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An enigmatic ammonite population from the late Callovian of Montreuil-Bellay (Maine-et-Loire, France)

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ABSTRACT

An enigmatic ammonite (Ammonoida, Ammonitida) population represented by ten immature specimens from the late Callovian (*Pseudopeltoceras leckenbyi* Horizon) of Montreuil-Bellay is documented in this work. No evident similarities can be found between the studied material and any previously described species overall, suggesting at first glance that this population represents a new taxon. However, a thorough literature review on ammonoid pathologies and a detailed investigation on the morphology and ornamentation of the specimens lead us to instead support the hypothesis that the studied population reflects abnormal specimens. More specifically, we suggest that the specimens described herein are genetically-induced abnormal (forma aegra circumdata) *Taramelliceras taurimontanum* Erni, 1934 specimens (or alternatively – although more unlikely – *Granulochetoceras hungaricum* Lóczy, 1915 specimens). In our opinion, additional material providing information on the adult morphology of this remarkable and extremely rare ammonite assemblage is required before completely ruling out the hypothesis that this population represents a new taxon.

KEY WORDS
Ammonoida,
Montreuil-Bellay,
Middle Jurassic,
late Callovian,
pathology.

RÉSUMÉ

Une population énigmatique d'ammonites du Callovien supérieur de Montreuil-Bellay (Maine-et-Loire, France).
Une énigmatique population d'ammonites (Ammonoida, Ammonitida) constituée de dix spécimens immatures du Callovien supérieur (Horizon à *Pseudopeltoceras leckenbyi*) de Montreuil-Bellay est documentée dans ce travail. Le matériel étudié ne montre de similitudes apparentes avec aucune espèce déjà connue de manière globale, ce qui suggère au premier abord que cette population représente un nouveau taxon. Cependant, un examen approfondi de la littérature sur les pathologies chez les ammonites, ainsi qu'une analyse détaillée de la morphologie et de l'ornementation des spécimens, nous conduit à plutôt soutenir l'hypothèse que le matériel étudié regroupe des spécimens présentant des anomalies. Plus précisément, nous suggérons que les dix spécimens décrits dans ce travail sont des individus de *Taramelliceras taurimontanum* Erni, 1934 (ou plus improbablement de *Granulochetoceras hungaricum* Lóczy, 1915) ayant souffert d'une anomalie *forma aegra circumdata* d'origine génétique. Il nous apparaît indispensable d'obtenir du matériel supplémentaire fournissant des informations sur la morphologie adulte de ce surprenant et rarissime assemblage pour que l'hypothèse d'un nouveau taxon puisse être définitivement rejetée.

MOTS CLÉS
Ammonoida,
Montreuil-Bellay,
Jurassique moyen,
Callovien supérieur,
pathologie.

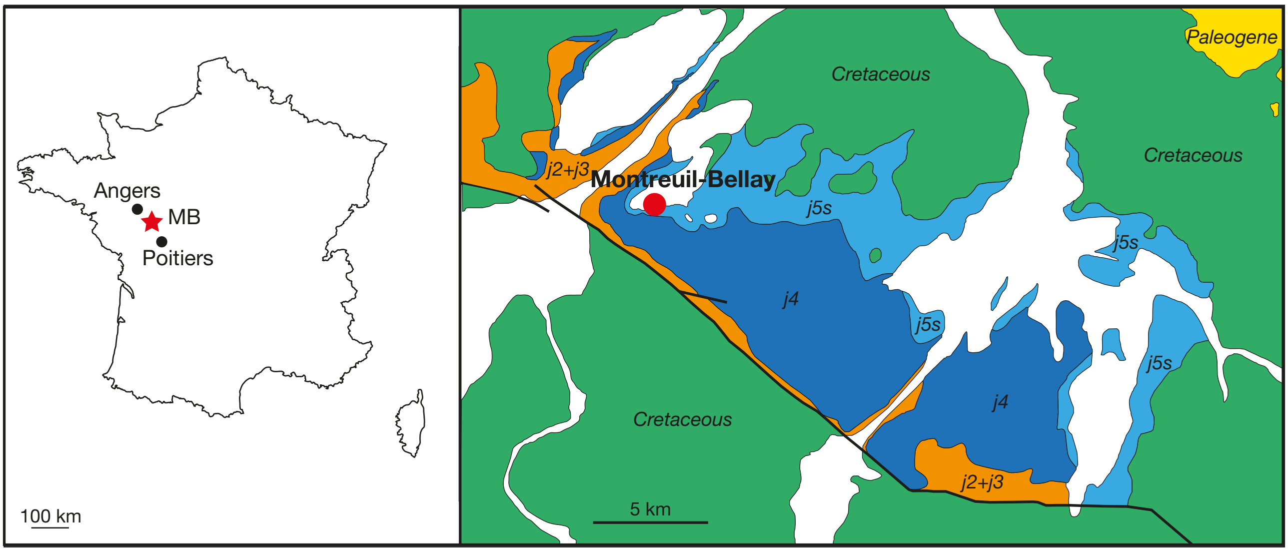

Fig. 1. — Geographical position of the Montreuil-Bellay locality: **A**, general location; **B**, close-up of the Montreuil-Bellay area with general chronostratigraphical information. Abbreviations: **j2**, Bajocian; **j3**, Bathonian; **j4**, Callovian; **j5s**, lower and middle Oxfordian. **White zones**, fluvial and alluvial deposits (Pleistocene?). Modified after Joubert *et al.* 2000.

INTRODUCTION

The Montreuil-Bellay locality (Maine-et-Loire, France; Fig. 1A) is historically well-known for its abundant and diverse late Callovian ammonite (Superorder Ammonoida Haeckel, 1866 and Order Ammonitida Haeckel, 1866; see Hoffmann *et al.* 2022) faunas (e.g., Millet de la Turtaudière 1854; Hébert 1855; Oppel 1858; Hébert & Eudes-Deslongchamps 1860; Grossouvre 1891; Couffon 1917-1919; Gérard & Contaut 1936; Cariou 1971, 1980; Bonnot 1996; Bonnot *et al.* 2005, 2008, 2014; Courville & Vullo 2016). Overall, several hundred ammonite species names have been cited from this locality. Within the remarkably extensive ammonite material documented from Montreuil-Bellay, a few specimens exhibit minor shell abnormalities, most commonly as the result of an exogenous injury or parasitism (see, e.g., Courville *et al.* 2019, fig. F.65). Recently, supposed gynandromorphic (i.e., having both male and female external shell features) specimens from this locality were recorded and used to define an abnormality coined 'forma hermaphrodita' (Frau & Boursicot 2021).

As mentioned by Jain *et al.* (2022), the types of irregularities or malformations in ammonoid shells that have been variously referred to as "monstrosities", "aberrations", "anomalies" and "abnormalities" are broadly categorized as "forma-types" (Hölder 1956). The latter were listed, revised and summarized in Hengsbach (1996), Keupp (2012), Hoffmann & Keupp (2015) and Jain *et al.* (2022). Abnormalities in ammonoids can provide information on their potential predators and predation modes (see Keupp 2012 for a review), on the impact of parasites on shell morphology (see Keupp 2012 and De Baets *et al.* 2015a for reviews), or on putative functions of ornamentation (e.g., Kröger 2002). In addition, the works by, e.g., Guex (1967, 1968), Morard (2002), Hammer & Bucher (2005), Keupp (2012) and Jattiot *et al.* (2019) well exemplify that pathologies in ornamental patterns constitute "natural experiments" that may help further deciphering the developmental mechanisms underlying regular shell secretion.

Here, we describe an enigmatic ammonite population represented by ten specimens from the late Callovian (*Pseudopeltoceras leckenbyi* Horizon) of Montreuil-Bellay (Figs 1; 2). Since no evident similarities can be found between the studied material and any previously described species overall, the main goal of this study is to determine whether this small population represents a new taxon or instead implicates a previously unknown and unusually uniform shell abnormality.

MATERIAL AND METHODS

This study is based on a total of ten ammonite specimens from the Montreuil-Bellay locality (*c.* 70 km NW of Poitiers and 45 km SE of Angers, western France; Fig. 1), all housed in the palaeontological collection of the Muséum national d'Histoire naturelle (MNHN, Paris, France). The specimens studied here were retrieved from the *Pseudopeltoceras leckenbyi* Horizon (Fig. 2) by one of us (PYB) between 1996 and 2024; they are part of a much larger ammonite collection sampled in this horizon (several thousand specimens; PYB's collection). The material was coated with magnesium oxide or ammonium chloride prior to photography to highlight morphological details (for a review of coating methods see Krogmann & Lehmann 2016). One incomplete specimen (MNHN.F.A99988) was cut transversally to reveal the whorl shape at earlier ontogenetic stages. Parts of two specimens (MNHN.F.A99984 and MNHN.F.A99988) were polished with sandpaper to reveal suture lines, which were subsequently drawn using a camera lucida. Suture lines of a specimen (MNHN.F.A99989) of *Granulochetoceras hungaricum* Lóczy, 1915 and two specimens (MNHN.F.A99990 and MNHN.F.A99991) of *Taramelliceras taurimontanum* Erni, 1934 from the same locality and

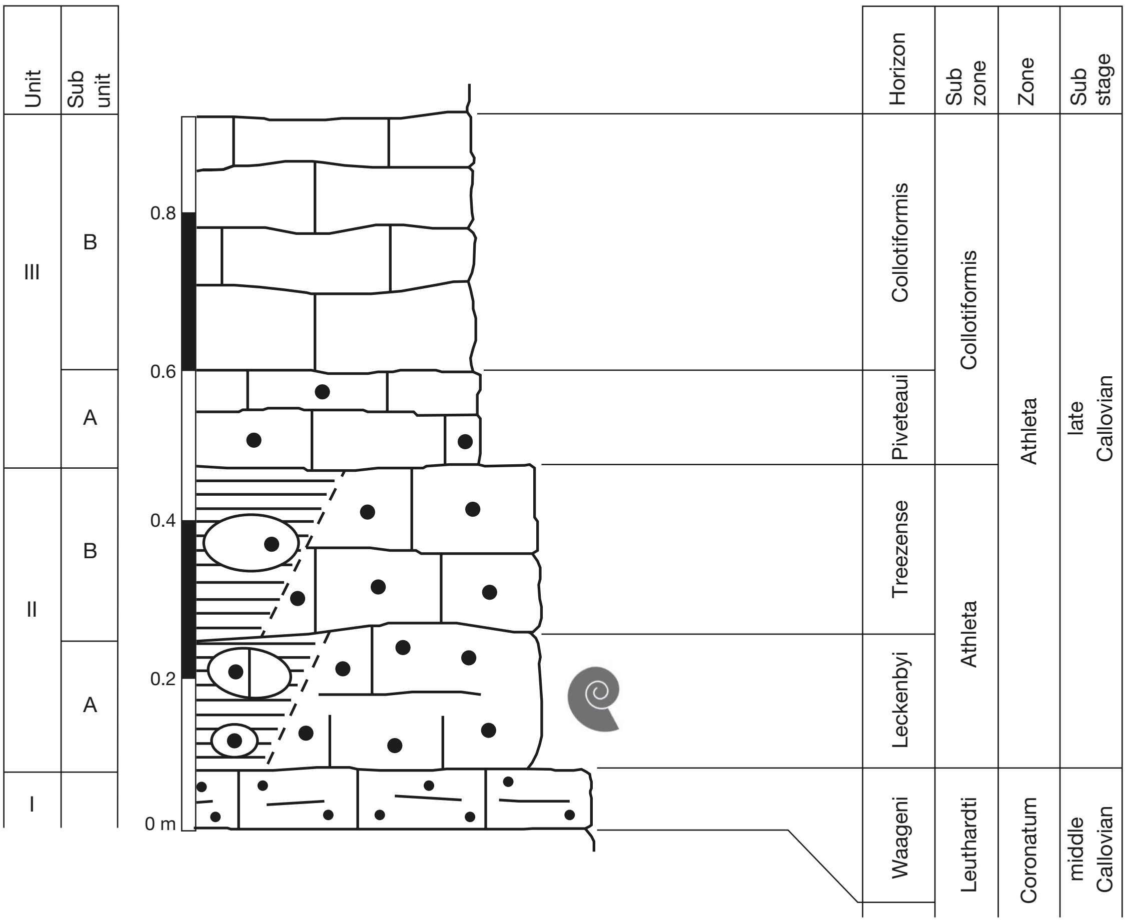

Fig. 2. — Biostratigraphy of the late Callovian in the Montreuil-Bellay area (modified after Bonnot *et al.* 2008).

horizon were also drawn for comparison. We use the suture terminology of Wedekind (1916), as applied by Kullmann & Wiedmann (1970) and modified by Korn *et al.* (2003): E, external lobe; A, adventive lobe (that is L of traditional nomenclature); and U, umbilical lobe. E/A (that is E/L of traditional nomenclature) is the saddle between E and A; A/U (that is L/U of traditional nomenclature) corresponds to the saddle between A and U. For each specimen, classical geometric parameters of the ammonoid conch (see Klug *et al.* 2015 for a review) such as shell diameter (D), and corresponding whorl height (H), whorl width (W) and umbilical diameter (U) were measured. Based on this, the three classical ratios H/D, W/D and U/D are used as descriptors of the conch shape. In addition, the ratio W/H is used as a descriptor of the whorl section, specifically.

Three specimens (MNHN.F.A99982, MNHN.F.A99984 and MNHN.F.A99986) were micro-CT scanned at the AST-RX ("Accès scientifique à la Tomographie à Rayons X") at the UMS 2700, MNHN (Paris, France), with the following parameters: voltage, 150 kV; current, 200 µA. A voxel size of 20.312 µm for MNHN.F.A99982, 22.628 µm for MNHN.F.A99984 and 23.465 µm for MNHN.F.A99986 was obtained. The original image stacks were optimized using ImageJ software (version 1.54f, National Institutes of Health). The images were cropped, rotated, converted to 8-bit grayscale and contrasted. Segmentation and 3D reconstruction were performed using Materialise Mimics innovation suite 24.0 (research edition).

Regarding terminology, as underlined by Hengsbach (1996), it can be extremely difficult in ammonoids to distinguish abnormalities that are prenatal in origin (i.e., "teratologies") from those that are postnatal ("pathologies"), particularly in the absence of obvious exogenous injuries. In this work, we opt for the principal use of the neutral term "abnormalities" to avoid possible confusions.

Institutional abbreviations

MNHN Muséum national d'Histoire naturelle, Paris;
MNHN.F Collection de Paléontologie, MNHN.

GEOLOGICAL SETTINGS

During the Callovian, the Montreuil-Bellay locality was located in the southwestern part of the Tethys (Cariou 1980). At this site, the near-entire Callovian (except for the Lamberti Zone) is represented by a condensed stratigraphic succession (up to 1.5 m thick; Fig. 2), in which 20 local horizons were originally identified (Cariou 1980). The reader is referred to Bonnot *et al.* (2008: 2; see also Bonnot *et al.* 2005) for detailed descriptions of the lithology and faunal composition of the *Pseudopeltoceras leckenbyi* Horizon.

Table 1. — Measurements (in mm) of the complete specimens studied. Abbreviations: **D**, diameter; **H**, whorl height; **W**, whorl width; **U**, umbilical diameter.

Specimen	D (mm)	H (mm)	W (mm)	U (mm)	H/D	W/D	U/D	W/H
MNHN.F.A99979	22.1	11.7	10.2	2.6	0.58	0.46	0.12	0.87
MNHN.F.A99980	25	13.1	11	3.7	0.52	0.44	0.14	0.84
MNHN.F.A99981	30.8	18.1	13.2	3.1	0.58	0.43	0.10	0.73
MNHN.F.A99982	29.5	17.2	11.7	3.8	0.58	0.4	0.12	0.68
MNHN.F.A99983	29.8	16.8	12.6	4.1	0.56	0.42	0.13	0.75
MNHN.F.A99984	33.9	19.8	15.3	4.6	0.58	0.45	0.13	0.77
MNHN.F.A99985	37.8	20.7	14.4	5.3	0.55	0.38	0.14	0.70
MNHN.F.A99986	44.6	25	19	5	0.56	0.42	0.11	0.76
MNHN.F.A99987	46	26.9	15.7	4.6	0.58	0.34	0.10	0.58
				Average:	**0.57**	**0.42**	**0.12**	**0.74**

RESULTS

Order AMMONITIDA Haeckel, 1866
Superfamily Haploceratoidea Zittel, 1884

Haploceratoidea fam., gen. and sp. indet.
(Figs 3; 4; 5; 6A, B; 7A, B; Table 1)

Examined material. — **France** • 10 specimens; Pays de la Loire, Maine-et-Loire, Montreuil-Bellay; late Callovian (*Pseudopeltoceras leckenbyi* Horizon); MNHN[MNHN.F.A99979, A99980, A99981, A99982, A99983, A99984, A99985, A99986, A99987, A99988].

Description

Most specimens are fully septate. Only MNHN.F.A99985 and A99987 (Fig. 3S-U, Y-AA) appear to preserve the beginning of the body chamber, since a very small portion of shell without suture lines can be observed at the adapertural end of their outer whorl. Yet, neither specimen shows any obvious signs of maturity (e.g., sutures approximation or distinctive change in ornamentation on the small portion of body chamber). All of the material (Fig. 3) is therefore interpreted as phragmocones of an immature assemblage, of which the adult morphology remains unknown for the time being.

The shell is very involute, with a U/D ratio of 0.12 on average (Table 1). The whorl section is moderately to weakly compressed (W/H ratio ranging from 0.58 to 0.87), elliptical. Noteworthy, the ventral shell outline is irregular in some specimens (i.e., a few ventral, discreet bulges are visible along the external whorl; Fig. 4A-C). The whorls are high; the ventral part is wide and rounded. Flanks are nearly parallel on their inner part and gently converging on their external part (e.g., Fig. 3C, I, U). Hence, maximum thickness is, overall, at mid-flank. The umbilicus is deep, with a high, nearly perpendicular wall. The umbilical shoulders are narrowly rounded and notably elevated, hence forming a distinct umbilical ridge. The umbilical region is slightly depressed. At earlier ontogenetic stages, the shell is more evolute and exhibits more depressed whorls with convex flanks (Fig. 5A-G). The ornamentation is characterized by biconcave ribs, with the point of convexity located slightly below mid-flank in all specimens. In the umbilical region, the ribs are extremely fine and dense. As a general rule, they then merge in pairs (or more) at the point of convexity to form a significantly thicker rib. Around the ventrolateral shoulders, some ribs irregularly bifurcate (see, e.g., Fig. 3Y). On the venter, the ornamental pattern often appears chaotic: a simple rib that bifurcates on one flank often correspond to two separate ribs on the opposite flank and the ribs pass through the venter in several disordered manners (Fig. 4D-F). The venter ribbing in specimen MNHN.F.A99984 is notably interrupted in the middle of the venter by a distinctive line (Fig. 3Q). Noteworthy, most specimens exhibit an extremely discreet spiral strigation, slightly more noticeable in specimens MNHN.F.A99984 and A99985 (Fig. 4G, H). In specimen MNHN.F.A99984, the spiral strigation is accompanied with an inconspicuous spiral ridge located at the point of convexity of the ribs (Figs 3S; 4H).

Suture lines of specimen MNHN.F.A99984 (Fig. 6A) are moderately complex, with trifid lobes and rather wide saddles. Suture lines of specimen MNHN.F.A99988 (Fig. 6B) slightly differ, with a wider lateral lobe and slightly more frilled, incised elements.

Importantly, no signs of exogenous physical injury (e.g., brutal change in shell morphology and ornamentation, or repaired shell areas) can be identified.

DISCUSSION

Here, we explore two hypotheses that could explain the existence of this previously undescribed population: either it reflects a previously unknown and unusually recurrent abnormality, or it represents a new taxon.

Hypothesis of a genetically-induced abnormality

As mentioned above, no signs of exogenous physical injury can be identified in the present material. As stressed by Hengsbach (1996: 586), in ammonoids, "paleopathies with no signs of exogenous physical injury might have been caused by genetic problems, parasitism, ecological/physiological problems, or some combination of these". Septal spacing irregularities in early whorls are commonly seen as reflecting brief episodes of slowed or interrupted growth, which may point to environmental stress or minor injuries (see, e.g., De Baets *et al.* 2013, 2015a; Beck *et al.* 2021). Although septal information is very limited in the three CT-scanned specimens, the apparent absence of septal spacing irregularities (Fig. 5B, D, F) supports the inference of

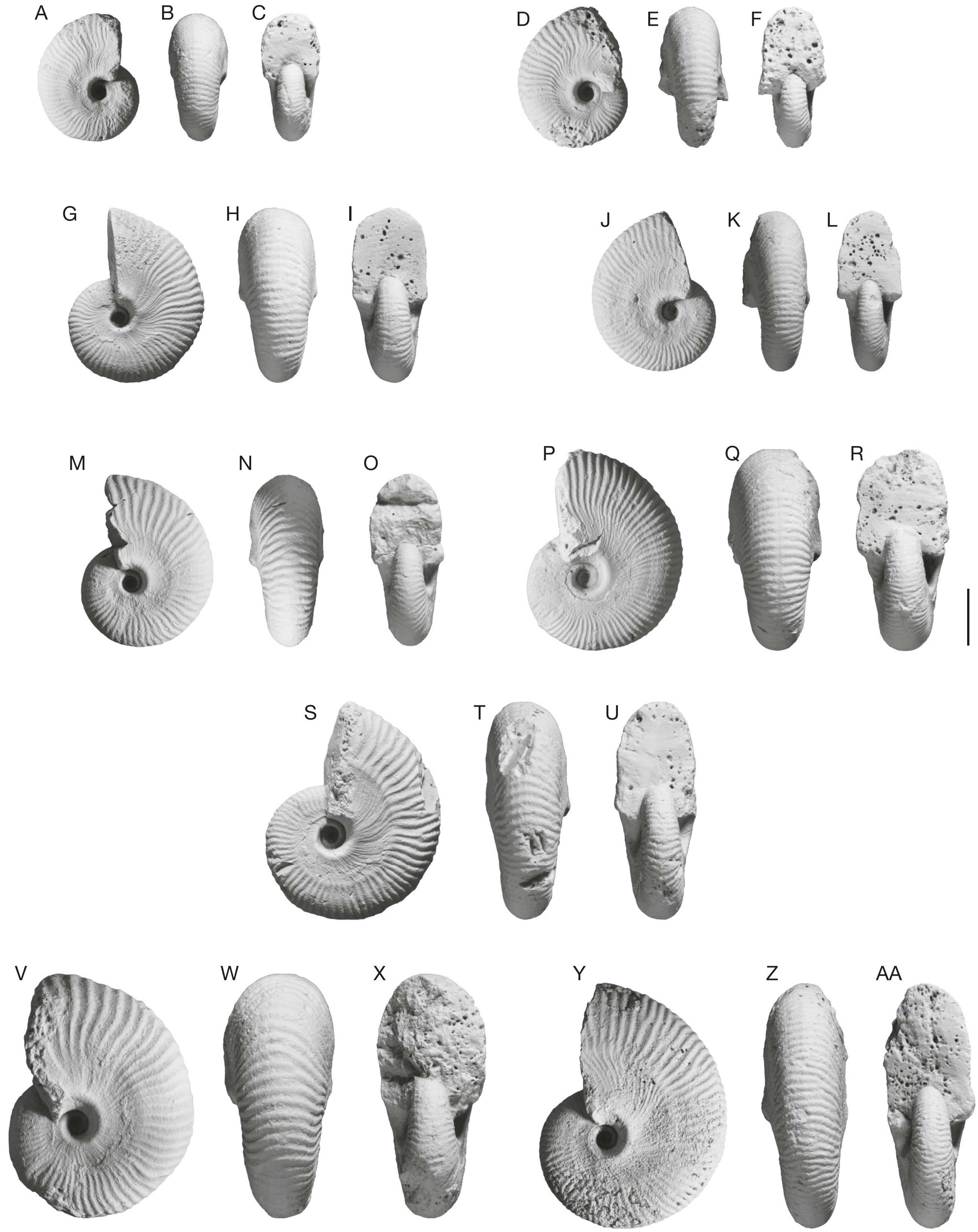

FIG. 3. — Studied specimens, tentatively assigned to 'Haploceratoidea Zittel, 1884, fam., gen., and sp. indet., late Callovian (*Pseudopeltoceras leckenbyi* Horizon), Montreuil-Bellay: **A**-**C**, MNHN.F.A99979; **D**-**F**, MNHN.F.A99980; **G**-**I**, MNHN.F.A99981; **J**-**L**, MNHN.F.A99982; **M**-**O**, MNHN.F.A99983; **P**-**R**, MNHN.F.A99984; **S**-**U**, MNHN.F.A99985; **V**-**X**, MNHN.F.A99986; **Y**-**AA**, MNHN.F.A99987. For each group of three photos, from left to right, lateral, ventral, and apertural views. Scale bar: 10 mm. Photos: Romain Jattiot.

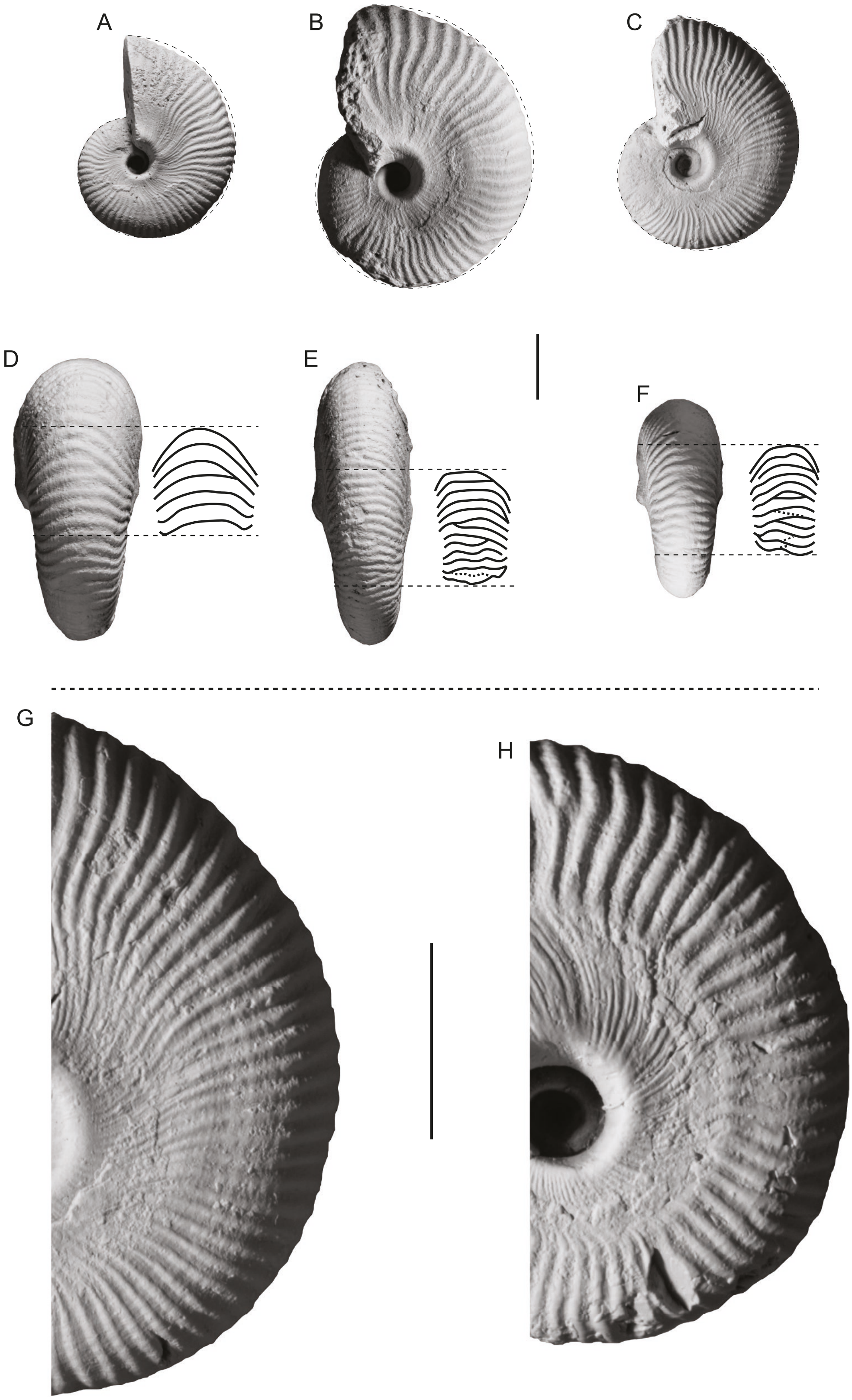

Fig. 4. — Morphological and ornamental details of the studied material of the specimens tentatively assigned to Haploceratoidea Zittel, 1884, fam., gen., and sp. indet.: **A**-**C**, slightly irregular ventral shell outline in specimens MNHN.F.A99981 (**A**), MNHN.F.A99986 (**B**) and MNHN.F.A99984 (**C**); **D**-**F**, chaotic ventral ornamental pattern in specimens MNHN.F.A99986 (**D**), MNHN.F.A99987 (**E**) and MNHN.F.A99983 (**F**); **G**, **H**, discreet spiral strigation in specimens MNHN.F.A99984 (**G**) and MNHN.F.A99985 (**H**). Scale bars: 10 mm. Photos and drawings: Romain Jattiot.

a relatively stable developmental environment. Additionally, no septal crowding is visible in shell portions where the major ribbing anomalies across the venter are observed (Fig. 4D-F). This suggests that apertural disturbances (such as those resulting from injury or parasitism) were not the cause.

Overall, genetic causes seem to better explain an abnormality occurring repeatedly in a consistent manner in specimens of a given ammonoid taxon (Hengsbach 1996). Yet, Hoffmann & Keupp (2015: 878) underline that "confirmation or identification of conch anomalies that are caused by genetic dysfunctions […] is difficult because the mutagenic character hinders a differentiation between intraspecific variation or speciation (development of new species). In many cases traumatic events during an early/juvenile ontogenetic stage that caused phenotypical modifications also in later ontogenetic stages were misinterpreted as being caused by genetic dysfunctions". However, here, we suggest that the observed shell morphology can be explained by a genetically-induced abnormality that occurred at the earliest ontogenetic stages ("Krüppel ab ovo" – cripple within the egg; Engel 1894) in each of the ten studied individuals. As such, under this hypothesis, the specimens are abnormal representatives of a previously described species remaining to be determined.

Firstly, we can exclude the present population from the Phylloceratoidea Zittel, 1884, as the suture lines (Fig. 6A, B) do not have the saddles with phylloid or spatulate endings typical of this superfamily. Based on the general shell morphology, the overall suture line patterns, and age of the present material, we instead believe that a potential candidate is to be found within the superfamily Haploceratoidea Zittel, 1884. According to Arkell *et al.* (1957), this superfamily includes ammonites that are keeled to unkeeled, typically compressed, discoidal, tending to oxycones, with smooth, usually falcoid or falcate ribbing (see also Quereilhac 2009). Within this superfamily, an affiliation of the present population to the family Haploceratidae Zittel, 1884 is ruled out. Indeed, this family typically includes unribbed taxa, and it seems unlikely that an abnormality could be expressed, in an originally unribbed taxon, by such complex ornamentation as observed in the studied material. Arkell *et al.* (1957: L271) provides a diagnosis of the family Strigoceratidae Buckman, 1924: "Compressed to oxycone, with or without keel, umbilicus narrow to minute; ribbing almost confined to outer half of whorl sides, simple or irregularly branched, not parallel to growth lines (which invariably are more projected than the ribs), whorl sides tending to be ridged or fluted spirally and strigate. Sutures moderately simple to complex, with long umbilical lobe, not retracted, bearing a graded series of auxiliaries". Several of the above listed characteristics are met in the present material (Figs 3; 4), such as the compressed shell morphology with narrow umbilicus, the ribbing generally confined to the outer half of the whorls, as well as the presence of a spiral strigation (although barely visible in the specimens studied here).

Within this family, we selected the genus *Granulochetoceras* Geyer, 1860 as a potential representative from which the present population might have originated. An emended diagnosis of this genus is provided by Schweigert *et al.* (2007: 46): "Small to medium-size oxyconic ammonite; shell with spiral strigation; narrow umbilicus; steep umbilical wall; rounded umbilical edge; one or two lateral furrows; falcoid ribbing, primaries starting from nodules at umbilical edge; secondaries starting from strong bases; ribs do not reach keel; serrate, partly undulating septicarinate keel".

Obviously, the most striking difference between typical representatives of the genus *Granulochetoceras* and the specimens studied here is that none of the latter possesses a keel. However, the asymmetry in rib ornamentation on the venter, with ribs that seem to stretch from one side to the other passing through the venter (see, e.g., Fig. 4D), as well as the presence of chaotic ventral ribbing patterns in most specimens (Fig. 4D-F), strongly point towards the abnormality forma aegra circumdata, defined by Morard (2002) as a confusing case of sculptural compensation. An example of this abnormality was first documented by Guex (1968; see also Keupp 1976: text-fig. 2; Morard 2002: fig. 2; as well as Keupp 2012 for a comparison with the abnormality forma aegra fastigata) in a *Hildoceras bifrons* (Bruguière, 1789) specimen. In the shift from the normal to the post-pathological ornamentation, the tricarinate-bisulcate venter is replaced by a rounded annularly ribbed periphery. In all cases later described, permanent post pathological keel-loss is always associated with the formation of annular ribs and a whorl section that becomes more rounded, losing its acute or squared shape.

Interestingly, Hölder (1970) distinguished circumdata-like forms, in which a triggering event (such as injury due to a predation attempt, accident, short parasitic infestation, or illness) can be observed on inner whorls, from true circumdata forms, for which there is no evidence of exogenous physical event (such as congenital malformation or mutation). Most importantly, regardless of the cause that affected the ammonite (parasitism, endogenous or exogenous), the healing process would remain the same overall (Morard 2002). Thus, to conclude, it can be reasonably hypothesized that the present population represents specimens of *Granulochetoceras* that were likely affected by a supposably genetically-induced abnormality at the earliest ontogenetic stages. This resulted in a significant change to the ornamentation on the flank, as well as the total replacement of the keel by annular ribs and a more rounded, thicker whorl section (instead of the typical oxyconic shell shape observed in *Granulochetoceras*).

Of note, a *Granulochetoceras* species, namely *Granulochetoceras hungaricum* Lóczy, 1915 is described by Schweigert *et al.* (2007: 62) as "an extreme rarity from the Late Callovian of France, Hungary, and Switzerland". 30 specimens of this species were retrieved in the Leckenbyi Horizon at Montreuil-Bellay by one of us (PYB; Fig. 6E-G); these are therefore contemporaneous of the present material. Despite some marked differences, the flanks of *G. hungaricum* (see Schweigert *et al.* 2007: fig. 26B, refigured here as Fig. 6D, E) are reminiscent of the present material as they have a nearly smooth inner half and an ornamented outer half, the two halves being separated by a lateral furrow (compare Fig. 3S with Fig. 6D, E).

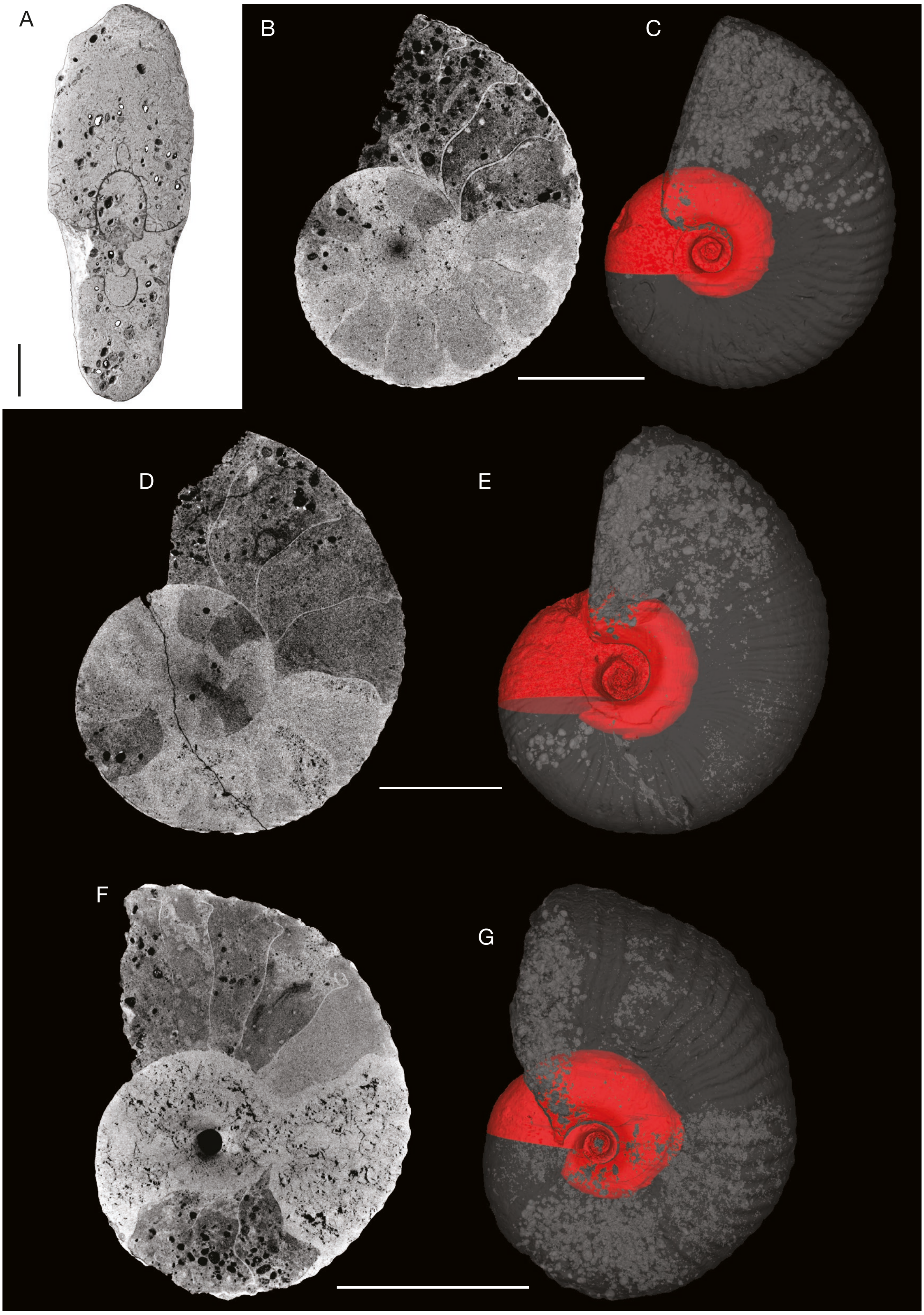

FIG. 5. — Inner whorls morphology of the studied material of the specimens tentatively assigned to Haploceratoidea Zittel, 1884, fam., gen., and sp. indet.: **A**, transversal cross-section of specimen MNHN.F.A99988; **B**-**G**, virtual longitudinal cross-section and 3D reconstructed inner whorls of specimens MNHN.F.A99982 (**B**, **C**), MNHN.F.A99984 (**D**, **E**) and MNHN.F.A99986 (**F**, **G**). Scale bars: 10 mm. Photos: A, Philippe Loubry; B-G, Nathalie Poulet-Crovisier.

In turn, it can be finally hypothesized that the material studied here represents genetically-induced abnormal (forma aegra circumdata) specimens of *G. hungaricum*, with total disappearance of the keel. Arguments in favour of this hypothesis are the overall similar shell morphology (very involute, compressed shell) and the ornamental pat-

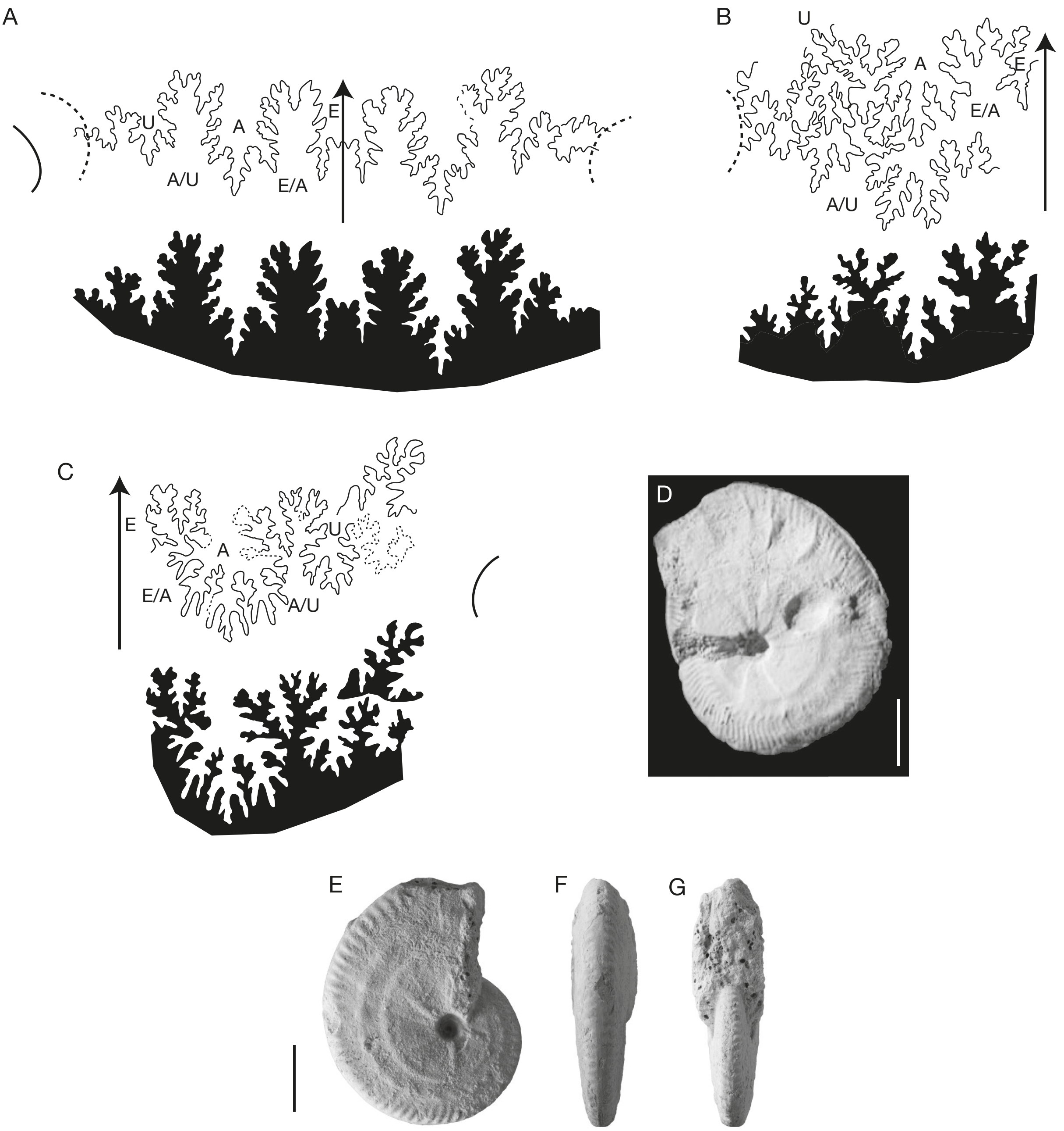

Fig. 6. — **A**, **B**, Suture lines of the studied material of the specimens tentatively assigned to Haploceratoidea Zittel, 1884, fam., gen., and sp. indet., specimens MNHN.F.A99984 (**A**; at H = 16 mm) and MNHN.F.A99988 (**B**; at H = 18 mm); **C**, suture lines of a *Granulochetoceras hungaricum* Lóczy, 1915 specimen (MNHN.F.A99989, late Callovian, *Pseudopeltoceras leckenbyi* Horizon, Montreuil-Bellay; at H = 18.5 mm); **D**, *Granulochetoceras hungaricum* specimen (after Schweigert *et al.* 2007: fig. 26B); **E**-**G**, *Granulochetoceras hungaricum*, specimen MNHN.F.A99989, late Callovian, *Pseudopeltoceras leckenbyi* Horizon, Montreuil-Bellay. **D**, **E**, lateral views; **F**, ventral view; **G**, apertural view. **Arrows**, middle of the venter. Scale bars: 10 mm. Drawings: Romain Jattiot; photos: E-G, Philippe Loubry.

tern, which consists of a marked differentiation between the inner and outer halves of the whorls. However, there are also notable arguments against this hypothesis. First, the suture lines of *G. hungaricum* differ from those of the present material as they are generally more complex and more divided. Specifically, the suture lines of *G. hungaricum* are characterized by a widely splayed trifid lateral lobe with much more deeply incised elements, as well as very narrow-stemmed saddles with more finely frilled, thin elements (Fig. 6C). Because they are slightly more complex than those seen in specimen MNHN.F.A99984, the suture lines of specimen MNHN.F.A99988 are somewhat reminiscent of that of *G. hungaricum* (compare Fig. 6B with Fig. 6C). Nevertheless, the suture lines of *G. hungaricum* still differ significantly in having a more widely splayed lateral lobe and more deeply incised elements. Another counter-argument is that a total of 30 specimens of *G. hungaricum* have been retrieved from the Leckenbyi Horizon at Montreuil-Bellay by one of us (PYB), implying a 25% (10/40) rate of occurrence for the supposed abnormality, which is a much higher rate than most known pathologies (0.05 to 3%, see, e.g., Guex 1967, Morard 2002). In rare instances, a prevalence of 70% or more can be observed, which might be due to specialized parasites; Hengsbach 1991, 1996; De Baets *et al.* 2015a).

Alternatively, it can be hypothesized that the present population represents genetically-induced abnormal (forma aegra circumdata) specimens of a taxa belonging to the family Oppeliidae Bonarelli, 1894 (superfamily Haploceratoidea Zittel, 1884), instead of *G. hungaricum* (family Strigoceratidae, superfamily Haploceratoidea Zittel, 1884). Noteworthy, a specimen similar to the ones described here is identified as “Oppeliidae indet.?” by Courville *et al.* (2019: fig. F.30). Although highly polymorphic (Roman 1938) and maybe polyphyletic, the family Oppeliidae overall includes compressed ammonites with an acute or narrowly rounded keeled venter, ornamented with flexuous, low ribs and ventrolateral clavi, as well as with a more or less developed (sometimes absent) groove at mid-flank. The suture lines of oppeliid taxa are uniform and characterized by the predominance of the lateral (A/U) saddle over the external (E/A) saddle. Within this family, we propose the genus *Taramelliceras* Del Campana, 1904 and more specifically the species *T. taurimontanum* Erni, 1934 (the only *Taramelliceras* species occurring in the Leckenbyi Horizon at Montreuil-Bellay) as a potential taxon from which the present population might have originated. The obvious difference between typical representatives of *T. taurimontanum* (holotype in Erni 1934: pl. 1, fig. 7a, b, refigured here as Figs 5E, 7F-K) and the present material is that none of the studied specimens possesses ventrolateral and siphonal clavi. Yet, it can again be hypothesized that the present population represents genetically-induced abnormal (forma aegra circumdata) specimens of *T. taurimontanum*, with total disappearance of usual venter ornamentation. As in the “*G. hungaricum* hypothesis”, one can note the overall similar shell morphology (very involute, compressed shell) and the rather similar ornamental pattern consisting in a marked differentiation between the inner and outer halves of the whorls (compare, e.g., Fig. 3S with Fig. 7F). Additionally, the sutures of the specimens studied here are closer to those of *T. taurimontanum* than those of *G. hungaricum* (they are simpler, with less deeply incised and less complex elements; compare Fig. 7A, B with Fig. 7C-E). Further, both specimens MNHN.F.A99984 and MNHN.F.A99988 have a more predominant lateral saddle than the E/U saddle (Fig. 7A, B), which is characteristic of the oppeliid (see diagnosis above and Fig. 7C-E). Of note, the external saddle of specimens MNHN.F.A99984 and MNHN.F.A99988 (Fig. 7A, B) appear slightly wider than those of *T. taurimontanum* (Fig. 7C-E). However, it can reasonably be argued that a marked, pathologically-induced change in venter morphology results in some correlated modifications of the suture line pattern on the ventrolateral shell area (see, e.g., Monnet *et al.* 2011 and Keupp 2012).

Finally, in contrast to *G. hungaricum*, the total number (about a thousand) of *T. taurimontanum* specimens sampled by one of us (PYB) in the Leckenbyi Horizon at Montreuil-Bellay is much more consistent with commonly observed rates of pathological specimens within a given ammonite population (*c.* 10/1000, i.e., *c.* 1%)

In sum, under the hypothesis that the present population consists of genetically-induced abnormal (forma aegra circumdata) specimens, *T. taurimontanum* appears as the most plausible taxon from which the present population might have originated.

Hypothesis of a new taxon

One could argue that the ornamentation and overall morphology observed in the present material is too complex, uniform among specimens, and singular to be the result of a genetically-induced abnormality in *Granulochetoceras hungaricum* or *Taramelliceras taurimontanum* individuals. In turn, another possibility is that the present material might represent a new taxon. However, there are two major impediments to this hypothesis. Firstly, we are unable to propose a genus and even a family affiliation for this potential new taxon. Under this hypothesis, it could only be stated with confidence that the new taxon belongs to the superfamily Haploceratoidea. Erecting a new species, a new genus, and a new family based solely on the limited present population appears highly inappropriate. Furthermore, and most importantly, the studied population is only represented by phragmocones, which means that the adult morphology remains unknown for the time being. In our opinion, this should strongly undermine any plan of erecting a new species. Although we do not completely reject this hypothesis, the current supporting arguments appear not robust enough to warrant further development or discussion as to whether the present population represents a new taxon. Overall, as underlined by De Baets *et al.* (2015b), strict typological approaches (by, e.g., erecting narrowly defined morphospecies) are not recommended as they lead to an artificial inflation of paleobiodiversity.

CONCLUSION

We described an enigmatic, small ammonite population from the late Callovian (*Pseudopeltoceras leckenbyi* Horizon) of Montreuil-Bellay. Based on their morphology and ornamentation, the studied specimens could not be affiliated with a previously described species. Although we cannot completely rule out the hypothesis that the material studied here represents a new taxon, the hypothesis of an abnormality appears to be the more parsimonious for the time being. Thus, we suggest that the most plausible explanation is that the present material consists of genetically-induced abnormal (forma aegra circumdata) *T. taurimontanum* specimens (or alternatively – although more unlikely – *Granulochetoceras hungaricum* specimens). Additional material providing information on the adult morphology of this population is required to definitely rule out one the two main hypotheses considered in this work.

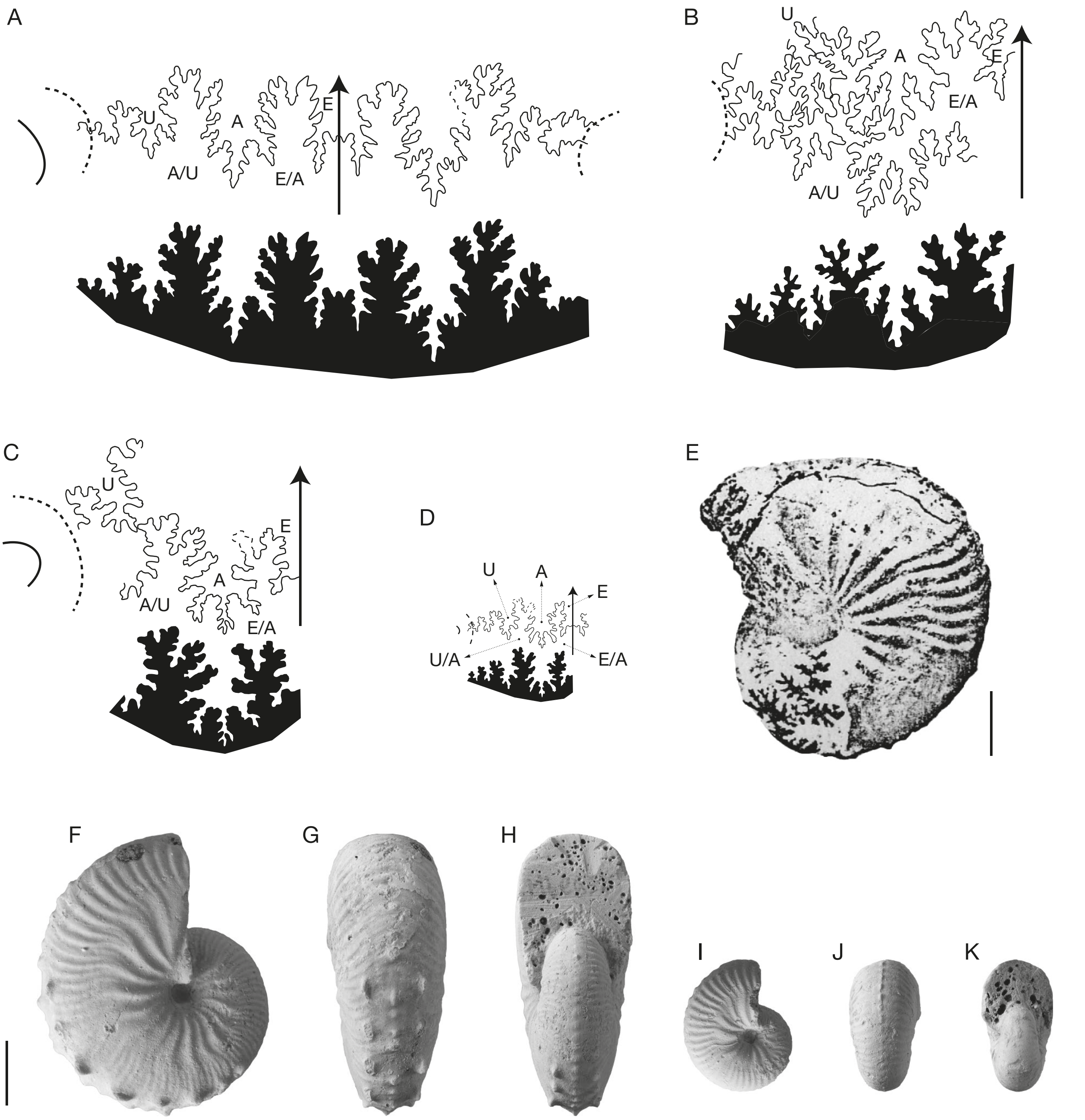

Fig. 7. — **A**, **B**, Suture lines of the studied material of the specimens tentatively assigned to Haploceratoidea Zittel, 1884, fam., gen., and sp. indet., specimens MNHN.F.A99984 (**A**; at H = 16 mm) and MNHN.F.A99988 (**B**; at H = 18 mm); **C**, **D**, suture lines of *Taramelliceras taurimontanum* Erni, 1934 specimens from the late Callovian (*Pseudopeltoceras leckenbyi* Horizon) of Montreuil-Bellay, MNHN.F.A99990 (**C**; at H = 14 mm), MNHN.F.A99991 (**D**; at H = 6.2 mm); **E**, holotype of *T. taurimontanum* (after Erni 1934: fig. 7); **F**-**H**, *Taramelliceras taurimontanum*, MNHN.F.A99990, late Callovian, *Pseudopeltoceras leckenbyi* Horizon, Montreuil-Bellay; **I**-**K**, *Taramelliceras taurimontanum*, MNHN.F.A99991, late Callovian, *Pseudopeltoceras leckenbyi* Horizon, Montreuil-Bellay. **E**, **F**, **I**, lateral views; **G**, **J**, ventral views; **H**, **K**, apertural views. **Arrows**, middle of the venter. Scale bars: 10 mm. Drawings: Romain Jattiot; photos: F-K, Philippe Loubry.

Finally, it here appears important to underline that there are known cases of abnormal ammonoid specimens that were mistaken for regular taxa; one of the most striking examples of such misinterpretations being the invalid ammonoid subfamily "Monestieriinae" Sapunov, 1965, which is based on an abnormal Grammoceratinae Buckman, 1904 (Morard 2002). In turn, the present case study appears as a strong reminder that much care must be taken when in presence of ammonoid material exhibiting unusual shell geometry and/or ornamentation.

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