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Description of the shark egg capsule *Palaeoxyris friessi* n. sp. from the Ladinian (Middle Triassic) of SW Germany and discussion of all known egg capsules from the Triassic of the Germanic Basin

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Abstract

The new shark egg capsule *Palaeoxyris friessi* n. sp. is described from the Hauptsandstein of the Lower Keuper (Erfurt Formation, Ladinian, Middle Triassic). The type and only specimen is complete and remarkably well preserved. With a length of 27 cm it is the longest complete *Palaeoxyris* egg capsule known so far. It is interpreted as an egg capsule of the hybodontid sharks *Polyacrodus polycyphus* or cf. *Polyacrodus keuperianus.* The capsule is associated with a rich flora, the brackish water bivalve *Unionites* and conchostracans, but other vertebrate remains were absent. All known records of Triassic and Lower Jurassic egg capsules from the Germanic Basin and their potential producers are discussed. All of the capsules have been found in deltaic or prodeltaic deposits.

Keywords: *Palaeoxyris friessi* n. sp., shark egg capsule, Erfurt Formation, Lower Keuper, Buntsandstein, Hauptsandstein, Rhaetian, Hettangian, Ilsfeld.

Zusammenfassung

Die neue Hai-Eikapsel *Palaeoxyris friessi* n. sp. aus dem Hauptsandstein des Unteren Keupers (Erfurt Formation, Ladinium, Mittlere Trias) wird beschrieben. Das Typusexemplar, der einzige Fund, ist außergewöhnlich gut und vollständig erhalten. Mit einer Länge von 27 cm ist sie die längste bisher bekannte *Palaeoxyris*-Eikapsel. Sie stammt vermutlich von den hybodontiden Haien *Polyacrodus polycyphus* oder cf. *Polyacrodus keuperianus*. Sie wurde zusammen mit einer reichen Flora, der Brackwassermuschel *Unionites* und Conchostraken gefunden, Reste von Wirbeltieren fehlten. Die Vorkommen der übrigen triassischen und unterjurassischen *Palaeoxyris*-Arten des Germanischen Beckens und ihre potentiellen Erzeuger werden diskutiert. Alle Eikapseln wurden in Delta- oder Prodelta-Ablagerungen gefunden.

Contents

1. Introduction

In the last few years new specimens of *Palaeoxyris* from the Triassic of Central Asia and North America have been described and the history of research and the different interpretations of this enigmatic fossil have been discussed in detail (FISCHER & KOGAN 2008, FISCHER et al. 2007, 2010). Today it is generally accepted that these spindle shaped fossils, which are known from the Carboniferous to the Cretaceous, are egg capsules of sharks, most probably of hybodontids. *Palaeoxyris* was first described from the Middle Triassic (Anisian) of the Vosges, France (*P. regularis*, BRONGNIART 1828). Later, in addition to several new species from the Carboniferous and two from the Cretaceous, further species were named from the Triassic of southern Germany: *P. becksmanni* (ORTLAM 1967) from the Upper Buntsandstein (Anisian) as well as *P. muensteri* (PRESL 1838), *P. quenstedti* (QUENSTEDT 1867, SCHIMPER 1870–74), and *P. muelleri* (FRENTZEN 1932b) from the Rhaetian.

Palaeoxyris has also been found from Triassic deposits outside Europe: *P. duni* from the Upper Anisian Hawkesbury Sandstone in New South Wales, Australia (DUN 1912, CROOKALL 1930), *Palaeoxyris* sp. from the Middle to Late Triassic (Ladinian–Carnian) of Kyrgyzstan, Central Asia (FISCHER et al. 2007), and *P. humblei* from the Late Triassic (Norian) of Arizona, USA (FISCHER et al. 2010).

In Europe (Fig. 1), the Triassic occurrences of *Palaeoxyris* are restricted to the Anisian (Upper Buntsandstein) and the Rhaetian (Upper Keuper). Around one hundred

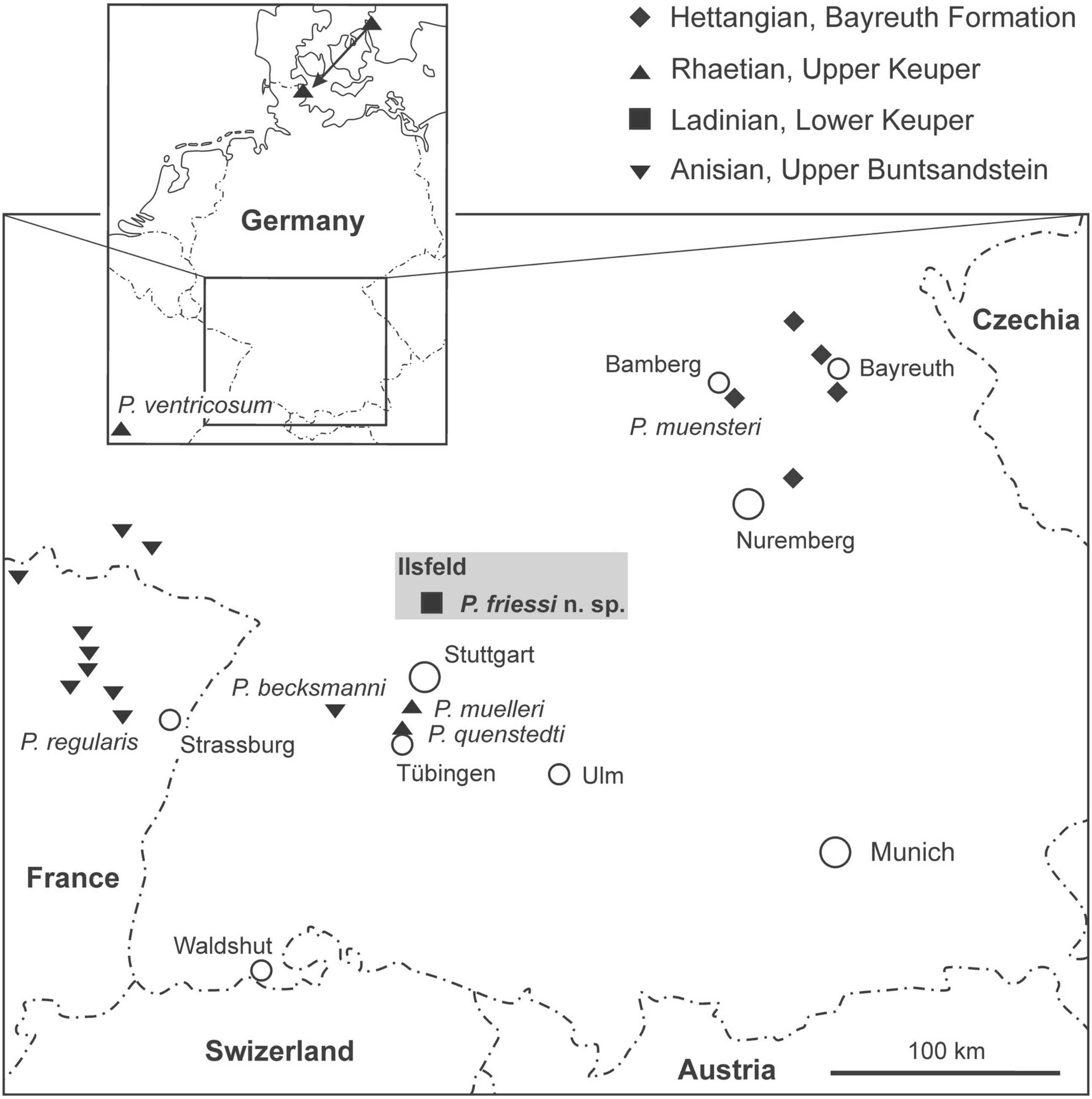

Fig. 1. Sketch map showing Triassic *Palaeoxyris* fossil localities in Germany, France, and Sweden and the type localities of the different species. The finding from Northern Germany has been transported during the Quaternary by glaciers from Southern Sweden (see text for further explanation) (after ENGELS & UNGER 1998, FRENTZEN 1932a, 1932b, GALL 1971, GOTHAN 1914, HAGEMANN 1984, NATHORST 1879, ORTLAM 1967, QUENSTEDT 1867, SCHENK 1867, SCHIMPER 1870–1872, SCHINDLER et al. 2009, WEBER 1968).

specimens of *P. regularis* have been collected in the Buntsandstein of the northern Vosges (GALL 1971, GALL & KRUMBEIN 1992). In adjacent areas of Germany *Palaeoxyris* is also known from contemporaneous layers in the Pfälzerwald of Rheinland-Pfalz (*P. regularis*, FRENTZEN 1932a: 535, SCHINDLER et al. 2009), and on the basis of a single specimen from the Schwarzwald (Black Forest) in Baden-Württemberg (*P. becksmanni*, ORTLAM 1967). *Palaeoxyris* is also known from the Buntsandstein of Majorca, Spain (*Palaeoxyris* sp., ZESSIN 2008).

In the Rhaetian *Palaeoxyris* is known from Tübingen in Baden-Württemberg (type area of *P. quenstedti* and *P.

muelleri, Quenstedt 1867, Frentzen 1932b). Also in the Rhaetian and/or Hettangian of Scania, Southern Sweden *Palaeoxyris* was found (Nathorst 1879, Vossmerbäumer 1966: 100), transported during the Pleistocene by glaciers as bed load also some 120 km to the North German coast (Fig. 1; Hagemann 1984). Also of Rhaetian age is *P. ventricosum* from Autun, France (Schimper 1870–1872, Courel 1980 (*Spirangium*)). Only slightly younger are the specimens from Bamberg, Kulmbach, Bayreuth, and Nuremberg in Franconia, northern Bavaria, type area of *P. muensteri* (Presl 1838, Schenk 1867, Gothan 1914, Engels & Unger 1998). Formerly known as the “Rhätolias” most of the plant-bearing horizons in that area are of Early Jurassic (Hettangian) age (Urlichs 1966, pl. 4, Weber 1968). It is probable that most, if not all specimens of *Palaeoxyris* from Franconia are of that age.

The aim of this paper is to describe the first specimen of *Palaeoxyris* from the Ladinian (Lower Keuper). It represents the largest complete *Palaeoxyris* specimen ever found.

Institutional abbreviations

GPIT	Institut für Geowissenschaften, Tübingen University, Germany
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany

Acknowledgements

I am most grateful to the private collector Gerald Friess (Großbottwar), who found the specimen described herein and donated one of the two slabs to the SMNS, and to Jan Fischer (Freiberg) for fruitful discussions and providing translations of some Russian literature. I further thank Philipe Havlik (Tübingen) for access to the *Palaeoxyris* specimen of the GPIT, Chris Duffin (Sutton) for improving the English, Rainer Schoch (Stuttgart) and Dieter Seegis (Schorndorf) for helpful comments.

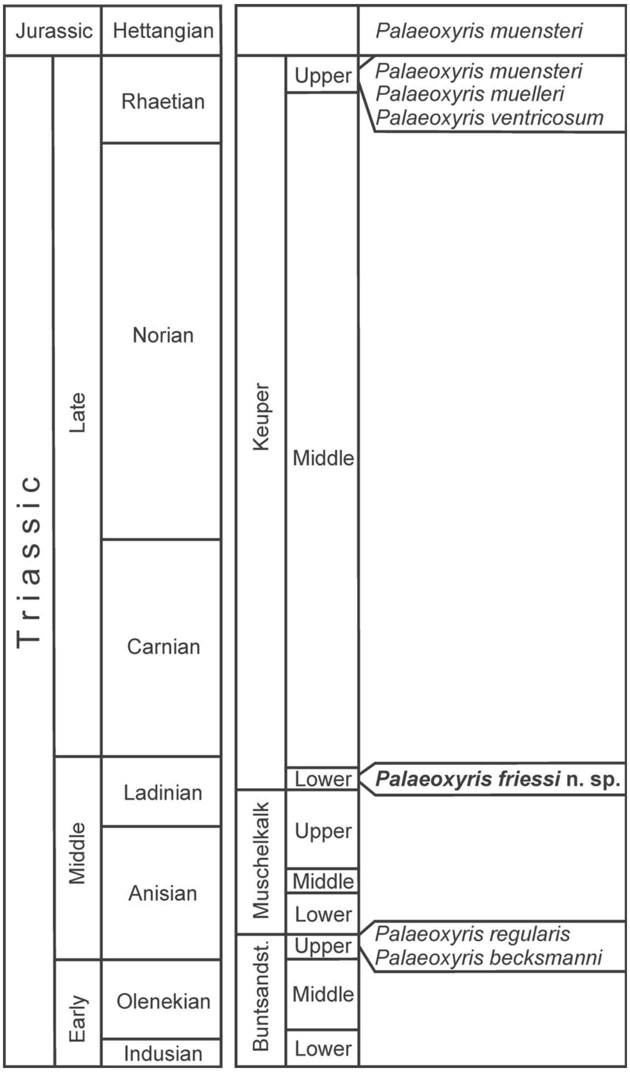

Fig. 2. Triassic stratigraphy in the Germanic Basin and occurrences of *Palaeoxyris* egg capsules.

2. Material and methods

2.1. Material

The new species of *Palaeoxyris* described here was found in 2009 by the private collector Gerald Friess, Großbottwar, Germany in the Bopp quarry near Ilsfeld north of Stuttgart, Baden-Württemberg (Fig. 1). It stems from near the top of a sand dominated channel of the Hauptsandstein in a laminated siltstone (Lower Keuper, Erfurt Formation, Ladinian; Fig. 2). For a detailed section of the Lower Keuper in the Bopp quarry see Pöppelreiter (1999: 120, outcrop photo fig. 15). Considerable information concerning the flora of the Hauptsandstein is given by Kelber (1990) and Kelber & Hansch (1995), a description of a new plant from the type horizon of the here described *Palaeoxyris* gave Rozynek (2008). In the same horizon the plants *Equisetites arenaceus*, *Neocalamites merianii*, *Danaeopsis arenacea*, *Cladophlebis distans*, *Taeniopteris* sp., *Schozachia donaea*, *Willsiostrobus* sp., *Swedenborgia* sp., the brackish water bivalve *Unionites* (Geyer et al. 2005), conchostracans, and coprolites have been found (pers. com. G. Friess, see also Rozynek 2008).

The egg capsule is compressed and preserved as part and counterpart. One plate is housed in the collection of the SMNS, while the other one remains in the private collection of G. Friess. Further specimens of Rhaetian age were studied in the SMNS and the collection of the GPIT.

2.2. Methods

Fischer et al. (2010, fig. 2) were the first to rationalise a descriptive terminology for *Palaeoxyris*, summarising their suggestions in a useful interpretative diagram. This necessity was apparent as early as 1928 when Crookall stated that descriptive terms "have often been very loosely used by certain authors." This comment applies particularly to the terms "segment" and "band". While in the past these two terms were often used synonymously (e. g. *P. pringeli*, Crookall 1928: 14 segments; Müller 1978: 14 bands) "band" now has a clearly defined meaning (Fig. 3a, b). A band surrounds the capsule and is repeated several times on the front side of it. A segment is a part of a band visible on the front side. As several segments of one band can be seen the number of segments is usually higher than the number of bands, but it can be also lower (*P. muelleri*: 3 segments, 4 bands). The wall of the spindle shaped capsule of *Palaeoxyris* consists of spirally twisted bands with slightly elevated ridges in between. The number of theses ridges or ribs has sometimes also been taken into account (Crookall 1930). The situation is similar to that of the bands: a ridge surrounds the capsule parallel to the bands, but counted was not the number of these ridges but the number of segments of all ridges visible on the front side.

While the number of bands in the twisted egg capsules of extant Bullhead sharks *(Heterodontus)* is two, in capsules of *Palaeoxyris* from the Mesozoic it is either four or six or even larger. No egg capsule appears to have an odd number of bands. If the capsule is compressed the number of bands is difficult to count. Also, in specimens preserved three dimensionally, the number is difficult to determine when the capsule is still partly embedded in sediment. They can be counted most easily at well preserved

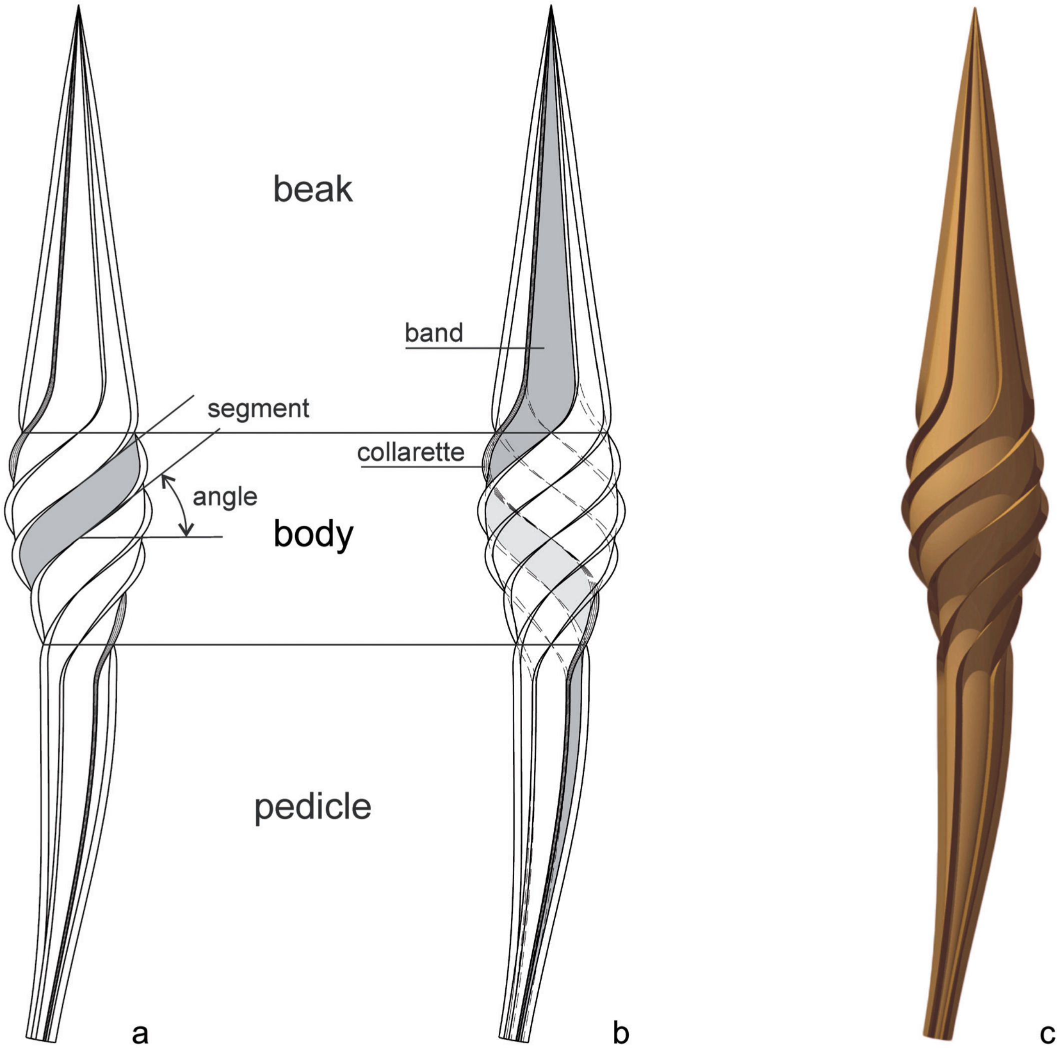

Fig. 3. Diagrammatic drawings of *Palaeoxyris friessi* n. sp. with the terminology used and a reconstruction. – **a**. Drawing of the front side. **b**. Drawing of front and backside, the usual view of compressed capsules, resulting in a rhomboidal pattern of the body of the capsule. **c**. Reconstruction.

cross sections (e. g. Nathorst 1879, pl. 6, figs. 2a, 3a, 4). The number of segments is easier to determine. The presence of a large number of segments may be due to a high number of bands, or a lower number of bands wound into a larger number of turns around the body.

The twisting is always to the right (clockwise, the capsule has a right-hand thread, Fig. 3) as in the egg cases of *Heterodontus* (see Zidek 1976), not to the left as shown in the reconstructions of *Spirangium* in Müller (1978, fig. 11D), of *Palaeoxyris* in Gall (1983, fig. 30), Fischer & Kogan (2008, fig. 5) and of *P. humblei* in Fischer et al. (2010, figs. 2, 7). This is clearly seen in all three-dimensionally preserved specimens but sometimes difficult to recognise in compressed egg cases. Since the ridges of the front side are preserved as elevated ribs while those on the back side are to be seen as furrows (Müller 1978: 12) it should be possible to distinguish the two sides in most cases and therefore the direction of twisting.

The capsules are usually divided into three morphological parts: the beak, the body, and the pedicle (Fig. 3a, b; Fischer et al. 2010, Müller 1978). The transition between beak and body is gradual while at the transition between the body and the pedicle the capsule is slightly constricted. In complete specimens, the pedicle is usually longer than the beak. Since most specimens are incomplete, usually only length and width of the body can be given. In all Palaeozoic species of *Palaeoxyris* the body and the pedicle are both twisted, but in Mesozoic specimens (with one exception) twisting is confined to the body (Fischer et al. 2008, Fischer & Kogan 2008). This means that the drawing given by Brongniart (1828) is not inaccurate in this point as was originally supposed by Crookall (1930).

The boundaries of the three parts are poorly defined. When compressed the ridges of the front and the back of the body cross each other resulting in a rhomboidal pattern (Fig. 3b). In this case the ends of the body are present at the last crossing points of the ridges (Müller 1978). If the capsules are preserved in three-dimensions, the boundaries are not so clearly defined. They are present where the ridges change their direction from spirally twisted to straight (Zidek 1976). In this case, therefore, it is not possible to give the exact length of the body.

The angle of the ridges with the cross axis of the capsule in the middle of the body is also often measured. Some confusion exists also with this character. Müller (1978) wrote “Der Winkel, den sie mit der Längsachse bilden, ist in der Mitte am kleinsten” (the angle they [the ridges] make with the longitudinal axis is smallest in the middle of the capsule). This statement is incorrect as there the angle is biggest if measured to the longitudinal axis. Since he and most other authors give the angle with the cross axis (also called the “angle of rising”, Zidek 1976) I have followed them (Fig. 3a). Some authors (e. g. Ortlam (1967), however, gave the angle with the longitudinal axis. For the sake of clarity it is best to compare the angle given by an author with the figures in order to decide which angle was measured. The angle formed at the ends of the body is of little value since they gradually increase up to nearly 90° in the pedicle or the beak. The angles are probably not influenced by taphonomic processes, except for the very rare case of upright embedding (see below).

The ridges between the bands are the basis of narrow flanges or collarettes (Fig. 3). The collarettes stand upright on the ridges in some species as seen, for example, in three-dimensionally preserved specimens of *P. muensteri*, *P. muelleri*, and *P. ventricosum* (material from the Rhaetian in SMNS and GPIT, see also Crookall 1930, pl. 3, fig. 4). This is different to the egg cases of *Heterodontus* where the collarettes are inclined (Zidek 1976).

3. Systematic palaeontology

Palaeoxyris Brongniart, 1828

Type species: *P. regularis* Brongniart, 1828, reproductions of the figure of the type specimen in Crookall (1930, pl. 5, fig. 4) and Fischer & Kogan (2008, fig. 1).

Type locality: Soultz-les-bains, 20 km West of Strassburg, France.

Type horizon: Grès à Voltzia, Upper Buntsandstein, Middle Triassic, Anisian.

Palaeoxyris friessi n. sp.

Figs. 3–5

Holotype: SMNS 95447 (Figs. 4a, 5), counterpart (Fig. 4b) in private collection Friess, Großbottwar.

Type horizon: Top of Hauptsandstein, Lower Erfurt Formation (Lower Keuper); Longobardian, Ladinian, Middle Triassic.

Type locality: Muschelkalk quarry Robert Bopp, west of Ilsfeld, Baden-Württemberg, SW Germany.

Etymology: Named after the private collector Gerald Friess, Großbottwar, who found the fossil and donated one of the two plates to the SMNS.

Diagnosis. – *Palaeoxyris friessi* n. sp. is characterised by its large size and the long beak, which is more than twice as long as the body, and a pedicle of the same size. The capsule consists of six bands making a turn around the body of only 300°. On the beak and the pedicle the bands run longitudinal. On the body six sections are visible on the front side. The collarettes have a width of 2 mm.

Description. – The type specimen is preserved in part and counterpart. Carbonaceous material, such as can be seen in plant remains from the same horizon, or a brownish shiny layer, which covers the conchostracans with their chitinous carapace, are not preserved in this fossil. The capsule has a complete length of about 275 mm. The lengths of the three sections of the capsule are: pedicle

Fig. 4. *Palaeoxyris friessi* n. sp., holotype; Hauptsandstein, Lower Keuper, Ladinian; Ilsfeld. – **a**. SMNS 95447. **b**. Private collection FRIESS.

about 110 mm, body 53 mm, beak 112 mm (Tab. 1). The beak is nearly straight with a pointed end, the pedicle is slightly curved. No tendrils are preserved at the end of the beak. Although completely preserved on one plate the end of the pedicle is not clearly visible (Fig. 4a), as seems to be usual in the genus (CROOKALL 1932: 129). The maximal thickness of the body including the collarettes is 39 mm. While the beak has a thickness of 25 mm at its base, the basal thickness of the pedicle is only 19 mm depending on the constriction at the body/pedicle transition. There are six bands 7 to 8 mm wide surrounding the body in a clockwise direction. On the beak they run in the direction of the longitudinal axis of the capsule, before making a turn of 300° on the body and than returning to a longitudinal trajectory on the pedicle. The angle of the ridges with the cross axis is 40° in the middle of the body (Fig. 3a). The flanges or collarettes are 2 mm wide (Fig. 5). They are preserved along all of the ridges and are bent at both sides of the capsule where they turn to the back side. This means that these structures are definitely not opened respirator slits (ZIDEK 1976). The collarettes show some faint longitudinal striation, while the bands lack any obvious structure (Fig. 5).

Discussion. – All Palaeozoic specimens of *Palaeoxyris* are characterised by a twisted pedicle, while in nearly all Mesozoic specimens the pedicle is not twisted (FISCHER et al. 2008, FISCHER & KOGAN 2008). Only one specimen from the Lower Barremian lithographic limestone of Lerida (Sierra del Montsec, Spain) seems to have a twisted pedicle (SAUVAGE 1903, see also DEAN 1906, fig. 13). As the new specimen has no twisted pedicle it needs only to be compared with Mesozoic species.

The types of the type species *P. regularis* BRONGNIART, 1828, as figured by the author and reproduced in CROOKALL (1930, pl. 5, fig. 4) and FISCHER & KOGAN (2008, fig. 1), have a body 35 to 40 mm in length and 13 mm in width (CROOKALL 1930). The angle of the ridges is 60° (CROOKALL 1930, MÜLLER 1978). Four to five segments are visible (MÜLLER 1978, FISCHER et al. 2010: four bands). The two type specimens are quite different from the specimens which GALL collected from the same area and horizon. His biggest specimen (GALL 1971, pl. 25, fig. 1), a complete capsule, has a total length of 180 mm and a body length of 40 mm. There seems to be wide variation in size, as the smallest capsules have a length of only 60 mm and a width of 10 mm (GALL 1971). It is not clear whether different size classes exist giving rise to discontinuous variation

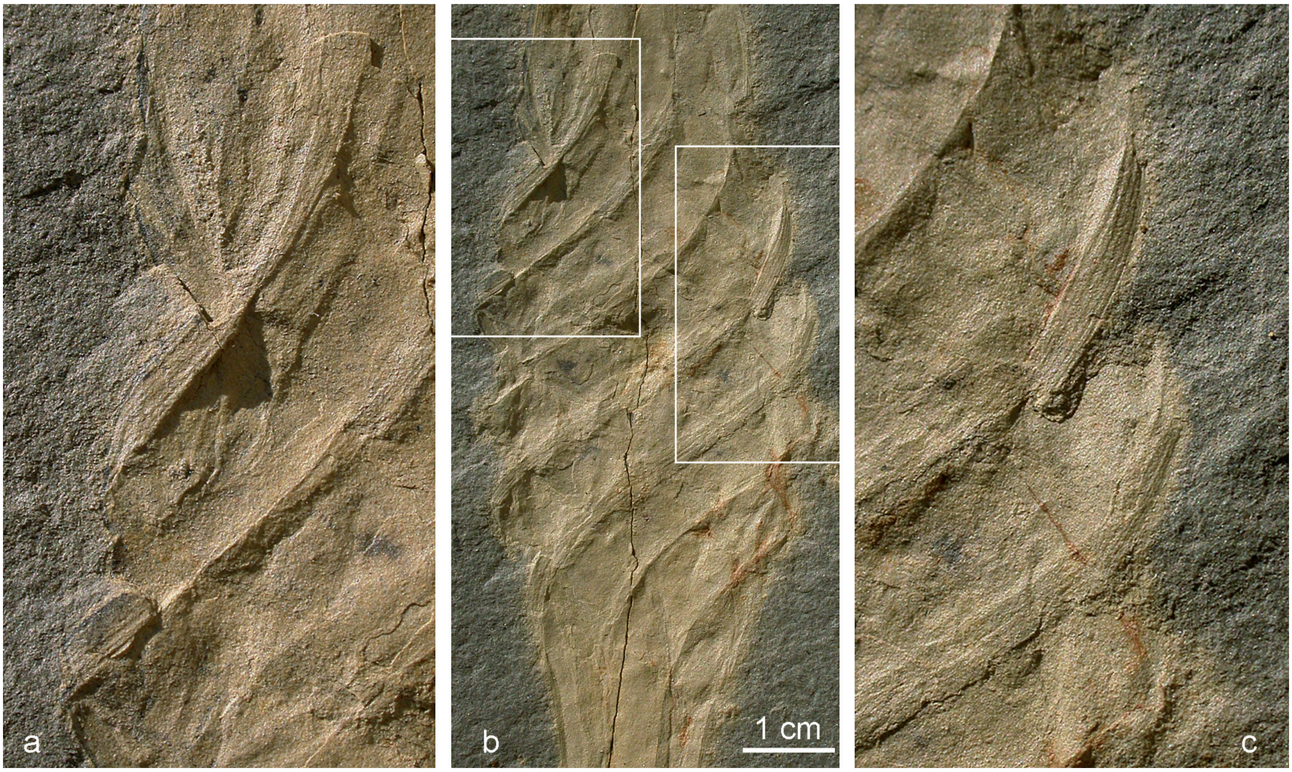

Fig. 5. *Palaeoxyris friessi* n. sp., holotype; Hauptsandstein, Lower Keuper, Ladinian; Ilsfeld; SMNS 95447. – **a**. Enlarged view from the left side of the body showing the collarettes from the front side crossing those of the back. **b**. The body, the middle section of the capsule. **c**. Enlarged view from the right side of the body showing the clearly striated collarettes.

or whether capsules show continuous variation. The capsule of *P. regularis* consists of six bands, and eight segments are visible. The angle of the ridges is only 30° in the middle of the body. If the drawing of Brongniart (1828) is correct, the specimens described by Gall (1971) would represent a different species. In any case, both differ from *P. friessi* n. sp. in their smaller size, the angle of the ridges (either bigger or smaller), and the number of sections. Furthermore the beak is shorter than the pedicle, whereas in the new species both are of almost the same length, and the beak is shorter in relation to the body (Tab. 1).

P. becksmanni (Ortlam, 1967), known by only one specimen from the Anisian Upper Buntsandstein of Rotfelden (northern Schwarzwald; Fig. 1), has a body length of ca. 15 mm and consists of only four bands. The angle of the ridges is 30° (Ortlam 1967 mentioned 60°, but he measured the angle with the longitudinal axis). This is the only specimen known so far to be embedded upright in sandstone. This might mean that it is somewhat compressed in longitudinal direction which could have reduced the angle. The drawing given by Ortlam (1967, fig. 15) seems to be somewhat schematic. It shows a symmetrical capsule in which it is unclear as to which end is the beak or the pedicle. On the fossil (Ortlam 1967, pl. 46, fig. 6) only the beak is well preserved. This structure is the lower end with four ridges in Ortlam's drawing. The other end is somewhat obscure in the fossil and shown in the drawing with six ridges. Also, the body seems to have too many ridges in the drawing, as compared to the actual specimen. Ortlam (1967) introduced the new genus *Triasocapsula* for this specimen, but differences between this and other species of *Palaeoxyris* are of only minor importance. *P. becksmanni* differs from *P. friessi* n. sp. in its smaller size and the smaller number of bands.

P. muensteri Presl, 1838 is known from the Hettangian, Lower Jurassic of Franconia and the Rhaetian of Tübingen and southern Sweden (Figs. 1, 6–8). The dimensions of the body are the subject of some difference of opinion. A length of 38 to 89 mm is given by Frentzen (1932b) and Fischer et al. (2010), as opposed to the 3 to 4 cm suggested by Crookall (1930) and ca. 4 cm by Müller (1978). These differences have their source in a block of Rhaetian Sandstone (Tübingen Sandstone) from Waldhausen near Tübingen (the original of Quenstedt (1867), housed in Tübingen (GPIT)). This block (dimensions ca. 11 × 8 × 10 cm) contains at least 14 capsules. A second, smaller block containing the remains of at least ten capsules is present in the Stuttgart collection (SMNS 89791), and probably belongs together with the GPIT specimen as they were both found in the same area and purchased in 1869 from the same collector (E. Kolb). The capsules in Tübingen belong to two size classes. There are 12 smaller capsules, one or two of which are probably the originals of Quenstedt's somewhat idealised drawings, and two bigger ones. The smaller capsules have bodies of ca. 35 mm in length and 16–18 mm in width (the biggest diameter measured parallel to the bedding plane), the longest preserved length of a somewhat incomplete capsule is 97 mm. This is the normal size range for *P. muensteri*, and also for compressed specimens from the Hettangian of Franconia. The complete specimens figured by Schenk (1867) and Engels & Unger (1998) each have a total length of 120 mm. The types figured by Presl (1838) are incomplete but seem to be approximately of the same length. The capsules consist of six bands which can be clearly discerned at the cross-sections of the beaks and peduncles. Crookall (1930) counted eight ribs. This does not equal the number of bands but is the number of sections of ribs visible on one side. This means that the number of the bands given by Frentzen (1932b), Müller (1978) and Fischer et al. (2010) for *P. muensteri* is too high and the number of four suggested by Fischer et al. (2010) is too low. The angle of the ridges is 30–40° (Crookall 1930; Müller 1978: 30°). The width of the collarettes can be measured as 1 mm in the three-dimensional specimens from the Rhaetian of Tübingen. This species differs from *P. friessi* n. sp. in its smaller size and the in relation to the body much shorter beak (Tab. 1).

P. quenstedti Schimper, 1870–1872 a name introduced for the specimen figured by Quenstedt (1867) from the Rhaetian of Waldhausen near Tübingen (Figs. 1, 7); Quenstedt did not give a species name for his material. The figure of Schimper (1874, pl. 80, fig. 3, reproduced in Schmidt 1928, fig. 3) is copied from Quenstedt (1867, pl. 82, fig. 9) but published in reverse as a mirror-inverted (note the twisting to the left). As suggested by Crookall (1930) the species represents a junior synonym of *P. muensteri*.

Tab. 1. Measurements of *Palaeoxyris friessi* n. sp. in comparison with other completely preserved Triassic species. The measurements are taken from: *P. friesii* n. sp.: holotype; *P. regularis*: Gall 1971, pl. 25, fig. 1; *P. muensteri*: Engels & Unger 1998, fig. p. 216; *P. muelleri*: types in SMNS, P.1066.

Length of	***P. friessi* n. sp.**			***P. regularis***			***P. muensteri***			***P. muelleri***		
beak	112 mm	41 %	211 %	55 mm	31 %	137 %	25 mm	21 %	68 %	17 mm	23 %	74 %
body	53 mm	19 %	100 %	40 mm	22 %	100 %	37 mm	31 %	100 %	23 mm	30 %	100 %
pedicle	110 mm	40 %	208 %	85 mm	47 %	212 %	58 mm	48 %	156 %	35 mm	47 %	152 %
total	275 mm	100 %		180 mm	100 %		120 mm	100 %		75 mm	100 %	

The two bigger capsules which are embedded together with *P. muensteri* in the same block in the Tübingen collection are preserved only as incomplete bodies. The preserved lengths are 78 and 108 mm and the diameters are 32 and 35 mm. A diameter of 14 lines (= 40.1 mm) is the only measurement given by QUENSTEDT (1867) in his description of both sets of specimens (a Württembergian line in 1867 equals 2.865 mm). FRENTZEN (1932b) obviously lumped together both size classes, giving a body width measurement ranging from 10 to 30 mm. The two forms are clearly differentiated by their size, however, and there are no intermediate forms. Thus, QUENSTEDT gave figures of *P. muensteri* but the body diameter for a different species. These fragmentary bodies are of similar size to *P. friessi* n. sp., but their incompleteness makes confident comparison difficult. MÜLLER (1978) gave a band (= segment) number of eight to nine, which could be correct, but is difficult to discern. The specimen might be identical with *P. ventricosum* (SCHIMPER, 1870–1872) from the "grès infraliasique" of the area of Autun, France (Fig. 1), which also seems to have a high number (10?) of bands (SCHIMPER 1874, pl. 80, fig. 4). Its preservation is nearly identical to the Tübingen specimens, as both beak and pedicle are missing. Besides the number of bands there is one clear difference to the new species: the collarettes have a width of 6 mm, whereas *P. friessi* n. sp. has collarettes only 2 mm wide.

P. muelleri FRENTZEN, 1932 known from around 13 specimens in one sandstone block from the Rhaetian near Waldenbuch between Tübingen and Stuttgart (Fig. 1) is clearly different from all other Triassic species (FRENTZEN 1932b; SMNS P.1066). The complete length might be around 75 mm, the length of the body 20–25 mm (Tab. 1), and its width 11 mm. As in *P. muensteri* the beak (17 mm) is shorter than the body and is about half the length of the pedicle (35 mm). The capsule is build of four bands which make a turn of only 180°. FRENTZEN (1932b) counted three "Spiralrippen" (spiral ribs), but their number is not identical with the number of bands. As the section of the capsule is quadrangular ("viereckig", FRENTZEN 1932b) it is clear that the capsule consists of four bands, not three (FISCHER et al. 2010). The angle of the ridges is ca. 55°. The width of the collarettes is ca. 2 mm at the beak. This species is clearly different from *P. friessi* n. sp. in the smaller number of bands, smaller size, and in relation to the body shorter beak (Tab. 1).

P. humblei FISCHER et al., 2010 from the Norian of Arizona is one of the smallest known species with a body length of up to 13 mm (FISCHER et al. 2010) whereas the new specimen is one of the largest, clearly separating the species.

P. duni CROOKALL, 1930 from the Anisian of Australia is similar in size (complete length unknown), identical in angle of the ridges and band number to the new species (DUN 1912). CROOKALL (1930) gave a segment number of eight (in the table) and 9 (in the text), but this is not identical with the number of bands (MÜLLER 1978: 8 Bänder), which is six. The figure given by DUN (1912) also shows that the collarettes seem to be identical in width with those of *P. friessi* n. sp. Body proportions differ between the two species, however. *P. duni* is longer and narrower (86 mm long, 27 mm wide = 1 : 0.31) than the new species (53 mm long, 39 mm wide = 1 : 0.74). The result is that the bands take a longer path around the body – more than one and a half turn as opposed to less than one turn in the new species. Thus, on the front side, eight segments are visible as compared to six in *P. friessi* n. sp. This is the main difference between the two species.

In addition to these Triassic species four further Mesozoic species have been named: *Palaeoxyris sino-coreana* (SZE, 1954), *P. taurica* CHABAKOV, 1949, *P. jugleri* (VON ETTINGSHAUSEN, 1852), and *P. versabunda* VIALOV, 1984.

P. sino-coreana from the Early(?) Jurassic of Pyongyang, North Korea, and Lingwu, Northwestern China is smaller in size and has broader collarettes than *P. friessi* n. sp. (KAWASAKI 1925, SZE 1954). From both occurrences only impressions of the capsules are known showing some similarities with *P. jugleri* figured by NATHORST (1879, pl. 7).

P. taurica from the Middle Jurassic (Bajocian-Bathonian) of Crimea (Ukraine) known by one three-dimensionally preserved body is somewhat smaller than *P. friessi* n. sp. (CHABAKOV 1949). As pedicle and beak are missing it is hardly to compare.

P. jugleri from the Early Cretaceous Wealden (Berriasian) of northern Germany and southern England (VON ETTINGSHAUSEN 1852, CROOKALL 1930) is clearly distinguished from the new specimen. The pedicle is up to twice as long as the beak (CROOKALL 1930) (new one: nearly equal in length). Although the capsule is smaller the collarettes are much wider than in *P. friessi* n. sp.

P. versabunda from the Late Cretaceous of the Aral area is incompletely known (VIALOV 1984). The three-dimensionally preserved bodies of the two known capsules are similar in size to *P. friessi* n. sp., but the ribs are quite different to all other Mesozoic species. They are very prominent, broad and with a rounded apex.

With a length of 27 cm *P. friessi* n. sp. is longer than any other completely preserved *Palaeoxyris* species. It is also longer than the spirally twisted egg capsules of the extant *Heterodontus portusjacksoni*, the biggest species of *Heterodontus* reaching a length of up to 1.65 m (COMPAGNO 1984). Its egg capsules are up to 17 cm long (SPRINGER & GOLD 1989), but they lack the long pedicles and beaks which make 80 % of the total length in *P. friessi* n. sp. On the other hand, a chimaeroid egg capsule is known from the Upper Jurassic with a length of 40 cm (FRICKHINGER 1994). It probably derives from a species of *Ischyodus* attaining a length of at least 1.5 m (STAHL 1999). Accordingly the remarkable length of *P. friessi* n. sp. does not disagree with its interpretation as a chondrichthyan egg capsule.

4. Nature and affinities of the *Palaeoxyris* capsules

4.1. Nature of the capsules

Recently Fischer & Kogan (2008) gave a detailed overview of the research history of *Palaeoxyris* in the form of an annotated bibliography, where most of the relevant literature is cited. While initially thought to be of vegetable origin, since the end of the nineteenth century the fossils have been associated with fishes. In particular the egg capsules of *Heterodontus* (Zidek 1976) but also those of chimaeroids (Fig. 6; Dean 1906, Brown 1950) show some resemblance to *Palaeoxyris*. One could say *Palaeoxyris* is somewhat intermediate in character: it has the shape of a chimaeroid capsule (the central spindle shaped cavity without their broad flanges) which is twisted like the capsules of *Heterodontus*. One point of difference is the number of bands: chimaeroid capsules have, as in all other oviparous chondrichthyans, a dorsal and a ventral side, also the capsules of *Heterodontus* consists of only two sides (bands) which are twisted. *Palaeoxyris* consists of at least four bands. Nevertheless, today the interpretation as shark egg capsule is generally accepted. But it shall not be concealed that there exist some problems with this interpretation.

Fig. 6. *Callorhynchus germanicus* (Brown, 1946), chimaeroid egg capsule; Upper Aalenian, Middle Jurassic; Heiningen, SW Germany. SMNS 5043.

Nearly all *Palaeoxyris* capsules, from the Carboniferous to the Cretaceous, a time span of around 250 million years, originate from brackish or fresh water deposits, often found together with plant remains or brackish water molluscs (Crookall 1932: 132). No shark teeth are generally found directly associated with the capsules, as is the case with the new specimen described here.

In the Triassic Germanic Basin all *Palaeoxyris* capsules have been found in marginal marine deposits (Fig. 2, 7). The Upper Buntsandstein is transitional between the fluviatile Middle Buntsandstein and the marine Lower Muschelkalk. The Lower Keuper is transitional between the marine Upper Muschelkalk and the limnic Middle Keuper, and the Rhaetian Sandstone and the Hettangian Bayreuth Formation in Franconia are transitional between the fluviatile upper Middle Keuper and the marine Lower Jurassic (Simon 1999). All of these occurrences are interpreted as deltaic to prodeltaic deposits.

The Upper Buntsandstein was deposited in a deltaic system where rivers originating from the southwest flowed into the sea, transgressing from a northeastern direction (Fig. 7; Gall & Grauvogel-Stamm 1999). A diverse fauna and flora including bony fishes and around hundred specimens of *Palaeoxyris regularis* (Gall 1971) but no shark remain is known from the northern Vosges (Gall et al. 1995). Agassiz (1839) described a tooth of *Acrodus braunii* Agassiz, 1839 from the Buntsandstein of Zweibrücken in Rheinland-Pfalz but the specimen probably comes from the marine Muschelsandstein (Udelfangen Formation) of the Lower Muschelkalk (Frentzen 1932a: 538, Hagdorn & Simon 2005, Schindler et al. 2009). The only shark remain from the Upper Buntsandstein is a small finspine from Waldshut (Fig. 1) in the southernmost part of the Black Forest (SMNS 95115), found together with remains of terrestrial and marine tetrapods (Wild 1998), demonstrating that sharks moved upstream together with nothosaurs far to the south.

In the Lower Keuper the situation is reversed. The Hauptsandstein was deposited by river systems which flowed from the Fenno-Scandian High in the northeast into marine waters moving from the southwest through

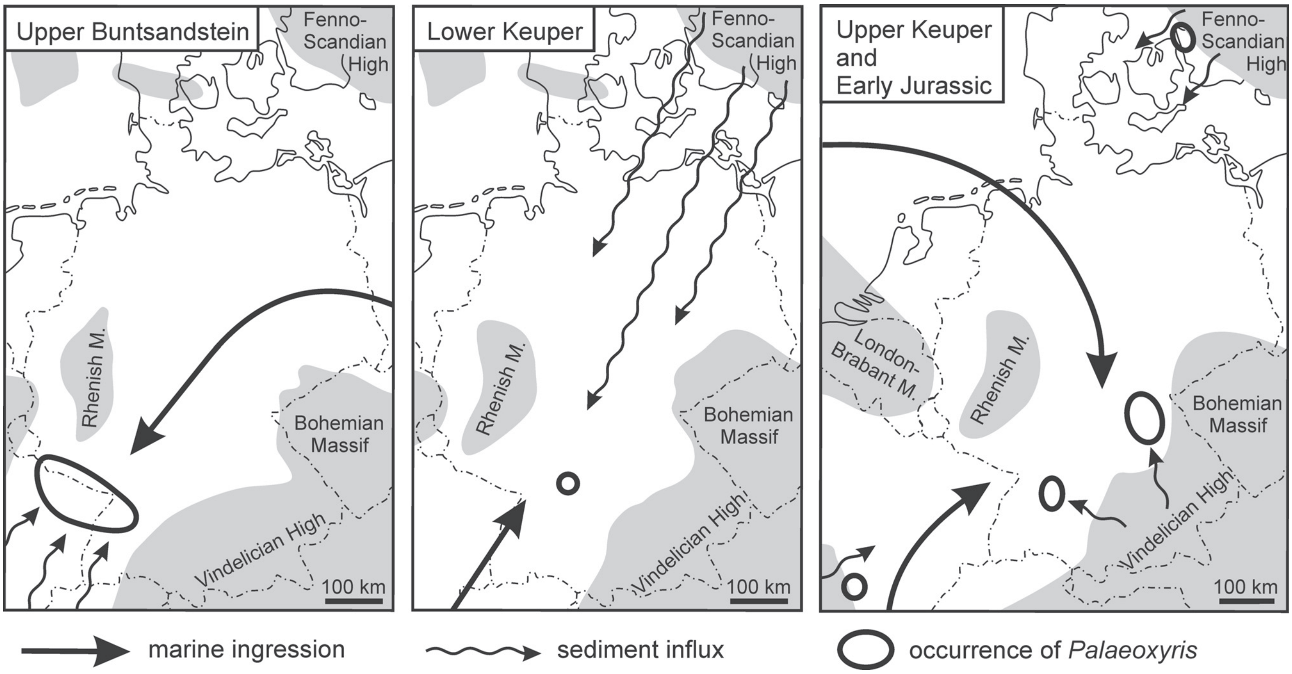

Fig. 7. Palaeogeographic maps of the central part of the Germanic Basin with occurrences of *Palaeoxyris* egg capsules (after MADER 1982, GALL & GRAUVOGEL-STAMM 1999, ZIEGLER 1982, BEUTLER & NITSCH 2005).

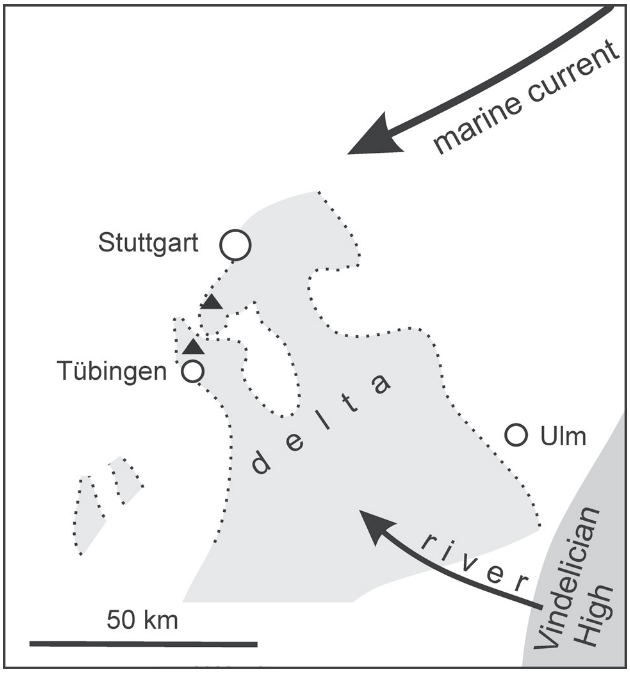

Fig. 8. Rhaetian palaeogeographic map of the area around Stuttgart and Tübingen with distribution of the deltaic Rhaetian Sandstone and *Palaeoxyris* occurrences (triangles) (palaeogeography after CARLÉ 1974, AEPLER 1974).

the Burgundian Gate (Fig. 7; BEUTLER & NITSCH 2005). Sharks lived in this transitional environment (see below) although no shark teeth have been found associated with *Palaeoxyris friessi* n. sp. The well preserved flora and the very sparse fauna point to a strongly reduced salinity.

In the Rhaetian rivers draining the Vindelician High flowed into a sea transgressing from southwestern and northerly directions (Figs. 7, 8; Tübingen-Sandstein, *contorta*-Schichten; AEPLER 1974, CARLÉ 1974, BEUTLER & NITSCH 2005). No shark teeth have been found together with the capsules but bone beds (Rhätbonebed) within and directly overlying the sandstone yield many shark remains (see below).

In the Hettangian of Franconia a river from the same high area flowed into the sea building a large delta (Figs. 7, 9; MEYER & SCHMIDT-KALER 1992) depositing sediments rich in plant remains of the Bayreuth Formation (Gümbelscher Sandstein) (BLOOS et al. 2005). Again no shark remains are known from these deposits. KUHN (1956) mentioned *Hybodus* from Strullendorf near Bamberg, the type locality of *Palaeoxyris muensteri*, but he also mentioned teeth of *Sargodon*, a typical element of the Rhaetian fauna. It is unclear, therefore, whether these fish teeth are really Jurassic in age or if they have been redeposited from the Rhaetian as is the case in the Tübingen area (see below). The Hettangian in general is very poor in fish remains (Delsate et al. 2002), but a few shark teeth are known from marine horizons in southern Germany (see below).

No capsule has been found together with stenohaline marine organisms, although most, if not all hybodonts probably lived in marine environments. It is to be expected that at least a few species would have laid their eggs under euhaline conditions but no specimen of *Palaeoxyris* has yet been found in this situation. No extant shark species lays their eggs in fresh water and the few species adapted to live in brackish or even fresh water are viviparous (Schultze & Soler-Gijón 2004). Of the Triassic sharks, known from the euhaline Muschelkalk, most species can also be found in the brackish deposits of the Lower Keuper, albeit to a different extent. At least one as yet undescribed hybodont species (cf. *Polyacrodus keuperianus*) and two species of problematic relationships (*Doratodus tricuspidatus* Schmid, 1861, *Steinbachodus estheriae* Reif, 1980) probably lived exclusively in brackish conditions. On the other hand, only one species lived exclusively in euhaline waters as its teeth are unknown from the Lower Keuper (except in the lowermost layers). This is the largest Middle Triassic shark *Acrodus gaillardoti* Agassiz, 1839, which obviously did not tolerate a lowering of the salinity. Thus, several sharks lived in brackish estuaries and lakes and were probably able to lay their eggs within that environment or were able to swim even further upstream to deposit them in virtually freshwater conditions. Shark embryos need several months to more than a year to develop (Carrier et al. 2004) and numerous predators feed on those eggs. At salinities of between 5 and 10 ‰, species diversity is at its lowest (Remane & Schlieper 1971) so the number of potential predators is also low. Therefore, it might have been advantageous to lay eggs in those environments. This means that hybodonts were probably more adapted to brackish conditions than extant neoselachians and thus also their embryos were able to develop in those environments. The question remains as to why *Palaeoxyris* has never been found in deposits of euhaline waters.

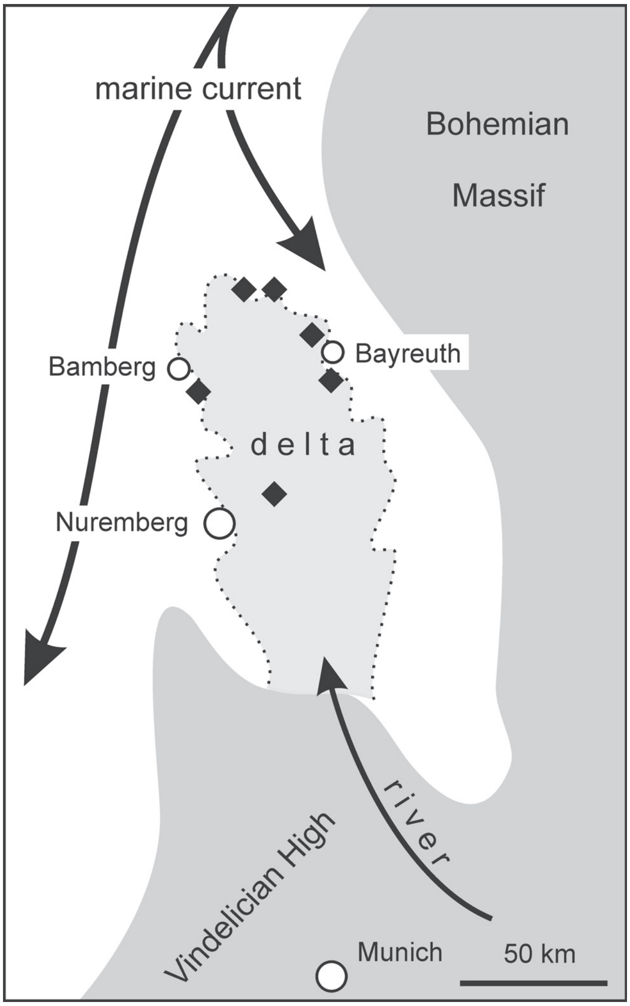

Fig. 9. Hettangian palaeogeographic map of Bavaria with *Palaeoxyris* occurrences (rhombs) (palaeogeography after Meyer & Schmidt-Kaler 1992).

In several cases, capsules have been found together in groups. Palaeozoic species are mostly preserved as single capsules; they are rarely found in pairs. In the Mesozoic up to 12 specimen clusters of *P. jugleri* (von Ettingshausen 1852) have been found in the Cretaceous (Berriasian), and up to 14 clusters in the Triassic (see above). Usually in these instances, individual capsules are arranged more or less parallel to each other, as fan-shaped clusters or in whorls; they are rarely found not showing special orientation. Whilst the unique capsular whorls of *P. jugleri* always have their beaks pointing toward the centre (Crookall 1932), in the Rhaetian *P. muelleri* the longer pedicles are directed along a common axis (Frentzen 1932b). This is the only exception known to date, since the paired Palaeozoic capsules are in contact with their beaks (Crookall 1932), as is the case with *P. duni* from the Triassic (Dun 1912). In the area of Bayreuth several specimen of *P. muensteri* have been found clustered in radially arranged whorls (Weber 1968: 16). Most oviparous sharks deposit one egg at a time from each oviduct (single oviparity, Musick & Ellis 2005). Furthermore, eggs from the two oviducts are deposited on separate occasions (Watson in Crookall 1932: 138). Extant chimaeroids usually lay a pair of eggs every seven to ten days (Didier 2004). This seems to have been the case in the Palaeozoic, where egg capsules are mostly discovered as isolated finds. By contrast, Mesozoic eggs are often found close together in clutches. It seems to be difficult, if not completely impossible for a single shark to deposit a dozen eggs in close juxtaposition to each other during a single egg-laying event. In *Heterodontus japonicus,* several females may lay their eggs at a single site, termed nests (Compagno 1984).

A small number of scyliorhinid species retain their eggs (up to about ten) in the oviduct before deposition (multiple oviparity, Musick & Ellis 2005). Thus, multiple oviparity or gregarious egg-laying cannot completely be ruled out as a means of explaining clutches of Mesozoic *Palaeoxyris*.

Crookall (1932: 125) referred to a notice of Nathorst (1879), who pointed to a figure given by von Ettingshausen (1852) showing capsules of different sizes within one whorl. Crookall (1932) held that "this difference in size does not exceed the normal amount of variation found in these fossils, and therefore calls for no special explanation." The capsules belong to a single clutch, however, and eggs so different in size within one clutch laid by a single shark would be impossible. The size differences are probably a consequence of different states of preservation. The larger specimens have collarettes, which are very wide in *P. jugleri*, while the smaller ones lack these structures (von Ettingshausen 1852, pl. 2, fig. 3).

The block from the Rhaetian Sandstone of Tübingen containing several capsules of two size classes raises the same question. In this case, however, the capsules are not arranged in a whorl but lie parallel to each other, and the two larger specimens are double the size of the smaller ones (*P.* sp. and *P. muensteri*, see above). Since it seems to be impossible for one female to lay eggs which are so different in size, this means that two shark species must have laid their eggs at exactly the same place. This is difficult to imagine, so maybe the capsules drifted together. Different sized capsules are reported to occur together in other species of *Palaeoxyris*. Crookall (1932) gave measurements of the Carboniferous species, *P. helicteroides* (Morris, 1840), with body lengths ranging from 27 to 60 mm and widths from 7 to 38 mm – a similar size range to those of the Triassic *P. regularis* (Gall 1971). This is much greater variability than that known from extant shark species and it is difficult to believe that one species could have produced eggs of such different sizes in the same environment (see also Watts in Moysey 1910). It would be sensible to check if these capsules really belong to one species as, in the Rhaetian, three species co-occur in the same area (see above).

In spite of these differences to the reproductive biology of extant neoselachians, and in the absence of any other suggestions, *Palaeoxyris* is taken to be the fossil egg capsule of a shark.

4.2. Affinities of the *Palaeoxyris* capsules

To which chondrichthyan species might the Triassic egg capsules belong? A holocephalian affinity for *Palaeoxyris* has been refuted by Zidek (1976). Although subsequently supported by McGhee (1982), this hypothesis can be ruled out as Triassic holocephalians are known only from the Rhaetian (Stahl 1999). Furthermore, chimaeroid egg capsules with a closely similar morphology to those of extant species are known from the Middle and Upper Jurassic (Fig. 6; Dean 1906, Frickhinger 1991); they are not twisted. With the exception of one extant chimaeroid species, which deposits its eggs in inshore bays and large estuaries in very shallow water (*Callorhinchus milii* Bory de Saint-Vincent, 1823; Last & Stevens 1994), no species is known to live in such an environment. Hence, the egg capsule must originate from a shark. Because of their wide stratigraphical range from the Upper Carboniferous to the Cretaceous *Palaeoxyris* capsules are generally agreed to be the egg cases of hybodont sharks (Fischer & Kogan 2008). Since they are largely restricted to brackish water deposits, the small so called "freshwater sharks" of the family Lonchidiidae (*Lissodus* and related genera), which were, in fact, mostly euryhaline marine fishes, are considered to be the producers.

As has already been mentioned, no fish remains were found directly associated with *Palaeoxyris friessi* n. sp. But the underlying sandstone and bone beds do yield a shark fauna locally (Hagdorn & Reif 1988). At the base of erosive channels cut into the underlying horizons these bone beds may contain teeth from reworked older horizons (Hagdorn & Reif 1988), but in Neidenfels near Crailsheim a silty layer was found containing many vertebrate remains especially small very fragile teeth (material in SMNS). This bone bed lacks all the criteria characteristic of bone beds at the base of the incised facies of the Hauptsandstein (wood fragments, reworked clasts and coarse quartz grains, Pöppelreiter 1999: 23) and the sandstone is not incised into the underlying sequence. Hence, this bone bed very probably contains no reworked material from older deposits but samples the remains of a contemporaneous fauna living in the estuary. The shark fauna, which is almost identical with that from the base of erosive channels (Hagdorn & Reif 1988), consists of *Lissodus nodosus* Seilacher, 1943, *Acrodus lateralis* Agassiz, 1839, *Polyacrodus polycyphus* Agassiz, 1843, cf. *Polyacrodus keuperianus* Winkler, 1880, *Polyacrodus* sp., *Steinbachodus estheriae* Reif, 1980, and *Doratodus tricuspidatus* Schmid, 1861. The large size of *P. friessi* n. sp. clearly demonstrates that members of the Lonchidiidae, usually supposed to be producer of *Palaeoxyris* egg capsules, could not have been the only sharks which produced such capsules. Lateral teeth of *Lissodus nodosus* measure up to 5 mm in length mesiodistally (Duffin 1985). Although there are no extant relatives of this species, the dentition of *Heterodontus* can act as a model in order to give some idea as to the length of the shark as its molariform lateral teeth show a gross morphology comparable to that of *L. nodosus*. *H. portusjacksoni* with a total body length of 1140 mm has teeth of 17 mm in length, whilst those of a 660 mm long *H. japonicus* are 9 mm long (Reif 1976).

L. nodosus was accordingly probably well below one meter in length. The teeth of *Steinbachodus estheriae* are even smaller. Reif (1980) supposed that the shark did not exceed 80 to 100 cm in length. Also the tiny very fragile teeth of *Polyacrodus* sp., an as yet undescribed species, are less than 3 mm in length. The molariform lateral teeth of *Acrodus lateralis*, the most frequent species in the Hauptsandstein, reach only a length of only 6 mm. This is less than in those from the marine Muschelkalk and the overlying Grenzbonebed, possibly due to the lower salinity in the Hauptsandstein. Thus all four species were obviously too small to produce *Palaeoxyris friessi* n. sp. *Doratodus tricuspidatus* has a strange tooth morphology differing from that of all other hybodont teeth; indeed, it is questionable as to whether it belongs to a hybodont at all (Duffin 1981).

The two bigger species, *Polyacrodus polycyphus* and cf. *Polyacrodus keuperianus*, remain. While *P. polycyphus* is a marine species also known from the Muschelkalk, cf. *P. keuperianus* is known only from the brackish deposits of the Lower Keuper. cf. *P. keuperianus* is similar to *P. keuperianus* from the Middle Keuper (Seilacher 1943, Dorka 2003) but probably represents a different species. The teeth of both species reach a length mesiodistally of up to 15 mm or even more. In order to judge the size of these sharks, the teeth were compared with those in skeletons of *Hybodus hauffianus* from the Lower Jurassic. The results suggest a total length of 2 to 2.5 m in *P. polycyphus* and cf. *P. keuperianus*. At this length it is conceivable that either of these two species could have been the producer of *Palaeoxyris friessi* n. sp.

To date, only the already mentioned small fin spine of an unknown shark species is known from the Upper Buntsandstein, while rare teeth of *Acrodus braunii* are described from the overlying lowermost Muschelkalk (see above). Woodward (1889) synonymised the latter species with *A. gaillardoti*, but this species is much bigger and probably did not live in waters with reduced salinity (see above). The more likely situation is that *Acrodus braunii* is a synonym of *A. lateralis*, a smaller species which is widespread in the Muschelkalk and the Lower Keuper.

From the Rhaetian sandstone and in particular its bone beds in the area between Stuttgart and Tübingen three shark species are known: the hybodonts *Lissodus minimus* (Agassiz, 1839) and *Hybodus cuspidatus* Agassiz, 1843 (= *Hybodus cloacinus* Quenstedt, 1868; Dorka 2003) and the neoselachian *Rhomphaiodon minor* (Agassiz, 1837). These could be the producers of *Palaeoxyris muensteri*, *P. muelleri*, and *P. ventricosum*.

From the marine Hettangian of southern Germany only a few shark teeth are known (besides redeposited teeth from the Rhaetian bone bed, Schweigert & Bloos 2008) belonging to species very similar to those known from the Sinemurian of Lyme Regis, England (Woodward 1889; material in the SMNS). Except for one tooth of *Acrodus nobilis* Agassiz, 1837 and a tooth of *Lissodus minimus* all other teeth are of the *Hybodus* type, in particular *H. delabechei* Charlesworth, 1839 and *H. reticulatus* Agassiz, 1837. Some of these teeth, together with a chimaeroid tooth plate (*Alethodontus bavariensis*, Duffin 1983), have been found in layers directly above the Bayreuth Formation in Franconia. One of these sharks could have been the producer of *P. muensteri* from the underlying fluvial deposits.

H. reticulatus shows some resemblance to *H. cuspidatus* from the Rhaetian. On the other hand Woodward (1889) figured some teeth from Lyme Regis which he tentatively assigned to *H. cloacinus* (see also Duffin 1993). Both point to the close affinities between Upper Triassic and Lower Jurassic species of *Hybodus*. Furthermore Rees (2008) has questioned the validity of the genus *Polyacrodus* Jaekel, 1889. The teeth of the type species *P. polycyphus*, which could be the producer of *Palaeoxyris friessi* n. sp., do not show any morphological characters that can be used to separate them from those of *Hybodus* (Rees 2008). As sharks of the genus *Hybodus* are also present in the Wealden (Woodward 1889), where *Palaeoxyris jugleri* is frequently found, species of *Hybodus* might have been the producers of Mesozoic *Palaeoxyris* egg capsules. This includes in particular species of *Hybodus* and *Polyacrodus* which are similar to the type species of *Hybodus*, *H. reticulatus*. But probably also other hybodontid species produced such egg capsules.

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