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ORIGINAL ARTICLE

Revisiting the chondrichthyan egg capsules inventory from the Pennsylvanian (Carboniferous) of Belgium: new data and perspectives

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Abstract

Records of chondrichthyan egg capsule morphotypes from the paralic deposits of the Belgian Coal Measures Group (Pennsylvanian; Bashkirian–Moscovian; Namurian B–Westphalian B according to the traditional subdivision) are presented and discussed. These include several species of the hybodontiform type *Palaeoxyris* as well as the putative holocephalian types *Vetacapsula* and *Crookallia*. Furthermore, the type specimens of *Scapellites cottoni* and *S. minor*, two additional putative and enigmatic egg capsules from the same lithostratigraphic unit, are figured and discussed. Altogether, a highly diverse egg capsule assemblage documented from the Belgian deposits implies the presence of at least eleven different Carboniferous chondrichthyan species using the ancient aquatic environments for spawning and as nurseries. The absence of the xenacanthiform morphotype *Fayolia*, known from surrounding coeval Coal Measures areas of northern France, the Netherlands, and Germany, is conspicuous. This lack may be a result of collecting bias and does not reflect a real pattern.

Keywords Elasmobranchii · Holocephali · Oviparity · Belgian Coal Measures · Bashkirian · Moscovian

Introduction

The recent study of the alleged fossil chondrichthyan egg capsules identified as *Spiraxis interstrialis* Stainier 1894 from the Upper Devonian (Famennian) of southern Belgium, demonstrating them not to be chondrichthyan egg cases (Mottequin et al. 2021), has led us to reconsider all other reports of alleged chondrichthyan egg capsules from the Palaeozoic of Belgium (Fig. 1). Although they are rare, these putative egg capsules are known from several Upper Carboniferous (Pennsylvanian) horizons of the Belgian Coal Field and were ascribed to *Palaeoxyris* (Stainier 1911; Pruvost 1930), *Scapellites* (Pruvost 1922, 1930), and *Vetacapsula* (Pruvost 1930; Stainier 1938, 1942). These fossils were all found during the active exploration and mining of coal in deep underground galleries. Since mining seized gradually from the 1950s and stopped fully in 1992 (Delmer et al. 2002), no further in-situ finds are to be expected, increasing the value of historically collected material surviving in collections today, not in the least because most of these records were not, or not properly, illustrated or described.

The aim of this paper is to overview, document, redescribe, and (re-)illustrate (in the case when the original material has been traced) the type material of the chondrichthyan egg capsules of the Upper Carboniferous of Belgium, described under their original specific names as *Scapellites cottoni* Pruvost 1922, *S. minor* Pruvost 1930, *Vetacapsula debildei* Stainier 1938, and *V. preati* Stainier 1942. Furthermore, the documented specimens assigned to the morphotypes *Palaeoxyris* and *Vetacapsula* by Pruvost (1930) are also figured in order to cover the subject as completely as possible.

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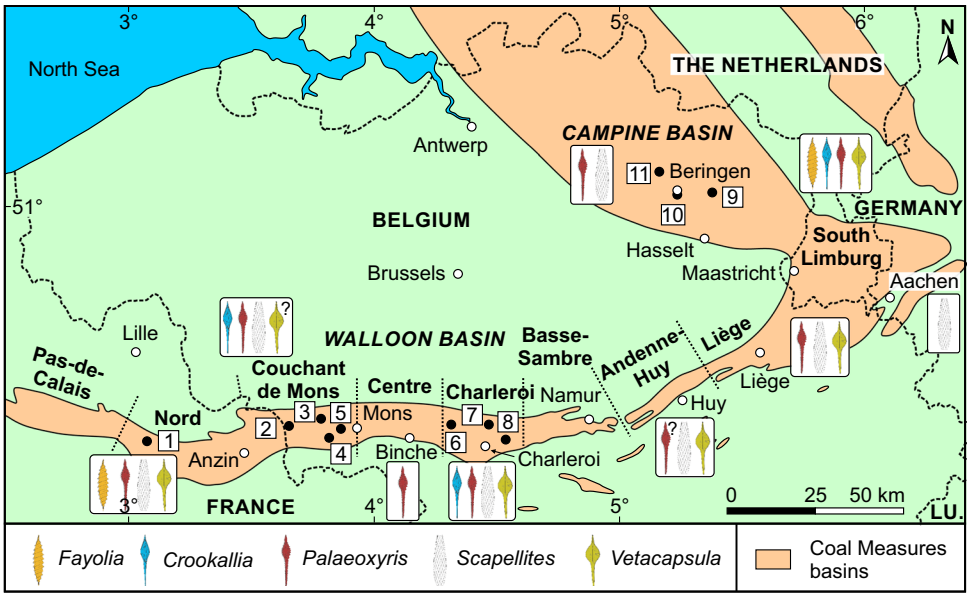

Fig. 1 Coal Measures basins of Belgium and neighbouring countries with indication of the districts and localities cited in the text (modified from Delmer and Graulich 1954) and with the distribution of the ascertained and putative/questionable chondrichthyan egg capsule morphotypes in Belgium (e.g. Pruvost 1930; Stainier 1938, 1942), northern France (Pruvost 1919, 1930), the Netherlands (southern Limburg; Pruvost 1927; van der Heide 1943), and Germany (Aachen area; Hahne 1939). *Vetacapsula* also includes the *Vetacapsula–Crookallia* morphotype see text). Localities: 1, L'Escarpelle; 2, Hensies; 3, Hautrage; 4, Pâturages; 5, Quaregnon; 6, Forchies; 7, Ransart; 8, Châtelineau; 9, Lillo; 10, Lummen-Gestel; 11, Kwaadmechelen-Veldhoven. Abbreviation: LU., Luxembourg

Geological setting

The material described and/or illustrated by Pruvost (1922, 1930), Stainier (1911, 1935, 1938, 1942), and Chaudoir et al. (1951) comes from the Pennsylvanian Belgian Coal Measures Group (Namurian B of 322 My to Westphalian B of 315 My (Aretz et al. 2020) according to the traditional subdivision; Fig. 2), which includes all the Carboniferous coal-bearing siliciclastics recognized in the two major Belgian coal basins separated by the Brabant Massif, namely the northern (or Campine) and southern (or Walloon) basins (Delmer et al. 2002) (Fig. 1). The Campine Basin corresponds to the continuation of the South Limburg coalfield (The Netherlands) and of the northern part of the Aachen and Ruhr coalfields in Germany, whereas the Walloon Basin extends from the French Nord–Pas-de-Calais in the west, and to the Aachen and Ruhr coalfields in Germany in the east (Delmer et al. 2002). The Walloon Basin was subdivided into several districts (e.g. Delmer and Ancion 1954a, b) that are plotted in Fig. 1. The reader is referred to the overviews of Paproth et al. (1983) and Delmer et al. (2002) for descriptions of the Andenne, Châtelet (Ransart and Floriffoux members) and Charleroi (Mons, As, and Eikenberg members) formations that yielded the material discussed here (Fig. 2).

Material and methods

The material studied in this paper is housed in the collections of the Royal Belgian Institute of Natural Sciences (RBINS, Brussels).

Quite a number of records were reported in publications of the 'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères (AEPSH)', subsequently rebaptised 'Centre national de Géologie houillère' in 1959. In the absence of a recent and exhaustive inventory of their immense collection (~ 8000 drawers, now at the RBINS), retracing all of these specimens is a colossal task that falls well beyond the scope of the present study. However, it is obvious that such a fossil hunt may be of considerable importance for future studies on Pennsylvanian chondrichthyan egg capsules.

All specimens, apart from those of *Scapellites cottoni*, were coated with ammonium chloride sublimate prior to being photographed. In addition to this, textured 3D models of the outer surface of the illustrated specimens (RBINS a7716, a7719, a7720–7722, a7769, and a13818) can be consulted via the RBINS Virtual Collections Platform (http://virtualcollections.naturalsciences.be/).

Except for *Scapellites*, the different chondrichthyan egg capsule morphotypes are presented following Fischer et al.'s

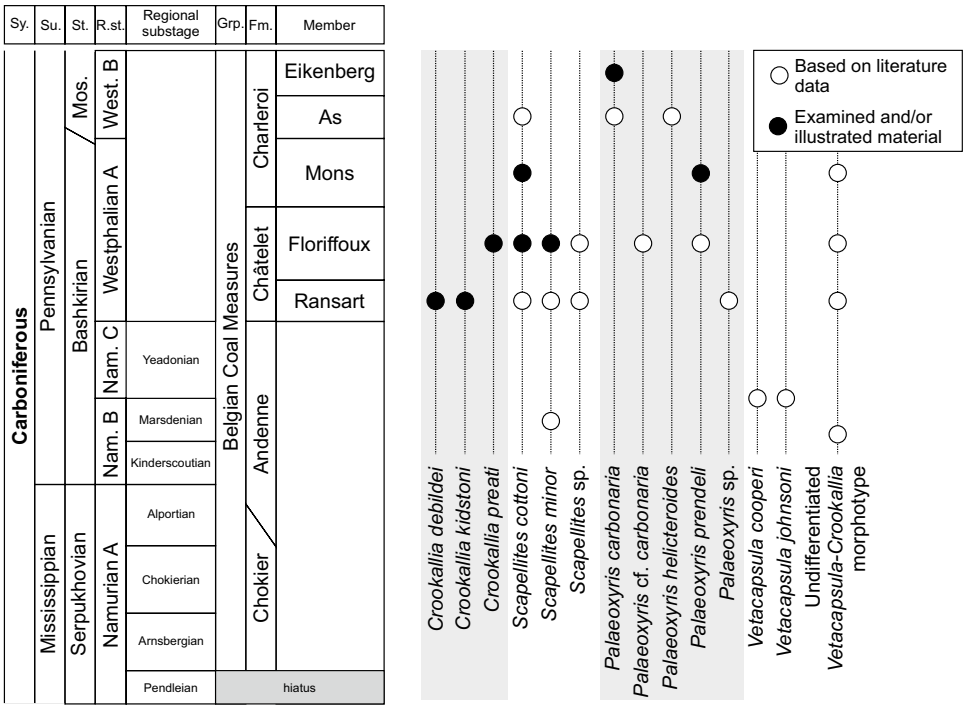

Fig. 2 Distribution of ascertained and putative/questionable chondrichthyan egg capsules within the Belgian Coal Measures Group based on literature data (see references in text; chrono- and lithostratigraphy after Delmer et al. (2002)). Abbreviations: Fm., Formation; Grp., Group; Mos., Moscovian; Nam., Namurian; R. st., regional stage; St., Stage; Su., Subsystem; Sy., System, West., Westphalian

(2014a) overview, with the species being alphabetically arranged under each genus. An exception was made for *Palaeoxyris* and *Vetacapsula*, whose representatives are only briefly discussed and, as far as possible, illustrated. Figure 3 presents the terminology used in the text.

The synonymy lists are non-exhaustive and primarily focussed on Belgian literature.

Systematic palaeontology

The classification of fossils egg capsules is parataxonomic, consisting of form groups because of their ambiguous orthotaxonomic position (Fischer and Kogan 2008). However, for practical reasons they are typically treated in accordance with the rules of the International Code of Zoological Nomenclature (Zidek 1976; Rössler and Schneider 1997; Fischer et al. 2011). An attempt by Vialov (1984) to create a distinct nomenclature for fossil egg capsules has not been adopted by subsequent authors (Fischer and Kogan 2008).

Genus *Crookallia* Chabakov 1949

Type species *Vetacapsula czernyshevi* Chabakov 1927; from the Middle Pennsylvanian (Late Moscovian, Westphalian D in the traditional subdivision) of the river Gnilusha, in the Krasnyy Sulin District of the Rostov Region, Russia, eastern outskirts of the Donets Basin (Nemyrovska and Yefimenko 2013).

General diagnosis Chondrichthyan egg capsule morphotype (Fig. 3a) with a three-fold division of a fusiform body tapering gradually at the anterior end into a shorter pointed beak and on the posterior one into a long and slender tail (pedicle). Its body is compressed, bulb-shaped, with a few untwisted longitudinal ribs (< 20) on the surface. In contrast to the similar, but more bulb-shaped *Vetacapsula* egg capsule morphotype (see below; Fig. 3b), a prominent middle ridge is not present. Altogether, body slightly non-symmetrical in its longitudinal direction. Distal part of the tail often showing a distinct kink. Moderate lateral flange (collarette) proved for at least one species comparable to the flanges in extant chimaeras.

Remarks Six species from the Pennsylvanian have already been documented from paralic strata of Europe (Fischer et al. 2014a, 2019). The producers most probably belong to the Holocephali (Fischer et al. 2014a).

Crookallia debildei (Stainier 1938) (Figs. 2, 4a and 5a)
1938 *Vetacapsula debildei* Stainier, p. 7–13, figs. 4–5.
1942 *Vetacapsula debildei*; Stainier, p. 4–5.

Type material The holotype (external mould), by monotypy, illustrated by Stainier (1938, figs. 4–5) and refigured here (Figs. 4a and 5a) is specimen RBINS a7769.

Type locality and horizon Hautrage colliery (Couchant de Mons district), top of the Ransart Member, 8 m below the base of the Floriffoux Member (Châtelet Formation), early Upper Bashkirian (Lower Westphalian A of the traditional subdivision) (Figs. 1 and 2) (see also Stainier's (1936) description of this colliery).

Description The single specimen is a 34-mm-long elongated fusiform capsule with distinct three-fold division. The needle-like beak is 6 mm long, the fusiform body is about

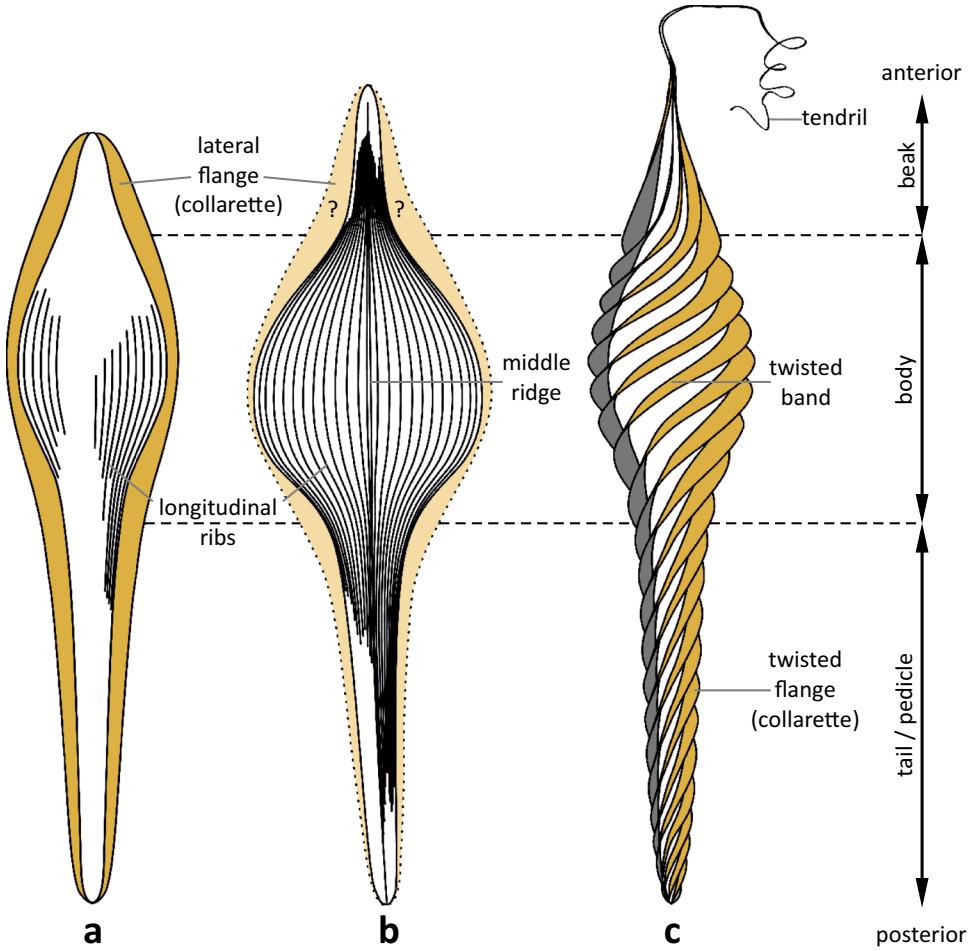

Fig. 3 Descriptive egg capsule terminology of *Crookallia* (**a**), *Vetacapsula* (**b**), and *Palaeoxyris* (**c**) used in the text according to Crookall (1928), Fischer et al. (2011), and Fischer et al. (2014a); egg capsules are not to scale (diagrammatic drawings by Frederik Spindler)

12 mm long and 4 mm wide at the widest point of the bulge. The pedicle is 16 mm long, has a uniform width of 1.5 mm, and shows a distinct kink of 45° distally. The transition from the body to the pedicle is very gradual. Up to 8 longitudinal ribs are visible on each hemisphere. The distance between them is maximum 0.4 mm on the body and 0.15 mm on the pedicle. A middle ridge between both hemispheres is not developed. The body shows also an oval depression corresponding to a protuberance on the positive. The most noticeable feature is a distinct, 1.4-mm-wide flange, which accompanies both margins and traces the capsule shape. It is not preserved over the entire length but is recognizable on the left side of the fossil on almost 80% of the longitudinal extension. In the area of the bulge of the body, it narrows to c. 1 mm, then it increases in width again.

Remarks The specimen was originally described as *Vetacapsula* by Stainier (1938) because of the combination of its three-fold division, fusiform shape, and longitudinal ribs. Due to the lack of a median ridge, Stainier (1938) had already noted that his new species was very close to *V. kidstoni* Crookall 1928, which was later ascribed to *Crookallia* by Chabakov (1949). Consequently, *V. debildei* was also assigned to *Crookallia* by Fischer et al. (2014a). The oval depression could maybe represent the outline of the former yolk sac (Stainier 1938, 1942), which at the beginning of embryonic development in chondrichthyans can still have such a size compared to its protective collagenous eggshell. However, this is pure speculation.

Crookallia kidstoni (Crookall 1928) (Figs. 2 and 4b)

1928 *Vetacapsula kidstoni* Crookall, p. 95–97, pl. 1, figs. 7–8.

1930 *Vetacapsula Johnsoni*; Pruvost, p. 134–135, pl. 2, fig. 7.

1938 *Vetacapsula johnsoni*; Demanet and Van Straelen in Renier et al., p. 238, pl. 144, Fig. 4 [copy of Pruvost (1930, pl. 2, fig. 7)]; text-fig. 126.

Material The specimen RBINS a7715 figured as *V. johnsoni* by Pruvost (1930: pl. 2, fig. 7) from the Charleroi district (Châtelet Formation, Ransart Member) has not been traced in the RBINS collections. Another specimen (RBINS a13818; Fig. 4b), slightly smaller than the former and better preserved, is from the Appaumée-Ransart colliery in the Charleroi district (e.g. Bellière and Harsée 1924; Stainier 1932), Châtelet Formation (Ransart

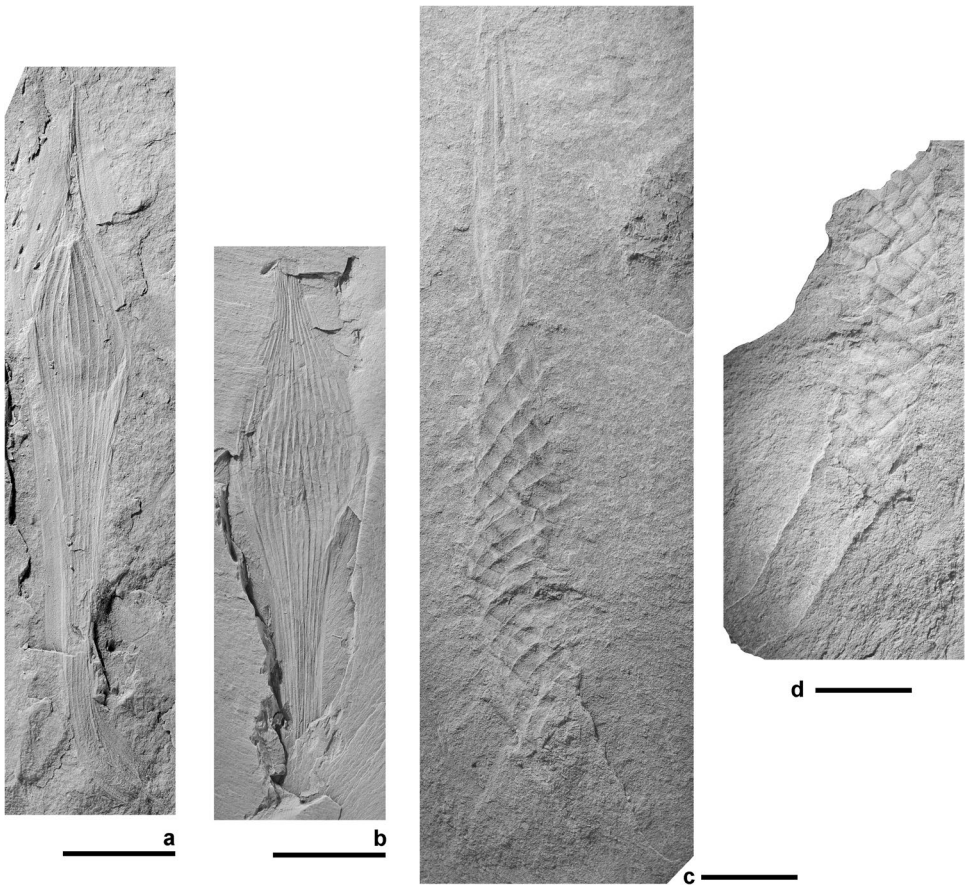

Fig. 4 **a** *Crookallia debildei* (Stainier 1938), holotype RBINS a7769 (Stainier 1938, figs. 4–5), from the Hautrage colliery, Châtelet Formation (top of the Ransart Member), Lower Westphalian A. **b** *Crookallia kidstoni* (Crookall 1928), RBINS a13818, almost complete specimen, Appaumée-Ransart colliery, Châtelet Formation (Ransart Member), Westphalian A. **c–d** *Palaeoxyris carbonaria* Schimper (in Stiehler 1850), RBINS a7716 (Pruvost 1930, pl. 2, fig. 8), almost complete specimen and its incomplete counterpart, Quaregnon, Les Produits colliery (northern Rieu-du-Cœur headquarters), Charleroi Formation (Eikenberg Member), Westphalian B. Scale bars represent 5 mm for all

Member) of Bashkirian age (Westphalian A of the traditional subdivision).

Description The incomplete fusiform capsule available reaches at least 21 mm in length and shows a slightly bulb-shaped body that gradually tapers into a pointed beak and a thicker, stretched pedicle. The body is 10.5 mm long and 6.2 mm wide at the widest point of the bulge. The incompletely preserved, 7.5-mm-long pedicle shows a uniform width of 2 mm. Altogether c. 8 longitudinal ribs are visible on each hemisphere. The distance between them is c. 0.4 mm on the body and much smaller on the pedicle. A middle ridge is absent.

Remarks There are discrepancies between the measurements given by Pruvost (1930) for the specimen RBINS a7715 that he assigned to *Vetacapsula johnsoni* and the single photograph provided as it is stated both in the caption and on the plate itself, that the specimen is enlarged twice. Although this specimen corresponds perfectly in shape to the type of *V. johnsoni* illustrated by Crookall (1928), the absence of the middle ridge, the reduced number of longitudinal ribs (18) on the surface, and the rather gradual tapering into the pedicle justify a re-assignment to the *kidstoni* type of *Crookallia*. If Pruvost's (1930) specimen reaches really 50 mm in length as indicated in Pruvost's description, thus almost double that of Crookall's (1928) *kidstoni* species, size alone should not be a criterion. As seen in fossil egg capsule whorls of the Cretaceous chondrichthyan capsule *Palaeoxyris jugleri* (von Ettingshausen 1852) (Fischer and Reich 2013) as well as in extant sharks (Zidek 1976), a distinct intraspecific variation in the size of capsules exists. All other capsule parameters, however, coincide with the characteristics of *C. kidstoni*. In contrast, the second specimen (RBINS a13818; Fig. 4b) fulfils all requirements, even the size. Therefore, both remains are regarded to represent specimens of *Crookallia kidstoni.*

Crookallia preati (Stainier 1942) (Figs. 2 and 5b–c).

1942 *Vetacapsula Preati* Stainier, p. 1–6, figs. 1–2.

Type material The only known specimen (a negative impression) (Fig. 5b–c), illustrated by Stainier (1942), has not been traced in the RBINS collections although he mentioned that the material was deposited there. However, the detailed documentation of the specimen by Stainier (1942) allows species validation and comparison.

Type locality and horizon Le Gouffre colliery (pit no. 10) at Châtelineau (Charleroi district) (Fig. 1), northern mine gallery (bouveau in French) at the depth – 855 m, Châtelet Formation, Floriffoux Member (base of Lower Bashkirian, Lower Westphalian A according to the traditional subdivision; see Stainier 1932).

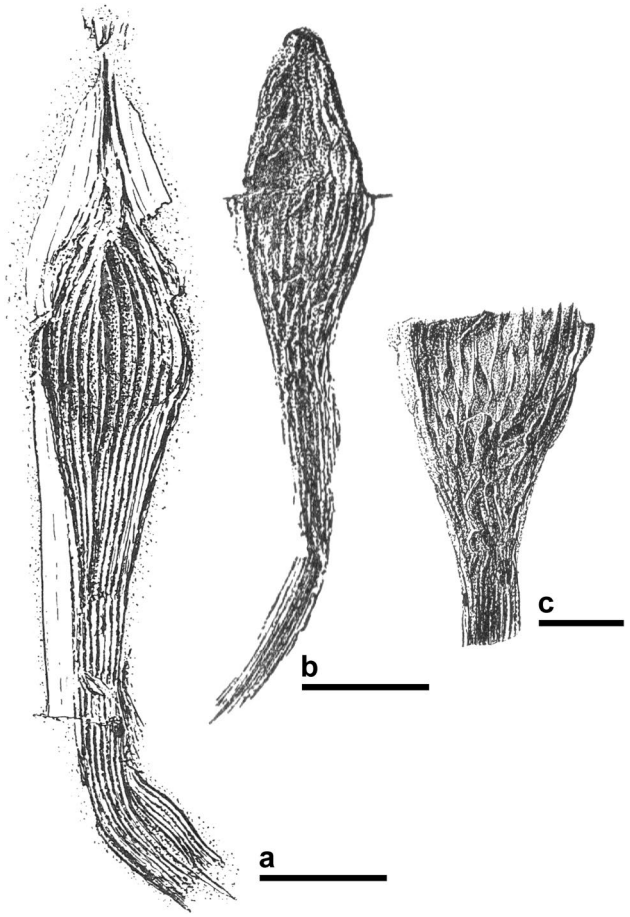

Fig. 5 **a** *Crookallia debildei* (Stainier 1938), holotype RBINS a7769 (facsimile of Stainier 1938, Fig. 4), from the Hautrage colliery, Châtelet Formation (top of the Ransart Member), Lower Westphalian A. **b–c** *Crookallia preati* (Stainier 1942), facsimile of Stainier (1942, figs. 1–2), from Le Gouffre colliery (pit no. 10) at Châtelineau, northern mine gallery at the depth − 855 m, Châtelet Formation (Floriffoux Member), Lower Westphalian A. Scale bars represent: 5 mm (**a–b**); 1 mm (**c**)

Description The single specimen is a 27 mm-long, elongated and fusiform capsule with distinct three-fold division. The beak is not preserved, the fusiform body is about 12 mm long and about 5 mm wide at the widest point of the bulge. The 15-mm-long pedicle has a general width of 1.6 mm and shows a kink of nearly 50° distally. The transition from the body to the pedicle is very gradual. Altogether, 8 longitudinal ribs are visible on the body. The distance between them is maximum 0.4 mm on the body and 0.2 mm on the pedicle. A middle ridge of any shape or form is not developed. In the front body area, in the direction of the former beak, an oval depression is weakly developed.

Remarks The lack of a prominent middle ridge, the low number of longitudinal ribs (only 8), the very gradual tapering into the pedicle and the distinct kink on it clearly justify the re-assignment to *Crookallia.* In a matter of size, shape and ribbing characteristics, *C. preati* is most similar to *C. debildei*. However, the very small number of longitudinal ribs and the lack of a lateral flange separate *C. preati* from the latter species and justify the assignment to a separate species according to current knowledge and underlying material. As already discussed and displayed by Stainier (1942, fig. 2), the ribs on the surface show a weak transverse rhomboidal pattern as a result of slight torsion during fossilization, a taphonomic phenomenon also known from few other specimens (Crookall 1928; Pruvost 1930; van der Heide, 1943).

Genus *Scapellites* Pruvost 1922

Type species *Scapellites cottoni* Pruvost 1922; from the Charleroi Formation (Mons Member, Early Bashkirian) of Pâturages (Couchant de Mons district), southern Belgium.

General diagnosis A morphotype with a slightly fusiform shape with a roughly textured surface of several narrow longitudinal, and often longitudinally twisted, filaments like a ball of wool.

Remarks Besides the type species, only *S. minor* Pruvost 1930 has been described. Pruvost (1922) noted the affinities of *Scapellites* with egg capsule morphotypes of *Palaeoxyris*, *Fayolia* and *Vetacapsula*. He considered his new genus as representing egg capsules of chondrichthyan fishes from the coal measures (*Cestracion* [=*Heterodontus*], *Helodus*), an interpretation already challenged by Lebrun (in Pruvost 1922), who suggested *Scapellites* to be eggs of molluscs or cephalopods, an opinion favoured by Renier (1942) due to their presence in horizons with marine influences (viz. *Gastrioceras subcrenatum* Horizon, base of the Ransart Member of the Châtelet Formation, Westphalian A) in the Liège district. However, neither Pruvost nor Lebrun substantiated their suggestions. Although exceptionally preserved fossils of early coleoid cephalopods are known from the Carboniferous of the USA (e.g. Mazon Creek and Bear Gulch Lägerstatten; Doguzhaeva et al. 2010; Wittry 2012; Klug et al. 2019; Whalen and Landman 2022) and despite the fact that there may be some resemblances with some egg clusters (egg strings or festoons) of some extant Coleoidea (e.g. octopods; see von Boletzky 1998), the cephalopods occurring within the marine horizons in the Belgian Coal beds, and thus those Renier (1942) referred to, namely ammonoids (abundant) and nautiloids (very rare), are presumed not to be the producers. The absence of any indication of embryonic shells being inside the egg cases, and the fact that no such structures are identified from any deposit elsewhere, argues against them being ammonoid or nautiloid egg cases. In addition, the great majority of nautiloids probably exhibited a K-strategy, like extant *Nautilus*, with a few and large individual eggs (Arnold 2010), thus differing from *Scapellites*. However, none of the above is discriminatory evidence. Although the producers are still unknown (Fischer and Kogan 2008), we follow the statement of Fischer

et al. (2014b) arguing that the weak rhomboidal patterns preserved on several remains may point to a chondrichthyan origin (Fischer et al. 2014b). Clearly, further study is needed to enlighten on the possible affinities and producers of the *Scapellites* fossils.

Occurrence Campine and Walloon Coal Measures basins of Belgium (Pruvost 1922 and references herein; Westphalian A and B of the traditional subdivision, and possibly from the Namurian B), northern France (Pruvost 1930; Westphalian A) and western Germany (Hahne 1939; Westphalian A) (Fig. 1). Crookall's (1930) suggestion that representatives of this genus may be present in the British Coal Measures has not yet been confirmed.

Scapellites cottoni Pruvost 1922 (Figs. 2, 6–7)

1922 *Scapellites Cottoni* nov. Pruvost, p. 151–155, text-figs. 1–4.

1926 *Scalpellites* [sic] sp.; Renier in Asselberghs, p. 646 [= *S. cottoni* after Pruvost (1930)].

1927 *Scapellites* sp.; Renier, p. 887 (= *S. cottoni* after Pruvost (1930)).

1930 *Scapellites cottoni*; Crookall, p. 22–23, pl. 5, figs. 1–3.

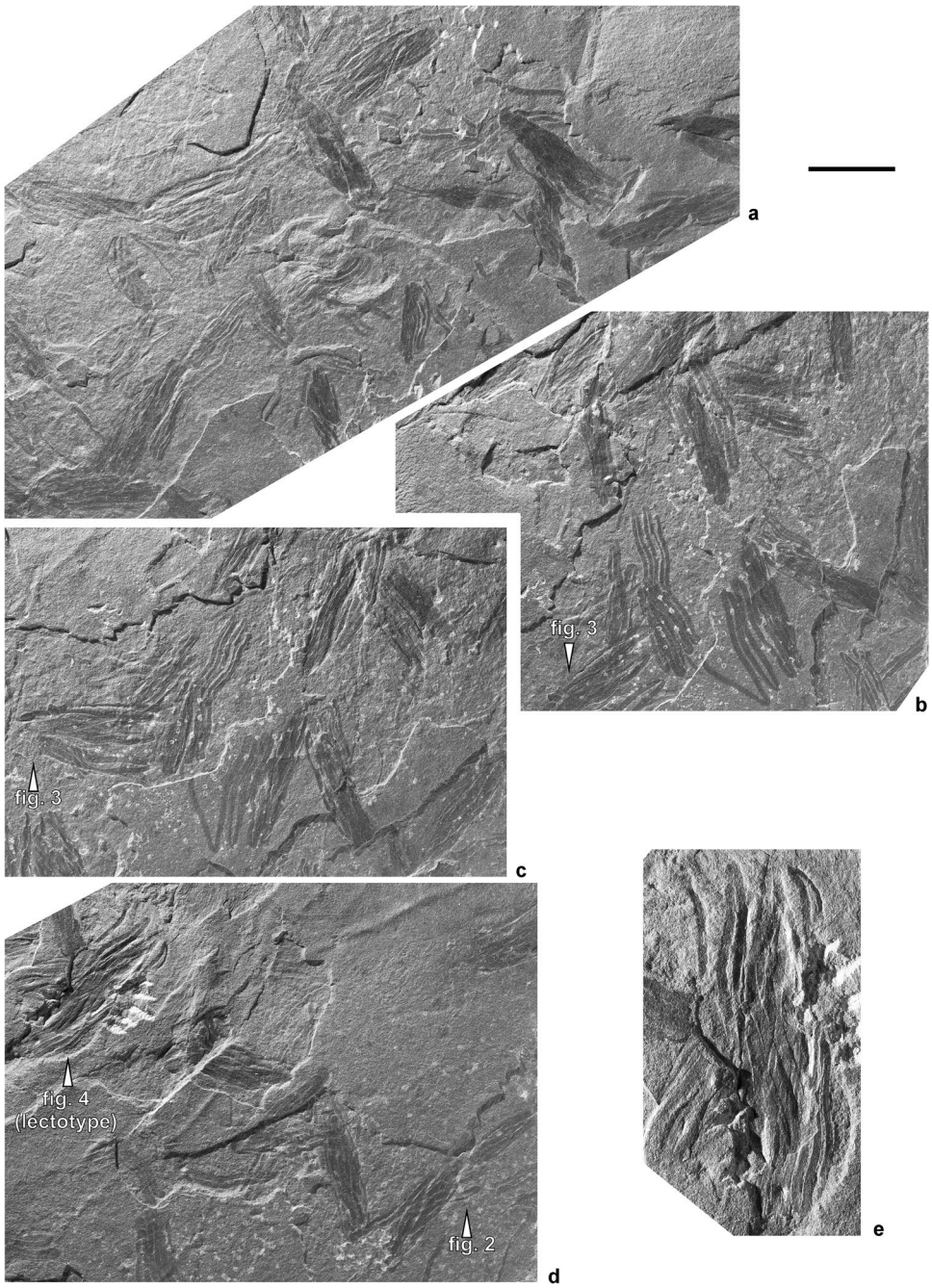

Fig. 6 *Scapellites cottoni* Pruvost 1922, from Pâturages (pit no. 10 known as Grisœuil, depth – 1150 m), Charleroi Formation (top of the Mons Member), Upper Westphalian A. **a–b** RBINS a7719, slab of black shale covered by numerous, differently oriented specimens (Pruvost 1922, text-fig. 1; Pruvost 1930, pl. 2, fig. 1). **c** RBINS a7719, close-up of specimen illustrated by Pruvost (1922, text-fig. 3). **d** RBINS a7719, detail of more or less dissociated capsules (Pruvost 1922, text-figs. 2 (= lectotype, RBINS a7719a), 4; Pruvost 1930, pl. 2, figs. 2–3). **e** close-up of lectotype with partly dissociated filaments, RBINS a7719a. Scale bar represents: 10 mm (**a–d**); 5 mm (**e**)

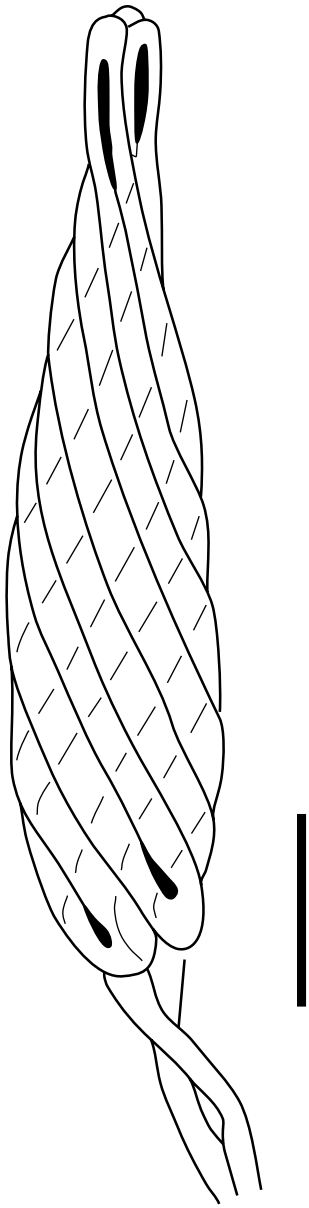

Fig. 7 Facsimile of the reconstitution of *Scapellites cottoni* Pruvost 1922 by Pruvost (1930, text-fig. 3). Scale bar represents 5 mm

1930 *Scapellites Cottoni*; Pruvost, p. 137–140, pl. 2, figs. 1–3; text-fig. 3.

1934 *Scapellites Cottoni*; Renier, p. 289.

1938 *Scapellites cottoni*; Demanet and Van Straelen in Renier et al., p. 239, pl. 144, fig. 5; text-fig. 129.

1938 *Scapellites cottoni*; Renier, p. 101–104.

1938 *Scapellites cottoni*; Renier in Renier et al., p. 275, 278, 279, 280, 282, fig. 141.

1939 *Scapellites cottoni*; Hahne, p. 223.

1950 *Scapellites cottoni*; Chaudoir et al., p. 13.

1951 *Scapellites cottoni*; Chaudoir et al., p. 41, 47, pl. 1, figs. 1–6.

1953 *Scapellites cottoni*; Chaudoir et al., p. 19, 64.

1976 *Scapellites cottoni*; Delmer and Tricot, p. 17, 23.

1995 *Scapellites cotoni* [sic]; Derycke et al., p. 346.

2008 *Scapellites cottoni*; Fischer and Kogan, p. 79.

Type material One black-coloured shaly slab (and its counter slab) (RBINS a7719) includes all the specimens illustrated by Pruvost (1922) (Fig. 6), but no holotype was designated in the original publication. Pruvost (1930) considered this slab as the type of the species. Although the term 'type' should act as a lectotype designation, this is incorrect according to Article 74.5 of the International Code of Zoological Nomenclature (fourth edition; International Commission on Zoological Nomenclature 1999) as the taxon had been based on more than one specimen.

The lectotype (RBINS a7719a) hereby designated corresponds to what is interpreted as a partly dissociated capsule figured by Pruvost (1922, text-fig. 4) and re-illustrated here in Fig. 6d–e. Pruvost's (1922) figured and unillustrated syntypes are to be considered paralectotypes.

Type locality and horizon Pâturages (pit no. 10 known as Grisœuil, depth -1,150 m) (Couchant de Mons district) (Fig. 1), top of the Mons Member (Charleroi Formation, Late Bashkirian (Late Westphalian A according to the traditional subdivision)), 25 m below the Quaregnon marine band (marking the base of the As Member, same formation) (Pruvost 1922; Renier 1922; Renier 1934, 1937; Renier in Renier et al. 1938).

Description Spindle-shaped capsules covering shale plates in the form of flattened but scattered impressions. They are on average 16 mm long and 4 mm wide. Their non-carbonaceous wall is composed of a kind of narrow longitudinal band folded into a loop at each of the two ends. This gives rise to a series of zigzag lines, the adjacent branches of which are closely joined, so that the whole forms a well-closed capsule. The whole capsule consists of at least 12 such folded bands; at one pole of the capsule there are at least 6 loops; at the other, there are one less. On one side of the capsule, the bands merge into a long pedicle. These capsules have a slight helical twist of one and a half turns about their long axis. By superimposing and compressing the front and back sides of the capsules, the bands of the lower side cross those of the upper side, forming small rhomboidal patterns. Often the bands no longer form a closed capsule, but are dissociated, spreading laterally and forming zigzag threads at wide intervals. This arrangement seems to be indicative of a very particular way in which these capsules are opened up by spreading of the bands. Sometimes the pedicles converge in a common stem of fibrous structure, suggesting that the original capsules were clustered.

Remarks Although only known originally by a limited number of specimens, several occurrences were subsequently reported (see references herein) and additional

specimens, from the Liège district, were illustrated by Chaudoir et al. (1951). It is not excluded that *Scapellites minor* was confused with *S. cottoni* by Renier (1937) and Humblet (1946) according to Chaudoir et al. (1951) (see below).

From a palaeoecological point of view, Chaudoir et al. (1950) mentioned *S. cottoni* in a m-thick level of laminar micaceous shale with sandy beds and thin shale intercalations that yielded various species of the freshwater bivalve *Anthracomya*. At the roof of the Homvent Layer (0.70 m thick), Chaudoir et al. (1951) indicated that some bedding planes of a 0.9-m-thick level of grey shale, with carbonate nodules, were literally covered by *Scapellites cottoni* and this level is interpreted as non-marine by Pastiels (in Chaudoir et al. 1951, legend of pl. 1). Pruvost's species as well as *S.* aff. *cottoni* Pruvost, *S.* sp., and cf. *S.* sp. are reported by Chaudoir et al. (1953) from more or less dark, micaceous shales, in association with the bivalve *Anthraconauta*. Several authors (e.g. Renier 1937, 1942; Chaudoir et al. 1953) recognised a *Scapellites* facies within the Westphalian of the Liège district and considered it as synchronous of an important marker known as the Bouxharmont Horizon but, according to Lambrecht et al. (1962), the *Scapellites* facies is older than this horizon.

Occurrence Besides the type locality, Pruvost (1922) also reported the species from the Charleroi district (Mons Member; Appaumée-Ransart colliery) (Fig. 1). Subsequently, *S. cottoni* was recognized by Pruvost (1930) at Hensies (Couchant de Mons district, base of the As Member of the Charleroi Formation; Moscovian, Westphalian B of the traditional subdivision) and in the Campine Basin (Fig. 1). There, this author indicated that the species was recovered in boreholes, within the Châtelet Formation: Ransart (Lummen-Gestel borehole (Fig. 1); see Renier 1927) and Floriffoux (Kwaadmechelen-Veldhoven borehole (Fig. 1); see Renier in Asselberghs 1926) members. However, according to Renier's (in Asselberghs 1926) description of the Kwaadmechelen-Veldhoven borehole, the species has been encountered at the base of the Charleroi Formation (Mons Member, Westphalian A).

Chaudoir et al. (1951) discussed the occurrence of this species in the Liège district (Fig. 1) where it was reported in the Châtelet Formation (base of the Floriffoux Member). Findings of slabs of shale covered with *Scapellites*, *S. cottoni* (Chaudoir et al. 1951) and *S. minor* (Renier 1937; Humblet 1946), were reported by Renier (1937, 1938) and Humblet (1946), which led them to consider this *Scapellites* facies as a local one at the base of the Floriffoux Member (Châtelet Formation) in the Liège district (see also Chaudoir et al. 1953), but *S. cottoni* was also reported from the Ransart Member by Delmer and Graulich (1958). Anyway, in the absence of illustration, all these identifications remain impossible to confirm.

Scapellites minor Pruvost 1930 (Figs. 2, 8)

1926 *Scalpellites* [sic] sp. nov.; Renier in Asselberghs, p. 657.

1930 *Scapellites minor*; Pruvost, p. 140, pl. 2, figs. 4–6.

1930 *Scapellites* sp.; Crookall, p. 23.

? 1937 *Scapellites minor*; Renier, p. B28, B31.

1938 *Scapellites minor*; Renier, p. 101–103.

1938 *S.* [*Scapellites*] *minor*; Demanet and Van Straelen in Renier et al., p. 239.

1939 *Scapellites minor*; Hahne, p. 222–223.

? 1946 *Scapellites minor*; Humblet, p. M15, M16, M22.

1951 *Scapellites minor*; Van Leckwyck et al., p. 16.

1957 *Scapellites minor*; Lambrecht et al., p. 17.

1995 *Scapellites minor*; Derycke et al., p. 346.

2008 *Scapellites minor*; Fischer and Kogan, p. 80.

Type material According to Pruvost (1930), the 'type' of the species corresponds to four slabs of a drill core covered by *Scapellites*. However, although Pruvost (1930) selected a holotype for all of his other species newly erected in his monograph, he did not designate one for *Scapellites minor*, possibly intentionally, given the poor state of preservation of the material. Nevertheless, for taxonomic purposes, a lectotype is hereby designated (RBINS a7720b; Pruvost 1930 (pl. 2, fig. 4, *partim*)) and is re-illustrated here in Fig. 8a–b. The other specimens present on the four slabs are thus to be considered paralectotypes.

Type locality and horizon Borehole no. 97 of Kwaadmechelen-Veldhoven (Campine Basin) (Fig. 1), depth – 1113.5 m, Floriffoux Member, Châtelet Formation (base of the Upper Bashkirian, Lower Westphalian A of the traditional subdivision). According to Pruvost (1930), the level with *Scapellites minor* is intercalated in a freshwater series yielding several species of the bivalve *Carbonicola*.

Description The capsules have an average length of 8 mm with a width of 2 mm. They are spindle-shaped, tapered at the ends, with walls composed of fine bands arranged longitudinally, side by side and very slightly spiraled around the spindle axis. The state of preservation of the fossils does not allow to see the folding of the bands at the ends. The capsules are preserved.

Remarks Pruvost (1930) distinguished *Scapellites minor* from *S. cottoni* on the basis of its markedly smaller size of only the half of the latter species and its less pronounced torsion. Renier (1938) noticed that whenever specimens of *Scapellites* are found in abundance, regardless of the species, they all have roughly the same size, but when they are found scattered in shaly deposits, it would be possible that the two species are sometimes associated. It is therefore not unlikely that both *S. minor* and *S. cottoni* are actually homotaxial and the size differences maybe are a result of different-aged and therefore sized producer; however, clarification needs further examination.

Occurrence In addition to the type horizon, Pruvost (1930) reported the species in the Lummen-Gestel

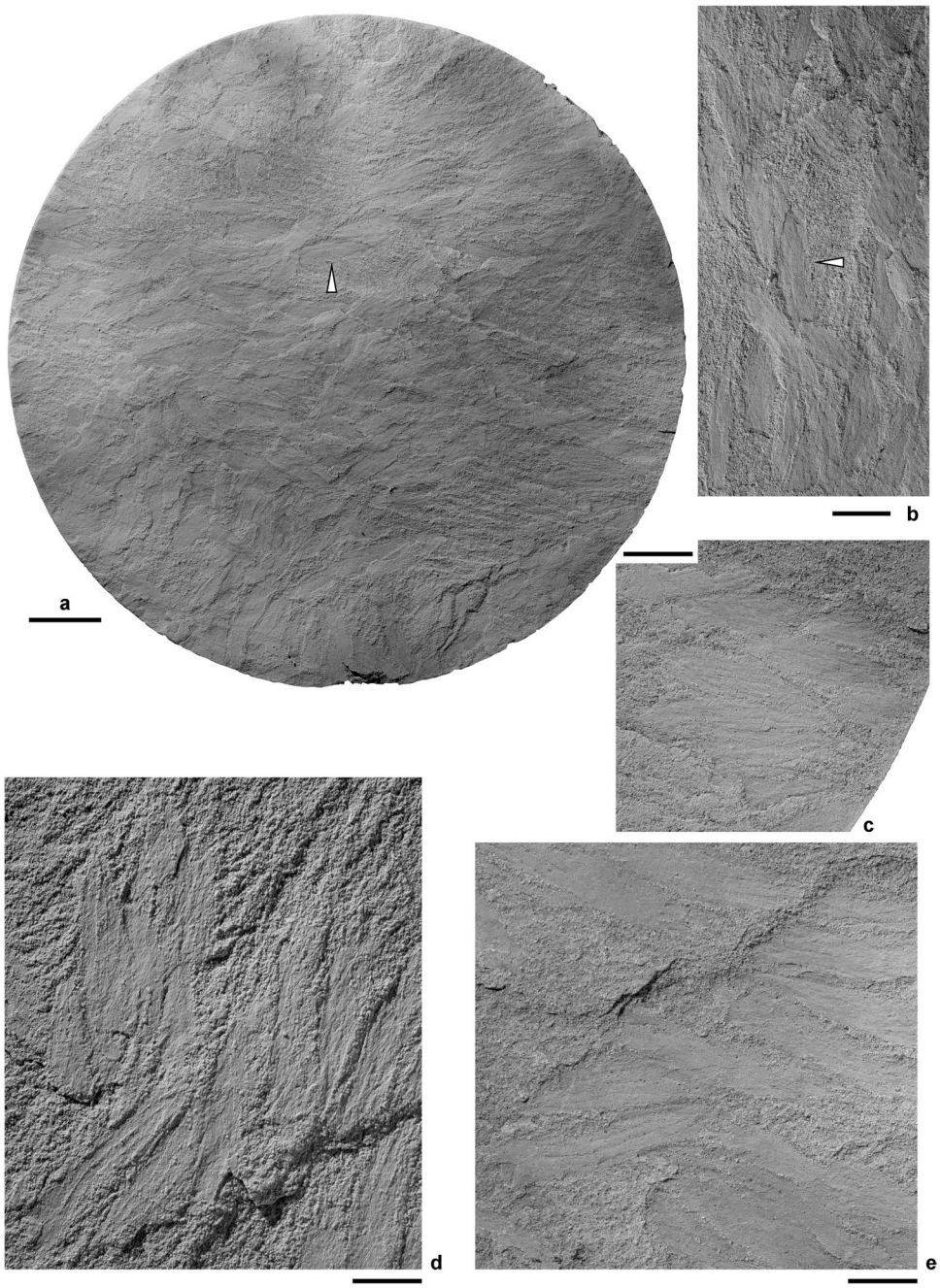

Fig. 8 *Scapellites minor* Pruvost 1930, from borehole no. 97 of Kwaadmechelen-Veldhoven, depth -1,113.5 m, Châtelet Formation (Floriffoux Member), Lower Westphalian A. **a–c** RBINS a7720a (Pruvost 1930, pl. 2, fig. 4), drill core surface covered by numerous specimens with localisation of the lectotype (RBINS a7720b, arrow) (**a–b**), and close-up (**c**) (Pruvost 1930, pl. 2, fig. 4a). **d** RBINS a7721 (Pruvost 1930, pl. 2, fig. 5), several specimens. **e** RBINS a7722 (Pruvost 1930, pl. 2, fig. 6), several specimens. Scale bars represent: 5 mm (**a**); 2.5 mm (**b**); 2 mm (**c–e**)

borehole (Campine Basin (Fig. 1), Renier 1927) within the Ransart Member of the Châtelet Formation. *Scapellites minor* was subsequently found in several Belgian coal districts although none of these records were illustrated. In the Charleroi district (Fig. 1), Van Leckwyck et al. (1951) reported the species in association with *S.* sp. within the upper part of the former upper Sippenaken Zone (upper Nm2a sensu Demanet (1941, 1943)), thus in the Marsdenian-aged part of the Andenne Formation (Bashkirian, Namurian B of the traditional subdivision) (Fig. 2). This would constitute the stratigraphically oldest record of *S. minor* and also of *Scapellites* as a genus. Furthermore, in this district, Aderca et al. (1958) reported *S.* aff. *minor* in the Floriffoux Member of the Châtelet Formation. Lambrecht et al. (1957) likewise noted the presence of the former in the Andenne–Huy district (Fig. 1) within the Floriffoux Member. Further to the east, Humblet (1946) mentioned a *S. minor* facies within the same lithostratigraphic unit in the Liège district (see also remarks related to *S. cottoni*).

Scapellites minor has also been recognized in northern France, at Anzin (Vicoigne Formation, Westphalian A of

the traditional subdivision; Pruvost 1930), and in western Germany, in the Aachen area (Westphalian A; Hahne 1939) (Fig. 1).

Scapellites sp. (Fig. 2)

Remarks Occurrences of *Scapellites* were mentioned by various authors from the Westphalian (Châtelet Formation) of the Charleroi and Liège districts without formal descriptions or illustrations (e.g. Van Leckwyck et al. 1951; Chaudoir et al. 1952, 1953; Aderca et al. 1958, 1965; Lhoest et al. 1958; Lambrecht et al. 1962). All these records were based upon in the AEPSH collection, and without the rediscovery of the specimens, they can only be referred to as *Scapellites* sp.

Comments on the other chondrichthyan egg capsules from the Pennsylvanian of Belgium

Next to *Crookallia* and *Scapellites*, there are quite a number of reports of occurrences of egg capsules in the Upper Carboniferous of Belgium that were assigned to the genera *Palaeoxyris* and *Vetacapsula*. An overview of these occurrences is presented below. However, for most of these occurrences, the specimens were not described in detail nor adequately figured, meaning that, without the rediscovery of the material these records are based upon (see Material and Methods), a full revision of these records cannot be executed at present.

Palaeoxyris Brongniart 1828 This chondrichthyan egg capsule morphotype (also known by its synonym *Spirangium*) is characterised by the three-fold division (Fig. 3c) of its fusiform body tapering gradually at the anterior end into a shorter pointed beak and on the posterior one into a long and slender tail. Its tail is normally as long as the body and beak combined. The body is composed of three or more parallel helicoidally twisted bands, the band margins being accompanied by spirally twisted membranous flanges (collarettes). Fine longitudinal striations on bands and flanges are possible. The apex of the beak is equipped with a coiled tendril for capsule attachment. In compressed specimens, the diagenetic compaction of the bands on the originally three-dimensional body results in a transverse rhomboidal pattern as a taphonomic phenomenon. Species distinction is based on the number and the possible breadth pattern of the capsule-forming bands. Twenty-six valid species of Early Carboniferous to Late Cretaceous age have been described yet (Fischer et al. 2014a) from predominantly freshwater to brackish deposits worldwide (except South America and Antarctica, Fischer et al. 2010). The most probable producers seem to be hybodontiform sharks (Zidek 1976; Schneider 1986; Fischer et al. 2011).

Stainier (1911) was the first to report on the presence of *Palaeoxyris* in the Belgian Coal Measures Group, notably in the Ransart Member (cited as *Palaeoxyris* sp. in Fig. 2) of the Châtelet Formation (Charleroi district) but also stratigraphically higher, i.e. within the As Member of the Charleroi Formation (see Stainier 1935) in the Campine Basin (Lillo borehole of the Helchteren–Zolder colliery, Fig. 1). Some authors reported on the presence of unidentified *Palaeoxyris* species or of specimens doubtfully assigned to this genus in the Ransart and Floriffoux members of the Châtelet Formation in the Andenne–Huy district (Lambrecht et al. 1957), and in the As Member of the Charleroi Formation in the Liège district (Ancion et al. 1948).

Besides these poorly documented reports, Pruvost (1930) illustrated two species from the Westphalian. The first is *P. appendiculata* Lesquereux 1870 (Pruvost 1930, pl. 2, figs. 8–9, text-fig. 2) (Fig. 4e–f)—a junior synonym of *P. carbonaria* Schimper (in Stiehler 1850) (Kidston 1886; Moysey 1910; Crookall 1928, 1930; Fischer et al. 2019)—from the As and Eikenberg members (Charleroi Formation) in the Couchant de Mons and the Centre districts (Fig. 1). *Palaeoxyris carbonaria* is formed by eight bands showing no breadth alternation. The second species is *P. prendeli* Lesquereux 1870 (Pruvost 1930, pl. 2, fig. 10) from the Mons Member (Charleroi Formation) in the Couchant de Mons district (Fig. 1). *Palaeoxyris prendeli* is characterized by four bands with identical breadth pattern. Unfortunately, most of the specimens illustrated by Pruvost (1930) and Demanet and Van Straelen (in Renier et al. 1938 = copy of Pruvost 1930) were not traced in the RBINS collections where they were supposedly deposited.

Stainier's (1911) specimen from the Campine Basin was assigned to *P. appendiculata* by Stainier (1935), who also reported *P. helicteroides* (Morris in Prestwich 1840), a *Palaeoxyris* species formed by eight bands with alternating breadth pattern (broad-narrow-broad-narrow), without illustration from the As Member in the same basin (Beringen colliery) (Figs. 1–2). In the Liège district, Chaudoir et al. (1952) mentioned *P.* cf. *appendiculata* at the base of the Floriffoux Member (Châtelet Formation) whereas, in the Charleroi district, Pastiels and Willière (1954) and Aderca et al. (1958) cited *P. prendeli* in the Floriffoux and in the Mons members, respectively.

In conclusion, the overview of the available data suggests the possible occurrence of three species of *Palaeoxyris* in the Belgian Coal Measures Group (Fig. 2): *P. carbonaria* (Fig. 4c–d), *P. prendeli* and *P. helicteroides*, of which only the two former were documented by photographs and thus verifiable.

Vetacapsula Mackie 1867 This chondrichthyan egg capsule morphotype (Fig. 3b) displays a three-fold division such as in *Crookallia* and *Palaeoxyris* (Fig. 3a, c) of a fusiform body abruptly tapering at the anterior end into a shorter pointed beak by forming a shoulder and on the posterior one into a long and slender tail. It is superficially almost identical

to *Crookallia* (both are sister taxa according to a phylogenetic analysis, Fischer et al. 2014a, b), however, the body is more bulb-shaped with a large number (> 20) of longitudinal ribs on the surface. Most diagnostic, a prominent middle ridge is present and lateral flange is not yet documented. Six species from the Pennsylvanian have been described up to now from paralic strata of Europe and the USA (Fischer et al. 2014a, b). As for *Crookallia*, the producers most probably belong to the Holocephali (Fischer et al. 2014a).

Due to the absence of illustrations and as noted in the preliminary remarks related to the collections, it is impossible to evaluate if the Belgian post-1945 reports concern either *Vetacapsula* or *Crookallia* (see above) since *Crookallia* was defined in a Russian work (Chabakov 1949)—on the basis of characteristics already noticed by Moysey (1913) and Crookall (1930)—which was unknown by the contemporary geologists/palaeontologists who studied the fauna from the Belgian Coal Measures Group. Therefore, a correct classification was not possible and all finds were understandably addressed as *Vetacapsula*.

Consequently, an undifferentiated *Vetacapsula–Crookallia* morphotype is indicated for the range based on these data in Fig. 2. Stainier (1938, 1942) stressed on the fact that remains (e.g. teeth) of elasmobranchs (other than egg capsules) are abundant within the rocks belonging to the Belgian Coal Measures Group contrary to the egg capsules of the *Vetacapsula* morphotype which are rare. In Belgium, few specimens originally assigned to *Vetacapsula* were illustrated (Pruvost 1930; Stainier 1938, 1942) and *V. debildei* was later referred to the genus *Crookallia* (Fischer et al. 2014a). Specimens belonging to the here used undifferentiated *Vetacapsula–Crookallia* morphotype were reported by different authors (unexhaustive list), i.e. from the Andenne Formation (Ancion et al. 1947), the Ransart (Stainier 1938; Van Leckwyck et al. 1951; Chaudoir et al. 1953) and Floriffoux (Aderca et al. 1958) members of the Châtelet Formation, and from the Mons Member of the Charleroi Formation (Chaudoir et al. 1952; Aderca et al. 1958; Lhoest et al. 1962).

Vetacapsula cooperi Mackie 1867, i.e. the type species of the *Vetacapsula* morphotype, was reported by several authors from the Belgian Coal Measures Group, but none of them illustrated material identified as such. The holotype (by monotypy) of Mackie's (1867) species from the British Coal Measures (unknown locality) was photographically illustrated by Crookall (1928, pl. 1, fig. 1). Crookall (1930, p. 31) cited the presence of *Vetacapsula cooperi* within the Coal Measures of Belgium, but this report seems to be based on an exchange of correspondence with Pruvost. Nonetheless, Pruvost (1930) did not mention this species among the Belgian fauna. Van Leckwyck in Laurentiaux (1952, p. 11) cited one specimen identified as such by A. Pastiels, without illustration, from the Monceau-Fontaine colliery at Forchies (Charleroi district) (Fig. 1) and associated with *V. johnsoni* (unfigured) in a shaly horizon rich in freshwater bivalves belonging to the middle or the upper part of the Andenne Formation (Bashkirian; Namurian B or C according to the traditional subdivision). Although this specimen has not yet been traced in the RBINS collections, it is to our knowledge the only report of this species in Belgium, but it remains unconfirmed until proven otherwise. In the western extension of the Belgian Coal Measures Basin, Pruvost (1930, p. 135) and Derycke et al. (1995, p. 346) mentioned the species (unillustrated) in the basal part of the Vicoigne Formation (Westphalian A of the traditional subdivision) at L'Escarpelle in northern France (Fig. 1). In the Netherlands, van der Heide (1943) described material identified as *V. cooperi* by Pruvost (1927) from the Namurian and Westphalian A of southern Limburg. In conclusion, the presence of *V. cooperi* in Belgium cannot be further documented and therefore remains uncertain (Fig. 2).

Another unconfirmed record is that of *Vetacapsula johnsoni* (Kidston 1886) (Fig. 2). Originally described from the British Coal Measures (Yorkian Series, Westphalian) of Coseley near Dudley (Staffordshire), Kidston's (1886) species was re-described and discussed by Moysey (1910) and Crookall (1928, 1930, 1932). The specimen identified as *V. johnsoni* by Pruvost (1930, p. 134–135, pl. 2, fig. 7) and Demanet and Van Straelen (in Renier et al. 1938, p. 238, pl. 144, fig. 4 [copy of Pruvost (1930, pl. 2, fig. 7)]; text-fig. 126) and thus Derycke et al. (1995, p. 346) is assigned here to *Crookallia kidstoni* (Crookall 1928) (see remarks above). The identification of another specimen made by A. Pastiels and reported by Van Leckwyck (in Laurentiaux 1952, p. 11) remains doubtful in the absence of illustrations (see comments related to *V. cooperi* above; same horizon). The species was reported in the Namurian and Westphalian A of southern Limburg by van der Heide (1943, p. 48).

Discussion

Although chondrichthyan remains were reported from various Carboniferous lithostratigraphic units of Belgium (e.g. Derycke et al. 1995), it is not until the Bashkirian (Namurian B of the traditional subdivision) that chondrichthyan egg cases (*Vetacapsula–Crookallia* morphotype) are first recognised in the Belgian succession (Fig. 2), thus in accordance with the literature data (e.g. Fischer and Kogan 2008; Fischer et al. 2014a). *Palaeoxyris*, *Crookallia*, and *Scapellites* are present in the paralic deposits of the Belgian Coal Measures Group, but uncertainties remain about the presence of *Vetacapsula* which may have been confused with *Crookallia* (e.g. Stainier 1938, 1942). More surprising is the current absence of representatives of the morphotype *Fayolia* Renault and Zeiller 1884 within the Belgian Coal

Measures whereas it is known from adjacent areas: Westphalian C of northern France (Pruvost 1919), Westphalian A of southern Limburg in the Netherlands (van der Heide 1943) and Westphalian D of the Piesberg quarry near Osnabrück in northwestern Germany (Fischer et al. 2019). This lack of fossils of the *Fayolia*-type, assigned to xenacanthiform chondrichthyans as the most probable producers (e.g. Pruvost 1919; Schneider and Reichel 1989; Schneider et al. 2005), probably does not reflect the original occurrence of this egg capsule type. This is suggested by its occurrence in the adjacent geographic areas as well as its repeated co-occurrence together with egg capsules of *Palaeoxyris*, *Vetacapsula*, and/or *Crookallia* in other Pennsylvanian localities (Mazon Creek, Wittry 2012; English Coal Measures, Crookall 1930; northern France, Pruvost 1930; the Netherlands, van der Heide 1943; northwestern Germany, Fischer et al. 2019; Czech Republic, Přibyl 1960). Especially the co-occurrence of *Fayolia* together with *Palaeoxyris* capsules in the same layers (e.g. Schneider et al. 2005; Fischer et al. 2011, 2019; Wittry 2012) and partly even on the same slabs (Schneider et al. 2005; Fischer et al. 2014c) indicates that necessary palaeoenvironmental conditions for the occurrence of *Palaeoxyris* were clearly also sufficient for *Fayolia*. Since *Palaeoxyris* is proven from Belgium, nothing speaks against the presence of *Fayolia* from a palaeoenvironmental point of view. The simplest and also most probable possibility for the lack of fossil evidence so far is, therefore, that the current absence is the result of collecting bias. Maybe some finds are already in museums or private collections, unidentified or wrongly assigned, awaiting scientific discovery. Assignment of fossil egg capsules to false morphotypes, which are morphologically much more different from each other than *Vetacapsula* and *Crookallia*, has been repeatedly documented, as with *Fayolia ellipticus* (Langford 1958) from Mazon Creek as *Palaeoxyris* (Fischer and Kogan 2008), *Vetacapsula marini* (Sampelayo 1946) from Spain as *Palaeoxyris* (Fischer and Kogan 2008), or *Vetacapsula johnsoni* (Kidston 1886) from England also as *Palaeoxyris* (Moysey 1910). Therefore, this case is not so unlikely. The alleged Upper Devonian (Famennian) *Fayolia* from southern Belgium (Stainier 1894, 1935), moreover, was reinterpreted by Mottequin et al. (2021) and rejected from the chondrichthyan egg cases assignment.

Nevertheless, the occurrence of the egg capsule morphotypes *Palaeoxyris*, *Vetacapsula*, *Crookallia*, and *Fayolia* from the central European realm is equivalent to the North American Mazon Creek area (Wittry 2012; Fischer and Wittry 2014) as well as the English Coal Measures (Crookall 1930) on morphotype and species level. It implies the presence of the same chondrichthyan genera and even species using the Pennsylvanian wetland environments for spawning and as nursery areas (Fischer et al. 2014a, 2019). These Mazon Creek-type wetland biota extended from North America throughout Europe, northern Africa to northern China along the palaeoequator, fringing the Pennsylvanian coastline of about 20 million square kilometres (Wittry 2012, 2020). Nowadays, egg capsules are considered fossil remnants of the ancient nurseries in these globally homogenous Late Palaeozoic wetland ecosystems tracing its extension. The Belgian diverse egg capsule inventory unequivocally demonstrates that this was linked with this global wetland environment.

Scapellites is a special case. Since its first description (Pruvost 1922), it has been repeatedly documented from Belgium (e.g. Pruvost 1930; Chaudoir et al. 1951). Nevertheless, outside Belgium, it has only been reported from nearby areas, namely in northern France (Pruvost 1930) and in western Germany (Hahne 1939). Thus, *Scapellites* could be either endemic from this large area, or its absence would be the result of a collection bias in all the other localities from North America to Ukraine. The latter hypothesis is possible but rather unlikely. *Scapellite*s is an unusually small remain whose chondrichthyan affinity is solely based on its formation of several twisted bands (Pruvost 1922). Its producer is still unknown. Other enigmatic small remains, formerly attributed to holocephalan chondrichthyans, have already been justifiably questioned (Obruchev 1967; Stahl 1999). The mass occurrences of *Scapellites* is not a criterion for exclusion from the chondrichthyan egg capsules since such accumulations of egg capsules are known from extant (Treude et al. 2011; Vazquez et al. 2016) as well as fossil (Schneider and Fischer 2011; Fischer and Reich 2013) chondrichthyan fishes. However, *Scapellites* always occurs in masses. Isolated specimens are not known, in contrast to all other capsule types where mass occurrence is an exception, not the rule. Altogether, *Scapellites* is in need of revision just like *Vetacapsula* and *Crookallia*.

Conclusions

Our detailed overview of the available data allows to state that, even though not all taxonomic uncertainties could be resolved, a highly diverse egg capsule assemblage can be documented from the paralic deposits of the Belgian Coal Measures Group (Pennsylvanian; Bashkirian–Moscovian; Namurian B–Westphalian B according to the traditional subdivision). The assemblage includes several species of the hybodontiform-type *Palaeoxyris*, several species of the putative holocephalian types *Vetacapsula* and *Crookallia*, and several species of the enigmatic type *Scapellites*. For the latter, the producers remain unknown.

In conclusion, at least eleven chondrichthyan species seem to have inhabited the ancient aquatic environments of the Belgian Coal Basin for spawning and as nurseries. The

latter number is supposed to be an underestimation, given that *Fayolia*, currently undocumented, is recorded from nearby and surrounding basins with similar palaeoenvironments, indicating that most probably the producers of *Fayolia* must also have been swimming in Belgian waters during the Carboniferous.

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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.

Code availability Not applicable.

Declarations

Competing interests The authors declare no competing interests.

References

Aderca BM, Willière Y, Demanet F, Pastiels A, Scheere J, Van Tassel R (1958) Étude géologique du bassin houiller de Charleroi – Le massif du Carabinier dans la division Marcinelle des Charbonnages de Monceau-Fontaine. Publications de l'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères 34:1–212

Aderca BM, Chesaux CH, Van Leckwijck WP, Pastiels A, Piérart P, Scheere J, Willière Y (1965) Étude paléontologiques, stratigraphiques et tectoniques dans le Westphalien du massif dit des dressants d'Anderlues du district de Charleroi. Publications du Centre national de Géologie houillère 10:1–63

Ancion Ch, Van Leckwyck W, Demanet F, Pastiels A, Willière Y (1947) Étude du Namurien et du Westphalien inférieur du bassin de Huy recoupés par la Galerie de Java (Couthuin, Belgique). Publications de l'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères 1:1–81

Ancion Ch, Dautrebande J, Van Leckwyck W, Pastiels A, Willière Y (1948) Étude géologique du bassin Houiller de Liège - La concession de Marihaye. Publications de l'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères 3:1–105

Aretz M, Herbig HG, Wang XD (2020) The Carboniferous Period. In: Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (eds) Geologic Time Scale 2020. Elsevier, Amsterdam, pp 811–874

Arnold JM (2010) Chapter 26 – Reproduction and embryology of *Nautilus*. In: Saunders W, Landman NH (eds) *Nautilus*, the biology and paleobiology of a living fossil, vol 6. Topics in Geobiology, pp 353–372. https://doi.org/10.1007/978-90-481-3299-7_26

Asselberghs E (1926) Le bassin houiller du Nord de la Belgique. Sondage n°97 (Veldhoven) (Concession Oostham-Quaedmechelen). Annales des Mines de Belgique 27:615–658

Bellière M, Harsée H (1924) Contribution à l'étude stratigraphique du terrain houiller du bassin de Charleroi. Annales des Mines de Belgique 25:347–365

Chabakov AV (1927) O nachodke w kamennougolnych otloshenijach SSSR jajzewych kapsul elasmobranchij *Palaeoxyris* i *Vetacapsula*. Westnik geologitscheskogo komiteta 1:33–34 (**([in Russian])**)

Chabakov AV (1949) O dwuch nowych formach problematitscheskich iskopajemych *Crookallia* is karbona Donezkogo bassejna i *Palaeoxyris* is jury Krima. Ann All-Union Paleontol Soc 13:83–87 (**([in Russian])**)

Chaudoir H, Ancion Ch, Pastiels A, Willière Y (1950) Étude géologique du bassin houiller de Liège – Le massif de Herve – Région orientale. Publications de l'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères 6:1–78

Chaudoir H, Ancion Ch, Pastiels A, Willière Y (1951) Étude géologique du bassin houiller de Liège – Le massif de Herve – Région occidentale. Publications de l'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères 8:1–66

Chaudoir H, Lambrecht L, Pastiels A, Willière Y (1952) Étude géologique du bassin houiller de Liège – La concession Espérance, Violette et Wandre. Publications de l'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères 15:1–132

Chaudoir H, Lambrecht L, Pastiels A, Willière Y (1953) Étude géologique du bassin houiller de Liège – Les concessions Cheratte et Argenteau-Trembleur. Publications de l'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères 17:1–109

Crookall R (1928) Palaeozoic species of *Vetacapsula* and *Palaeoxyris*. Summ Prog Geol Surv Great Britain Museum Pract Geol for 1927 2:87–107

Crookall R (1930) Further morphological studies in *Palaeoxyris*, etc. Summary of progress of the geological survey of great britain and the museum of practical geology for 1929 3:8–36

Crookall R (1932) The nature and affinities of *Palaeoxyris*, etc. Summary of Progress of the Geological Survey of Great Britain and the Museum of Practical Geology for 1931 2:122–140

Delmer A, Ancion Ch (1954a) Le Namurien. In: Fourmarier P (ed) Prodrome d'une description géologique de la Belgique. Société géologique de Belgique, Liège, pp 323–352

Delmer A, Ancion Ch (1954) Le Westphalien. In: Fourmarier P (ed) Prodrome d'une description géologique de la Belgique. Société géologique de Belgique, Liège, pp 353–367

Delmer A, Graulich JM (1954) Tableau synoptique des échelles stratigraphiques des gisements houillers de Belgique. In: Fourmarier P (ed) Prodrome d'une description géologique de la Belgique. Société géologique de Belgique, Liège, inset plate

Delmer A, Graulich JM (1958) Solution de quelques problèmes de stratigraphie houillère par la découverte de niveaux à goniatites. Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie 67:425–453

Delmer A, Tricot J (1976) Le sondage de Buvrinnes au lieu-dit: 'Le Luce.' Belgian Geological Survey, Professional Paper 10:1–24

Delmer A, Dusar M, Delcambre B (2002) Upper Carboniferous lithostratigraphic units (Belgium). Geologica Belgica 4:95–103. https://doi.org/10.20341/gb.2014.045

Demanet F (1941) Faune et stratigraphie de l'étage namurien de la Belgique. Mémoires du Musée royal d'Histoire naturelle de Belgique 97:1–324

Demanet F (1943) Les horizons marins du Westphalien de la Belgique et leurs faunes. Mémoires du Musée royal d'Histoire naturelle de Belgique 101:1–66

Derycke C, Cloutier R, Candilier AM (1995) Palaeozoic vertebrates of northern France and Belgium: Part II – Chondrichthyes, Acanthodii, Actinopterygii (uppermost Silurian to Carboniferous). Geobios, Mémoire Spécial 19:343–350. https://doi.org/10.1016/s0016-6995(95)80136-7

Doguzhaeva LA, Mapes R, Mutvei H (2010) Evolutionary patterns of Carboniferous coleoid cephalopods based on their diversity and morphological plasticity. In: Tanabe K, Shigeta Y, Sasaki T, Hirano H (eds) Cephalopods – Present and Past. Tokai University Press, Tokyo, pp 171–180

Ettingshausen C von (1852) Ueber *Palaeobromelia*, ein neues fossiles Pflanzengeschlecht. Abhandlungen der kaiserlich-königlichen geologischen Reichsanstalt I (3. Abth.):1–10

Fischer J, Kogan I (2008) Elasmobranch egg capsules *Palaeoxyris*, *Fayolia* and *Vetacapsula* as subject of palaeontological research–an annotated bibliography. Freiberger Forschungshefte, C 528:75–91

Fischer J, Reich M (2013) On the Early Cretaceous chondrichthyan egg capsule *Palaeoxyris jugleri* (von Ettingshausen) also known as *Spirangium*. In: Schwarz C, Kriwet J (eds) 6th International Meeting on Mesozoic Fishes. Diversification and Diversity Patterns, 4–10 August 2013, Vienna, Abstracts. Verlag Dr. Friedrich Pfeil, Munich, p 24

Fischer J, Wittry J (2014) The unique Pennsylvanian chondrichthyan multi-taxa nursery of Mazon Creek. Schriftenreihe Der Deutschen Geologischen Gesellschaft Für Geowissenschaften 85:121

Fischer J, Axsmith BJ, Ash SR (2010) First unequivocal record of the hybodont shark egg capsule Palaeoxyris in the Mesozoic of North America. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 255:327–344. https://doi.org/10.1127/0077-7749/2009/0028

Fischer J, Voigt S, Schneider JW, Buchwitz M, Voigt S (2011) A selachian freshwater fauna from the Triassic of Kyrgyzstan and its implication for Mesozoic shark nurseries. J Vertebr Paleont 31:937–953. https://doi.org/10.1080/02724634.2011.601729

Fischer J, Licht M, Kriwet J, Schneider JW, Buchwitz M, Bartsch P (2014a) Egg capsule morphology provides new information about the interrelationships of chondrichthyan fishes. J Syst Palaeontol 12(3):389–399. https://doi.org/10.1080/14772019.2012.762061

Fischer J, Licht M, Schneider JW, Kriwet J, Kogan I (2014b) Chondrichthyan egg capsule card – overview about the chondrichthyan egg capsule morphotypes. https://doi.org/10.13140/2.1.2322.5922

Fischer J, Schneider JW, Rössler R, Spindler F, Hoffmann U (2014c) An Early Carboniferous mass occurrence of shark egg capsules from freshwater deposits. the oldest chondrichthyan multi-taxon nursery. Society of Vertebrate Paleontology 74th Meeting Program & Abstracts: p 130

Fischer J, Hartkopf-Fröder C, Leipner A, Schneider JW, Wittry J, Sowiak M (2019) A highly diverse chondrichthyan egg capsule assemblage from the Late Pennsylvanian Piesberg Quarry, Northwest Germany. Kölner Forum für Geologie und Paläontologie 23:105–106

Hahne C (1939) Ein seltenes Spinnentier (*Trigonomartus dorlodoti* Pruvost) und ein bemerkenswerter Fischrest (*Scapellites minor* Pruvost) aus dem Aachener Steinkohlengebirge. Paläontologische Zeitschrift 21:218–223

Humblet E (1946) Quelques observations supplémentaires sur l'assise de Châtelet dans le bassin houiller de Liège. Zones de Beyne et d'Oupeye. Annales de la Société géologique de Belgique 69:M3–M29

International Commission on Zoological Nomenclature (1999) International Code of Zoological Nomenclature, 4th edn. International Trust for Zoological Nomenclature, London

Klug C, Landman NH, Fuchs D, Mapes RH, Pohle A, Guériau P, Reguer S, Hoffmann R (2019) Anatomy and evolution of the first Coleoidea in the Carboniferous. Communications Biology 2:280. https://doi.org/10.1038/s42003-019-0523-2

Kidston R (1886) On the species of the genus *Palæoxyris*, Brongniart, occurring in British Carboniferous rocks. Proceedings of the Royal Physical Society of Edinburgh 9:54–65

Lambrecht L, Pastiels A, Willière Y (1957) Étude géologique du gisement houiller d'Andenne-Huy – Le Westphalien inférieur dans la concession Halbosart-Kivelterie-La Paix Dieu (province de Liège). Publications de l'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères 29:1–55

Lambrecht L, Bouckaert J, Pastiels A, Scheere J, Van Tassel R, Willière Y (1962) Contribution à l'étude de la zone à *Gastrioceras* dans le synclinal de Liège. Publications du Centre national de Géologie houillère 7:5–35

Langford G (1958) The Wilmington coal flora from a Pennsylvanian deposit in Will County, Illinois. Esconi Associates, Downers Grove:295–302

Laurentiaux D (1952) Découverte d'un homoptère prosboloïde dans le Namurien belge. Publications de l'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères 14:1–16

Lesquereux L (1870) Organs of uncertain affinity. Geological Survey of Illinois. IV, Springfield: 464–467

Lhoest A, Pastiels A, Willière Y, Stockmans F, Scheere J, Van Tassel R (1958) Étude géologique du bassin houiller de Liège – La concession Belle-Vue et Bienvenue. Publications de l'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères 36:1–112

Lhoest A, Pastiels A, Willière Y (1962) Stratigraphie, paléontologie et tectonique au siège de Milmort à l'extrême nord du synclinal de Liège. Publications du Centre national de Géologie houillère 6:1–45

Mackie SJ (1867) Undescribed Vegetable Fossil. The Geological and Natural History Repertory 1 (pro 1865–67):79–80

Mottequin B, Goolaerts S, Hunt A, Olive S (2021) The erroneous chondrichthyan egg case assignments from the Devonian: implications for the knowledge on the evolution of the reproductive strategy within chondrichthyans. The Science of Nature 108(36):1–16. https://doi.org/10.1007/s00114-021-01751-z

Moysey L (1910) On *Palaeoxyris* and other allied fossils from Derbyshire and Nottinghamshire Coalfield. Quarterly J Geol Soc London 66:329–345. https://doi.org/10.1144/gsl.jgs.1910.066.01-04.18

Moysey L (1913) Some further Notes on *Palaeoxyris* and other allied fossils, with special reference to some new features found in *Vetacapsula*. Report of the 83rd meeting of the British Association for the Advancement of Science:492–493

Nemyrovska TI, Yefimenko VI (2013) Middle Carboniferous (Lower Pennsylvanian). In: Gozhyk PF (eds) Stratigraphy of the Upper Proterozoic and Phanerozoic of Ukraine. Vol. 1. Stratigraphy of the Upper Proterozoic, Paleozoic and Mesozoic. Institute of geological sciences NAS of Ukraine, Kiev, pp 283–303 (in Ukrainian)

Obruchev DV (1967) Fossil chimaera egg capsules. Int Geol Rev 9:567–573

Paproth E, Dusar M, Bless MJM, Bouckaert J, Delmer A, Fairon-Demaret M, Houlleberghs E, Laloux M, Piérart P, Somers Y, Streel M, Thorez J, Tricot J (1983) Bio- and lithostratigraphic subdivisions of the Silesian in Belgium, a review. Annales de la Société géologique de Belgique 106:241–283

Pastiels A, Willière Y (1954) Etude géologique du Bassin Houiller de Charleroi – La concession Trieu-Kaisin. Publications de l'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères 20:1–196

Prestwich J (1840) On the Geology of Coalbrook Dale. Trans Geol Soc London Ser 2 5(3):413–495. https://doi.org/10.1144/transgslb.5.3.413

Přibyl A (1960) Nové poznatky o svrchnokarbonské sladkovodní a kontinentální fauně z ostravsko-karvinské oblasti. Rozpravy Česoslovenské Akademie Věd 70(6):43–48 (**([in Czech])**)

Pruvost P (1919) Introduction à l'étude du terrain houiller du Nord et du Pas-de-Calais. La faune continentale du terrain houiller du Nord de la France. Mémoires pour servir à l'explication de la Carte Géologique détaillée de la France. Imprimerie Nationale, Paris, i–xxxii, 1–584

Pruvost P (1922) Description d'un fossile nouveau (*Scapellites Cottoni* nov. gen. et sp.) du Westphalien supérieur du Couchant de Mons. Annales de la Société scientifique de Bruxelles (Documents et Comptes Rendus) 42:150–155
Pruvost P (1927) Distribution de la faune continentale dans le terrain houiller du Limbourg. Geologisch Bureau Voor Het Nederlandsche Mijngebied Te Heerlen, Jaarverslag 1926:78–83
Pruvost P (1930) La faune continentale du terrain houiller de la Belgique. Mémoires du Musée royal d'Histoire naturelle de Belgique 44:103–280
Renault B, Zeiller R (1884) Sur un nouveau genre de fossiles végétaux. Comptes rendus hebdomadaires des séances de l'Académie des Sciences 98:1391–1394
Renier A (1922) La position stratigraphique du gisement profond du siège n° 10 (Grisœuil), de la Compagnie de Charbonnages Belges. Annales de la Société géologique de Belgique 45:B80–B85
Renier A (1927) Le sondage de Lummen-Gestel (n° 103). Annales des Mines de Belgique 28:870–894
Renier A (1934) Détermination de l'exacte position de l'horizon de Quaregnon dans le massif du Borinage, au Couchant de Mons. Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie 44:281–290
Renier A (1937) Contribution à l'étude du bassin houiller de Liège, spécialement dans sa partie orientale. Annales de la Société géologique de Belgique 61:B20–B33
Renier A (1938) Quelques observations sur des *Scapellites*. Annales de la Société scientifique de Bruxelles, 2ème série, 58:100–104
Renier A (1942) Quelques remarques sur les variations de facies de l'horizon à *Gastrioceras subcrenatum* dans le bassin de Liège. Annales de la Société géologique de Belgique 65:M8–M24
Renier A, Stockmans F, Demanet F, Van Straelen V (1938) Flore et faune houillères de la Belgique. Introduction à l'étude paléontologique du terrain houiller. Patrimoine du Musée royal d'Histoire naturelle de Belgique, Bruxelles
Rössler R, Schneider JW (1997) Eine bemerkenswerte Paläobiocoenose im Unterkarbon Mitteleuropas - Fossilführung und Paläoenvironment der Hainichen-Subgruppe (Erzgebirge-Becken). Veröffentlichungen Museum Für Naturkunde Chemnitz 20:5–44
Sampelayo PH (1946) Estudios acerca del Carbonifero en España. Boletín del Instituto Geológico y Minero de España 59:1–19
Schneider JW (1986) *Limnoselache* n. g.—ein Süßwasserhai der paläozoisch-mesozoischen Familie Tristychiiade (Hybodontoidea). Freiberger Forschungshefte C 410:77–87
Schneider JW, Fischer J (2011) A late Viséan shark nursery – transition from anadromous to stationary freshwater lifestyle? Ichthyolith Issues Special Publication 12:43–44
Schneider JW, Reichel W (1989) Chondrichthyer-Eikapseln aus dem Rotliegenden (Unterperm) Mitteleuropas - Schlußfolgerungen zur Paläobiologie paläozoischer Süßwasserhaie. Freiberger Forschungshefte C 436:58–69
Schneider JW, Hoth K, Gaitzsch B, Berger HJ, Steinborn H, Walter H, Zeidler MK (2005) Carboniferous stratigraphy and development of the Erzgebirge Basin, East Germany. Zeitschrift der Deutschen Gesellschaft für Geowissenschaften 156:431–466. https://doi.org/10.1127/1860-1804/2005/0156-0431
Stahl BJ (1999) Chondrichthyes III – Holocephali. Handbook of Paleoichthyology 4. Verlag Dr. Friedrich Pfeil, Munich
Stainier X (1894) Un *Spiraxis* nouveau du Dévonien belge. Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie (Mémoires) 8:23–28.
Stainier X (1911) Matériaux pour la faune du Houiller de Belgique (5e note). Annales de la Société géologique de Belgique 39:B79–B87
Stainier X (1932) Stratigraphie des assises inférieures du bassin houiller du Hainaut. (Assises de Châtelet, d'Andenne et de Chokier). P. Hosdain, Jumet
Stainier X (1935) Matériaux pour la faune du Houiller de Belgique (6e note). Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie 45:15–42
Stainier X (1936) Le Houiller inférieur au charbonnage d'Hautrage. Coupe du sondage d'Hautrage. Bulletin de la Société belge de Géologie, de Paléontologie et d'Hydrologie 46:203–228
Stainier X (1938) *Belinurus* et *Vetacapsula* nouveaux du Houiller belge. Bulletin du Musée royal d'Histoire naturelle de Belgique 14(32):1–13
Stainier X (1942) Un *Vetacapsula* nouveau du Houiller belge. Bulletin du Musée royal d'Histoire naturelle de Belgique 18(47):1–6
Stiehler AW (1850) Herr Stiehler an Herrn v. Carnall Zeitschrift der Deutschen Geologischen Gesellschaft 2:181–184
Treude T, Kiel S, Linke P, Peckmann J, Goedert JL (2011) Elasmobranch egg capsules associated with modern and ancient cold seeps: A nursery for marine deep-water predators. Mar Ecol Prog Ser 437:175–181. https://doi.org/10.3354/meps09305
Van der Heide S (1943) La faune ichtyologique du Carbonifère supérieur des Pays-Bas. Mededeelingen van de Geologische Stichting, Series C-4 3(2):1–65
Van Leckwyck W, Biot A, Demanet F, Pastiels A, Willière Y (1951) Etude géologique du bassin houiller de Charleroi – La concession Tergnée-Aiseau-Presle (première partie). Publications de l'Association pour l'Étude de la Paléontologie et de la Stratigraphie houillères 9:1–155
Vazquez DM, Mabragaña E, Gabbanelli V, Díaz JM (2016) Exploring nursery sites for oviparous chondrichthyans in the Southwest Atlantic (36°S–41°S). Mar Biol Res 12(7):715–725. https://doi.org/10.1080/17451000.2016.1203948
Vialov OS (1984) Nowaja nachodka jaizewych kapsul elasmobranchij *Palaeoxyris*. In: Vialov OS, Gawrilischin WI, Didikovski WJ, Sosimovitsch WJ, Makridin WP, Masulin NW, Eynor OL (eds) Paleontologija i stratigrafija fanerosoja Ukrainy. Naukova dumka, Kiev, pp 99–103 (**[in Russian]**))
Von Boletzky S (1998) Cephalopod eggs and egg masses. Oceanogr Mar Biol Ann Rev 36:341–371
Wittry J (2012) The Mazon Creek Fossil Fauna. Earth Science Club of Northern Illinois: Downers Grove
Wittry J (2020) A Comprehensive Guide to the Fossil Flora of Mazon Creek. Earth Science Club of Northern Illinois, Downers Grove
Whalen CD, Landman NH (2022) Fossil coleoid cephalopod from the Mississippian Bear Gulch Lagerstätte sheds light on early vampyropod evolution. Nat Commun 13:1107. https://doi.org/10.1038/s41467-022-28333-5
Zidek J (1976) A new shark egg capsule from the Pennsylvanian of Oklahoma, and remarks on the chondrichthyan egg capsules in general. J Paleontol 50:907–915

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