypothetical producer can be discussed. It is difficult and impractical for assigning coprolites to the extinct animals responsible for them, except for a few specimens (Häntzschel et al. 1968; Bishop 1975; Sarjeant 1975; Boucot 1990; Brett 1990; Pollard 1990). Although there is an extensive literature on faecal deposits, including the nature of their content, studies which systematically review their morphology and size in Recent vertebrates and invertebrates are very rare or absent according to the different groups (Häntzschel et al. 1968; Boucot 1990; Hunt et al. 1994). In spite of differences in general organisation and shape of different invertebrates and vertebrates, the anatomical and functional conditions which determine the properties of faeces are the same (Häntzschel et al. 1968; Schäfer 1972; Hunt et al. 1994). The number of possible modifications of the external shape of the faeces is small and they are not typical for species and not even for higher taxa. So, only speculations can be made for assigning the double alignments of Valanginian aptychi interpreted as cylindrical coprolites to a hypothetical ammonoid-eater responsible for them. An overview of the predation on Palaeozoic and Mesozoic ammonoids is proposed in order to give some elements of comparison. Among this list of potential ammonoid-eaters, some of them cannot be the producer of the double alignments of aptychi interpreted as coprolites.

Ammonoid remains preserved within predator's coprolites provide some data concerning the predator/prey relationship (Bishop 1975; Boucot 1990; Pollard 1968, 1990; Hunt et al. 1994), but the evidence of predation on Palaeozoic and Mesozoic ammonoids (and more generally on cephalopods) is derived mostly from studies of shells displaying mechanical injuries (for example, "forma seccata" and "forma mordata"), and remains preserved in stomach contents of predators (Brett 1990; Mapes et al. 1995; Hengsbach 1996 and references therein; Maeda and Seilacher 1996). Some ammonoid shells have been cut (forma seccata) by crabs (Roll 1935; Hölder 1955; Kennedy and Cobban 1976; Lehmann 1981) or by other cephalopods (teuthoids, Mehl 1978b; belemnites, cannibalistic ammonoids, Guex 1967). The double alignments of Valanginian aptychi cannot probably be caused either by crustaceans or cephalopods. Faecal material produced by invertebrates is usually in the form of discrete pellets (microcoprolites; Pollard 1990). Aptychi are generally entire and not cut by the predators. Recent cephalopods are predators and carnivores (Engeser 1996); they have to cut the prey (and so the aptychi) with their strong beaks as their brain is very close to the oesophagus.

Nowadays, sharks and bony fishes are considered to be the most important predators on Recent cephalopods (Cappetta 1987; Benjamins 2000; for predation on modern coleoids and *Nautilus* see Chamberlain et al; 1981; Lehmann 1981b, Ward 1983, 1987; Saunders et al. 1987; Tanabe 1988, Tanabe et al. 1988) and these vertebrates could have been ammonoid-eaters. Only in a few instances, has it been possible to establish fish predation on ancient ectocochleate cephalopods: predation on *Dactylioceras* (Lehmann 1981b); symmoriid shark predation on nautiloid and ammonoid (Mapes and Hansen 1984; Hansen and Mapes 1990) or on *Goniolobocerasa* (Mapes et al. 1995); and semionotid fish predation on *Kosmoceras* (Martill 1990). However, as spiral coprolites have been attributed to primitive fishes (Jain 1983; McAllister 1985; Hunt et al. 1994 and references therein), sharks cannot be the producer of the double alignments of aptychi, interpreted as both parts of a cylindrical coprolite. In the stomach of a present-day shark, Tanabe (1988) has found *Nautilus* jaws for which the anterior calcified portion has been dissolved by the reaction with acidic gastric juice. This observation also tends to exclude sharks as possible ammonoid-eaters, considering that aptychi of double alignments are relatively well-preserved. The Early Cretaceous is a period of the radiation of large teleost fishes (Massare 1987) and they could have been the producers of these hypothetical coprolites as teleosts are not characterized by spiral intestinal valves (Hunt et al. 1994).

Numerous examples of ammonoid predation are recognizable by bite marks (forma mordata) and correspond to an attack by vertebrates. Ammonoids appear to have formed part of the diet of marine reptiles which were the main predators of the Mesozoic times (Massare 1987; Brett 1990). Since Kauffman and Kesling's (1960) paper, numerous marks on ammonoids have been interpreted as the teeth marks of mosasaurs (Bishop 1975; Saul 1979; Pollard 1990; Hewitt and Westermann 1990; Kauffman 1990). Doubts over the interpretation of bite marks on Cretaceous ammonoids have

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been raised. Marks on most of the shells are holes bored or dissolved in the ammonite shells from limpets or other forms of gastropods (Kase et al. 1994, 1995, 1998). However, mosasaur predation can be disregarded in the study of Valanginian coprolites, as the first mosasauroids appeared during the Cenomanian in Europe and the Western Interior Sea (Everhart 2005). Among the earlier marine reptiles, there were probably some that fed on ammonoids (Lehmann 1981b) but data is less abundant or does not exist (Kauffmann 1990). Predation of some marine reptiles on ammonoids could be limited due to their different habitats: most ammonoids lived in deeper waters and were inaccessible to some marine reptiles like sea crocodiles or plesiosaurs (Lehmann 1981b); proximal versus distal palaeoenvironments can also be evoked. The recent finding of cephalopod jaws in the stomach content of a Cenomanian polycotylid plesiosaur provides further evidence to support the hypothesis of reptile predation activity on cephalopods (Sato and Tanabe 1998). These authors have found about 30 small (5–15 mm in length), isolated and disarticulated ammonoid (desmoceratids?) jaw apparatuses, a shark's tooth, molluscan shells and stomach stones. All the cephalopod jaws are made of black, horny material and lack any trace of calcification. The absence of ammonoid shells is probably due to the effects of stomach acid and/or preferential selection by the plesiosaur before swallowing (Sato and Tanabe 1998). It seems that ichthyosaurs predominantly fed on belemnites and fish (Pollard 1968, 1990; Lehmann 1981b; BBC News 2002; National Geographic News 2002; Pour La Science 2002), and Lehmann (1981) suggested that their jaws were not suited to cracking the shells of ammonoids. Judging by their behaviour towards the Recent *Nautilus* (Lehmann 1981b; Ward 1987), marine turtles could prey on ammonoids (Lehmann 1981b). As previously evoked for sharks (see above, Tanabe 1988), aptychi which would have been swallowed by plesiosaurs, ichtyosaurs or turtles would have been partly dissolved by digestive fluids from their stomach. Lower jaws of double alignments are relatively well preserved and so large marine reptiles may be excluded as ammonoid-eaters responsible for these Valanginian coprolites. However, it is also possible that the reaction of dissolution by digestive fluids was too slow for calcitic material (see belemnites swallowed by ichthyosaurs, BBC News 2002; National Geographic News 2002; Pour La Science 2002). In such a case, it would be rather difficult to differentiate the effect of gastric dissolution and the one caused by diagenetic processes. Moreover, to our knowledge, no direct evidence showing aptychi partly dissolved by gastric juice is available in literature.

Even if vertebrates are the most probable candidates, the assignment of these hypothetical Valanginian coprolites to a specific producer is not possible here for the reasons evoked previously (see Boucot 1990; Pollard 1990). Also, because data on marine Valanginian vertebrates of the Southeast France Basin are generally very rare (mainly sharks' teeth and vertebra) and limited to systematic-biostratigraphic studies (Thieuloy 1965; Cappetta 1987, 1990; Pucéat et al. 2003). However, Hunt et al. (1994: 235) emphasized that "even if the producer cannot be identified, the contents of the coprolite can indicate diet and hence something of the ecology of the producer". Some features of the ammonoid-eater can be evoked such as its size, mode of life and ecology.

It is rather difficult task to estimate the size of the ammonoid-eater as it could have measured from a few decimetres up to one meter in length. The size of the faecal mass can give an idea of the size of the animal (defecator). Many animals produce faecal masses that are proportional to their size but it is not always a reliable criterion as large animals can produce small faecal masses (Hunt et al. 1994). This depends, for example, on if the animal was a predator or a necrophagous, a marine reptile or a fish. Two parameters must be taken into account: the size of the prey and the dimensions of the hypothetical coprolites. The mean adult-size of the Valanginian ammonoids recorded in the Vocontian Basin is generally smaller than 130 mm in diameter and rarely exceeds 150 mm (Reboulet 1996, 2001). An aptychus of 12 mm in length (comparable in size to the aptychi of the double alignments) has been found in the body chamber of a Valanginian haploceratid *Neolissoceras grasianum* which is 35 mm in diameter (Reboulet 1996: pl. 34: 6). The dimensions of the hypothetical coprolites are 50–70 mm in length and around 10 mm in diameter. As it has often been the case for Recent cephalopods (Benjamins 2000), and as evoked by some authors (for example see Barthel and Janicke 1970) in palaeontological studies, it is possible to consider that ammonoids were swallowed whole by their predators. In the Valanginian case, two kinds of data could be in favour of this interpretation: the small size of the ammonoid shells (see above) and the aptychi are generally whole. The absence of ammonoid shells (entire or fragmented) in the Valanginian coprolites can be explained by a differential preservation as the shells and aptychi are respectively aragonitic and calcitic. Firstly, the ammonoid shells can be digested by the animal more easily than aptychi. Secondly, ammonoid shells could also have been dissolved during the diagenetic processes. But, most probably, only the soft parts of ammonoids can have been swallowed by the ammonoid-eater (as suggested for the case of plesiosaur), without chewing them, as aptychi are generally entire, or with limited mastication thus explaining the presence of broken aptychi in two examples (FSL 710904, Fig. 5B; FSL 710905, Fig. 5C). In this case, the whole buccal mass was also probably swallowed by a predator and so upper jaws and radulas should be found in double alignments of aptychi (lower jaws). This supposes that chitinous elements of buccal mass have not been dissolved by the acidic gastric juice of predators responsible for these hypothetical coprolites. The beaks of modern coleoids, made of chitin (Hunt and Nixon 1981), are remarkably resistant to the digestive juices of animals and are often found in the stomach of predators (Lehmann 1981b; Ward 1987; Benjamins 2000). So, it is possible to consider that upper jaws and radulas were originally present in these Valanginian coprolites, but they have been dissolved during diagenesis due to their composition

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(chitinous substance; Lehmann 1981b). Wholly chitinous upper jaws (and also inner chitinous layer of lower jaws) are not usually preserved in limetsone-marl facies but they are relatively well fossilized in shales and calcareous or phosphate nodules in muddy sediments (Lehmann 1981b; Maeda and Seilacher 1996; Nixon 1996; Tanabe and Landman 2002 and references therein). The preservation of radula has always been very rare (Lehmann 1981b; Maeda and Seilacher 1996). The consuming of the soft parts by a predator would have been easier if ammonoid arms had not been retractable (but nothing is known about this, see Engeser 1996) and if aptychi had behaved only as lower jaws and had not functioned as opercula (Morton 1981; Morton and Nixon 1988; Nixon 1996 and references therein). In the case of predation by a marine reptile, the stomach region of the animal probably had no stomach stones, as aptychi of the double alignments are well-preserved (and generally not fragmented). It can also be evoked that the body of the ammonoid was not extracted and consumed by a predator. After the death of the ammonoid, the separation of the body from the shell could have been due to its decomposition, the activity of scavengers, or the deterioration of muscle-shell attachment areas (see studies on modern *Nautilus*; Chamberlain et al. 1981). Fallen to the sea floor, the soft parts of ammonoids could have been swallowed whole by a scavenger which searching for food near the bottom. As well for a scavenger as for a predator, a nekto-benthic mode of life (occasional or permanent) for the ammonoid-eater can be demonstrated by the presence of a bivalve in one of the coprolites. Moreover, to have aptychi well-arranged in a double alignment, the ejection of excrements by the ammonoid-eater must have been done relatively close to the sea bottom (see "Result of biological processes"). Some predators like plesiosaurs could have been in part bottom-feeders, as bivalves and gastropods have been found in their stomach contents (Sato and Tanabe 1998; McHenry et al. 2005).

Conclusion

A quantitative study of the mid-Valanginian macrofauna of the limestone-marl alternations of the Vergol section (Vocontian Basin, SE France) enabled to find nearly 20,000 ammonoids and 4,800 aptychi (lower jaws of ammonoids). Aptychi (*Lamellaptychus*) frequently occur in isolation; they are often single (one of the pair of plates) and sometimes bivalved with the paired structure preserved. A new kind of fossilization of aptychi is described in six well preserved samples. Aptychi are arranged in two parallel rows, which are generally 50 mm in length and separated by 4 mm. The fact that aptychi are convex-up and their harmonic margin always run parallel to the direction of the alignment can be related respectively to the fact that this is the most stable position for transported bowl-shaped material and also a preferential orientation by bottom current. However, some features do not correspond to the occurrence of a resedimentation process. The double alignments of aptychi have also been considered as trace fossils which could correspond to bromalites (fossilized regurgitation, stomach or intestinal contents, faeces). This newly described arrangement of fossilized aptychi can be more likely interpreted as a form of coprolite (fossilized excrement). Both the parallel rows of aptychi probably correspond to both halves of cylindrical faeces which would have been separated in two parts just after the animal defecated. This hypothesis supposes that: (1) aptychi were arranged with their convex side towards the intestinal wall of the hypothetical ammonoid-eater; (2) a particular anatomy (like a bulge in the ventral part) of the anus or cloaca allowed the division of the cylindrical faeces (following the long axis) when the animal defecated; and (3) the ejection of excrements probably occurred when the animal was close to the sea-bottom allowing optimal preservation of the coprolite in a double alignment with their convex side to the viewer. Among potential marine predators, vertebrates (e.g., teleost fishes, plesiosaurs, ichthyosaurs, marine turtles, crocodiles) are the most probable candidates. However, data on double alignment of Valanginian aptychi and knowledge on the faeces of fossils and Recent animals are insufficient to determine assignment to a specific producer.

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