3D imaging of shark egg cases (*Palaeoxyris*) from Sweden with new insights into Early Jurassic shark ecology

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**ABSTRACT**

Several shark species produce egg cases as protective casings in which their embryos develop. These casings are composed of multiple layers of collagen and are extremely durable, making them prone to fossilisation. Here we document *Palaeoxyris* (*Spirangium*) — fossil shark egg cases from Lower Jurassic successions of southern Sweden. We present high-resolution 3D images of *Palaeoxyris* based on microfocus X-ray computed tomography (µCT) of seven specimens, including fossils that were embedded within a sandstone matrix. Our examination of the internal structure of the egg cases revealed the possible remnants of a yolk and foetus in one specimen. The cases were most likely produced by hybodont sharks, as outlined in previous studies, and the occurrence of hybodont teeth from Lower Jurassic successions of Sweden support this. Palynological analysis of the matrix from one of the specimens hosting *Palaeoxyris*, indicates an early Hettangian age. The high percentage of spores (c. 60%) reveals that the egg cases were laid during the Transitional Spore Spike Interval following the end-Triassic mass extinction. The egg cases are found in conjunction with fossil horsetails; with the broader palynological and sedimentological evidence, this suggests an estuarine depositional setting, and potentially indicates that newborn sharks were living in habitats comparable to modern mangroves, as is often the case today.

**Introduction**

Modern shark reproduction and egg case production

Elasmobranchs (sharks, rays and skates) have evolved many adaptations over their 400-million-year evolutionary history, including complex reproductive modes. Their reproductive strategies are diverse and in many cases remain poorly understood. Different species exhibit a variety of brood sizes, ovarian cycles, gestation periods, mating systems and the utilisation of nurseries (Carrier et al. 2004). Ray-finned fishes produce large numbers of eggs and sperm, and fertilisation occurs in the water; this simple form of oviparity provides no protection for the egg, and thus predation of the egg is common. Should fertilisation occur, the embryo survives on a small amount of yolk, and if the juvenile finally hatches, the hatching is still underdeveloped and highly vulnerable to predators and the environment. To overcome the dangers of simple ovoviviparity, Chondrichthyan fishes are some of the earliest vertebrates to have evolved internal fertilisation.

Internal fertilisation is ubiquitous among elasmobranchs, but the duration throughout which the female retains the fertilised eggs varies. Ovoviparous forms (egg laying) keep their eggs for a short period of time before depositing them in substrate or attaching them to structures (Carrier et al. 2004). Viviparous (live bearing) forms retain the embryo internally, allowing development to complete within the uterus, before giving birth to live young. In both forms the young hatch (or are born) fully developed; this is in contrast to the more primitive mode of reproduction of ray-finned fishes, where the young hatch undeveloped and require time outside the egg to complete their development. Sharks owe much of their success to this shift from the ancestral, simple form of oviparity to internal fertilisation (Carrier et al. 2004).

Modern sharks are mostly viviparous, but only three families utilise oviparity – the Heterodontidae, Scyliorhinidae, and Orectolobidae. However, both viviparous and oviparous forms produce egg cases. For viviparous species there are several different ways that the egg case is treated. For example, in viviparous species the egg case may be treated as an intermediary stage, whereby the embryo develops within the egg case, and once hatched, continues to develop *in utero*. In other examples, the egg case is present throughout the entire developmental cycle *in utero* and can even be incorporated into the uterus (Wourms 1977). Recently, a new mode of oviparity, described as “sustained single oviparity”, was discovered in the *Cephaloscyllium sarawakensis* shark of the South China Sea. This is characterised by an extended period of time for which a single egg case in an oviduct is retained until the embryo attains a sizable length, and the egg case can be deposited outside of the mother’s body (Nakaya et al. 2020). Recent discoveries such as this highlight the complex and poorly understood nature of the embryonic development of Chondrichthyans.

Elasmobranch egg cases consist of the egg case membrane, embryonic jelly, egg yolk, and a developing embryo (Musa et al. 2018). The egg case is secreted by the kidney-shaped oviducal glands (also known as shell glands, and in viviparous elasmobranchs, the nidamental gland), which is found in the upper third of each oviduct. The gland has identical dorsal and...
ventral sides, which are made of several long tubular glands, each of which produces one of the two walls of the egg case. The two sides also create a dorsoventrally flattened lumen, within the gland, into which the egg case is extruded. The size of the oviducal gland changes during the sexual cycle, for example: in Scyliorhinus canicula the gland is characterised by a pronounced and discrete thickening and grows to about 3.5 cm by 2.5 cm in fully mature females, but is only visible as a slight thickening in immature females (Knight et al. 1996). The spiral shape and coiling of the tendrils of modern elasmobranch egg cases is thought to be a result of rotation as it forms within the oviducal gland (Knight et al. 1996). The oviducal gland may also play an important role in sperm storage, a phenomenon seen frequently in captive sharks which are able to lay fertilised eggs without the presence of a male (Knight et al. 1996; Hamlett et al. 1998). A detailed description of the morphology of the oviducal glands and a discussion on the terminology used to describe the gland is presented by Hamlett et al. (1998).

The oviparous sharks produce enclosed eggs, which are protected by a tough, leathery case. The cases are either deposited on a substrate or attached to structures in the benthic zone, often in pairs, and serve as the only protection for the embryo. Once deposited, the embryo is left to grow on its own, feeding on the large yolk inside the egg case. Incubation can vary greatly among species, generally lasting a few months, and in other species over a year.

The morphology of egg cases is highly varied among different shark groups. In general, skates (but also some sharks) produce quadrangular egg cases with horn-like processes which protrude from the corners. Chimeras tend to produce tadpole shaped cases which are often intricate and complex in their morphology. Sharks generally produce rounded, ellipsoidal egg cases, however there are many exceptions to this morphology. Each ellipsoidal shark egg case or “capsule” has a flange that spirals the side of the structure and has been shown to be made up of many different collagen layers (Carrier et al. 2004; Hamlett et al. 2005). The toughness of the egg cases increases their preservation potential in the fossil record and serves as a propensity for the fossilisation process, and several fossilised egg cases are known from around the world that can preserve intricate morphologies (Fischer et al. 2014).

**Egg cases in the fossil record**

In the fossil record, sharks and chimaeroids are known from the Middle Ordovician (Sansom et al. 2012), but usually only their hard parts, i.e. their teeth (oral odontodes) and scales (skin odontodes), are preserved. In rare circumstances, fin spines, pectoral girdles (Maisey et al. 2017), brain cases (Maisey 2001; Maisey & Anderson 2001; Coates et al. 2017) and even complete specimens have been discovered (Miller et al. 2003). Fossilised chondrichthyan egg cases have been recovered from Visean (Late Mississippian) to Upper Cretaceous strata (Stainier 1894; Fischer et al. 2014), but most are known from the Palaeozoic. Identification of these fossils has, however, proven highly problematic and controversial over the century following their discovery. Although initially described incorrectly, Brongniart (1828) was the first to document fossil shark egg cases. Bearing a resemblance to the inflorescence of the extant angiosperm *Xyris*, the cases were named *Palaeoxyris regularis*. Schenk (1867) later considered the cases to be similar to cones of cycads, but noted that they also bore similarities with the egg cases of extant sharks. Schimper (1869) renamed the egg cases under the genus *Spiranium* (meaning “spiral capsule”) as an alternative to *Palaeoxyris*, as he realised that *Palaeoxyris* had no relationship to the living *Xyris*. Mackie (1867) also described shark egg cases under the name *Vetacapsula*, a new type of what he interpreted as seed pods, from the UK. Further studies would also erroneously describe shark egg cases as plant organs and algae (Nathorst 1879). A further form, named *Fayolia*, was found in France and described as a possible seed or fructification (Renault & Zeiller 1884). But spurred on by earlier suggestions by Schenk in 1867, Renault & Zeiller (1888) conducted a study on *Palaeoxyris* and *Fayolia* and concluded that these were in fact egg cases of fish, and not botanical remains. Further studies were carried out on *Palaeoxyris*, *Fayolia* and *Vetacapsula* by various authors, and eventually a comprehensive series of papers was published by Crookall (1928a, 1928b, 1930, 1932), showing that these fossils were the egg cases of elasmobranchs. Crookall’s work also demonstrated that *Palaeoxyris*, *Fayolia* and *Vetacapsula* occurred in fresh or brackish water deposits, and the cases were secured to plants by structures at the apex of their beaks (see Fig. 1). Throughout the 1900s there was still scepticism that these fossils were the remains of shark eggs, but today this is widely accepted. An exhaustive review of the literature and history of *Palaeoxyris*, *Fayolia* and *Vetacapsula* was presented by Fischer & Kogan (2008), which chronicles the development of research regarding these fossil egg cases since their discovery. Following Crookall’s research, much work has been done to unravel the evolution and morphologies of ancient Chondrichthyan egg cases. Today there are 10 distinct morphotypes of chondrichthyan egg cases (Fischer et al. 2014).

Many *Palaeoxyris* specimens preserve a rectangular rhombic pattern, which Brongniart (1828) referenced as tile-like rhombic scales. This is indeed why *Palaeoxyris* was given its name, as this pattern resembled that of *Xyris* seed heads. This pattern is the product of taphonomy, and is the result of the collarettes on each side of the egg case forming overlapping ribbing in completely compressed specimens. However, this common form of preservation is not found within the Early Jurassic Swedish Museum of Natural History (NRM) *Palaeoxyris* collection, as all specimens are preserved in 3D with screw-like morphology which is similar to extant *Heterodontus francisci* (see Fischer et al. 2008), or as a negative imprint of a single surface of the egg cases.

*Palaeoxyris* (Brongniart 1828) is the most common fossil shark egg case. It is present in Palaeozoic and Mesozoic successions, albeit in slightly different forms, and is found in brackish and freshwater deposits (Fischer et al. 2010). There are several Mesozoic species from Europe, Asia and Australia (Schmidt 1928; Crookall 1930; Müller 1978), and recent finds have revealed examples from Upper Cretaceous strata of the USA (Fischer et al. 2010). *Palaeoxyris* thus ranges from the early Carboniferous to the Late Cretaceous. Curiously, the fossil record of *Palaeoxyris* is extremely poor throughout the Permian, from which only a single specimen
has been recorded (Fischer & Kogan 2008; Hamad et al. 2016). The fossil egg cases are rarely found in association with skeletal remains of sharks, and therefore the producer of *Palaeoxyris* has remained uncertain. Today, the consensus view is that hybodontid sharks produced *Palaeoxyris*; these are the only group of elasmobranchs that span the geological range of *Palaeoxyris* (Zidek 1976). However, several similarities have been noted between egg cases of the extant heterodontid sharks (*Heterodontus*) and *Palaeoxyris*, including egg case construction, general shape and collarette attachment (Schenk 1867; Zidek 1976; Fischer et al. 2007; Böttcher 2010).

Morphologically, *Palaeoxyris* has a three-fold division (Fig. 1) consisting of a spindle-shaped body, pointed beak (posteriorly) and a long slender pedicle (anteriorly). The case body is flanked by a spirally twisted flange, known as a collarette. Palaeozoic specimens exhibit a spiral collarette extending down the long slender pedicle, whereas Mesozoic specimens have a parallel arrangement (Fischer et al. 2014). Typically, the junction at which the beak can be distinguished from the body is gradual in nature. The junction between the body and pedicle is more pinched and constricted, and generally the pedicle is longer than the beak. In some specimens, the division between the different parts of the case may be difficult to discern, hampering differentiation between the beak and the pedicle. At the posterior end of the beak, *Palaeoxyris* has a spiral tendril functioning as an attachment mechanism to bottom structures and aquatic plants in order to secure the case in place (Fischer et al. 2014), a feature which is shared with modern oviparous shark egg cases. It is common to find the pedicle broken and/or incomplete. Including the beak, body and pedicle, *Palaeoxyris* can reach a total length of up to 27 cm (Böttcher 2010).

Examples of *Palaeoxyris* have previously been documented from “Rhaeto-Liassic” successions of Skåne, Sweden (Nathorst 1879), under the genus *Spirangium* (Schenk 1867). Nathorst’s (1879) study was based on specimens collected by Angelin and Lundegren in 1860. Nathorst (1879) rejected a zoological affinity and concluded that *Spirangium* were gigantic *Chara*, fresh-water green algae (stone-worths). Nathorst (1879)

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Figure 1. Morphology of the Mesozoic *Palaeoxyris* fossil chondrichthyan egg case. The egg case consists of three sections: the beak, body and pedicle. A long tendril extended from the beak which aided in the anchoring and attachment of specimens to bottom structures and aquatic plants. A collarette flanks the side of the egg case and is distinctive for different species. The collarette in the Mesozoic form of *Palaeoxyris* extends down the pedicle in a vertical manner, a different morphology from that of Palaeozoic specimens. Illustration after (Fischer et al. 2014).
applied the genus *Spirangium*, interpreting the algae as growing in pairs on stalks. Based on their co-occurrence with plant remains, fresh-water molluscs and insects, Nathorst (1879) inferred a fresh-water lake or lagoonal setting for *Spirangium* in the uppermost Rhaetian deposits of Bjuv and the specimens from the supposedly Hettangian deposits of Helsingborg (Gravarana).

The aim of this study is to illustrate the range of shark egg cases housed in the collections of the NRM and reconstruct the environment that hybodont sharks inhabited during the Early Jurassic in Sweden. We further aim to examine potential interior morphological characters or contents of the egg cases (e.g. for the possible remains of shark embryos) using X-ray tomography.

**Geological setting**

Mesozoic sedimentary rocks in Sweden occur only in the southernmost province, Skåne (Fig. 2), where Triassic–Cretaceous successions may reach a thickness of up to 2000 m in the southwestern part of the province, resting on the crystalline basement (Brotzen 1945, 1950; Norling & Bergström 1987; Norling et al. 1993; Larsson et al. 2000; Vajda 2001; Lindström & Erlström 2006). While Cretaceous deposits are missing in the northwestern part of Skåne, Upper Triassic and basal Jurassic sediments are well-represented, reaching thicknesses of 100–1000 m (Norling & Bergström 1987; Pieńkowski 1991; Ahlberg et al. 2003a, Ahlberg et al. 2003b).

![Figure 2. Geological map of Skåne, southern Sweden with Mesozoic successions colour coded, sample localities marked: Bjuv, Helsingborg. Modified after Norin (1953).](image-url)
The geographical location of Upper Triassic–Lower Jurassic sedimentary successions of southern Sweden is a reflection of the ancient topography, and the depositional and tectonic conditions, with structural highs separating different areas (Erilstrom & Guy-Ohlson 1999; Vajda & Wigforss-Lange 2009). The oldest Mesozoic successions preserved in Sweden are of Late Triassic, Norian age and are mainly expressed as alluvial fan deposits, with conglomerates to sandstones to sandstones (Qvarnstrom & Niedzwiedzki 2018). Fossils are rare in these deposits, charophytes being the only representatives so far recorded (Qvarnström & Niedzwiedzki 2018). The Triassic and Jurassic successions were chiefly deposited in a range of continental settings, such as alluvial plains, deltas, tidal zones, and coastal plains, but the Lower Jurassic deposits also record shallow, near-shore marine conditions (Pieńkowski 1991; Ahlberg et al. 2003a, Ahlberg et al. 2003b).

The Rhaetian successions are part of the Högänäs Formation, which is divided in three parts: the Vallåkra, Bjuv and Helsingborg members (Fig. 3). The basal Vallåkra Member mainly comprises mudstones interbedded with sandstones containing siderite concretions (Sivhed 1984). This is overlain by the Bjuv Member (Sivhed 1984; Lindstrom & Erlstrom 2006), which mainly comprises mudstones bracketed by two coal seams, A and B (Lundblad 1950; Sivhed 1984). The uppermost coal seam (seam A) is generally overlain by non-marine carbonaceous mudstones and poorly sorted sandstones (Boserup beds). The sandstones are traditionally referred to as Liassic in age and are part of the Helsingborg Member, the uppermost member of the Högänäs Formation. This is overlain by mainly marine sand- and mudstones, marking the base of the Rya Formation, indicating an Early Jurassic marine transgression in this region (Troedsson 1950; Sivhed 1984).

**Material and methods**

**Fossil egg cases**

The Palaeoxyris specimens studied here are housed in the Department of Paleobiology, at the NRM. The majority of these specimens were collected by Angelin and Lundegren during the mid- and late 1800s from Helsingborg (Gravarna), northwestern Skåne, from sandstones of Hettangian age. Nathorst collected additional specimens in 1875, from north of Helsingborg in what he described as “an iron-rich clays tone” of Sinemurian age. As previously outlined, these fossils were interpreted as seeds, buds or chara (Nathorst 1879). Therefore, we surveyed both the palaeobotanical and palaeozoological collections of the NRM for Palaeoxyris specimens. Fifty-nine specimens were identified, some nearly complete, while only the negative mould was available for others. Selected specimens were measured, illustrated (by tracing) and photographed (Fig. 4).

**Microfocus X-ray computed tomography (µCT)**

Microfocus X-ray computed tomography (µCT) is now widely applied in palaeontology. While the benefits of this non-destructive scanning technique are obvious for the examination of internal morphological features of fossils, µCT data can also assist in the investigation of external features, and has been applied to numerous groups and types of preservation, e.g. therapsids (e.g. Krüger et al. 2018), hominins (e.g. Berger et al. 2015), dinosaurs (e.g. Bates et al. 2009), invertebrates (e.g. Afriat et al. 2020) and taphonomic traces (e.g. Randolph-Quinney et al. 2018). For this study we apply µCT for the investigation of internal structures and the reconstruction of surface data, which would otherwise be difficult to extract from the host sediment.

Seven Palaeoxyris egg cases curated at NRM (S064340, S064388, S064387, S064341, S064390, S066495 and S064578) were scanned using microfocus X-ray computed tomography

| System   | Stage     | Formation | Member          | Miospore Zone               |
|----------|-----------|-----------|-----------------|-----------------------------|
| Jurassic | Lower     | Rya Fm    | Rydebäck Mb    | Sphenopollenites-Leptolepidites |
|          |           |           | Katslösa Mb    | Chasmatosporites             |
|          |           |           | Pankarp Mb     | C. macroverrucosus          |
|          |           |           | Döshult Mb     |                             |
|          | Sinemurian|           | Helsingborg Mb | Pinuspollenites-Trachysporites |
| Triassic | Upper     | Höganäs Fm| Bjuv Mb         | Transitional Spore-spikes     |
|          |           |           | Vallåkra Mb    | Corollina - Ricciisporites   |
|          | Norian    | Kågeröd Formation | Undefined               |

Figure 3. Stratigraphic scheme of the sedimentary units spanning the Triassic-Jurassic boundary in Skåne, correlated with local pollen zones (from Koppelhus & Nielsen 1994; Larsson 2009). The green band illustrates the stratigraphic interval from where the Palaeoxyris egg cases derive. Modified after Vajda et al. (2013).
Figure 4. Photograph and illustration of hybodontid egg cases *Palaeoxyris*. Specimen A. S064585; B. S065911; C. S065910-01; D. S066490. Scale bars = 1 cm. Illustrations not to scale.
(μCT) at Stockholm University Brain Imaging Centre (SUBIC) using the ZEISS Xradia Versa 520 X-ray microscope (Figs. 5–8). μCT scanning of the specimens enabled the non-destructive investigation of the internal structure of the shark egg cases, and subsequent segmentation of external structures to visualise their morphology. These seven specimens were selected for their overall completeness of the corpus, and because they are preserved in 3D. Small cylindrical specimens were placed inside 50 ml falcon tubes to be mounted to the Xradia’s stage platform and make use of the system’s autoloader function. Larger specimens were placed in modified plastic tubes or tubs that were cut to size and glued to mounting brackets. Each specimen was scanned at 120 kV and 10 W with 1601 projections. Visualisation and segmentation were accomplished in Object Research Systems (ORS) (Montreal, Quebec Canada) Dragonfly software using a non-commercial license.

Figure 5. Palaeoxyris specimen S064578 in lateral view (A, B). C: Digitally segmented specimen (in blue) from the rock matrix (grey). The ribbing of the collarettes are more clearly visible as they have not been weathered out due to surface exposure. The pedicle ribbing junction is clearly visible as the ribbing changes gradually to a parallel form and extends vertically down the pedicle. D, E: Two-dimensional slices of the μCT data set showing the morphology of the collarettes (as indicated by red arrows) are visible and still preserved within the rock matrix. Scale bars = 1 cm.
Figure 6. Three-dimensional (3D) models of the surface of Palaeoxyris specimens extracted from the μCT data sets. Lighting and rendering of the surface of the models was manipulated utilising ORS Dragonfly and various lookup tables (LUTs) to exaggerate the surface morphology, allowing more clear investigation and characterisation of external morphology. *Palaeoxyris* specimen: A. S064578; B. S066495; C. S064388; D. S064387; E. S064341; F. S064390; G. S064340. Mica inclusions are seen throughout the specimens (as indicated by white specs in 2D μCT slices in H). Scale bars = 1 cm.
One rock sample from the sandstones hosting *Palaeoxyris* (S064398) was analysed for palynology to: (i) date the sediments, and (ii) improve reconstructions of the palaeoenvironment. The sample was processed according to standard palynological procedures at Global Geolab Ltd., Canada: c. 5 g of sediment was first treated with hydrochloric acid (HCl) to remove calcium carbonate, and further macerated in 45% hydrofluoric acid (HF).
to dissolve silicates. The organic residue was sieved using a 5 μm mesh and mounted in epoxy resin on a glass slide. Over 300 pollen and spores were counted using light microscopy. Palynofacies analysis was also carried out to assess the depositional environment. Over 500 organic grains were counted, and the following groups were identified: opaque phytoclasts, translucent phytoclasts, spores, pollen (non-saccate), pollen (saccate) and amorphous organic matter (AOM). The palynological organic residue was then examined using scanning electron microscopy (SEM). For SEM analysis, organic residues were spread across stubs and gold coated before analysis, using an ESEM FEI Quanta FEG 650 SEM at the NRM. Slides, SEM stubs and residues are housed in the collections of the NRM and illustrated specimens are identified by S-numbers.

**Results and discussion**

Fifty-nine specimens assigned to *Palaeoxyris*, curated at the NRM, were observed for this study. Most specimens were damaged and missing their pedicle and/or beak. This is unsurprising as the long and slender morphology of the pedicle is likely to be damaged during fossilisation and the collection process. The body (or corpus) is more robust and therefore may withstand overburden pressures following burial. Two sedimentary rock blocks (S066535 and S064583) possess several *Palaeoxyris* specimens, supporting the hypothesis that hybodont sharks laid their eggs in clutches (Fischer et al. 2011). Many extant holocephalans are known to spawn two egg cases simultaneously – one from each oviduct (e.g. Carrier et al. 2004; Hamlett et al. 2005), although in some individuals only one ovary is functional (Carrier et al. 2004; Rêgo et al. 2013). For the *Palaeoxyris* specimens studied here, measurements for the total length (beak, body, pedicle) and maximum width (of the body) were taken where possible and an average measurement of the spacing between ribbing (collarettes) was also recorded. Specimen numbers and measurements are presented in Table 1.

To visualise weathered specimens more clearly (such as S064578; Fig. 5) μCT scanning was used. The scanning proved to be useful for visualising the morphology of the shark egg.
Table 1. Palaeoayris muensteri specimens curated at the Naturhistoriska riksmuseet. Measurements for total length (where possible), body width and average width between bands (ribbing) recorded in mm.

| Catalogue N. | Author | Collector | Storage | Area | Site | Lithology | Length (mm) | Width (mm) | ID |
|--------------|--------|-----------|---------|------|------|-----------|-------------|------------|----|
| S064339      | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | 38 | 9.5 | Body | 4 |
| S064340      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | 16 | Body | 4 |
| S064341      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | 29.5 | 15.1 | Body | 4 |
| S064381      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | - | - | Unidentified | - |
| S064382      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | - | 10 | Body mold | 4 |
| S064383      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | - | 11.5 | Body mold | 4 |
| S064384      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | - | -12 | Body | 4 |
| S064385      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | - | 12.2 | Beak/pedicle | - |
| S064386      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | 24 | 12.2 | Body | 4 |
| S064387      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | 33 | 13.1 | Body | 3 |
| S064388      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | 40 | 17.2 | Body | - |
| S064389      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | 12 | 10 | Pedicle incomplete | - |
| S064390      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | 19 | 11 | Body incomplete | 3 |
| S064391      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | - | 14 | Body | 4 |
| S064392      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | - | - | Body | 3.5 |
| S064393      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | - | - | Body | 2 |
| S064394      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | 71.5 | 10.1 | Almost complete | 3 |
| S064395      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | - | - | Unidentified | - |
| S064415      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | 28.1 | - | Pedicle incomplete | 4 |
| S064416      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | - | - | Beak/pedicle | 3.9 |
| S064417      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | 33 | 14 | Body, incomplete, missing pedicle | 4.1 |

| Catalogue N. | Author | Collector | Storage | Area | Site | Lithology | Length (mm) | Width (mm) | ID |
|--------------|--------|-----------|---------|------|------|-----------|-------------|------------|----|
| S064418      | Carlson, A. F. | Silica | Helsingborg | Helsingborgs tegelbruk | Silica | - | 13 | Cast | 4 |
| S06451      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | - | Unidentified | 4 |
| S06452      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | - | Pedicle | - |
| S06453      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | 15.9 | Body | 5 |
| S06454      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | - | Body | 4.5 |
| S06455      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | - | Body | 5 |
| S06456      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | 24 | 14 | Beak? | 5 |
| S06457      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | - | Unidentified | - |
| S06458      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | 54 | 15.1 | Body | 3 |
| S06459      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | -41.8 | 8 | Body | 3 |
| S06460      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | 22.5 | 6 | Pedicle? | 3 |
| S06461      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | 34 | 11 | Beak? | 3 |
| S06462      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | - | Beak? | - |
| S06463      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | - | A number of specimens | - |
| S06464      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | - | Beak (?) | 5 |
| S06465      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | 51.9 | -14.8 | Body, parts of pedicle and beak | 5 |
| S06466      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | - | Mold | 6 |
| S06467      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | - | Unidentified | - |
| S06468      | Schimp. | Nathorst, A. G. | Cast | Helsingborg | Gravarna | Sandstone | - | 9 | Complete | 4 |
| S065910-01  | Pred | Nathorst, A. G. | Cast | Höganäs | Site 6 | Sandstone | 58 | 10 | Almost complete | 3 |
| S065910-02  | Schimp. | Nathorst, A. G. | Cast | Höganäs | Site 6 | - | - | Unidentified | - |
| S065911      | Pred | Nathorst, A. G. | Cast | Höganäs | Site 6 | Höganäs | 49.5 | -10 | Body and beak | 4 |
| S065912      | Pred | Nathorst, A. G. | Cast | Höganäs | Site 6 | Höganäs | - | - | Beak? | - |
| S066232      | Angelin | Cast | Höganäs | Site 6 | Höganäs | 30.5 | 4 | Body, pedicle | 3 |
| S066233      | Angelin | Cast | Höganäs | Site 6 | Höganäs | 55 | -9.3 | Almost complete | 3 |
| S066489      | Schimp. | Nathorst, A. G. | Cast | Höganäs | Site 9 | Höganäs | 56 | 14.8 | Beak? | - |

(Continued)
Table 1. (Continued).

| Catalogue N. | Author       | Collector       | Storage | Area  | Site  | Lithology | Length (mm) | Width (mm) | ID                  |
|-------------|--------------|-----------------|---------|-------|-------|------------|-------------|------------|---------------------|
| S066490     | (Ettingsh.)  | Nathorst, A. G. | Cast    | Höganäs| Site 9| Sandstone  | 57          | 23.5       | Beak?               |
| S066491     | Schimp.      | Nathorst, A. G. | Cast    | Höganäs| Site 9| Sandstone  | -           | -          | Unidentified         |
| S066492     | Schimp.      | Nathorst, A. G. | Cast    | Höganäs| Site 9| Sandstone  | -           | -          | Unidentified         |
| S066493     | (Ettingsh.)  | Nathorst, A. G. | Cast    | Höganäs| Site 9| Sandstone  | -           | -          | Unidentified         |
| S066494     | Schimp.      | Nathorst, A. G. | Cast    | Höganäs| Site 9| Sandstone  | 43          | 11         | 4 specimens, body, parts of beak and pedicle |
| S066495     | Presl        | Nathorst, A. G. | Cast    | Höganäs| Site 9| Sandstone  | 38.5        | -7.6       | Body, parts of pedicle and beak 2-3 |
| S066496     | Presl        | Nathorst, A. G. | Cast    | Höganäs| Site 9| Sandstone  | -           | 14         | Body mold 5         |
| S066497     | Presl        | Nathorst, A. G. | Cast    | Höganäs| Site 9| Sandstone  | 16          | 9          | 2                   |
| S066498     | Presl        | Nathorst, A. G. | Cast    | Höganäs| Site 9| Sandstone  | ~44         | ~11.2      | Body and beak 4      |
| S066535     | Schimp.      | Nathorst, A. G. | Cast    | Helsingborg| Gravarna | Sandstone | -           | ~13.9      | 8 + specimens 5     |
| S070396     | Presl        | Nathorst, A. G. | Cast    | Möllebacke| Site 1 | -          | -          | -          | -                   |
| S075976     | Malling, C.  | 265:19:07:12     | Impression | Sofiero | N om parken | -          | -          | Body and pedicle 8   |
cases still embedded in their rock matrix. The ribbing of the collarettes is more clearly defined in specimens that are surrounded in a sedimentary matrix as their surfaces have not been exposed to weathering. Digital segmentation of such specimens enables visualisation of the morphology of the ribbing without invasive destruction and exposes the junction between the body and pedicle ribbing (Fig. 5C). Visualisation of 2D slices (Fig. 5) clearly shows the morphology of the egg case in posterior view (D) and ventral view (E). Remnants of the collarettes are indicated with arrows (Fig. 5D, E).

The internal contents of Palaeoxyris specimens were further examined using µCT scanning. Most specimens analysed were infilled with sandstone, suggesting that any original organic contents were replaced during fossilisation. However, abundant mica inclusions were seen throughout the specimens (as indicated by white specs in 2D µCT slices; Fig. 6H). Three-dimensional (3D) models of the surface of the specimens were also extracted from the µCT data sets (Fig. 6). Adjustments to the lighting and rendering of the surface of the models may enhance the visibility of structural features, allowing more clear investigation and characterisation of external morphology.

Internal investigation of one specimen (S066495) revealed a notable void in the posterior section (towards the beak) (Fig. 7). Upon further examination and manipulation of grey scale values of the X-ray data set, a set of globular structures were observed. Utilising visualisation software and built in lookup tables (LUTs), image intensity was mapped to on screen colour. This allowed the clearer visualisation of these globular structures (Fig. 8). The structures may be reminiscent of the developing shark embryo and yolk which can be observed in modern oviparous shark egg cases. Posteriorly a smaller sized void can be observed, taking up approximately a fifth of the total length of the case. This void is then separated by a high-density inclusion (Fig. 8A), followed by a much larger void, which is approximately half the length of the case (Fig. 8B, C). We interpret these as the possible remnants of a yolk and embryo. This may represent the first observation of a shark embryo recorded in an egg case in the fossil record, however, we would caution this diagnosis until further examination of egg case cases can be undertaken, perhaps with various other scanning methodologies.

In Skåne, Jurassic shark teeth assigned to hybodonts have been documented from Plinsbachian and Sinemurian successions of the Rya Formation (Katsåsö) (Rees 2000), supporting hypotheses that Palaeoxyris was produced by hybodonts (Zidek 1976; Fischer et al. 2011). During most of the Triassic and Early Jurassic, hybodont sharks dominated amongst the selachians and most of them were adapted to both fresh-water and marine environments (Rees & Underwood 2008). During the Late Jurassic, however, the hybodonts were outcompeted in open marine environments by the neoselachians and became restricted to fluvial and restricted marine environments (Rees 2000; Rees & Underwood 2008). Investigation of modern sharks’ (such as Heterodontus) nursery and egg laying activities (Powter & Gladstone 2008a, Powter & Gladstone 2008b; Day et al. 2019) has led some researchers to use Heterodontus as a modern analogue for understanding the associated behaviour of the sharks which laid Palaeoxyris egg cases (Böttcher 2010; Fischer & Reich 2013). Heterodontus is known to have complex nursing strategies and may possess a high spatial memory, often returning to specific resting sites (O’Gower 1995). Future research beyond the models of Heterodontus, from both viviparous and oviparous extant sharks may shed light on the behaviour of Palaeoxyris laying sharks and their ancient nurseries.

**Palynology**

Well preserved spores, pollen and marine palynomorphs were recorded from sample S064398; 29 taxa were identified (Table 2), composed of 13 spore, 13 pollen and three marine taxa. The assemblage is dominated by spores and pollen derived from land plants (~96%), with minor marine palynomorph abundances (~4%) (Fig. 9). Spores comprise ~59% of the assemblage, which are overwhelmingly dominated by Deltoidospora toralis (Fig. 9B; ~49%), a fern spore probably produced by a member of the Matoniaceae, possibly Dictyophyllum (Larsson 2009). With the exception of Calamospora tener (Fig. 9A; ~4%), Trachysporites fuscus (~2%) and T. asper (~1%), all other spore taxa comprise subsidiary components (<1% of the total assemblage each). Pollen comprises ~36% of the assemblage, of which the most abundant taxon is Pinus pollenites spp. (~10% of the total assemblage), with relatively low abundances of Classopolis spp. (~6%) and Perinapolilites elataoides (~5%). The overall composition of the

| Table 2. Palynological count data from sample S064398. “+” refers to taxa that were present in the slide, but not in the count. |
|--------------------------------------------------|
| Raw abundance | Relative abundance (%) |
|----------------|------------------------|
| **Mosses** (Bryophytes) | + | + |
| Foraminisporis jurassicus | + | + |
| Stereisporites spp. | 1 | 0.3 |
| Club-mosses (Lycopophytes) | + | + |
| Retiniletes australclavatides | 1 | 0.3 |
| Sphenophytes/Ferns | + | + |
| Calamospora tener | 14 | 4.3 |
| Ferns | + | + |
| Bucalcutisporites caomumensis | 1 | 0.3 |
| Cibotiumspora jur assessment | 2 | 0.6 |
| Conbacularisporites mesoaequus | 1 | 0.3 |
| Deltoidospora australis | 3 | 0.9 |
| Deltoidospora toralis | 157 | 48.6 |
| Loevagiosporites spp. | 1 | 0.3 |
| Marattisporites scabrus | + | + |
| Trachysporites asper | 4 | 1.2 |
| Trachysporites fuscus | 7 | 2.2 |
| Pollen (saccate) | + | + |
| Araucariaceae australis | 1 | 0.3 |
| Cerebropollenites thiartgi | 2 | 0.6 |
| Chasmatosporites spp. | 5 | 1.5 |
| Classopolis spp. | 19 | 5.9 |
| Monosulcites minimus | 1 | 0.3 |
| Monosulcites punctatus | + | + |
| Perinapolilites elataoides | 17 | 5.3 |
| Pollen (saccate) | + | + |
| Alisporites spp. | 1 | 0.3 |
| Alisporites radialis | 2 | 0.6 |
| Alisporites robustus | + | + |
| Pinus pollenites spp. | 32 | 9.9 |
| Quaenacllaeana malaformis | 2 | 0.6 |
| Unidentifiable bisaccate pollen | 35 | 10.8 |
| Marine palynomorphs | + | + |
| Dinoflagellata | 1 | 0.3 |
| Leiospherae | 8 | 2.5 |
| Michystridium spp. | 5 | 1.5 |
| Total | 323 | 100 |
Figure 9. Light microscope (A–E, G) and SEM (F, H) images of spores and pollen from sediment sample S064398 that hosts Palaeoxyris. A. Calamospora tener; B. Deltoidospora toralis; C. Trachysporites fuscus; D. Perinopollenites elatoides; E–F, Classopolis spp; G–H. Pinuspollenites spp. I–J. Neocalamites hoerensis (I, specimen S064406; J, specimen S064394). Scale bar in A = 10 µm for A–H, scale bar in I = 1 cm for I–J.
palynological assemblage, in particular, the relatively high abundances of Pinuspollenites spp. and the presence of Trachysporites spp., suggest that this sample belongs to the Hettangian Pinuspollenites–Trachysporites Zone (Dybkjær 1988, 1991; Larsson 2009). This is further supported by the absence of classic Rhaetian taxa, such as Riccisporites tuberculatus, and the absence of Cerebropollenites macroverrucosus, the first appearance of which marks the onset of the overlying Sinemurian C. macroverrucosus Zone (Dybkjær 1991; Larsson 2009; Peterfy et al. 2016). However, the dominance of fern spores, in particular D. toralis, suggests that the sample may belong to the Transitional Spore Spike Interval (TSI) sensu Larsson (2009), an informal interval of spore-dominance following the end-Triassic mass extinction. The absence of Rhaetian taxa suggests that this sample originates from the uppermost part of the TSI. Although the palynology reveals that the parent flora was dominated by ferns, abundant pollen from large trees, including Pinuspollenites spp., Classopolis spp. and P. elatoides, indicate that the regional vegetation comprised a mixture of opportunistic (i.e. ferns) and more well-developed elements (i.e. large gymnosperms), suggesting that this represents a seral/intermediate successional community following the end-Triassic mass extinction.

**Environmental setting**

The overwhelming dominance of terrestrial organic matter within the palynological and palynofacies data (Fig. 10) points to a predominantly freshwater depositional environment with limited marine influence, situated close to the palaeoshoreline. Notably, the eggs are found in close association with the stems of the fossil horsetail plant, Neocalamites hoerensis (Equisetales) (Fig. 9I–J). Extant horsetails often grow as emergent aquatic plants (Hauke 1979), and exhibit high tolerances to several environmental stresses, including increased salinity (Husby et al. 2011; Husby 2013). Jurassic horsetails are commonly found in situ in coastal plain and deltaic deposits that record evidence of marine influence (e.g. Spicer & Hill 1979; Slater & Wellman 2015). The Neocalamites macrofossils associated with shark egg cases here support previous observations that Palaeoxyris egg cases were attached to the stems of horsetails (e.g. see Fig. 5 in Fischer & Kogan 2008). Interestingly, Calamospora tener, a probable Equisetales spore (Larsson 2009), was recorded in relatively high abundances (~4%) within the palynological count. Spores equivalent to Calamospora tener have been found in situ from Echinostachys verticillata, an isolated reproductive organ recorded from the Triassic of France. Echinostachys verticillata is similar in organisation to living Equisetum and is presumed to be part of an Equisetites fossil species (Grauvogel-Stamm 1978; Grauvogel-Stamm & Lugardon 2009). The co-occurrence of C. tener and N. hoerensis in our material suggests a spore–parent plant connection, and further points to a possible link between Echinostachys-type organs and N. hoerensis. The monospecific nature of the plant macrofossil assemblages of N. hoerensis recorded here, in association with the varied orientation of egg cases preserved in their sandstone matrix, are further suggestive of a relatively high-energy depositional environment. Based on comparisons of plant macrofossil and spore-pollen assemblages from Jurassic deposits elsewhere (Slater & Wellman 2015), Calamospora is considered to have had a low preservation potential, due to its thin wall and low sporopollenin content (Traverse 2007; Grauvogel-Stamm & Lugardon 2009). Hence, the relative high abundances of C. tener in conjunction with its probable parent plant strongly suggests that horsetails comprised a major component of the local parent vegetation. Although we interpret that the monospecific macrofossil assemblages of N. hoerensis indicate that horsetails were growing locally in probable shallow brackish water and sharks were attaching their eggs to these plants (Fig. 11), the palynological data demonstrates that the regional vegetation was more diverse. The palynofacies counts (Table 3; Fig. 10) are overwhelmingly dominated by opaque (~56%) and translucent (~41%) phytoclasts. A large portion of the opaque phytoclasts are probably the fragmented remains of macroscopic charcoal inclusions, visible within

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**Figure 10.** A. Pie charts of the relative abundances of various plant groups based on palynology, and palynofacies categories. B. Ternary chart of palynofacies composition (see Tyson 1995). Red dot = composition of sample 5064398.
Figure 11. Reconstruction of Early Jurassic estuarine ecosystem with *Palaeoxyris* egg cases attached to *Neocalamites (Equisitum)* stems, and hybodont sharks in the background. Illustration © Michael Rothman.
Table 3. Palynofacies count data from sample S064398.

| Description                  | Raw abundance | Relative abundance (%) |
|------------------------------|---------------|------------------------|
| Opaque phytoclasts           | 289           | 56.2                   |
| Translucent phytoclasts      | 213           | 41.4                   |
| Spores                       | 7             | 1.4                    |
| Pollen (non-saccate)         | 1             | 0.2                    |
| Pollen (saccate)             | 1             | 0.2                    |
| Amorphous organic matter     | 3             | 0.6                    |
| TOTAL                        | 514           | 100                    |

the sediment matrix. When palynofacies data are plotted in a ternary chart of phytoclast vs. palynomorph vs. AOM relative abundances (Fig. 10B), the position of the sample supports a high-energy depositional environment (Tyson 1995). Together, the palynofacies, plant macrofossils and the lithology of sandstones, indicate high-energy conditions, with possible flash flooding events following torrential rains during which the shark egg cases may have been buried.

Today, juvenile sharks often live in brackish water, amongst shallow water mangrove roots, as such habitats host prey for the young sharks and offer protection from predators (Nagelkerken et al. 2008). Although mangroves were not present in the Jurassic, the emergent aquatic horsetails reconstructed here would have provided a comparable habitat for newborn sharks, with the stems of the Neocalamites hoerenis plants acting as an ideal substrate for hybodont sharks to attach their eggs to (Fig. 11).

Conclusions

The application of CT-scanning of fossil shark eggs provides additional information of the gross morphology of the external structure of Palaeoxyris cases and is especially useful when such specimens are concealed by a rock matrix. The internal contents of the shark eggs analysed here remain somewhat elusive, and most specimens do not show evidence of fossilised embryos, suggesting that the original embryos either: (i) successfully hatched and the empty case was later fossilised; (ii) were predated on; (iii) were empty and unviable to begin with; or (iv) the embryo and accompanying yolk were destroyed during fossilisation. However, the contents of one specimen (S066495) reveal faint globular structures that may be the remnants of the original yolk and/or shark embryo. Assuming the two cavities separated here represent the yolk and embryo, this would be the first time such a find has been reported. Further investigation should be undertaken, possibly utilising synchrotron X-ray scanning to ascertain the true nature of this anomaly. The possible future discovery of a Palaeoxyris case with an indisputable shark foetus would settle any outstanding debate on the affinity of these fossils and pave the way for future research into the reproduction and possible nursing strategies of extinct hybodont sharks.

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