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Didier NÉRAUDEAU, Baptiste COUTRET, Damien GENDRY,
Bastien LESAGE, Alfredo LOI & Marc POUJOL

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Elliptical body fossils from the Fortunian (Early Cambrian) of Normandy (NW France)

Didier NÉRAUDEAU
Géosciences, Université de Rennes, CNRS, F-35000 Rennes (France)
didier.neraudeau@univ-rennes1.fr (corresponding author)

Baptiste COUTRET
Géosciences, Université de Rennes, CNRS, F-35000 Rennes (France)
and Department of Earth and Atmospheric Sciences, University of Alberta,
Edmonton T6G 2E3 (Canada)

Damien GENDRY
Bastien LESAGE
Géosciences, Université de Rennes, CNRS, F-35000 Rennes (France)

Alfredo LOI
Dipartimento di Scienze della Terra, Via Trentino, 51, 09127 Cagliari (Italy)
alfloi@unica.it

Marc POUJOL
Géosciences, Université de Rennes, CNRS, F-35000 Rennes (France)

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ABSTRACT

Body fossils have been discovered in the Fortunian deposits of the Rozel Cape, in Normandy (NW France). The material consists of about 80 specimens preserved on a shale surface, recently observed at the base of a cliff at the Cap Rozel, in the Cotentin region. The fossils, centimetric in size, have an elliptical outline, with a peripheral bulge, generally without other conspicuous ornamentation, but showing sometimes concentric or radial lines possibly of taphonomic origins. In addition, these body fossils are preserved parallel to the bedding plane, locally rich in horizontal trace fossils (e.g. *Archaeonassa* Fenton & Fenton, 1937, *Helminthoidichnites* Fitch, 1850, *Helminthopsis* Heer, 1877) and also complex treptichinids burrows (e.g. *Treptichnus pedum* (Seilacher, 1955)) sometimes associated with microbial mats. The sedimentological characteristics of these deposits (ripple marks, syneresis cracks) correspond to a shallow marine shelf environment, with a variable hydrodynamism in the intertidal zone, low for surfaces showing elliptic fossils and syneresis cracks, higher for surfaces with ripple marks. These new discoveries unravel the potential of the Fortunian strata from Normandy and provide new information about the early Cambrian biocenoses.

KEY WORDS
Elliptical body fossils,
Fortunian,
Normandy,
NW France.

RÉSUMÉ

Organismes fossiles elliptiques du Fortunien (Cambrien inférieur) de Normandie (NO France).

Des organismes fossiles ont été découverts dans les dépôts d'âge Fortunien, en Normandie (NO France). Le matériel comporte environ 80 spécimens préservés sur une même surface, dans des siltites récemment observées à la base des falaises du Cap Rozel, dans le Cotentin. Les fossiles, de taille centimétrique, ont un contour elliptique, avec un bourrelet périphérique, généralement sans autre ornementation nette, mais comportant exceptionnellement des structures radiales ou concentriques pouvant être d'origine taphonomique. Ces fossiles sont associés à diverses traces fossiles horizontales (e.g. *Archaeonassa* Fenton & Fenton, 1937, *Helminthoidichnites* Fitch, 1850, *Helminthopsis* Heer, 1877), et des terriers complexes de type treptichinides (e.g. *Treptichnus pedum* (Seilacher, 1955)). Les organismes et traces fossiles sont recouverts de mattes algaires. Les caractéristiques sédimentologiques de ces dépôts (rides oscillatoires et unidirectionnelles, fentes de synérèse) correspondent à un environnement de plateforme marine peu profonde, avec un hydrodynamisme variable en zone intertidale, faible pour les surfaces à organismes elliptiques ou fentes de synérèse, plus forte pour les faciès à rides de vagues. Ces découvertes révèlent le potentiel des couches fortuniennes de Normandie et apportent de nouvelles informations fondamentales pour la connaissance des biocénoses du Cambrien basal.

MOTS CLÉS
Organismes fossiles elliptiques,
Fortunien,
Normandie,
NO France.

INTRODUCTION

The Fortunian biota (541-529 Ma) represents the first step of the Cambrian metazoan biodiversification referred as the "Cambrian explosion" (Conway Morris 1989; Erwin *et al.* 2011; Kouchinsky *et al.* 2012). The stratotype defined in Newfoundland, Canada, is located at the Fortune Head locality in the north of the Burin peninsula. The palaeontological content is mainly documented by ichnofossils (e.g. Mángano & Buatois 2017; Laing *et al.* 2019), especially treptichnids like *Treptichnus pedum* (Seilacher, 1955), an ichnospecies long considered as the stratigraphical marker of the Cambrian GSSP (Narbonne *et al.* 1987; Brasier *et al.* 1994). However, treptichnids *lato sensu* (*Treptichnus ichnosp.* indet.) are known in older levels (Buatois 2017) and the Precambrian/Cambrian boundary is not so easy to define. As far as body fossils are concerned, the end of the Fortunian is marked by an increase in Small Shelly Fossils or worm imprints in various areas worldwide (Landing *et al.* 2013), and especially well documented in China (e.g. Shao *et al.* 2015; Zhang *et al.* 2015, 2017).

Fortunian fossilized organisms are documented by several localities throughout the world in addition to the outstanding stratotype. Until now, limited data are available from the western part of Europe and no body fossils have been described from well-dated early Cambrian deposits from France. Only a few elliptical fossils, close to *Nimbia* Fedonkin, 1980, have been mentioned in the Brioverian deposits of Brittany, more likely late Ediacaran in age (Néraudeau *et al.* 2016, 2018; Gougeon *et al.* 2019). However, Normandy (NW France) may be regarded as an optimal geological framework to record early Fortunian organisms. Indeed, the Cotentin peninsula, at the NE of the Armorican Massif, provides large exposures of marine early Cambrian strata (Jenkins 1984). On the one hand, body fossils (archaeocyathids, hyolithids, trilobites) were recorded in the southern and younger outcrops of the local Cambrian, especially near Carteret and Saint-Jean-De-La Rivière (Bigot 1925; Pillola 1993; Doré 1994; Pillola *et al.* 1994; Went 2020; Néraudeau *et al.* pers. obs. 2020) (Figs 1B; 2). On the other hand, a lot of ichnofossils have been found in the northern and older part, of Fortunian age, at the Rozel Cape (Doré *et al.* 1984; Doré 1994; Went 2020).

This paper presents the first potential body fossils from the Fortunian of France, in deposits well dated by the abundance of the ichnostratigraphical index *Treptichnus pedum* and U-Pb zircon dating.

GEOLOGICAL FRAMEWORK

The Cambrian series from the Rozel Cape

The North of the Cotentin peninsula, at the NE of the Armorican Massif, provides large exposures of marine Paleozoic strata (Fig. 1A). On the western coast, the Cambrian series outcrop mainly at the northern and southern parts, Ordovician and Devonian deposits outcropping in the intermediate areas (Fig. 1B). At the north, an Hercynian granitic intrusion has intersected the previous deposits and widely outcroups around Flamanville (Fig. 1B). The Cambrian series are deposited unconformably on top of a volcanic basement (Cadomian orogeny) from the Saint-Germain-le-Gaillard complex, outcropping near the Grosville village (Guerrot *et al.* 1992; Doré 1994) (Figs 1B; 2). On the Rozel Cape cliffs and shore, the contact between the fossiliferous Cambrian strata and the volcanic rocks cannot be observed, the coast being 2 kms away from the basement outcrops.

The Cambrian deposits are progressively younger from the North, at the Rozel Cape (with *Treptichnus pedum*), to the South, on the coast of Carteret and Saint-Jean-de-La Rivière (containing archeocyathids, hyolithids and trilobites) (Fig. 2). At the Rozel Cape, the deposits are mainly sandstones and siltstones, showing many sedimentary structures (ripple marks, syneresis cracks, diagenetic nodules) and sometimes conspicuous microbial mats (Fig. 1C). The elliptical fossils studied herein come from the older Cambrian layers, outcropping on the Rozel Cape coast.

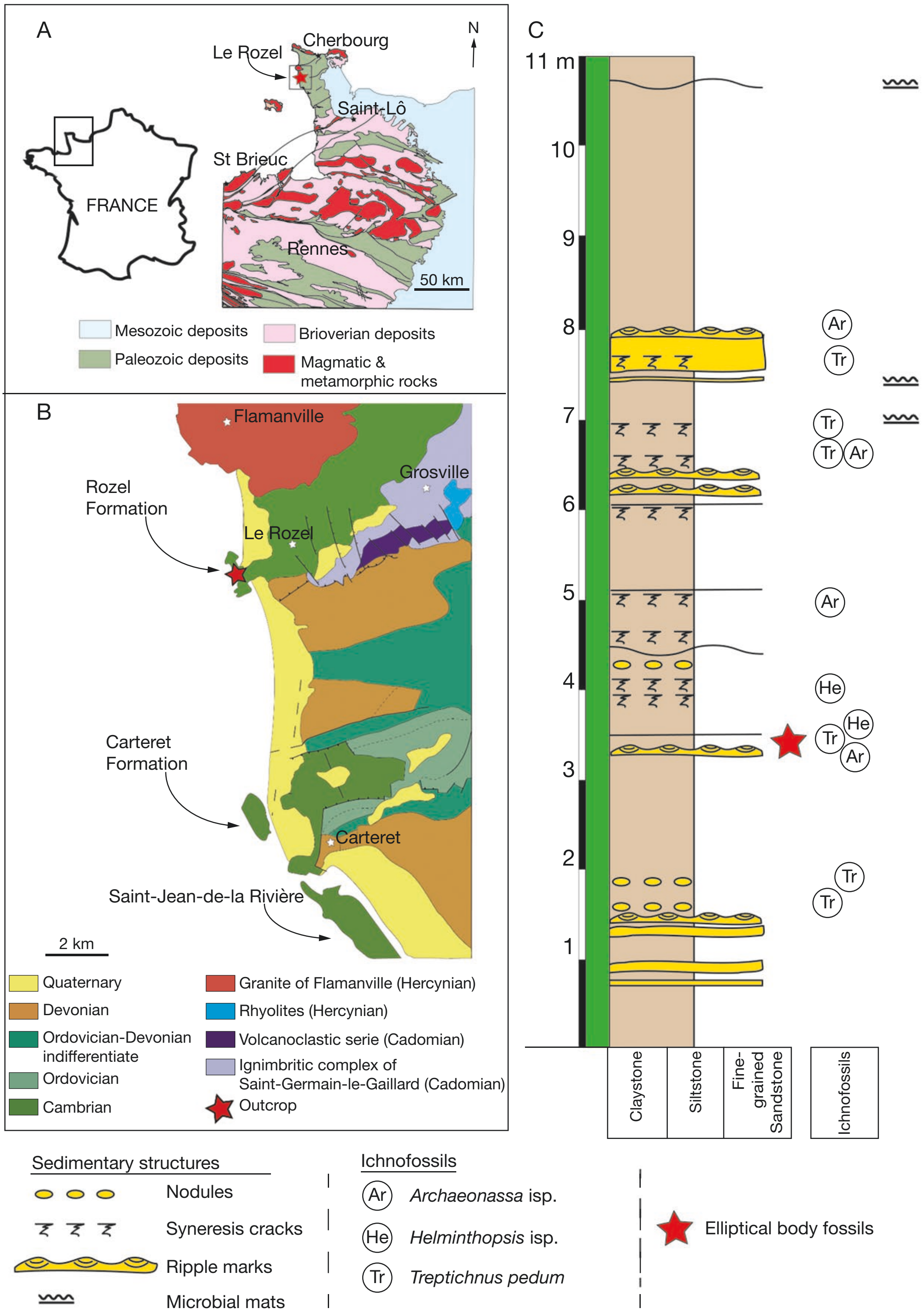

FIG. 1. — **A**, Geological location of the Cambrian fossiliferous outcrops from the Rozel Cape, in Normandy (NW France); **B**, detailed geological map of the Rozel Cape area, with location of the earlymost Cambrian formation of the Rozel Cape and the younger Cambrian formation of Carteret; **C**, simplified sedimentological section of the Rozel Cape with location of the main ichnofossils and the level providing elliptical fossils.

The fossiliferous facies

The fossiliferous layer (Figs 1C; 3B) is located on a fine micaceous siltstone surface (Fig. 1C) extremely rich in well preserved exquisite and various ichnofossils (mainly *Treptichnus pedum*), typical of the early Cambrian (Fig. 4). This layer is about 2 m above two key horizons with large (*c.* 10 cm) diagenetic nodules

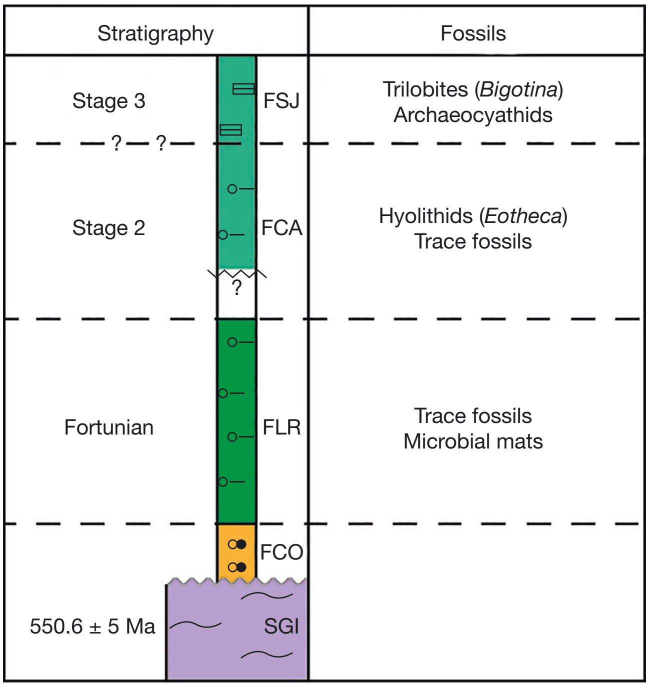

Fig. 2. — Synthetic stratigraphy of the Ediacaran-Cambrian geological units of the Cotentin peninsula, in Normandy (NW France). Abbreviations: **FCA**, siltstones and sandstones of the Carteret Formation; **FCO**, conglomerates and arkoses of the Couville Formation; **FLR**, siltstones and sandstones of the Rozel Cape Formation; **FSJ**, limestones of Saint-Jean-la-Rivière Formation?; **SGI**, ignimbrites complex of Saint-Germain-le-Gaillard; U-Pb dating on zircon gave a radiochronological age about 551 ± 5 Ma. Credits: Doré 1994, modified by the authors.

and 2 m under 5 m of deposits especially rich in syneresis cracks (Fig. 1C). The fossiliferous surface shows a few sedimentary structures due to sedimentary transport processes:

– ripples are present, but of small wavelengths (about 150 mm) and width (about 20 mm), inconspicuous with a very faint relief (Fig. 4A); large and conspicuous ripple marks can be observed on younger (3 m above) and older (2 m under) beds only (Fig. 1C);

– all the elliptical fossils have the same orientation, their alignment by the current being approximately SW-NE and crossing the previous slight ripples with an angle about 45°;

– most of the elliptical fossils have been tilted by the current, their “northern” edge being in relief on the substrate when their “southern” edge is hidden by sediment;

– the cluster of elliptical structures located at the NE of the fossiliferous surface includes several overlappings or repeated slippings of elliptical imprints; specimens have been accumulated either displaced on the substrate surface;

– two isolated elliptical specimens seem out of current effects and are more horizontal, with a more visible complete outline: the first one at the northern part of the shale bed surface (Fig. 4A: 1) and the other one at the southern part, near a treptichnid trace fossil (Fig. 4B: 2);

– two parts of the fossiliferous surface can be distinguished: a part with a lot of ichnofossils and elliptical structures and a part where fossils are rarer but load cast cup imprints very abundant (area in the lower mid part of Fig. 3B, beginning in the left lower side of Fig. 4B).

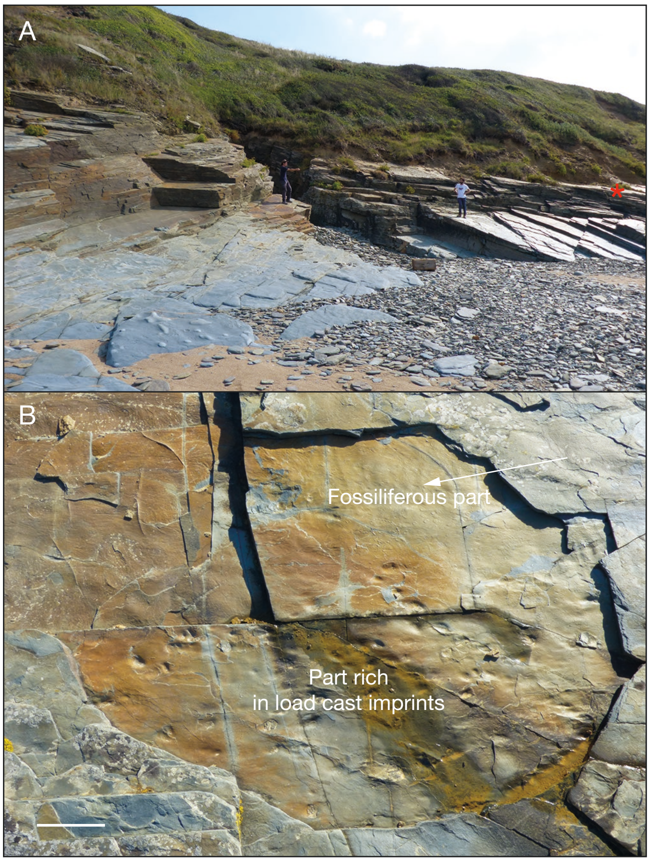

Fig. 3. — General views of the outcrop providing the elliptical fossils: **A**, part of the cliff where have been found the elliptical fossils – the **red star** indicates the level providing the elliptical fossils; **B**, overview of the surface bearing elliptical fossils (they are located in the area pointed by the yellow arrow, in the upper right quarter of the picture). Scale bar: 20 cm. Photo credit: Didier Néraudeau.

Except for the ripple marks present in various levels of the section, above the fossiliferous layer the sediments are rich in syneresis cracks (Fig. 1C). Thus, sedimentary and ichnological characteristics are compatible with a very shallow platform environment, periodically subjected to unidirectional current on a tidal flat area. The activity of the burrow makers and the elliptical fossils preservation took place during mud deposition at low energy levels.

MATERIAL AND METHODS

The elliptical fossils are preserved on a single shale surface, observed at the base of a cliff at the Rozel Cape, during field trips in February 2021 (Figs 1C; 3). The precise location of the fossiliferous outcrop is 49°28’19.46”N, 1°50’42.06”O. The shale surface shares approximately 80 specimens. However, it is difficult to precise their real number because they are more or less complete and covered by sediments (Fig. 4). The specimens are gathered in two clusters, with a first one on the cliff side of the outcrop (Fig. 4A), and the other one on the seaside (Fig. 4B). The total size of the shale bed is about 50 cm long and 30 cm width. The shale bed was collected and is housed at the University of Rennes, in the Collections of the Geological Institute, with the number IGR-23261A.

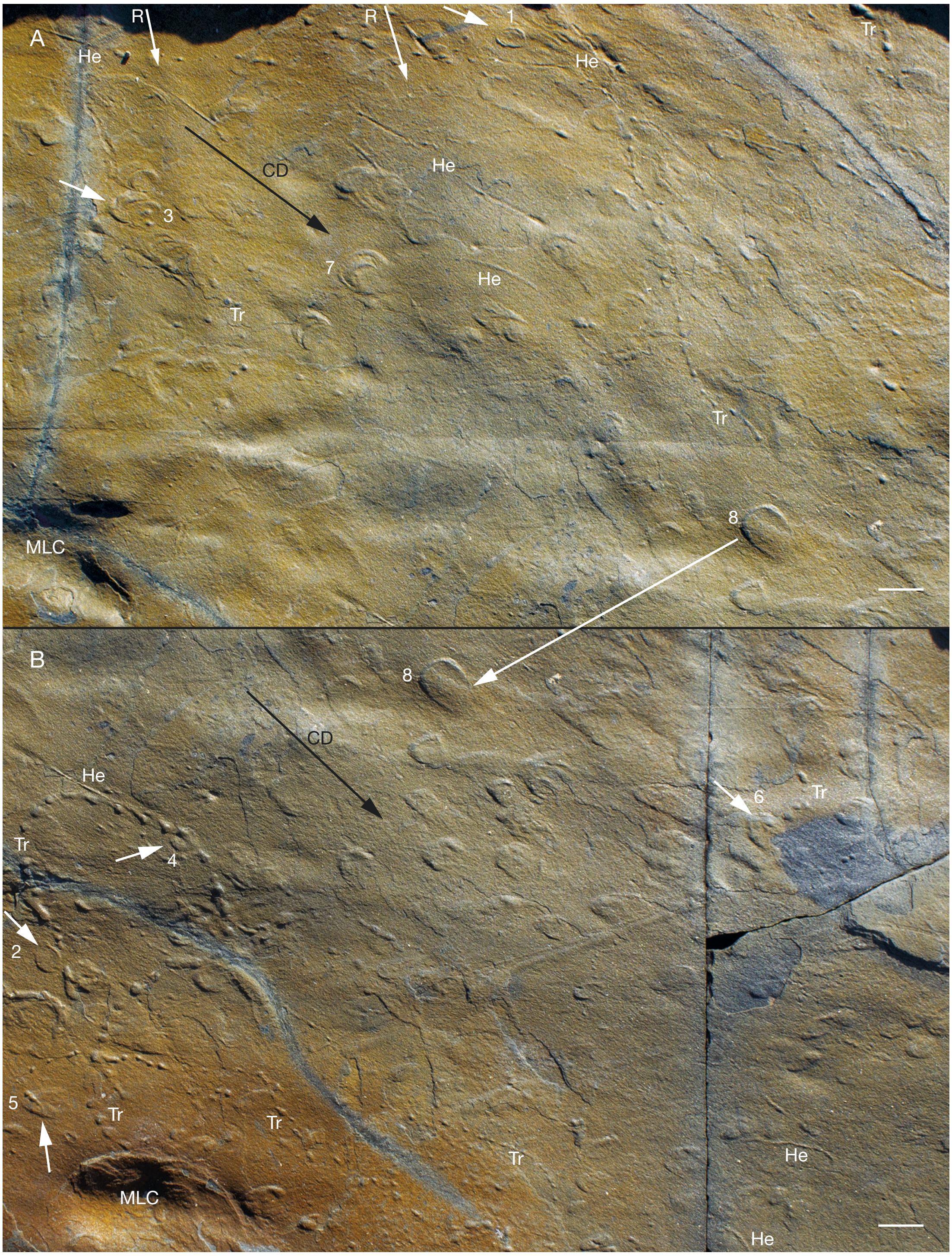

Fig. 4. — Details of the shale surface providing the two clusters of elliptical fossils: **A**, cluster on the cliff side where several elliptical structures are “duplicated” (overlapping or rebound) and are associated to slight ripples, and trace fossils, some burrows “piercing” previous body fossils imprints (specimen 3), a single elliptical structure being almost complete (specimen 1); a load cast from a younger layer deform the elliptical fossils bearing surface; **B**, cluster on the sea side where several elliptical structures are associated to trace fossils, some burrows “piercing” or crossing previous body fossils imprints (specimens 4, 5, 6), a single elliptical structure being almost complete (specimen 2); a load cast from a younger layer deform the elliptical fossils bearing surface. Abbreviations: **CD**, current direction; **He**, *Helminthopsis* Heer, 1877 or *Helminthoidichnites* Fitch, 1850 segments; **MLC**, load cast; **R**, slight ripples; **Tr**, *Treptichnus* Miller, 1889. Scale bars: 20 cm. Photo credit: Didier Néraudeau.

A thin section of the fossiliferous shale (IGR-23261B) has been realized, crossing three elliptical fossils, to understand if they are surface reliefs only or 3D structures.

A sample (GRO21-2) from the Saint-Germain-le-Gaillard ignimbrite was collected in a small quarry along the road D367 (49°31’02.1”N/1°44’16.6”O), near the Grosville village

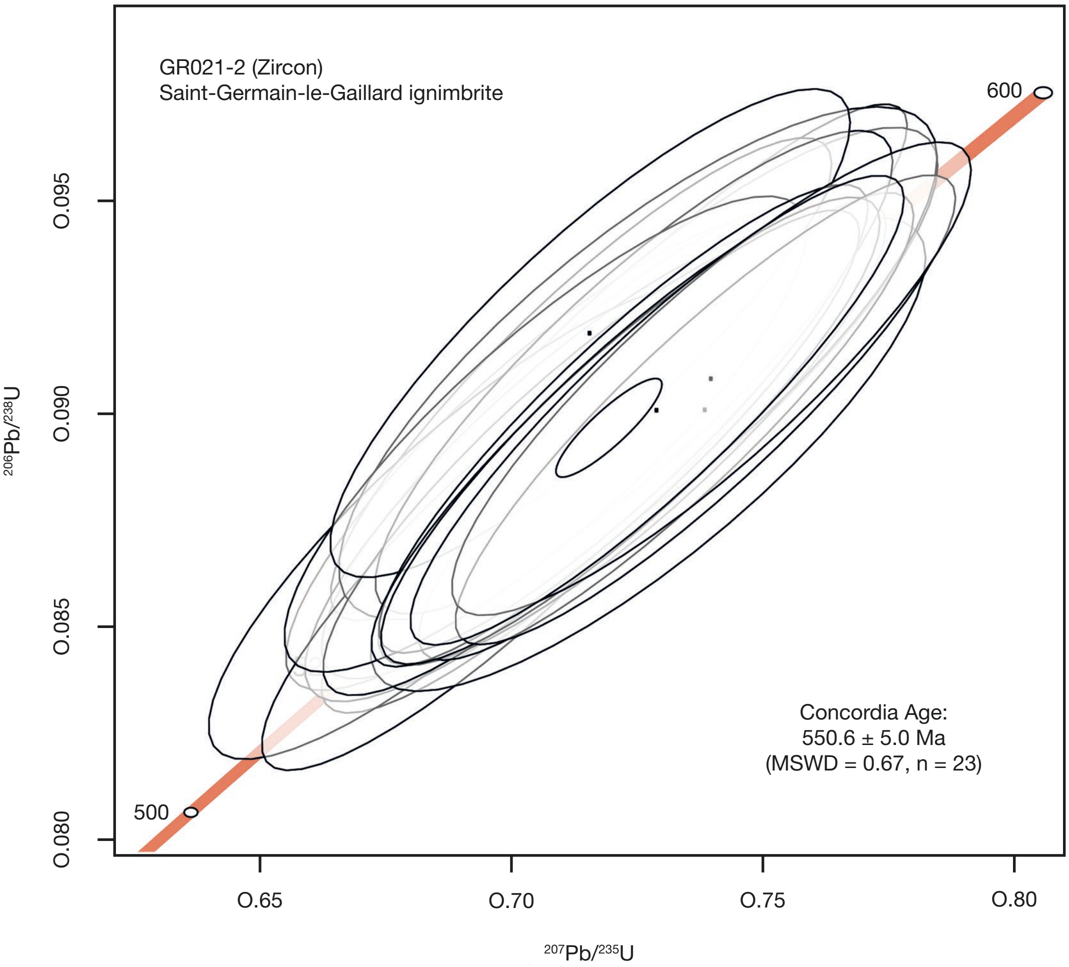

FIG. 5. — Wetherill U-Pb concordia diagram for the zircon grains from the Saint-Germain-le-Gaillard ignimbrite.

(Fig. 1). After the crushing and the mineral separation, magmatic zircon grains were mounted in an epoxy puck, polished to expose their inner parts and imaged by cathodoluminescence. The U-Pb dating was performed in the GeOHeLiS analytical platform (Université de Rennes) by laser ablation ICP-MS (LA-ICP-MS). More information on the analytical protocol can be found in Manzotti *et al.* (2015) and in Appendix 1.

GEOCHRONOLOGICAL CONSTRAINTS

Twenty-three analyses were acquired on 20 different zircon crystals (Appendix 2). Reported in a Wetherill's concordia diagram (Fig. 5), they all plot in a concordant position yielding a concordia age of 550.6 ± 5 Ma (MSWD (conc+Equiv) = 0.67, n = 23) that we interpret as the emplacement age for this volcanic flow. This age is within error of the poorly constrained evaporation age of 531 ± 20 Ma (Guerrot *et al.* 1992), demonstrating that the volcanic activity in the region took place during the late Ediacaran. As the fossiliferous sediments from the Rozel Cape were unconformably deposited on top of these ignimbrites, their oldest possible deposition age is therefore late Ediacaran.

The suite of the sedimentation of the Rozel Cape outcrops 10 kms to the south, in the Carteret coast (Fig. 1B) where it has been dated to the lower and mid-Cambrian by stratigraphical fossil index such as hyolithids and trilobites (Pillola *et al.* 1994).

Thus, the Cambrian deposits from the Rozel Cape are older than Cambrian series containing hyolithes or trilobites and younger than 550 Ma ignimbrites basement. Consequently, the Rozel Cape fossils can only be the earliest Cambrian in age, probably Fortunian.

Biostratigraphically, complex burrows such as *Treptichnus pedum* (Dzik 2005), typical of the base of the Cambrian, are abundant in the Fortunian strata from Rozel Cape and are associated to simple horizontal trails on the shale bed surface with the elliptical fossils studied in this paper.

ICHNOFOSSILS AND MICROBIAL MATS

ICHNOLOGY

Trace fossils are associated with the elliptical fossils. The first part of the ichnofossils corresponds to elongated, straight (*Helminthoidichnites* Fitch, 1850) to slightly meandering (*Helminthopsis* Heer, 1877) horizontal trails, with a constant millimetric diameter

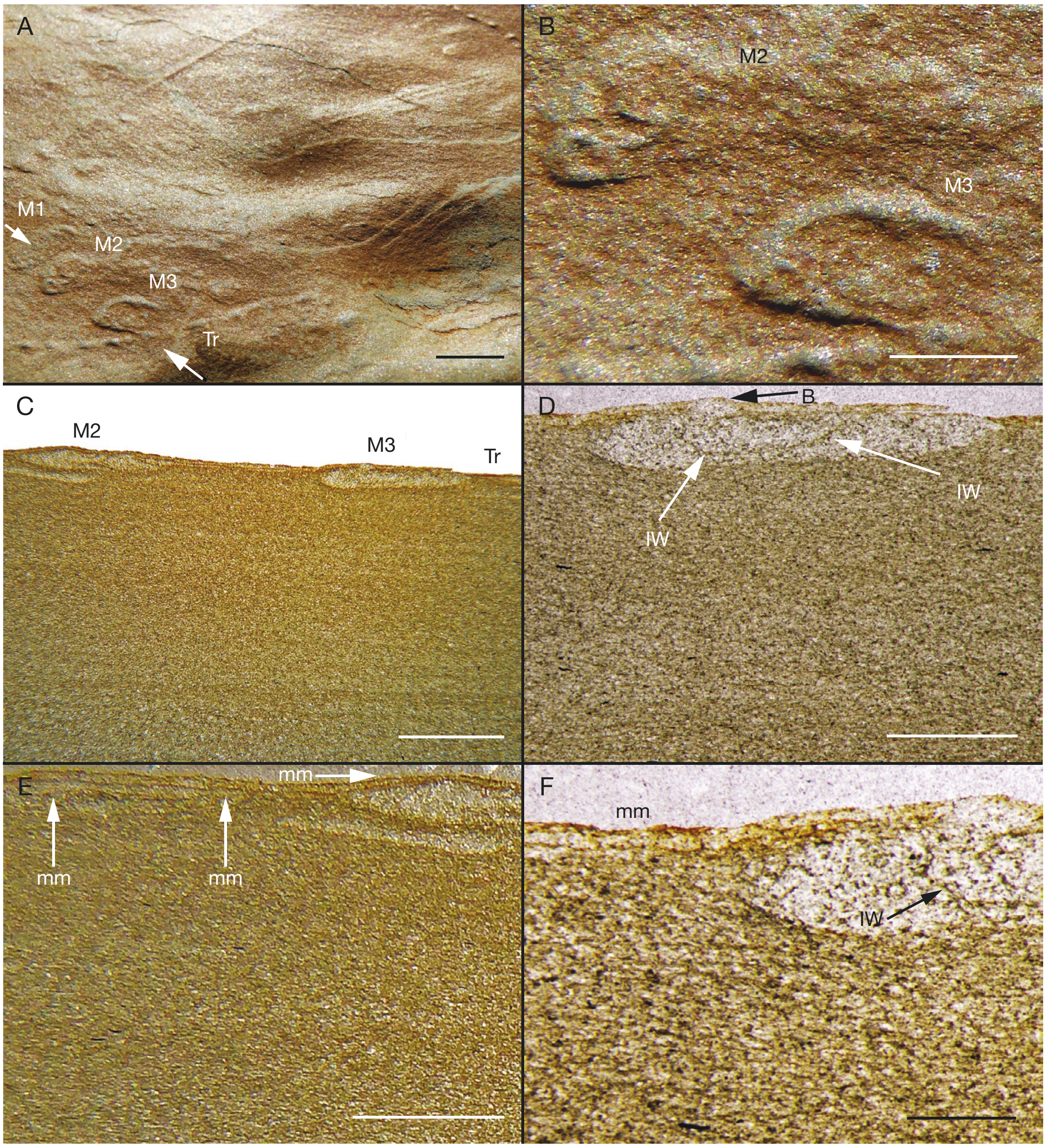

Fig. 6. — Thin section (IGR-23261B) of elliptical fossils from the Fortunian of the Rozel Cape, Normandy: **A**, general view of the shale part where the thin section has been realized, between the two arrows; the section crosses three specimens (M1, M2, M3) and one treptichnid ichnofossil; **B**, zoom on the two main specimens (M2, M3) crossed by the thin section, and the adjacent treptichnid; **C**, general view of the thin section showing the profile of the elliptical fossils M2 and M3 and the adjacent treptichnid, deposited on fine-grained sediment made of quartz and phylosilicates; phyllosilicates are lacking in the inner structure of the elliptical fossils; **D**, zoom on the specimen M3, showing its "pancake" shape covered by a microbial mat, excepted the arched bulge (B) visible in surface (A, B), and inside a structure delimited by an inner wall; **E**, zoom on the left side of the specimen M2 showing its covering by a microbial mat made of three layers (a clear layer one between two brownish ones); **F**, high magnification on the specimen M3 (with position of its inner wall), showing that the microbial mat does not coat the elliptical fossil. Abbreviations: **IW**, inner wall; **mm**, microbial mat; **Tr**, treptichnid ichnofossil. Scale bars: A, 10 mm; B, C, 5 mm; D, E, 2 mm; F, 1 mm. Photo credit: Didier Néraudeau.

("He" on Fig. 4). A few horizontal trails with lateral levees have a larger, plurimillimetric, diameter (*Archaeonassa* Fenton & Fenton, 1937). Other ichnofossils correspond to varying typical treptichnids, with a rectilinear ("Tr" on Fig. 4A) or an arched arrangement ("Tr" on Fig. 4B). When arched, their alignment constitutes an oval arrangement of 2.5 by 2 cm. It can be noticed that the two areas where elliptical fossils are numerous and make clusters are close to *Helminthopsis* and *Helminthoidichnites* when the areas rich in treptichnids are very poor, but not devoid, of elliptical specimens, a complete elliptical structure being close to *Treptichnus* Miller, 1889 (Fig. 4B: specimen 2), and a few other ones being crossed by treptichnid burrows (Fig. 4A: specimen 3; B: specimens 4- 6). As treptichnids "pierce" the elliptical fossils, it can be concluded that these burrows were realized after a first step of body fossil preservation.

Microbial mats

Like in Present-day marine environments, the Fe oxidation of the bedding surface bearing elliptical fossils can be related to a microbial mat (Chan *et al.* 2016). A thin section of the fossiliferous layer, crossing three elliptical fossils (Fig. 6A, B) and a treptichnid, reveals a triple layer mat, with a clear lamina between two dark, brownish laminae (Fig. 6C-F). The mat covers the elliptical fossils and could have played a key role in the preservation of these structures very uncommon in the Cambrian series from the Rozel Cape. The elliptical fossils are not microbial mat folds or fragments, nor elliptical holes in a microbial mat due to gas bubbles, like the ones illustrated by Davies *et al.* (2016: fig. 10G). Finally, no conspicuously wrinkled mats, observed in overlaying layers (Fig. 1C), can be distinguished in association with the elliptical fossils.

ELLIPTICAL FOSSILS

Description

The elliptical fossils from the Rozel Cape have been deposited on a fine-grained mud, without load effect deforming the sediment, and cannot be confused with load casts (Fig. 6C-F). They have the same SW-NE orientation by currents, but are not lengthened by elongated impressions that characterize flute casts and tool marks (Figs 4; 6A; 7A, B). They correspond to both reliefs on the shale surface and 3D structures within the sediment. They have a “pancake” shape in section view, with an unconspicuous inner wall and a clear sedimentary content different from the surrounding sediment, darker and richer in phyllosilicates with a sub-horizontal arrangement (Fig. 6C-F). The zoom observation of the thin section, both in natural and polarized light, shows that the phyllosilicates are present with various orientations within the elliptical fossils and correspond to a re-crystallization and not to a sedimentary filling. The elliptical fossils are relatively irregular in size, ranging between 5 mm and 12 mm in length. However, their precise size is sometimes difficult to measure, when their right end (SE, according to the orientation on Fig. 6A; 7A, B, D) slightly dives or disappears in the sediment (Fig. 6B). They are often slightly tilted by the currents in the mud, like the similar specimens from the Brioverian of Brittany described by Néraudeau *et al.* (2018) (Fig. 7G, H). Their thickness, about 0.8-1 mm, generally increases and forms a larger bulge on the upstream side (on the left of the section) (Fig. 7D-F). The bulge crosses partly the microbial mat covering (Fig. 6C, D). On the shale surface, the peripheral bulge is 1 to 2 mm in width, and surround a large central disc, generally flat or slightly depressed (Figs 6; 7C, E).

The elliptical fossils stand on a single sediment surface, but are not regularly spaced, with two main clusters and a few isolated specimens. The first cluster, located at the NW of the shale bed surface, is composed of specimens with a conspicuous peripheral bulge, some imprints seeming to overlap other ones (Fig. 7A, B, E, F). It is difficult to distinguish between two possibilities: first, it corresponds to the real overlapping of several specimens, gathered by the current; secondly a single elliptical fossil produced several imprints, after repeated slipping. The second cluster, located at the SE of the shale bed surface, is composed of specimens with a less conspicuous peripheral bulge and a more variable shape. The more conspicuous and complete specimens are relatively small (6 mm), uncommon and isolated near treptichinid trace fossils (Fig. 4: 1, 2). Apart from these small, isolated specimens, the elliptical fossils have the same orientation and the same NW-SE axis of elongation in their clusters, with always the northern part conspicuous with a crescent of marginal bulge on the upstream side.

DISCUSSION

According to their conspicuous elliptical outline and “pancake” profile, their permanent peripheral bulge, their little variable size, and their overlappings, the fossils of the Rozel Cape cannot correspond to sedimentary structures such as load cast or groove casts, or even raindrop imprints, and no more to surface openings of burrows (e.g. *Monocraterion* Torell, 1870; Schlirf & Uchman 2005).

According to their single peripheral bulge, without ornamentation, elliptical fossils from the Rozel Cape clearly differ from typical Ediacaran discoid fossils such as *Aspidella* Billings, 1872, *Cyclomedusa* Sprigg, 1947, *Liaonanella* Liu & Yang, 1988, *Marsonia* Raghav et al., 2005 and *Medusinites* Sprigg, 1949 which show strong concentric lines or regular radial structures (Wade 1972; Narbonne & Hofmann 1987; Narbonne & Aitken 1990; McCall 2006; Zhang *et al.* 2006; McGabhann 2007; Kumar & Ahmad 2012; Burzynski & Narbonne 2015; Tarhan *et al.* 2015). The “pseudo-concentric” lines observed on few specimens from Le Rozel correspond to overlapping or repeated slipping of their elliptical imprints (Fig. 7A, B, E, F). The overlappings and slippings group generally two (Fig. 7E, F) to four or five specimens (Fig. 7A, B), with 220 to 280° of they elliptical outline being conspicuous. It is clearly different from the linear series of numerous arches or lobes forming the fossil *Palaeopascichnus* Palij, 1976 (Palij 1976; Dong *et al.* 2022). The fossils from the Rozel Cape more likely correspond to elliptical organisms accumulated on fine sediment surface. The unconspicuous radial lines observed between two consecutive concentric bulges (overlapping or repeated slipping) of a single specimen are probably linked to slipping and taphonomic folds of its body (central specimen of Fig. 7A, F).

The low thickness, the peripheral bulge and the lack of a deep central depression differentiate the Fortunian specimens of Normandy from the Intrites punctatus of Ediacaran deposits of United Kingdom and from the very variable and unconspicuous “*Medusinites* aff. *asteroides*” from the same outcrops (McIlroy *et al.* 2005; Liu 2011).

The elliptical outline, the thick peripheral rim and the lack of both fine concentric lines and dome shape challenge an affinity with most of the convex rounded fossils corresponding to *Beltanelloides*-like structures such as the *Beltanelliformis*, *Beltanelloides*, and *Nemiana* known from the Ediacaran-Cambrian transition in South America (*Beltanelloides* sp. from Argentina; Aceñolaza & Aceñolaza 2005), in North America (*Beltanelliformis brunsae* Menner *in* Keller, Menner, Stepanov & Chumakov, 1974 from Canada; Hofmann *et al.* 1983; Narbonne & Hofmann 1987; McCall 2006), in China (*Beltanelliformis* sp.; Xiao *et al.* 2013), in Europe (*Beltanelliformis minutae* McIlroy *et al.*, 2005 and *B. brunsae* from United Kingdom; McIlroy *et al.* 2005; *B. brunsae* from United Kingdom; Liu 2011; *B. brunsae* from Romania; Saint

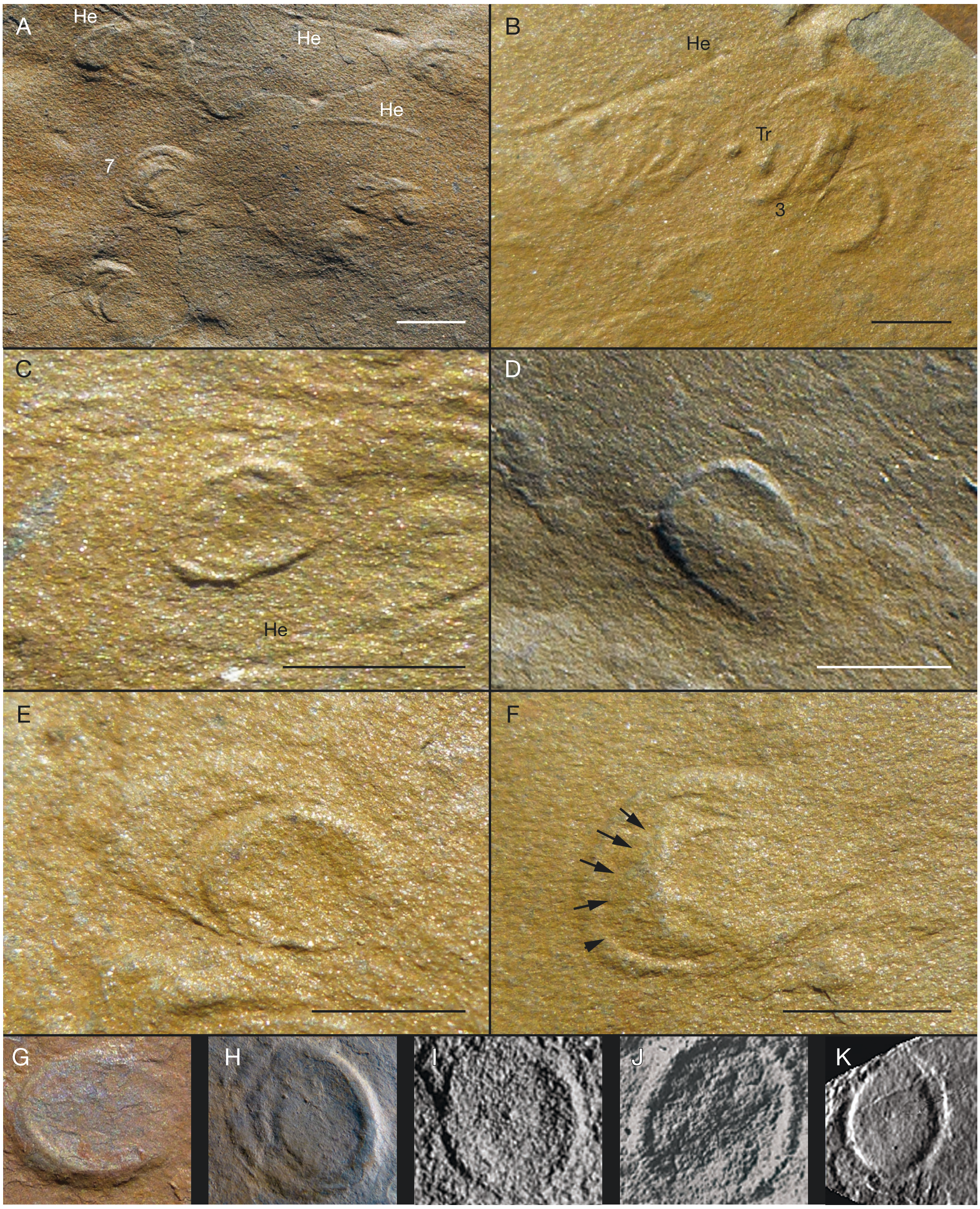

Fig. 7. — **A**-**F**, *Nimbia* sp., Fortunian of the Rozel Cape, Normandy, shale IGR-PAL-23261: **A**, cluster with several elliptical fossils showing overlapping or/and slipping, close to *Helminthoidichnites* trace fossils. The specimen no. 7 from Figure 4 shows unconspicuous radial lines; **B**, group of specimens showing overlapping or/and slipping, with some of them crossed by the pustular structures of treptichnids, along a *Helminthoidichnites* Fitch, 1850 trace fossil; **C**, almost complete specimen (no. 1 in Fig. 4) with its peripheral bulge, close to a *Helminthoidichnites* trace fossils; **D**, specimen with a single crescentic bulge (no. 8 in Fig. 4); **E**, **F**, specimens with overlapping or slipping showing pseudo-concentric arched lines; the specimen of picture F (no. 7 from Fig. 4) shows unconspicuous radial lines (pointed by the **arrows**) on its left side; **G**, **H**, *Nimbia* sp., Brioverian of Saint-Gonlay, Brittany, shale IGR-PAL-2778: **G**, specimen IGR-PAL-2778a; **H**, specimen IGR-PAL-2778b; each specimen size is about 10 mm; **I**-**K**, specimens of *Nimbia* published in previous works (their sizes vary from a few millimeters to almost two centimeters): **I**, type specimen from Siberia; **J**, specimen from West Africa; **K**, specimen from Kazakhstan. Abbreviations: **He**, *Helminthoidichnites*; **Tr**, treptichnids. Photo credits: A-H, Didier Néraudeau; I, Fedonkin 1980; Fedonkin *et al.* 2007; J, Bertrand-Sarfati *et al.* 1995; K, Meert *et al.* 2011. Scale bars: 1 cm.

Martin & Saint Martin 2018), and in Siberia (*Beltanelliformis sorichevae* Sokolov, 1965; Leonov & Rud'ko 2012; Ivantsov *et al.* 2014) or Ukraine (*Nemiana simplex*; Leonov 2007).

The flat elliptical fossils observed at the Rozel Cape strongly differ from the lower Cambrian plug-shape burrow *Bergaueria*, such as *Bergaueria perata* Prantl, 1945 or *B. langi* (Hallam, 1960) (Jensen 1997; Paczesna 2010; Hosgör & Yilmaz 2018). In fact, *Bergaueria* is present in Le Rozel Formation within the siltstone bearing the elliptical structures and are clearly different (Coutret *et al.*, in prep). However, the ichnospecies *B. sucta*

Seilacher, 1990, corresponding doubtfully to the same ichnogenus, is rather similar to the specimens from the Rozel Cape according to their subcircular disc shape displaying laterally a repeated pattern of crescent-shaped impressions (Hofmann *et al.* 2012), but without a conspicuous peripheral bulge. *Bergaueria sucta* has probably to be considered as an ichnological species belonging to another ichnogenus than *Bergaueria*, considered as a short, plug-shaped, vertical sea anemone burrow (Prantl 1945; Pickerill 1989; Lima & Netto 2012), and not as the imprint of the disc shape base of an actinian cnidarian, as suggested by Seilacher (1990), the laterally repetitive crescentic pattern recording the sideway-migration of the trace-maker.

Finally, according to their elliptical shape, their conspicuous peripheral rim, their size, and the lack of central depression, the Fortunian elliptical fossils from Normandy are similar to the Cambrian discoidal structures from New Brunswick (Hagadorn & Miller 2011: fig. 4g, h), and the elliptical fossils from California (Sappenfield *et al.* 2017: fig. 3h). In addition the fossils described herein are close to *Nimbia* occlusa from the White Sea, in Russia (Fedonkin 1980; Fedonkin *et al.* 2007; Fig. 7A, B), or from the Ediacaran of Africa (Bertrand-Sarfati *et al.* 1995; Fig. 7C), Kazakhstan (Meert *et al.* 2011; Fig. 7D) and Nevada (Hagadorn & Waggoner 2000), even to other specimens without central tubercle (Crimes & McIlroy 1999; Fig. 3C; McGabhann 2007). However, they are different from the *Nimbia* from Brazil (Becker-Kerber *et al.* 2020) and East Siberia (Liu *et al.* 2013), much bigger and circular (about 30 mm and 80 mm respectively), and the *Nimbia* occlusa from Eire that have a large central tubercle (Crimes *et al.* 1995). The Fortunian specimens from Normandy are finally close to the elliptical structures recently described from the Ediacaran-Fortunian beds (Brioverian) from Brittany, putatively referred to "*Nimbia*-like" fossils (Fig. 7E, F) (Néraudeau *et al.* 2018).

The biological attribution of *Nimbia* is not consensual and different interpretations are possible. *Nimbia* was generally viewed as a cnidarian (Fedonkin 1980; Sepkoski 2002; Meert *et al.* 2011) or as a microbial mat structure (Grazhdankin & Gerdes 2007; Liu *et al.* 2013). Sometimes *Nimbia* as been interpreted as a scratch circle formed by the site of attachment of organisms (Jensen *et al.* 2002). However, various elliptical fossils were named *Nimbia* and the genus is probably a catch-all term. Consequently, Erwin *et al.* (2011) removed the three classical species of the genus (*N. dniestrei*, *N. occlusa*, *N. paula*) from their phylogenetic analysis of the Ediacaran biota because they consider the taxa poorly or incorrectly described.

The *Nimbia* occlusa from Eire, interpreted as scratch circles by Jensen *et al.* (2002), were previously interpreted as transported rigid-bodied fossils by Crimes *et al.* (1995) and correspond to two possibilities linked to body fossils. But generally, the alternative is between a "medusoid" body fossil option and a microbial mat one.

Grazhdankin & Gerdes (2007) have considered that many enigmatic discoïdal fossils from the Neoproterozoic, such as *Cyclomedusa* or *Paliella*, are microbial mats only, when Young & Hagadorn (2020) have concluded that medusan preservation is attested for Cambrian strata but not for Neoproterozoic ones. Unfortunately, these two last publications do not illustrate their conclusion by any microstructural observation provided by thin sections or Microtomographic Imaging of the fossils. Even if their conclusions are questionable, they refer to Ediacaran circular or elliptical fossils very different in shape and size of the small, centimetric and non-concentric typical *Nimbia sensu* Fedonkin (1980). On the other hand, the big non-concentric Ediacaran *Nimbia* published by Liu *et al.* (2013) as microbial mats do not correspond to the centimetric elliptical fossils from the Brioverian of Brittany and the Fortunian of Normandy. Overall, by combining both observations from thin sections or microtomography, the elliptical fossils reveal 3D structures with a "pancake shape", clearly covered by a microbial layer, but not corresponding to a fold, a fragment, or a development of a microbial mat, nor a sedimentary structure as a load cast. We tentitavely consider the elliptical fossils from the Rozel Cape as body fossils, possibly ctenarian comb jellies such as the modern *Pleurobrachia pileus* (O.F. Müller, 1776), also named "sea gooseberry", a centimetric and ovoid gelatinous animal.

The deposit environment of the *Nimbia*-like fossils from the Rozel Cape was coastal and shallow, according to the abundance of ripple marks and syneresis cracks at different levels in the geological formation. It is difficult to compare the palaeoenvironmental characteristics of these body fossils with the ones of the previously published specimens because various fossil structures have been named *Nimbia* (see above). *Nimbia*-like fossils are known generally in shallow water sequences, but Crimes *et al.* (1995), mentioned deep-water habitat for the Eire specimens with a central tubercle. However, at the scale of the Armorican Massif, the Fortunian *Nimbia* from Normandy had probably a slightly shallower habitat than the ones from the Ediacaran of Brittany, found in sedimentry series poor in ripple marks and devoid of syneresis cracks (Néraudeau *et al.* 2018).

CONCLUSIONS

The body "pancake" fossils from the Rozel Cape are slightly elliptical with a pancake profile, a peripheral bulge and a centimetric size. In addition they have a dominant orientation and the composition of their filling is like the surrounding sediments. According to the characteristics previously described, we assume that the elliptical fossils from the Rozel Cape cannot be interpreted as surface sedimentary structures (e.g. load-cast imprints), nor as burrow openings. Therefore, we suggest that they could be interpreted as body fossils close to the genus *Nimbia*, previously related to elliptical fossils found in late Ediacaran-Fortunian deposits from Brittany, approximately 200 km away from the Rozel outcrop. U-Pb dating on magmatic zircon grains extracted the Saint-Germain-le-Gaillard ignimbrite yields a late Ediacaran (*c.* 550 Ma) maximum deposition age for this sample, a result compatible with an early Cambrian age for this fossiliferous shale. This new discovery reveals the interest of the Cambrian series from Normandy to investigate the biodiversity evolution around the Ediacaran-Cambrian boundary in NW Europe.

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Appendices

Appendix 1. — Operating conditions for the LA-ICP-MS equipment.

Laboratory & sample preparation	
Laboratory name	GeOHeLiS Analytical Platform, OSUR, University of Rennes 1, France
Sample type/mineral	Magmatic Zircon
Sample preparation	Individual crystals mounted in an epoxy puck
Imaging	CL: RELION CL instrument, Olympus Microscope BX51WI, Leica Color Camera DFC 420C
Laser ablation system	
Make, Model & type	ESI NWR193UC, Excimer
Ablation cell	ESI NWR TwoVol2
Laser wavelength	193 nm
Pulse width	<5 ns
Fluence	5.4 J/cm2
Repetition rate	4Hz
Spot size	30 µm
Sampling mode / pattern	Single spot
Carrier gas	100% He, Ar make-up gas and N2 (3 ml/mn) combined using in-house smoothing device
Background collection	20 seconds
Ablation duration	60 seconds
Wash-out delay	15 seconds
Carrier gas flow (He)	0.80 l/min
ICP-MS Instrument	
Make, Model & type	Agilent 7700x, Q-ICP-MS
Sample introduction	Via conventional tubing
RF power	1350 W
Sampler, skimmer cones	Ni
Extraction lenses	X type
Make-up gas flow (Ar)	0.85 l/min
Detection system	Single collector secondary electron multiplier
Data acquisition protocol	Time-resolved analysis
Scanning mode	Peak hopping, one point per peak
Detector mode	Pulse counting, dead time correction applied, and analog mode when signal intensity > ~ 106 cps
Masses measured	204(Hg + Pb), 206Pb, 207Pb, 208Pb, 232Th, 238U
Integration time per peak	10-30 ms (207Pb)
Sensitivity / Efficiency	23000 cps/ppm Pb (50 µm, 10 Hz)
Data Processing	
Gas blank	20 seconds on-peak
Calibration strategy	GJ1 zircon standard used as primary reference material, Plešovice used as secondary reference material (quality control)
Common-Pb correction, composition and uncertainty	No common-Pb correction.
Reference Material info	GJ1 (Jackson *et al.* 2004), Plešovice (Sláma *et al.* 2008)
Data processing package	Iolite (Paton *et al.* 2010)
Uncertainty level and propagation	Ages are quoted at 2 sigma absolute, propagation is by quadratic addition according to Horstwood *et al.* (2016). Reproducibility and age uncertainty of reference material are propagated.
Quality control / Validation	Plešovice: concordia age = 339.9 ± 4.5 Ma (n = 6; MSWD (conc + Equiv) = 0.94)

Appendix 2. — U-Pb data obtained on the zircon grains from the Saint-Germain-le-Gaillard ignimbrite. f206c % = (207Pb/206Pbm – 207Pb/206Pb*)/(207Pb/206Pbc – 207Pb/206Pb*) x 100; if Age206Pb/238U < 1000 Ma concordance % = (Age206Pb/238U / Age207Pb/235U) * 100; else concordance % = (Age207Pb/235U / Age207Pb/206Pb) * 100. Uncertainties on ages include secondary standard uncertainty propagation as proposed by Horstwood *et al.* 2016.

19 May 2021, GeOHeLiS Platform, Université de Rennes 1						Data for Tera-Wasserburg plot					Data for Wetherill plot					Dates						
Identifier	Grain number	f206c %	Uppm	Th/U	Pbppm	238U/ 206Pb	2se%	207Pb/ 206Pb	2se%	rho	207Pb/ 235U	2se%	206Pb/ 238U	2se%	Rho	207Pb/ 206Pb	2se (abs)	206Pb/ 238U	2se (abs)	207Pb/ 235U	2se (abs)	% conc
Sample GR21-2																						
S-190521a-01.d	Zr 1	0,00	399	0.09	93	11.31	5.0	0.05795	4.0	0.37	0.7109	5.6	0.08839	5.0	0.89	527	87	546	26	545	23	100.1
S-190521a-02.d	Zr 2	0.00	1056	0.15	365	10.91	5.0	0.05769	3.8	0.19	0.7295	5.5	0.09167	5.0	0.91	517	83	565	27	556	23	101.6
S-190521a-03.d	Zr 3	0.00	281	0.15	94	11.23	5.1	0.05835	4.5	0.35	0.7061	5.9	0.08907	5.1	0.86	542	99	550	27	542	25	101.4
S-190521a-04.d	Zr 4	0.00	325	0.25	185	11.19	5.1	0.05845	4.4	0.39	0.7128	5.8	0.08936	5.1	0.87	546	97	552	27	546	25	101.0
S-190521a-05.d	Zr 5	0.00	233	0.12	65	10.98	5.1	0.05882	4.7	0.38	0.7310	6.0	0.09105	5.1	0.84	559	103	562	27	557	26	100.8
S-190521a-06.d	Zr 6	0.00	789	0.16	282	11.01	5.1	0.05773	4.1	0.34	0.7138	5.7	0.09082	5.1	0.89	518	89	560	27	547	24	102.5
S-190521a-07.d	Zr7a	0.00	214	0.16	80	11.26	5.1	0.05824	4.5	0.40	0.7102	5.9	0.08879	5.1	0.86	538	98	548	27	545	25	100.6
S-190521a-08.d	Zr7b	0.00	314	0.29	204	11.43	5.2	0.05815	4.7	0.36	0.6914	6.1	0.08746	5.2	0.86	534	102	541	27	534	25	101.3
S-190521a-09.d	Zr8	0.00	374	0.09	80	11.48	5.1	0.05773	4.2	0.40	0.6991	5.7	0.08707	5.1	0.89	518	93	538	26	538	24	100.0
S-190521a-10.d	Zr9	0.12	80	0.26	51	11.23	5.1	0.05952	4.8	0.34	0.7271	6.2	0.08905	5.1	0.83	585	105	550	27	555	26	99.1
S-190521a-11.d	Zr10	0.06	285	0.17	121	11.16	5.0	0.05915	4.2	0.38	0.7239	5.7	0.08958	5.0	0.88	572	91	553	27	553	24	100.0
S-190521a-12.d	Zr11	0.00	128	0.18	55	10.97	5.4	0.05802	5.7	0.38	0.7251	6.7	0.09119	5.4	0.80	530	124	563	29	554	28	101.6
S-190521a-13.d	Zr12a	0.00	542	0.10	129	11.26	5.0	0.05813	4.1	0.30	0.7122	5.7	0.08883	5.0	0.88	534	89	549	26	546	24	100.5
S-190521a-14.d	Zr12b	0.03	423	0.13	143	11.15	5.0	0.05894	3.9	0.40	0.7307	5.5	0.08971	5.0	0.90	564	85	554	26	557	24	99.4
S-190521a-15.d	Zr12c	0.00	529	0.13	169	10.99	5.1	0.05801	4.2	0.24	0.7243	5.8	0.09098	5.1	0.87	529	92	561	27	553	25	101.5
S-190521a-16.d	Zr13	0.00	106	0.29	74	11.17	5.1	0.05728	4.6	0.43	0.7067	6.0	0.08953	5.1	0.85	501	101	553	27	543	25	101.8
S-190521a-18.d	Zr15	0.00	577	0.17	228	10.88	5.1	0.05707	4.4	0.35	0.7156	5.9	0.09190	5.1	0.86	493	97	567	27	548	25	103.4
S-190521a-19.d	Zr16	0.00	429	0.25	266	11.12	5.0	0.05805	3.9	0.39	0.7222	5.5	0.08989	5.0	0.90	530	85	555	26	552	23	100.5
S-190521a-20.d	Zr17a	0.00	607	0.10	149	11.18	4.9	0.05836	3.8	0.35	0.7206	5.5	0.08943	4.9	0.90	542	84	552	26	551	23	100.2
S-190521a-21.d	Zr17b	0.02	701	0.07	115	11.16	5.0	0.05885	4.1	0.35	0.7236	5.6	0.08961	5.0	0.89	561	89	553	27	553	24	100.1
S-190521a-22.d	Zr18	0.08	583	0.14	209	11.10	5.0	0.05938	3.9	0.34	0.7385	5.5	0.09010	5.0	0.90	580	84	556	26	562	24	99.0
S-190521a-23.d	Zr19	0.03	213	0.27	145	11.01	5.0	0.05906	4.2	0.35	0.7397	5.7	0.09083	5.0	0.88	568	91	560	27	562	25	99.7
S-190521a-24.d	Zr20	0.00	451	0.13	148	11.10	5.0	0.05861	3.9	0.31	0.7289	5.5	0.09009	5.0	0.90	552	85	556	26	556	24	100.0