



The erroneous chondrichthyan egg case assignments from the Devonian: implications for the knowledge on the evolution of the reproductive strategy within chondrichthyans

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Abstract

Spiraxis interstitialis, and its junior synonym *Fayolia mourloni*, an uppermost Famennian (Upper Devonian) fossil first described as algae and subsequently interpreted as the oldest known chondrichthyan egg case, is reinvestigated based on the discovery of several additional specimens in Belgian collections. New data, in particular from micro-CT imaging, allow to refute *S. interstitialis*, and by extension also *Spiraxis major* (the type species of *Spiraxis* Newberry, non Adams) and *Spiraxis randalli* from the Famennian of New York and Pennsylvania, as chondrichthyan egg cases. Alternative interpretations of these enigmatic helicoidal fossils are discussed. The first occurrence of oviparity in the fossil record of chondrichthyans is thus not as old as previously thought and is close to the first occurrence of viviparity in this group, both being recognised now in the Mississippian. The question of which of both conditions is plesiomorphic within chondrichthyans, and more widely within vertebrates, is discussed. Also, the presence of the genus *Spiraxis* in both the USA (east coast) and Belgium reinforces the strong faunal resemblance already observed in both palaeogeographical areas. It suggests important faunal exchanges between these regions of the Euramerica landmass during the Famennian.

Keywords Fish egg cases · Bioturbations · Coprolites · Micro-CT imaging · Chondrichthyans · Reproductive strategy

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Introduction

Extant chondrichthyans ('cartilaginous fishes') dominantly have a viviparity mode of reproduction and oviparity, characterised by fertilised eggs within capsules (or egg cases), which is a much less common mode of reproduction (Wourms and Lombardi 1992; Blackburn 2005, 2015; Musick and Ellis 2005; Wyffels 2009). Whether viviparity preceded oviparity in the evolution of chondrichthyans, and vertebrates in general, remains debated (e.g. Grogan and Lund 2011; Carr and Jackson 2018; Fischer et al. 2014a; Trinajstić et al. 2019).

Stainier (1894) described a singular helicoidally enrolled fossil under the name *Spiraxis interstitialis* from the Upper Devonian (Famennian) of southern Belgium that he considered related to algae. This enigmatic fossil was later reinterpreted as a chondrichthyan egg case notably by Pruvost (1919) and Crookall (1928). This determination must be considered doubtful given its age and morphology compared to other chondrichthyan egg cases. However, it is still regarded as the oldest occurrence of chondrichthyan egg case, notably by Fischer et al. (2014a) who recognised one

egg case morphotype in the Belgian Famennian, i.e. *Fayolia*, previously *Spiraxis* (Stainier 1894, 1935). Yet, Poschmann and Schindler (1997, table 1), in their inventory of all *Fayolia* species, scored the Belgian species with half of the characters as unknown ('nicht erhalten'). That should have raised suspicions, but the assignment of the Belgian material to egg cases has never been questioned until this paper, which consequently has implications for the knowledge on the evolution of the reproductive strategy in chondrichthyans.

The search for the type material led us to revise the interpretation of Stainier's (1894) species, which was considered until now the oldest examples of chondrichthyan egg capsules (e.g. Fischer and Kogan 2008; Fischer et al. 2011, 2014a). Careful examination of undescribed similar material challenges such an explanation. The aim of this paper is therefore not only to re-evaluate this assignment, but also to document and to re-illustrate topotypes of the so-called Devonian Belgian chondrichthyan egg cases described under their original specific names as *Spiraxis interstitialis* Stainier, 1894 and *Fayolia mourloni* Stainier, 1935. It led us also to question similar and contemporaneous specimens from the USA (New York and Pennsylvania) originally described as *S. major* and *S. randalli* by Newberry (1885), and to discuss palaeobiogeographic considerations and the evolution of the reproductive strategy in vertebrates.

Geological setting

The putative chondrichthyan egg cases (Stainier 1894, 1935) were collected from now disused and almost completely backfilled quarries located around the village of Isnes-Sauvage (now Les Isnes) (Fig. 1), c. 10 km WNW of Namur (Namur Province, Belgium). These quarries previously exploited the micaceous, often dolomitic sandstones of the Bois de la Rocq Formation (Delcambre and Pingot 2008) for the purpose of building construction and interior design. The sequence is estimated to be up to 45 m thick and fossiliferous at some levels, dating, with some uncertainty, from the uppermost Famennian (Strunian) to the lowermost Tournaisian (Hastarian) (Poty et al. 2002). Nevertheless, a latest Famennian age has to be considered for the quarried levels, as only the topmost part (max. 2–3 m in thickness) of the Bois de la Rocq Formation is Hastarian in age (Delcambre and Pingot 2008). From a tectonic viewpoint, these quarries are situated in the Brabant Parautochthon (e.g. Belanger et al. 2012) (Fig. 1), and were located along the southern margin of Euramerica during the Late Devonian.

At Les Isnes, those quarries exploiting sandstones of the Bois de la Rocq Formation are now almost completely backfilled (Delcambre and Pingot 2008) preventing new finds and observations. A few kilometres to the east, between Les Isnes and Rhisnes (Fig. 1), there is still one active quarry

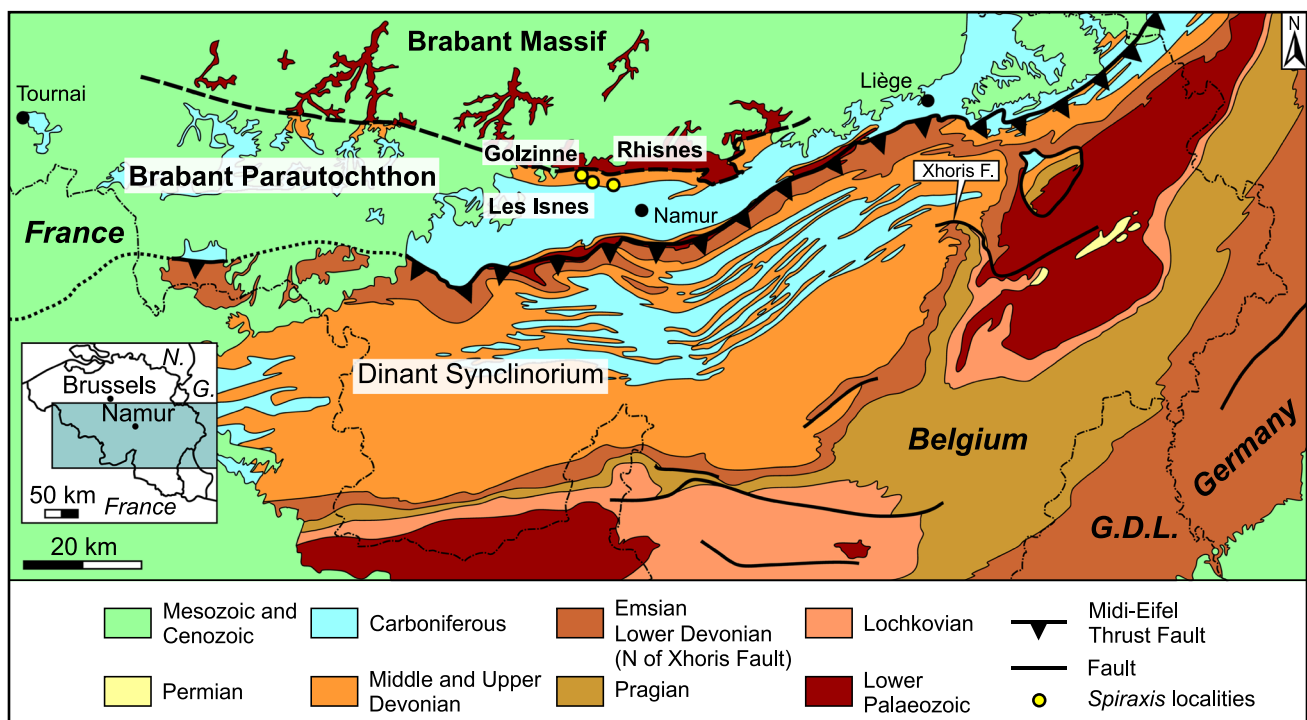


Fig. 1 Location and schematic geological map of southern Belgium and neighbouring countries with indication of the localities cited in the text (modified from de Béthune, 1954). Abbreviations: F., fault; G.D.L., Grand Duchy of Luxembourg; G., Germany; N., the Netherlands

exploiting sandstones of the Bois de la Rocq Formation (see Delcambre and Pingot 2015). No specimens have yet been collected from the latter, and given the small number of specimens of *Spiraxis* that have been found and reported, it is likely that these fossils are probably rare. According to Mourlon (1875), the macrofauna recovered from the ‘Psammites du Condroz’ in the Les Isnes area includes marine invertebrates such as brachiopods, orthoconic cephalopods and bivalves (see also Stainier 1922; Asselberghs 1936), as well as the edrioasteroid *Dinocystis barroisi* (Discocystinae, Edrioasteroidea). Although detailed accounts on the depositional and palaeoenvironment of the sediments from the Bois de la Rocq Formation are lacking, these fossils indicate that at least some of these sediments were deposited in a (shallow) marine environment not far from the coast.

Material and methods

The bulk of the material studied in this paper is stored in the collections of the Royal Belgian Institute of Natural Sciences (Brussels, Belgium, numbers with prefix RBINS; three specimens). Additional illustrated specimens are in the collections of the ‘Centre Grégoire Fournier’ (Maredsous Abbey, Denée, Belgium, number with prefix CGF; one specimen) and of the University of Liège (Liège, Belgium, number with prefix PA.ULg.; one specimen). North American specimens mentioned herein are in the Paleobotany Department of the Yale Peabody Museum of Natural History (New Haven, CT, USA, numbers with prefix YPM PB).

Three specimens (RBINS a13524 and a13525, and PA.ULg. 2020.11.19/1) were analysed using the RBINS micro-CT scan RX EasyTom 150, at 150 kv and 200 μ A in middle spot mode, with voxel sizes of 20.8908 μ m (RBINS a13524), of 20.8936 μ m (RBINS a13525) and at 150 kv 135 μ A in middle spot mode with voxel size of 39.9447 μ m (PA.ULg. 2020.11.19/1). After scanning, extraction into 16-bit TIFFs was performed with the X-Act software, and 3D-rendering and segmentation with Dragonfly ORS (version 4.10 for Windows). Figures of the scanned specimens were produced with the ‘export screenshot’ function, after optimising the 3D rendering by adjusting the histogram, contrast, shading, light source position, hard gradient and turning off all annotations except the scale bar. In a final step, an image processing software was used for the scaling to 600 dpi. In addition to this, 3D-models of the outer surface of RBINS a13524 and a13525 can be consulted via the RBINS Virtual Collections Platform (<http://virtualcollections.naturalsciences.be/>) and of specimen PA.ULg. 2020.11.19/1 via <https://www.morphosource.org/projects/000379486>. The primary scanning data and the set of Y slices are stored on Belspo’s LTP platform and can be

consulted upon request to the RBINS palaeontology collection manager.

All specimens were coated with ammonium chloride sublimate and photographed traditionally.

Systematic palaeontology

Incertae Sedis

Genus *Spiraxis* Newberry 1885, non Adams 1850

Type species *Spiraxis major* Newberry 1885 from the Conewango Group (Famennian), southern NY, USA, is hereby designated as type species following the recommendation 69.A.10 of the International Code of Zoological Nomenclature (fourth edition, 1999).

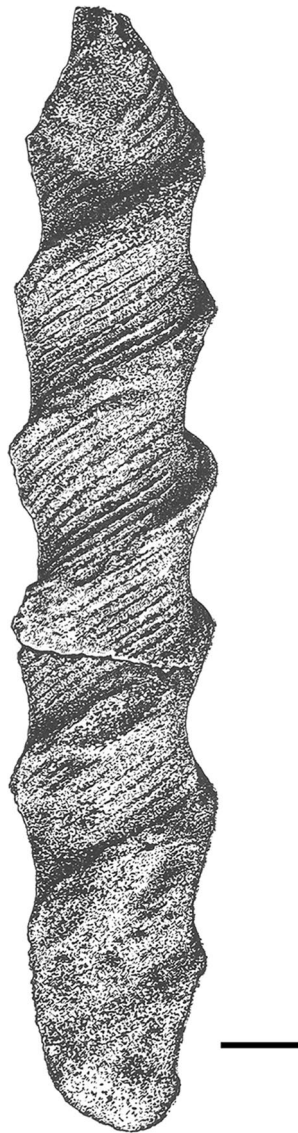
Diagnosis Emended from Newberry (1885): body cylindrical, or subfusiform, somewhat abruptly conical above, more gradually tapering below; surface traversed by two parallel revolving spiral ridges, in some species closely spaced, in others separated by an interval half as wide as the diameter; traces of internal structure; no distinct surface-markings visible, or only thin continuous, spiral and parallel ridges.

Included species Besides the type species, *Spiraxis randalli* Newberry 1885 and *Spiraxis interstitialis* Stainier 1894.

Remarks Newberry (1885) assigned two species to his new genus *Spiraxis* (no type species was selected in the publication), namely *S. major* from southern New York State (Newberry (1885, pl. 18, Fig. 1): specimen YPM PB 027,174) and *S. randalli* from the Warren area of northern Pennsylvania (Newberry (1885, pl. 18, Figs. 2–3): specimens YPM PB 027,172–027,173). Photographic illustrations of the specimens figured by Newberry (1885) are available via the website of the Yale Peabody Museum. Facsimile of Newberry’s figured specimens was published by Lesley (1890) and Crookall (1928); to our knowledge, Crookall (1930, pl. 4, Fig. 6) was the first to provide a photographic illustration of the species *randalli*. Moreover, soon after his first description, *Spiraxis* Newberry 1885, was renamed as *Prospiraxis* by Williams (1887) due to a primary homonymy issue with the recent gastropod genus *Spiraxis* Adams 1850, although this action is only strictly necessary if *Spiraxis* is to be placed in the Animalia and not in the Plantae Kingdom (see discussion on possible affinities of *Spiraxis* below). Hay (1902) selected *Spiraxis major* Newberry 1885, as the type species of *Prospiraxis*. Zeiller (in Renault and Zeiller 1888), who was unaware of Williams’ (1887) publication, considered *Spiraxis* a synonym of *Fayolia* Renault and Zeiller 1884, and he thus transferred both Newberry’s species to the latter genus.

Crookall (1930), who did not examine Newberry’s material, but rather specimens from the Warren area collected by F.A. Randall in Hall’s collection (now in New York State

Fig. 2 Original Stainier's (1894) illustration of the holotype (not traced) of *Spiraxis interstitialis* Stainier 1894, from the Bois de la Rocq Formation (latest Famennian), Isnes-Sauvage (Belgium). Scale bar represents 10 mm



Museum, Albany), came to the conclusion that (1) *Fayolia randalli* and *F. major* correspond to a single species, and (2) these should be united under *F. randalli*. Crookall (1930) likewise discussed the age of *F. randalli* from the Warren area based on (written or oral) communications provided by W. Goldring according to the observations of G.H. Chadwick and Ch. Butts. It appears that the *randalli* specimens were collected in two quarries exploiting the Salamanca conglomerate, thus the middle part of the Conewango Formation, which is the lowest Mississippian (Bradfordian) in age according to Ch. Butts. For this reason, Crookall (1930) considered *Spiraxis interstitialis* the oldest Upper Devonian *Fayolia* species, a view followed by subsequent workers such as Poschmann and Schindler (1997) and Fischer and Kogan (2008). A more detailed look onto the age of the material from northern Pennsylvania reveals that the Chemung is a now obsolete stratigraphic term for nearshore to outer-shelf

sandstones, siltstones and shales belonging to different formations of Late Devonian age (Harper and Kollar 2015). According to Chadwick (1935), the fossils are confined to the Devonian-aged Conewango Group (a term introduced by Butts (1910)), of southern New York and Pennsylvania. The Conewango Group includes, from base to top, the Venango and Riceville formations that are Famennian in age (e.g. Harper and Kollar 2015), and the Salamanca conglomerate (e.g. Willard et al. 1939) is now part of the Venango Formation. In conclusion, both North American species described by Newberry (1885) are Late Devonian (Famennian) in age.

Spiraxis interstitialis Stainier 1894 (Figs. 2–6)

1894 *Spiraxis interstitialis* Stainier, p. 26–27, unnumbered text-fig.

1910 *Spiraxis* [*Fayolia*] *interstitialis*; Moysey, p. 341.

1919 *Spiraxis* [*Fayolia*] *interstitialis*; Pruvost, p. 447.

1928 *Spiraxis* [*Fayolia*] *interstitialis*; Crookall, p. 326, 365.

1932 *Fayolia interstitialis* (Stainier [sic]); Crookall, p. 134.

1935 *Fayolia Mourloni* Stainier, p. 35.

1950 *S.* [*Spiraxis*] *interstitialis* Stainier; Brown, p. 596.

1997 *F.* [*Fayolia*] *interstitialis* (Stainier); Poschmann and Schindler, p. 30–31, table 1.

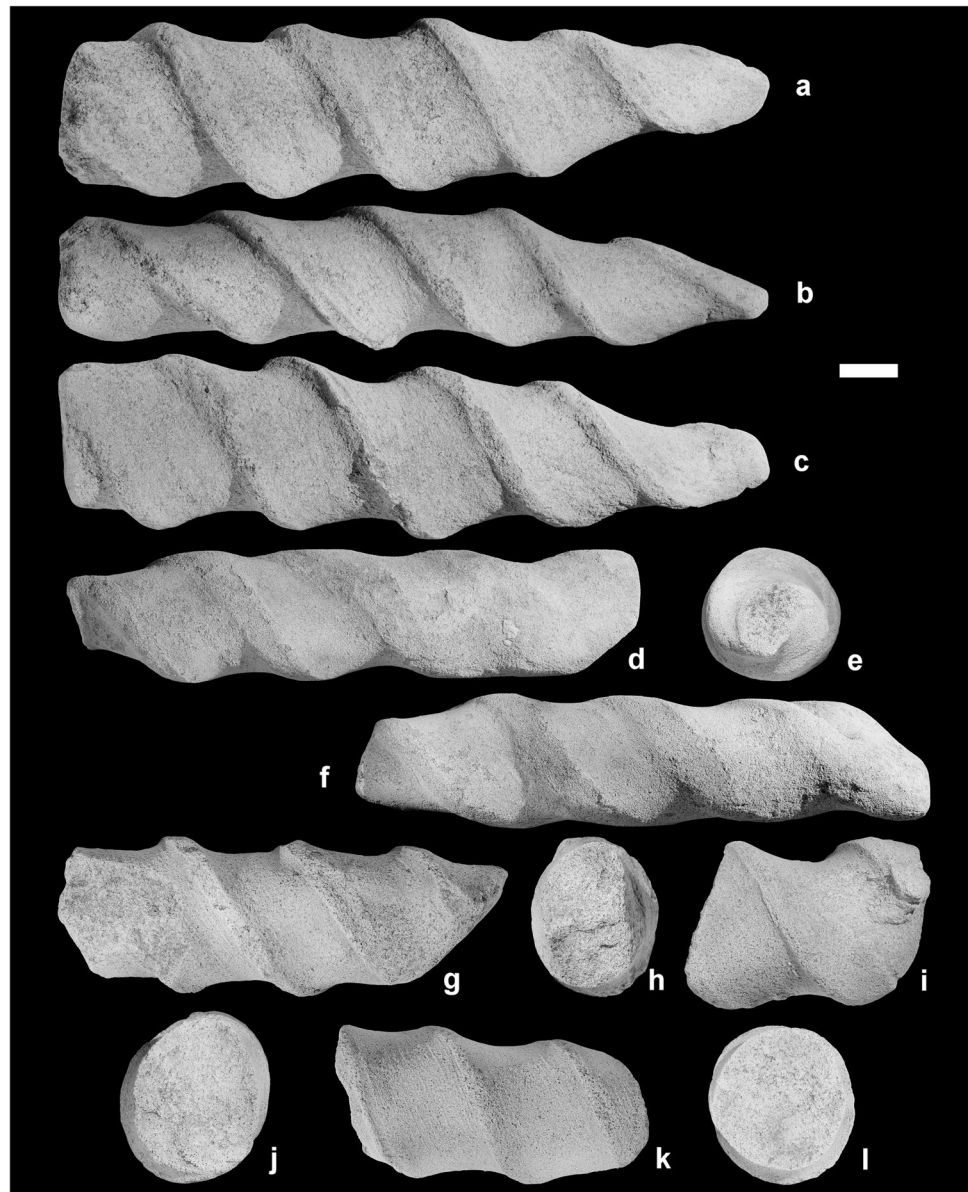
2008 *Spiraxis* [*Fayolia*] *interstitialis*; Fischer and Kogan, p. 79.

2018 *Spiraxis* of Stainier 1894 [sic]; Carr and Jackson, p. 384.

2021 *Spiraxis interstitialis*; Mottequin, p. 38.

Material Stainier (1894) reported that only one specimen from the ‘Psammites du Condroz’ (see above) was collected in the quarries of Isnes-Sauvage by M. Mourlon and can therefore be considered the holotype by monotypy. According to an exchange of correspondence between X. Stainier and G. Fournier (famous monk who gathered the largest collection of specimens from the Carboniferous (Viséan) Denée conservation Lagerstätte that made the CGF famous: Mottequin 2008; Mottequin et al. 2015) preserved in the archives of the CGF, the holotype was in 1894 present in the collections of the Muséum d’Histoire naturelle de Belgique (now RBINS). However, from a letter addressed by E. Maillieux (the curator of these collections) to G. Fournier, it can be learned that in 1925, the specimen was considered lost. Recent searches in the collections of the RBINS (including the Belgian Geological Survey) were in vain. Therefore, this specimen may be considered presumably lost, exactly as did Maillieux almost a century ago. Nevertheless, the search for this specimen resulted into the discovery of other and formerly unreported specimens: (i) three specimens in the RBINS collection (RBINS a13524 (Figs. 3g–h, 4a–h), 13,525 (Figs. 3i–j, 4i–n) and 13,526 (Fig. 3k–l)) identified (on label, by E. Maillieux) as *Fayolia mourloni* Stainier 1935, from Les Isnes (including the villages of Isnes-Sauvage and Isnes-Les-Dames) that

Fig. 3 *Spiraxis interstitialis* Stainier 1894, from the Bois de la Rocq Formation (latest Famennian). **a–c** PA.ULg. 2020.11.19/1 (neotype) in lateral views; Isnes-Sauvage. **d–f** CGF 2020.11.20/1 in lateral (**d–e**) and terminal (base, **f**) views; Golzinne area. **g–h** RBINS a13524 in lateral (**g**) and terminal (top, **h**) views; Les Isnes. **i–j** RBINS a13525 in lateral (**i**) and terminal (base, **j**) views; Les Isnes. **k–l** RBINS a13526 in lateral (**k**) and terminal (top, **l**) views; Les Isnes. Scale bar represents 10 mm



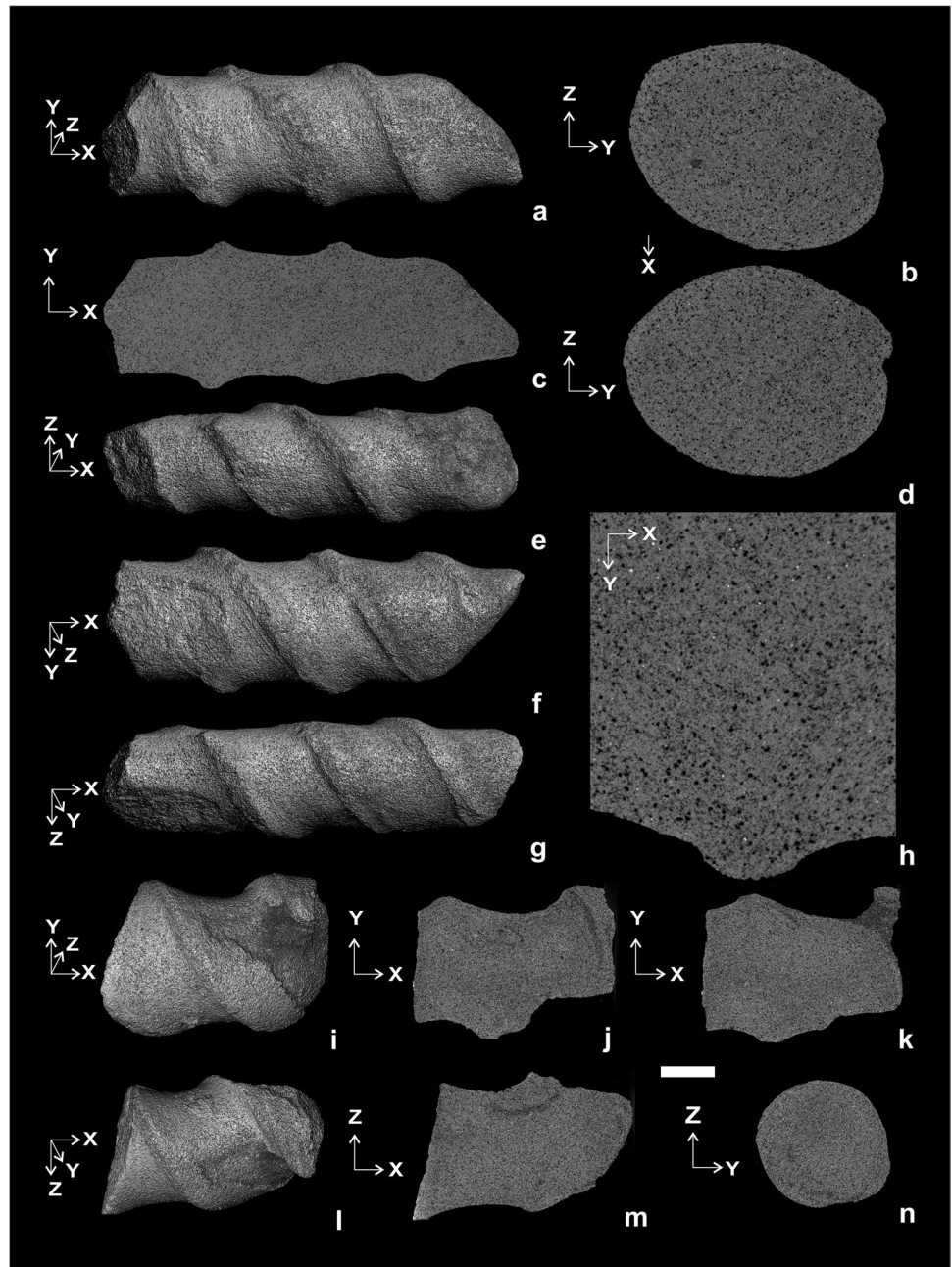
were acquired by the RBINS in 1930 (one specimen from Malaise's collection, IG 9340) and in 1932 (two specimens from Piret's collection, IG 9694); (ii) one specimen in the palaeontological collections of the Université de Liège (PA. ULg. 2020.11.19/1; Figs. 3a–c, 5, 6; former Henne's collection) labelled as *Spiraxis interstitialis* and coming from Isnes-Sauvage, which is hereby designated as the neotype; (iii) one specimen in the collection of the Centre Grégoire Fournier (CGF 2020.11.20/1; Fig. 3d–f), without locality and stratigraphy details other than 'Golzinne area' (Golzinne is near to Les Isnes). This specimen was the subject of the correspondence between G. Fournier, E. Maillieux and X. Stainier (see above).

Type locality and horizon Isnes-Sauvage (now Les Isnes) (Fig. 1), latest Famennian part of the Bois de la Rocq

Formation (formerly 'Psammites du Condroz') (Thorez et al. 2006; Delcambre and Pingot 2008).

Original description Stainier (1894) provided a detailed description (in French) and drawing (refigured here in Fig. 2) of the single specimen available at that time, i.e. the holotype (lost). His description is as follows: total length 140 mm, maximum width 25 mm. One end is quite pointed, the other one is more rounded. The object has noticeably the same width, but its middle part is slightly swollen. Its cross section is ellipsoidal, but this may be the result from compression phenomena during the fossilisation. The surface bears a kind of ridge spiralling around the object, starting from the top right, and extending to down left, in making an angle of c. 45 degrees with the vertical axis of the object. Towards the top of the

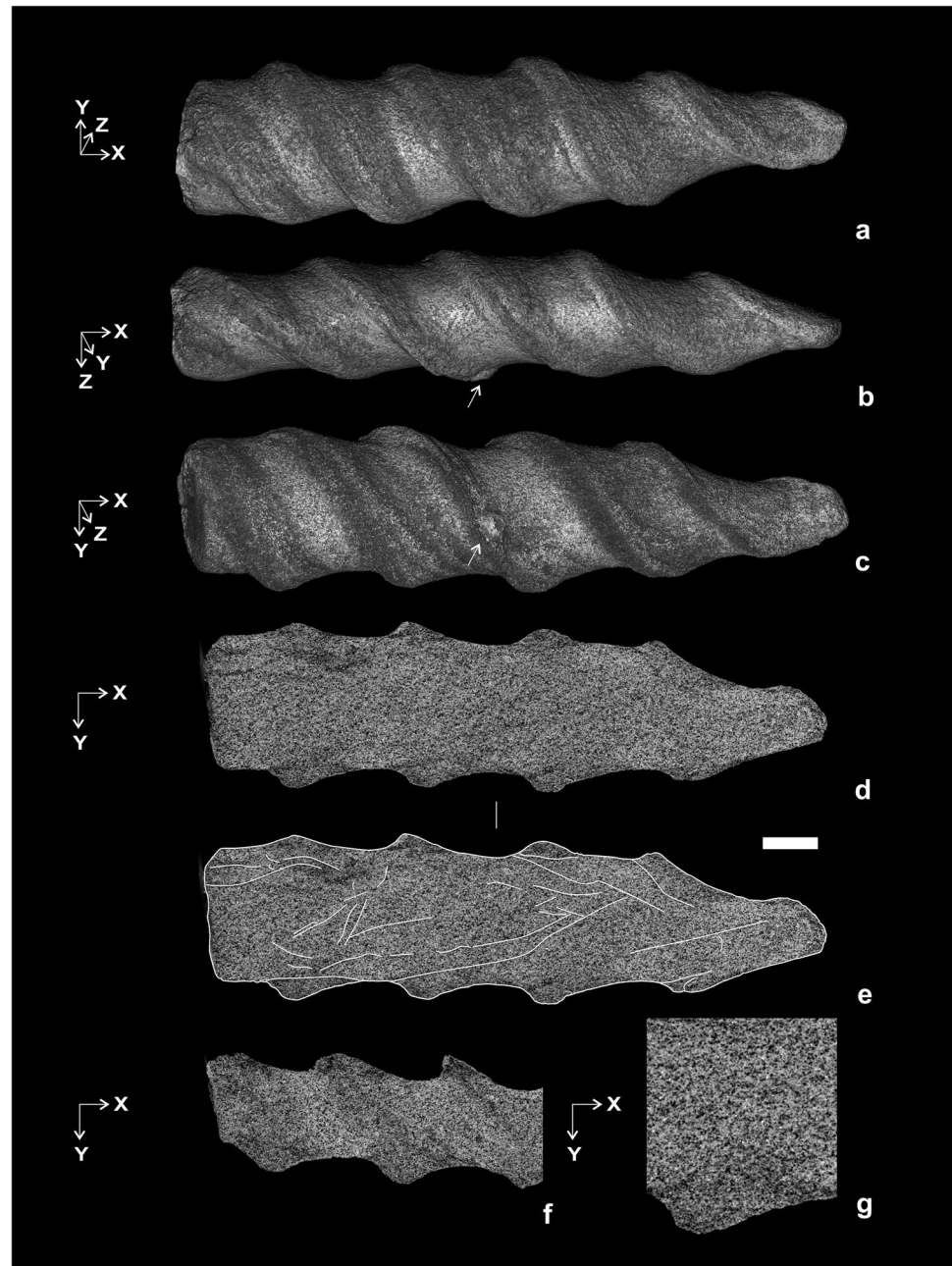
Fig. 4 *Spiraxis interstitialis* Stainier, 1894, from the Bois de la Rocq Formation (latest Famennian). **a–h** RBINS a13524. **i–n** RBINS a13525. Different views on 3D surface renderings (**a, e–f, i, l**) and virtual sections through the specimens (**b–d, h, j–k, m–n**). Scale bar represents: 10 mm (**a, c, e–g, i–o**); 5 mm (**b, d**); 2.5 mm (**h**)



fossil, the ridge has a sharp edge and its upwards-turned flank falls steeply into the depression, whereas, downwards, this slope gradually decreases towards the depression. On this slope oriented bottomwards, the main ridge is accompanied throughout its development by a secondary one that is less prominent, less distinct and less acute than it. Both ridges rotate together around the axis of the object but as one moves from top to bottom, the secondary ridge moves further and further away from the main one and becomes more prominent, almost as prominent as the latter. As both ridges diverge from each other, two very small spiral protrusions gradually appear in the hollow

between them and are especially visible in the fourth turn from the top. Towards the top of the fossil, the prominence of the main ridge gives to the spiral turns the appearance of a sharp ridge on one side. Between each turn, there is a very pronounced depression with a width of c. 25 mm measured perpendicularly from the main crest to main crest. The depression displays up to nine thin continuous, spiral and parallel ridges. The latter are spaced from 2 mm and become more and more distinct and more protruding bottomwards and for each interval comprised between two spiral tours of the main ridges.

Fig. 5 *Spiraxis interstitialis* Stainier 1894, from the Bois de la Rocq Formation (latest Famennian). **a–g** PA.ULg. 2020.11.19/1 (neotype) in different views on a 3D rendering (**a–c**) and virtual sections through the specimen (**d–g**), close to the centre (**d–e, g**) and to the proximity (**f**) of the specimen. X, Y, the horizontal axes; Z, the vertical axis. Scale bar represents: 10 mm (**a–f**); 5 mm (**g**)



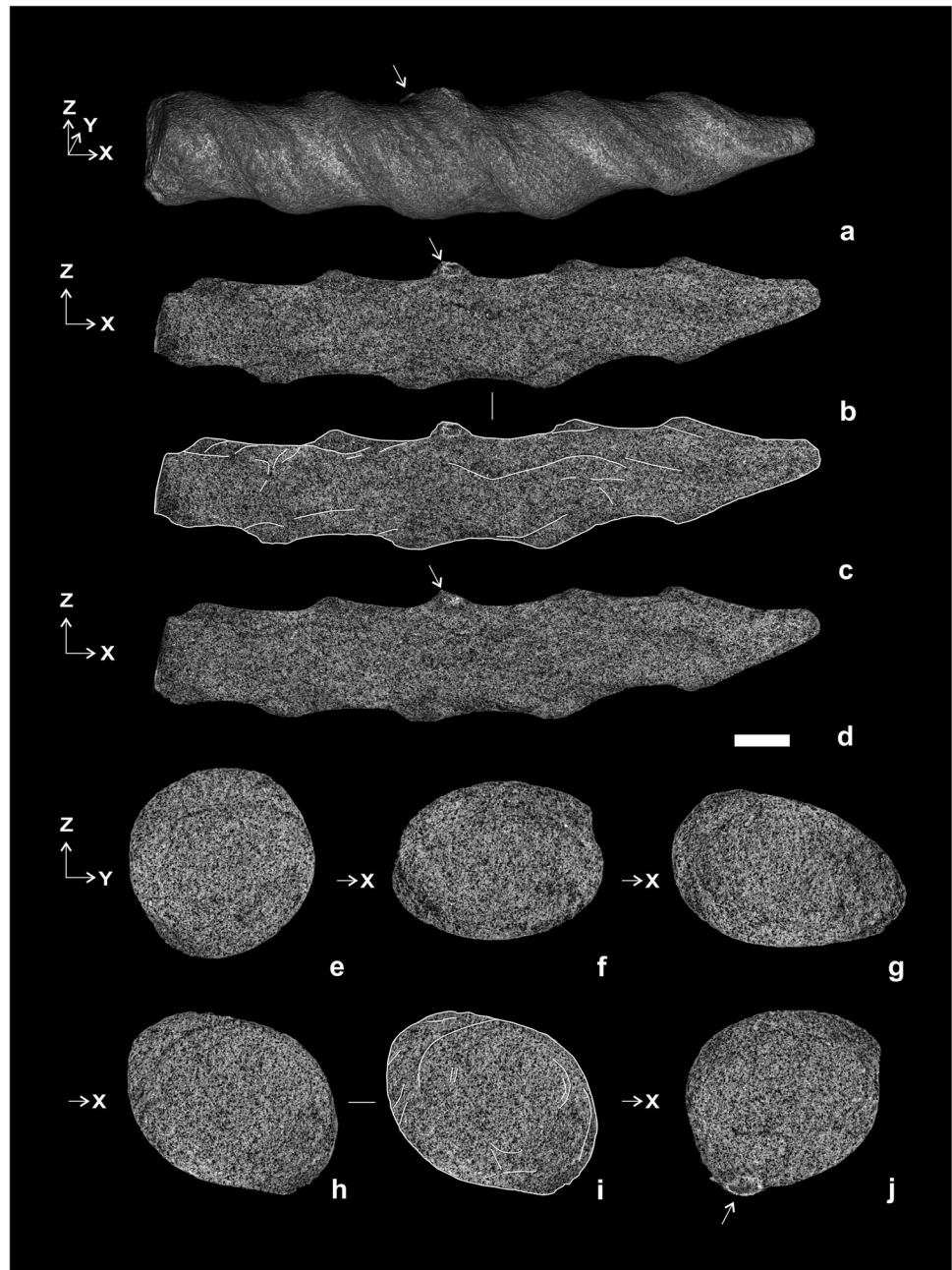
Stainier (1894) stressed on the fact that the specimen was composed of yellow, very micaceous sandstone that was absolutely identical to the rock in which it was found.

Description of additional specimens All the additional specimens are fully three-dimensional fossils, devoid of any traces of carbonate or dark-coloured organic matter. They are all loose, devoid from surrounding rock. All these specimens have some degree of distortion along — what is interpreted as — the vertical axis. Most probably this is due to sediment compaction, as a similar degree of distortion can be observed in e.g. bivalves from the same layer and localities that are in the RBINS collections. These bivalves are

also fully decalcified and exhibit a slightly different taint of yellow than their surrounding sediment. The nature of the distortion allows to firmly state that all the additional specimens must have lied, at time of fossilisation, horizontally in the sediment.

All of these additional specimens are interpreted as being incomplete; only one of the extremities of PA.ULg. 2020.11.19/1 (Fig. 3a–c), the largest of the additional specimens, may be a (nearly) complete extremity. The sedimentary matrix, these fossils are made out of, is rich in mica (the rock is called a psammite), and thus there is a concentration of mica plates on the outer surface of PA.ULg.

Fig. 6 *Spiraxis interstitialis* Stainier 1894, from the Bois de la Rocq Formation (latest Famennian). **a–j** PA.ULg. 2020.11.19/1 (neotype) in 3D rendering (**a**) and virtual sections through the specimen (**d–j**), close to the centre (**b–d**) and different sections along the X axis (**e–j**). Scale bar represents: 10 mm (**a–d**); 5 mm (**e–j**)



2020.11.19/1. On the outer surface of the other specimens, this is less prominent (RBINS a13524 (Fig. 3g–h), a13526 (Fig. 3k–l)) to even absent (RBINS a13525 (Fig. 3i–j)). In the latter case, however, there seems to be an overall lesser amount of mica in the sediment. Similar concentrations of mica plates are also observed on the surface of bivalves from the same beds, and for these bivalves, there is also no void left between the matrix and the mica-coated surface of the bivalves.

An additional factor that varies from one specimen to the other is the preservation of the ornament of delicate ribs, which is absent in PA.ULg. 2020.11.19/1 (Fig. 3a–c), only

faintly preserved in RBINS a13525 (Fig. 3i–j), with the exception of one circular spot where it is better preserved, and much better preserved in RBINS a13524 (Fig. 3g–h) and a13526 (Fig. 3k–l). Specimen RBINS a13526 displays more than 12 thin ridges in the depression.

Micro-CT imaging of three specimens allow to study and visualise the internal build-up of *Spiraxis interstitialis*. Of these three, the internal structures are most easily observable in PA.ULg. 2020.11.19/1 (Figs. 5d–g, 6b–j). The most prominent and largest internal structures are oriented at angles between 10 and 20 degrees to the main length axis (Figs. 5d–e, 6d), implying that the structure is made from

partly overlapping whorls that are 3.5–4.8 mm thick. Virtual sections taken much closer to the outer surface (Fig. 5f) reveal additional structures which align with the inclination of the outer ridges and also some that make an angle with these of 5–15 degrees.

Next to these larger-scale features, the virtual sections allow to identify a (relatively large) number of faintly to very faintly traceable structures. For none of these structures, there is certainty that these are directly related to the fossil itself. One of these possibly unrelated structures that easily can be observed both on the outer surface of PA.ULg. 2020.11.19/1 and in the virtual sections is what is termed here as the ‘nipple’ (arrow on Figs. 5a–c, 6a–d, j). Its overall shape is spherical, although deformed, it has a maximal diameter of 4.5 mm, and based on the different grey values, it must have a different chemical composition than the rest of the sedimentary fill of the fossil. This nipple was not observed in any of the other *Spiraxis* specimens.

Remarks As stated above, Stainier (1894) introduced *Spiraxis interstitialis* based on a single specimen that, according to the author, differs from the two species of Newberry (1885) by the presence of an outer ornament of thin ridges in the depressions separating the crests. More than 40 years later, Stainier (1935) mentioned the discovery of a second specimen (currently untraced; see above), and although this second specimen displayed the same characters as the first, surprisingly, these two were used to name the new taxon *Fayolia mourloni* Stainier 1935. For unknown reasons, the second specimen was not illustrated, and from Stainier (1935), it is also impossible to deduce whether the second specimen is the one mentioned by G. Fournier in two letters dating to 1925, one to X. Stainier and one to E. Mailleux, which Fournier said he received from an unnamed friend. *Fayolia mourloni* is thus to be regarded as a junior synonym of *Spiraxis interstitialis*.

Occurrence Les Isnes area (Brabant Parautochthon), southern Belgium (Fig. 1).

Discussion

Specimens of *Spiraxis* are not egg cases

Of all the different interpretations that have been proposed for *Spiraxis* (see below), it is the one of chondrichthyan egg capsules that received the most attention and which is still the one prevalent in the recent literature. However, it is noteworthy that the general morphology of *Spiraxis* only bears some vague resemblances with true representatives of chondrichthyan egg cases like those of the genus *Fayolia* Renault and Zeiller 1884 (compare with Fischer et al. 2011). In addition, the nearly undistorted 3D nature of the *Spiraxis* fossils is notable. This is notable because ‘fish’ egg capsules

are organic structures that may have some rigidity, and thus, one would expect their fossils to be flattened or to only retain limited 3D preservation. However, some exceptional examples of fully 3D specimens, corresponding to the moulds of the external structure during the decay of the original egg capsule in the sediment, are reported, in particular of Mesozoic *Palaeoxyris* (Frentzen 1932; Vialov 1984; Böhme et al. 2012), all found in broadly similar sandy lithologies, which are sediments with very limited dewatering compaction.

Internal helicoidal cavities for chondrichthyan egg capsules do not exist. The only extant chondrichthyan producing helicoidally shaped egg capsules is the Port Jackson shark genus *Heterodontus*, but this helicoidally shaped structure is external. The internal cavity of *Heterodontus* egg cases is ovoid-shaped with smooth surfaces (e.g. Powter and Gladstone 2008, Fig. 2), thus differing largely from the fossils named *Spiraxis interstitialis*. If we only consider here the type species of *Spiraxis* (*S. major* Newberry 1885) and that of *Fayolia* (*F. dentata* Renault and Zeiller 1884, from the Upper Pennsylvanian (Gzhelian, Stephanian) of the Commeny Basin in the Allier department (France)), it becomes evident that, except for the helicoidal shape, both genera do not have many similarities. Moreover, the surface pattern of *S. interstitialis* includes ridges (see Fig. 2) that are clearly distinct, a feature not observed in *Fayolia* representatives.

Nevertheless, the most convincing evidence for refuting the egg case hypothesis for *Spiraxis interstitialis* comes from the micro-CT imaging, revealing its internal structure, which is not conformable with an egg case interpretation.

Thus, what could *Spiraxis* be?

Stainier (1894) was not sure what *S. interstitialis* could be. The author was not even sure whether it should belong to the Animalia or the Plantae. His best guess was that it was related to the algae. But Stainier (1894) also briefly discussed several other possible assignments of *S. interstitialis*, but without presenting substantial evidence to support or disprove any of the hypotheses that he proposed. For example, he hypothesized a possible affinity with the spiralled fenestrate bryozoan *Archimedes* but immediately overruled this hypothesis because of the absence of preserved internal structures or remnants of calcium carbonate. Nevertheless, as already detailed above, the bivalves and brachiopods in the Bois de la Rocq Formation have also lost their carbonate shell, and the micro-CT imaging of *S. interstitialis* specimens revealed the presence of internal structures. He also reflected on a possible vegetal origin, specifically, he hypothesized it to be the fruit of an unknown plant, but there is, to our knowledge, not a single Devonian plant producing fruits that even vaguely resemble Stainier’s species. Moreover, as is the same for the types of *S. randalli* and *S. major*, there are no traces of

charcoal on the outer surface, although Williams (1887) reported on the presence of charcoaled chips of wood in the same beds in which *Spiraxis* is known from in Genesee, NY. Stainier (1894) also evoked the possibility for *S. interstitialis* to be the internal mould of soft-bodied sponges, but again, the nearly undeformed three-dimensional nature of the specimens in combination with the absence of flattened specimens makes assignments with soft-bodied organisms devoid of rigid structures questionable. In addition, an assignment to siliceous sponges (Dictyospongiidae), well-known in the Famennian of Belgium and northern France (e.g. Legraye 1929; Waterlot 1946), cannot be considered here as the fossils are devoid of the characteristic reticulate pattern usually present on the internal moulds of these sponges (e.g. Hall and Clarke 1899).

What Stainier did not consider was that the spiralled shape of *Spiraxis* vaguely recalls that of some coprolites (suggested by Hollick (1893) for the North American material) and burrows.

Chondrichthyans and other ‘fishes’ such as placoderms, actinistians, dipnoans, chondrosteans, amiids and lepisosteids have one of two architectures of valvular intestines (*valvula volute*: scroll valve) and (*valvula spiralis*: spiral valve) which produce spirally shaped faeces (Parker 1885; Owen 1866; Williams 1972; McAllister 1987). *Spiraxis interstitialis* has spirals that are distributed evenly along the long axis in lateral view, a morphology that would be termed amphipolar if it were a coprolite (Neumayer 1904). There are coprolites with broadly similar morphology to *Spiraxis*, notably *Helicocoprus* (Hunt et al. 2015), but they are apatitic in composition. In addition, the internal structuring of *Helicocoprus* remains unknown, and the ornament of the outer surface differs largely from *Spiraxis interstitialis*. There are uncommon coprolites of filter feeders that are composed of sandstone and are known from the Silurian and Permian (Gilmore 1992; Retallack and Krull 1999). However, these coprolites differ from *Spiraxis* in having a pronounced spiral internal structure and lack spiral ridges on the exterior.

Some eurypterids possessed a partially spiralled gut (Waterston et al. 1985), but there is no evidence that they produced spirally shaped coprolites. Caster and Kjellesvig-Waering (1964) described a putative eurypterid coprolite containing fragments of the exoskeleton of the eurypterid *Megalograptus ohioensis* and a trilobite cephalon, in association with body fossils of this eurypterid species from the Ordovician of Ohio, as evidence of cannibalism. Unstructured masses containing disarticulated agnathan fragments are common in the Monks Water fish bed in the Silurian Hagshaw Hills inlier in Scotland, together with the eurypterid *Lanarkopterus dolichoschelus*, and these were interpreted as eurypterid coprolites (Selden 1984) as were bodies comprising *Logania* denticles from the Lesmahagow inlier

(Rolfe 1973). These examples suggest that eurypterid coprolites consist of unstructured material that does not have a spiral shape. In addition, although some of the structures seen in the virtual sections of *S. interstitialis* may hypothetically be remains of other biological entities, none of them can be unequivocally recognised as fragments of eurypterids, trilobites or vertebrate skeletons.

Poschmann (2015), in the description of *Helicodromites*, overviewed a number of (sub)horizontal nearly straight unbranched burrows. However, like *Helicodromites*, all of these consist of a single spiralling cylindrical tube, and thus differing from *S. interstitialis*. Resemblances to *Skolithos helicoidalis* Volohonsky et al. 2008 are also only superficial and more importantly, this ichnotaxon is vertically oriented, and thus, it is not a match.

A very different interpretation can be made by considering that originally, *Spiraxis interstitialis* may have been a hard structure, possibly composed out of Ca-carbonate. This would explain its similar mode of preservation (largely undeformed three-dimensional fossils, concentration of mica plates on the outer surface) compared to the other macrofossils known from the Bois de la Rocq Formation. It would also explain the variation in the preservation of the outer ornament of thin ribs, varying from being well-preserved all over the entire external surface (e.g. Stainier’s (1894) specimen (Fig. 2), at least, if the drawing was not enhanced), to being only partly present or even fully absent. This variation also questions the validity of the presence of thin ribs as a discriminator between *S. interstitialis* and the two American species. It needs further investigation, but the absence of these thin ribs in the type of *S. major* may simply relate to preservation bias, and, in addition, faint traces of these ribs seem also to be present on one of the two types of *S. randalli* (YPM PB 027,173). The latter specimen also reveals an additional feature that may hint for the hard nature of the original structure; it seems to lie torn or broken in the sediment, at least in two spots. Interestingly, in the interpretation that *Spiraxis* has a hard ‘skeleton’, it may well have been a vertical structure, rather than a horizontal one. Stainier’s (1894) reference to the bryozoan *Archimedes* was maybe not that far-fetched after all. However, *Archimedes* has a different mode of coiling, and all evidence of fronts is missing.

Palaeogeographical comments

While none of the above discussed hypotheses seems able to undoubtedly clarify the higher taxonomic position of *Spiraxis*, there are some striking similarities between the localities from which *Spiraxis* fossils derive. Until now, *Spiraxis* has only been reported from a small number of localities in Belgium, NY, and Pennsylvania exposing

shallow marine sandy sediments that were deposited at a very similar palaeolatitude during the Famennian, at a not too far a distance from the shores of the Euramerican continent, however, with a mountainous region on that continent in between the Belgian and American localities. Apart from a remarkable similarity in the composition of the other macrofossils found at these localities, faunal and floral similarities between both regions as a whole were previously already identified, i.e. for plants (Kenrick and Fairon-Demaret 1991; Cressler et al. 2010; Prestianni and Gerrienne 2010) and for vertebrates (Olive et al. 2015, 2016; Daeschler et al. 2019).

Implications for the evolution of the reproductive strategy in chondrichthyans

For chondrichthyans, viviparity is sometimes considered the plesiomorphic condition (Grogan and Lund 2004; Musick and Ellis 2005) since it has been evidenced in Carboniferous holocephalans, which are regarded as basal chondrichthyans (Lund 1980; Grogan and Lund 2004, 2011; Fig. 7a: number 2). Viviparity has also been observed in various groups of placoderms (ptyctodonts, Long et al. 2008, 2009; Trinajstić et al. 2015; arthrodires, Long et al. 2009; Johanson and Trinajstić 2014; Newman et al. 2021; Fig. 7b–c: numbers 7, 8 and 10), the sister-group (in part or in full if they are, respectively, considered a grade or a clade, see below) of chondrichthyans and osteichthyans. However, oviparity is more often cited as the ancestral condition for chondrichthyans (Compagno 1990; Wourms and Lombardi 1992; Dulvy and Reynolds 1997; Carrier et al. 2004; Fischer et al. 2014a), since (i) the fossil evidence for oviparity preceded that of viviparity (Famennian (viz. *Spiraxis*) versus Late Mississippian (Grogan and Lund 2011)), (ii) it is the only known mode of reproduction in the stem-group elasmobranchs Xenacanthiformes and Hybodontiformes (Fischer et al. 2014a; Fig. 7a), (iii) it has been observed in holocephalans (Fischer et al. 2014a) and (iv) it has been suggested in placoderms (e.g. Ritchie 2005; Carr and Jackson 2018; probably also Downs et al. 2011 since oviparity is suggested by hatchlings (Trinajstić et al. 2019)).

Nevertheless, in the present study, we refute the fossil evidence of egg cases dating to the Famennian. *Spiraxis interstitialis* was previously considered by various authors a representative of *Fayolia* (e.g. Fischer et al. 2014a), and *Fayolia* egg cases considered egg cases of Xenacanthiformes (Fischer et al. 2014a). Therefore, the geologically oldest egg cases for the latter group are from the Viséan Hainichen Subgroup (e.g. Schneider et al. 2005) in southern Saxony (Germany), namely *Fayolia* sp. from the Asbian Ortelsdorf Formation of Chemnitz–Glösa (Fischer et al. 2014b) and *Fayolia sterzeliana* Weiss 1887 (e.g. Moysey 1910; Crookall 1928; Nindel 1920; Müller 1978; Rössler and Schneider

1997) from the Brigantian Berthelsdorf Formation of the Chemnitz–Borna area. The Lower Mississippian age of *F. crenulata* Moysey 1910, from Derbyshire (Shipleigh Manor Claypit, near Ilkeston) reported by Poschmann and Schindler (1997, table 1) is incorrect, and a Pennsylvanian age (top hard coal seam, Westphalian B of the traditional subdivision) has to be retained for this species (e.g. Frost and Smart 1979; Guion 1987).

For chondrichthyans as a group, the oldest evidence of oviparity by fossilised egg cases is now to be the Viséan *Palaeoxyris* from Chemnitz–Glösa (Schneider et al. 2005; Fischer et al. 2014b) and the aforementioned *Fayolia* species. This implies that there is no remaining evidence for chondrichthyans developing oviparity prior to the Viséan, and that the argument for choosing oviparity over viviparity as the plesiomorphic condition in chondrichthyans is weakened with now only a few millions of years between the oldest evidence of both (Fig. 7a).

Both oviparity and viviparity possess a long fossil record, and both have strong arguments being the ancestral condition in chondrichthyans. However, the fossil record of these evidence is too scarce for this group yet (Fig. 7a), and new discoveries are needed. Also, the phylogenetic relationships of placoderms, in which both oviparity and viviparity have been observed (Fig. 7b–c), need to be clarified since they have been resolved as either paraphyletic (Brazeau 2009; Davis et al. 2012; Long et al. 2015) or monophyletic (Goujet and Young 2004; Young 2010; King et al. 2017; King and Rücklin 2020). Placoderms are the sister group (in part or in full if they are considered a grade or a clade, respectively) of chondrichthyans and osteichthyans and their monophyly — or not — has obviously consequences on the considerations on the evolutive history of their reproductive strategies. Also, new discoveries of viviparous and/or oviparous placoderms are needed to infer the ancestral state, since our knowledge is too scattered (see Fig. 7b–c and the incompleteness of data regarding reproductive strategies within placoderms). Finally, the condition in most basal groups of vertebrates such as Osteostraci or Galeaspida is currently completely unknown, and it would be precious to decipher the plesiomorphic condition of the reproduction mode in vertebrates. Recently, Chevrin et al. (2018) demonstrated the presence of internal fertilisation in the jawless fish *Euphanerops* from the Miguasha Lagerstätte (Canada). Unfortunately, this discovery does not inform on the oviparity or viviparity condition but remains promising for future discoveries.

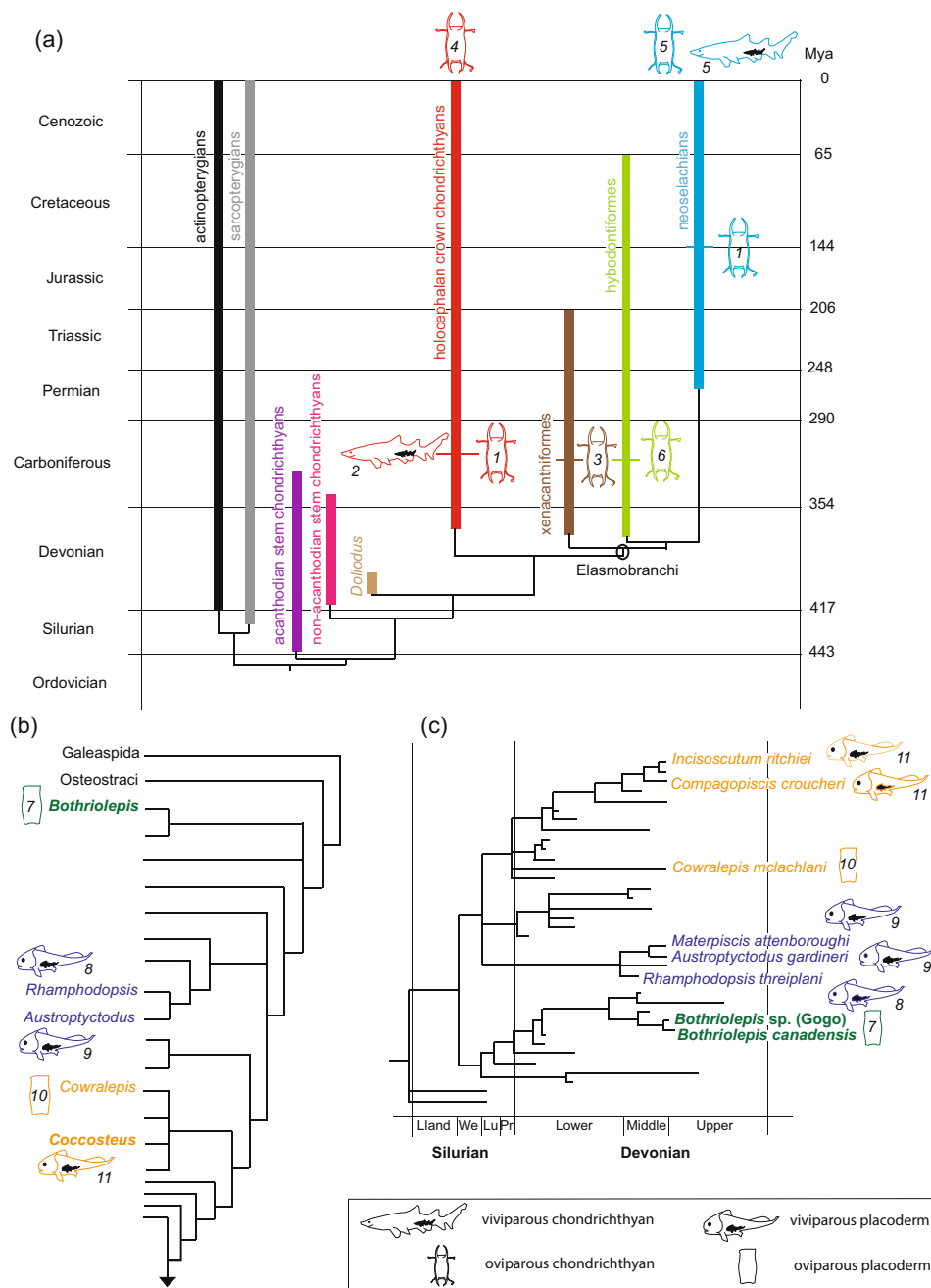


Fig. 7 Distribution of oviparous and viviparous modes of reproduction in chondrichthyans and placoderms. **a** Chondrichthyan phylogeny, modified from Coates et al.’s (2018) and Boisvert et al.’s works (2019). Horizontal bars on the coloured columns indicate the oldest fossil evidence of oviparity (by egg case symbol) and of viviparity (by ‘fish’ symbol) in the fossil record. ‘Fish’ and egg case symbols on top of the coloured columns represent modes of reproduction in extant chondrichthyans. **b** Placoderm phylogeny (paraphyletic), modified from Coates et al.’s work (2018). Arrowhead points towards chondrichthyans. **c** Placoderm phylogeny (monophyletic), modified from King and Rücklin (2020). For b and c, colour coding: dark green: antiarchs, dark blue: ptyctodonts, orange: arthrodires; taxa in bold are sister groups of taxa where oviparity/viviparity has been observed but not considered in the phylogenies (*Coccoosteus* for *Inc-*

soscutum and *Compagopiscis*, *Bothriolepis* and *B. canadensis* for *B. sp.* from PA, USA). Only placoderm taxa with a known reproductive strategy are named in terminal position for clarity purpose; the names of the other terminal taxa are available in Coates et al.’s (2018) and King’s and Rücklin’s (2020) works. Abbreviations: Lland, Llandovery; Lu, Ludlow; Pr, Pridoli; We, Wenlock. Colours of egg case and ‘fish’ symbols refer to their taxonomic assignments. Italicised numbers refer to the following bibliographical references, 1: Fischer et al. (2014a), 2: Grogan and Lund (2011), 3: Fischer et al. (2014b), 4: Wourms (1977), 5: Wourms and Lombardi (1992); Blackburn (2005, 2015), 6: Fischer et al. (2014b), 7: Downs et al. (2011); Trinajstic et al. (2019), 8: Trinajstic et al. (2015), 9: Long et al. (2008, 2009), 10: Ritchie (2005) and 11: Long et al. (2009); Johanson and Trinajstic (2014)

Conclusions

The interpretation prevailing in recent literature (e.g. Fischer et al. 2014a) that *Spiraxis interstitialis* Stainier 1894, and its junior synonym *Fayolia mourloni* Stainier 1935, represent the geologically oldest fossil evidence of chondrichthyan oviparity must be refuted, and this new insight weakens the widely traditionally accepted concept of pleisomorphy of oviparity over viviparity in chondrichthyans. A detailed study of previously unconsidered specimens of *S. interstitialis*, in particular by the aid of micro-CT scanning, is presented, increasing the knowledge of both the external and the internal structuring of this fossil. Nevertheless, other than confirming that it is a biological and neither a sedimentary nor a diagenetic structure, the higher taxonomic affinities and even its position within or the Plantae or Animalia remains unresolved. A further in-depth study of the North American Newberry's (1887) species *S. major* and *S. randalli*, by micro-CT scanning, may bring additional insights into these enigmatic fossils. Nevertheless, a revision of their age revealed that they have a nearly identical age to the Belgian occurrences, dating to the Famennian.

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Data availability All studied specimens are housed in official repositories guaranteeing their long-term safekeeping and availability to other researchers for future studies. Metadata and 3D models of the specimens from the RBINS can be consulted via the RBINS Virtual Collections Platform (<http://virtualcollections.naturalsciences.be/>). The primary scanning data and the set of Y slices are stored on Belspo's LTP platform and can be consulted upon request to the RBINS palaeontology collection manager.

Code availability Not applicable.

Declarations

Competing interests The authors declare competing interests.

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