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Ammonite aptychi from the Lower Jurassic (Toarcian) near Whitby, North Yorkshire, UK

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SUMMARY: Ammonite aptychi from the Lower Jurassic of Port Mulgrave near Whitby, U.K., are reported for the first time in association with ammonites of the Family Hildoceratidae, Subfamily Harpoceratinae. The aptychi are preserved in shale, varying in their completeness and exhibiting a range of sizes, but are identified as *Cornaptychus* sp. and cf. *Lamellaptychus* sp. Some *Cornaptychus* specimens are preserved with ammonites identified as *Tiltoniceras antiquum*. The aptychi, especially *Cornaptychus*, are comparable with aptychi associated with ammonites of the Harpoceratinae elsewhere, notably in the Posidonia Shale of Toarcian age in Germany. The ammonite aptychi were further analysed using an Environmental Scanning Electron Microscope (ESEM) in order to determine their composition and assess whether this might have implications for their occurrence and preservation potential compared with that of the ammonite shells.

The term aptychus (plural: aptychi) is a general name given to calcareous or corneous structures (Moore & Sylvester-Bradley 1957) considered to be isolated hard parts of ammonoid shells. Aptychi have been documented in the fossil record since the 19th century (Meyer 1831; Voltz 1837; Quenstedt 1856–58) and superficially resemble the shells of bivalves, for which they have been mistaken in the past (Parkinson 1811). Their function has been discussed extensively in the literature. They have been regarded as opercula (Arkell 1957), i.e. hard plate-like structures used to close the aperture of the shell when the animal was retracted, as jaws of ammonites (Lehmann 1979), or as a combination of the two (Lehmann & Kulicki 1990; Seilacher 1993). They are now generally interpreted as plates that covered the outer surface of ammonite lower jaws (Tanabe & Landman 2002).

Aptychi have been recorded from Palaeozoic and Mesozoic successions. Mesozoic occurrences were reviewed by Engeser & Keupp (2002) and aptychi from the Upper Cretaceous were discussed by Tanabe & Landman (2002). Mesozoic records, which show their widespread geographical distribution, include those from the upper Toarcian of Spain (Martínez 2007), the Middle–Upper Jurassic of Russia (Rogov 2004*a*, *b*) and the Lower Cretaceous of Antarctica (Thomson 1972). Ammonite specimens from the Upper Jurassic (Tithonian) Solnhofen Limestone of Germany have yielded complete jaw apparatuses (Keupp 2007), including the first Jurassic ammonite jaw apparatus preserved *in situ* and in three dimensions (Schweigert 2009).

Aptychi have been found associated with ammonites in, for example, the Upper Cretaceous of Slovenia (Summesberger *et al*. 1996) and the Middle Cretaceous of Skye, Scotland (Morton 1973). Such discoveries have helped to develop an understanding of the relationships between aptychi and ammonites. They provide information on the function of aptychi relative to their shape, size and morphology, and in recent years have focussed attention on the feeding habits of ammonites and their feeding apparatus (Andrew *et al*. 2010; Kruta *et al*. 2011; Tanabe 2011).

Aptychi recorded from the Lower Jurassic of England include isolated specimens from Whitby, which were referred to *Trigonellites whitbyensis* (Simpson 1884), Ilminster (Moore 1851) and Northamptonshire (Morris 1852). Here, we describe aptychi associated with Harpoceratid ammonites from the Lower Jurassic Lias Group of the Yorkshire Coast at Port Mulgrave near Whitby, and investigate their preservation potential.

1. GEOLOGICAL SETTING

Aptychi described in this paper were collected at Port Mulgrave, north of Whitby on the Yorkshire coast (Fig. 1). There, Lower Jurassic rocks of Toarcian age form the Grey Shale Member and the overlying Mulgrave Shale Member, the lowest two members of the Whitby Mudstone Formation of the Lias Group. The Grey Shale Member comprises 13.56 m of grey silty mudstone with beds of calcareous siderite concretions. The Mulgrave Shale Member (formerly Jet Rock Member) consists of fissile, bituminous, dark grey mudstone and is up to about 31 m thick; the Jet Rock comprises the lowest third of the member. The base of the Mulgrave Shale Member is at the base of a bituminous mudstone with large concretions (Bed 33 of Howarth 1973) that rests conformably on non-bituminous shaly mudstone of the Grey Shale Member (Bed 32 of Howarth 1973). The Grey Shale Member correlates with the *Dactylioceras tenuicostatum* Ammonite Biozone, and beds of the member with subzones of the *tenuicostatum* Biozone as shown in Figure 1. The Mulgrave Shale Member correlates with the *Harpoceras falciferum* Biozone. Bed 32 of the Grey Shale Member correlates with the *semicelatum* Subzone of the *tenuicostatum* Zone (Fig. 1). Numerous ammonites including *Tiltoniceras, Dactylioceras* and *Eleganticeras* are present at several levels within the Grey Shale Member, and belemnites are present almost throughout. Large numbers of juvenile *Tiltoniceras antiquum* are found crushed throughout Bed 32. Specimens of *Dactylioceras semicelatum*, the index of the *semicelatum* Subzone, are also present, and the bivalve *Bositra radiata* is common (Howarth 1973).

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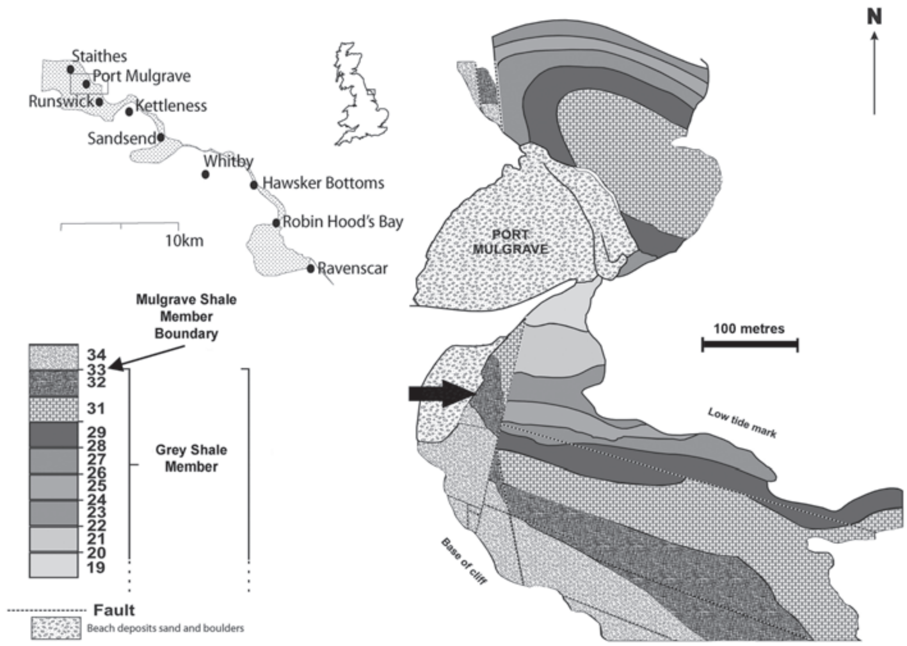

STRATIGRAPHIC COLUMN

	STAGE	ZONE	SUBZONES	FORMATIONS	MEMBERS	BEDS
LOWER JURASSIC	TOARCIAN	*Dactylioceras tenuicostatum*	*D. semicelatum*	Whitby Mudstone Formation	Grey Shale Member	28 - 32
			D. tenuicostatum			20 - 27
			D. clevelandicum			18 - 19
			Protogrammoceras paltum			3 - 17

Fig. 1. Geological map of Port Mulgrave after Howarth, 1973. The thick black arrow indicates the *in situ* location of WHITM:2011/44 in Bed 32 of the Grey Shale Member, Whitby Mudstone Formation. Inset maps show the location of Port Mulgrave on the Yorkshire coast.

2. Material and Methods

Four of the aptychi described in this paper were collected in 2008 by one of the authors (BGH) and were donated to the Whitby Museum in 2011 with the accession numbers WHITM:2011/16.1 to WHITM:2011/16.4. These specimens were collected loose on the foreshore at Port Mulgrave. WHITM:2011/16.2 and WHITM:2011/16.3 are associated with ammonites identified as *Tiltoniceras antiquum* (Wright). A further specimen, WHITM:2011/44, was found *in situ* in the Grey Shale Member at Port Mulgrave in 2011 by one of us (DRL), and is also associated with *Tiltoniceras antiquum* (Wright). Additional material, also examined, includes an isolated single aptychus valve present in the supratemporal fenestra of a specimen of the marine crocodyliform *Steneosaurus* cf. *bollensis* in the Doncaster Museum (DONMG:ZG425). Measurements were made with dial callipers, recorded to the nearest 0.1 mm. With the exception of WHITM:2011/16.4, the aptychi discussed herein consist of single valves.

In addition, the aptychus and matrix of specimen WHITM:2011/16.1 were investigated using an EDAX ESEM (Environmental Scanning Electron Microscope) at the University of Manchester in order to establish their composition and consider aspects of taphonomy.

Abbreviations used are WHITM, Whitby Museum, Whitby, and DONMG, Doncaster Museum and Art Gallery, Doncaster.

3. DESCRIPTION

A large number of aptychi genera have been described in the literature, with six of the better known illustrated by Lehmann (1990, fig. 4.3). They include *Cornaptychus* and *Lamellaptychus*, which are relevant to the specimens discussed in this paper. *Cornaptychus* is identified by fine, tightly packed radiating growth lines (inner surface) with a strong symphysis, and is completely chitinous. *Lamellaptychus* has strong, coarse ribbing, and the aptychus is organic and calcitic. Recent taxonomic revision (Měchová *et al*. 2010) has resulted in many Early Cretaceous species formerly attributed to *Lamellaptychus* being placed in separate genera within the family Lamellaptychidae, including *Lamellaptychus* Trauth 1927, *Beyrichilamellaptychus* Turculet 1994, *Mortilletilamellaptychus* Měchová *et al*. 2010, *Thorolamellaptychus* Turculet 1994 and *Didayilamellaptychus* Turculet 1994. In this paper, *Lamellaptychus* is used in its original broad sense. Four of the aptychi described below have been identified as *Cornaptychus* sp. (Riegraf et al. 1984, fig. 41; Lehmann 1990, fig. 4.3a) and the remaining aptychus as cf. *Lamellaptychus* sp. (Lehmann 1990, fig. 4.3b; Thomson 1972, fig. 2).

3.1. Aptychus morphology and terminology

Morphological terminology used below follows Moore & Sylvester-Bradley (1957) and Měchová *et al*. (2010). In Moore & Sylvester-Bradley's (1957) terminology, 'aptychus' refers to all types of calcareous or corneous structures now considered to be ammonite lower jaws. Aptychi that comprise two discrete valves are classed as diaptychi (singular diaptychus), and the valves are referred to as left and right. The joint between the two valves comprises the symphysal margin (Měchová *et al*. 2010). Aptychi that are univalved are referred to as anaptychi (singular anaptychus). Aptychus morphology is illustrated in Figure 2.

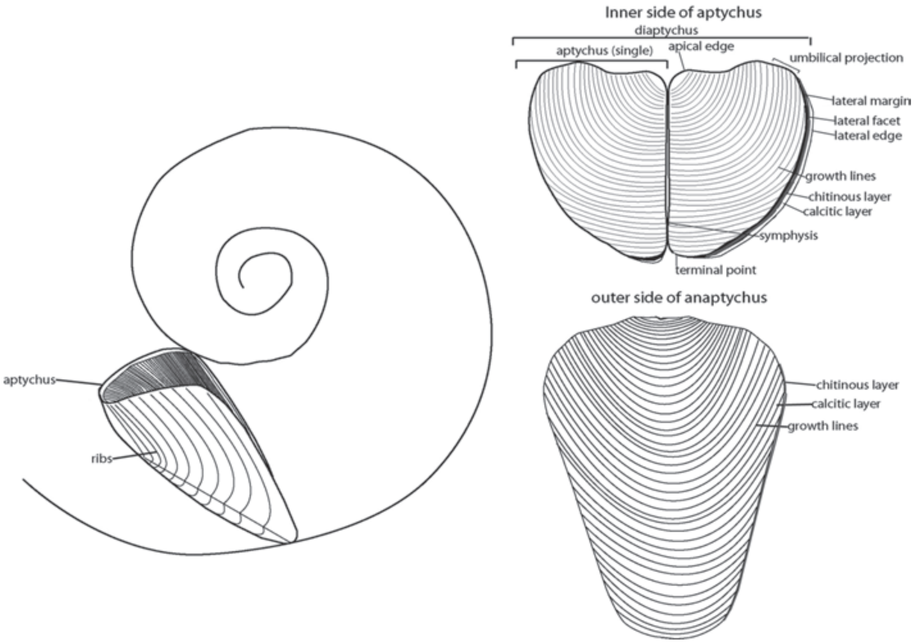

Fig. 2. Sketch of ammonite showing position and orientation of aptychus in the living chamber, and illustrations of diaptychus and anaptychus types of aptychi. Terminology from Měchová *et al*. (2010).

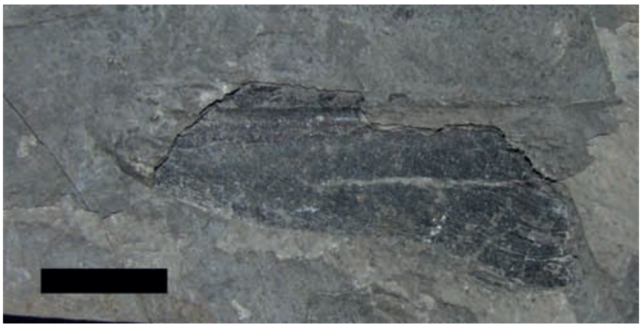

Fig. 3. WHITM:2011/16.1, the largest isolated aptychus discussed in this paper. Scale bar = 1 cm.

3.2. WHITM:2011/16.1

WHITM:2011/16.1 is an isolated specimen and the largest specimen assigned to *Cornaptychus* here. It comprises the concave inner surface of a left valve, which is worn and appears partly overlain by matrix at the terminal and apical points. The growth lines, however, are evident. The symphysis is only partly preserved and shows no evidence of any changes in width, but the negative impression is present and enables determination of the total length (46 mm) and width (17 mm) of the valve. The umbilical projection has been removed by weathering, while the lateral margin has been preserved intact and shows a slight constriction two thirds the way up towards the umbilical projection (Fig. 3).

3.3. WHITM:2011/16.2

The specimen, attributed to *Cornaptychus*, comprises an aptychus preserved directly on top of an ammonite. Only the left valve is present and its orientation shows only the inner surface. The aptychus is incomplete and partially fragmented, partly obscured by matrix and worn due to weathering after exposure. Nevertheless, the full length of the valve can be estimated at 29 mm and its width as approximately 7 mm. The weathering of this aptychus has removed parts of the umbilical projection and parts of the lateral margin, thus preventing comparison with these features on the other specimens discussed. The symphysis, although partially weathered, can still be seen and tapers from the apical edge towards the terminal point. The associated ammonite is preserved as a negative mould and does not display any shell material or suture marks, although the orientation of the whorl impressions and ribbing suggest that it belongs to the Harpoceratinae (Howarth 1992*b*). Determination of the genus is difficult, however, as no shell material remains. It is here tentatively identified as cf. *Harpoceras* sp. or cf. *Eleganticeras* sp. on the basis of similar specimens found within the Mulgrave Shale Member. At least two more aptychi are preserved on the matrix of this specimen, along with at least two more ammonites preserved as negative moulds, most probably Harpoceratids (Fig. 4).

3.4. WHITM:2011/16.3

WHITM:2011/16.3 is the smallest of the aptychi discussed. It comprises a left valve showing the inner surface with characteristic growth lines and falls within the range of variability of *Cornaptychus*. The valve is nearly complete, missing only a small fraction of the symphysis. It measures 12 mm in length and 6 mm at its widest point. The umbilical projection is present, although broken along the top apical edge. The curvature of the umbilical projection and the tapering of the symphysis suggest that the umbilical projection extended slightly above the apical edge. The lateral margin shows a slight constriction, although it is not as pronounced as that seen in specimen WHITM:2011/16.1. The symphysis in this specimen is clearly visible and tapers from the terminal point towards the apical edge. The aptychus is preserved in close association with the impression and partly preserved shell of an ammonite identified as *Tiltoniceras antiquum*. The aptychus is located in the most anterior section of the ammonite, slightly displaced from the aperture. We consider it to belong to the same ammonite (Fig. 5).

Fig. 4. WHITM:2011/16.2. Harpoceratid ammonite and aptychus association. Note the additional aptychi circled. Scale bar = 2 cm.

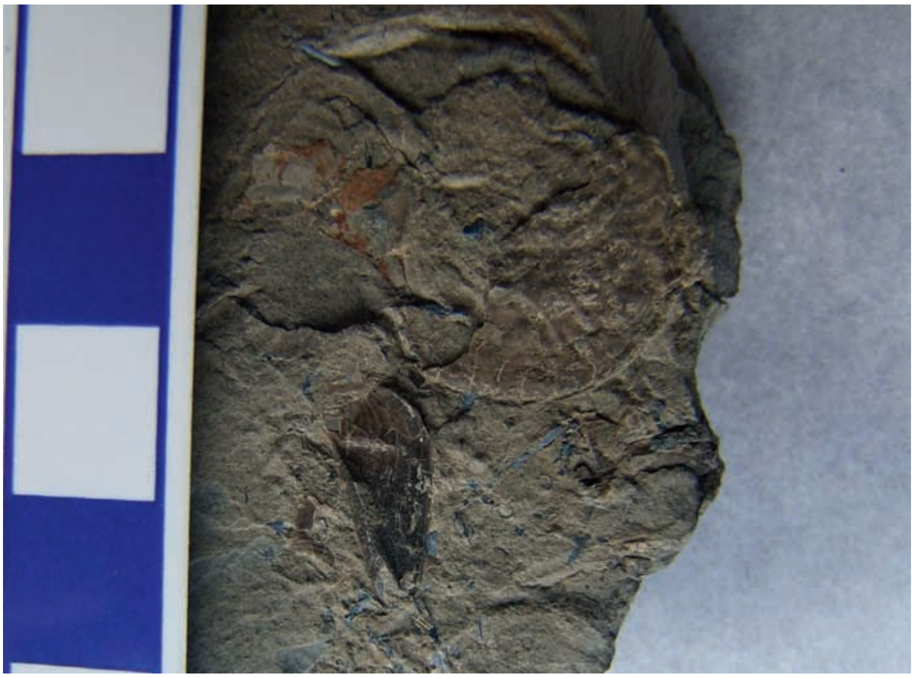

Fig. 5. WHITM:2011/16.3. Specimen of the ammonite *Tiltoniceras antiquum* with little original shell material; note the aptychus slightly displaced from the aperture of the ammonite. Scale bar = 4 cm.

3.5. WHITM:2011/16.4

WHITM:2011/16.4 comprises a well preserved and complete diaptychus, presenting the outer convex surface of both valves. The total length of the diaptychus measures 29 mm, with the width of a single valve estimated at 18 mm. The specimen displays an umbilical projection that tapers downwards and a lateral margin that shows no constrictions. The strong ribbing evident on this diaptychus is more indicative of ornamentation preserved on the upper surface rather than the growth lines seen in the other specimens from the underside. Unfortunately the specimen is not associated with any ammonite. This specimen is tentatively identified as cf. *Lamellaptychus* (Thomson 1972, fig. 2) on the basis of its strong detailed ribbing and comparable shape to other *Lamellaptychus* species (Fig. 6). However, a strong symphysis is preserved through half of the specimen, between the inner margins of the two valves. This is not typical of other *Lamellaptychus*-type aptychi and could suggest that the affinity of this specimen lies elsewhere and requires further investigation.

3.6. WHITM:2011/44

WHITM:2011/44 was collected *in situ* from the Grey Shale Member while attempting to determine the provenance of the aptychi recovered from the foreshore at Port Mulgrave, and is identified as *Cornaptychus* sp. It consists of a small aptychus preserved with the ammonite *Tiltoniceras antiquum* (Wright), and surrounded by many more ammonites of the same genus (Fig. 7). Although the aptychus is represented by a fragment rather than a complete specimen, some details can be determined. The fragment represents the underside of a single valve with closely packed growth lines. This may show that just a

Fig. 6. WHITM:2011/16.4, a complete diaptychus identified as cf. *Lamellaptychus*. Scale bar = 2 cm.

Fig. 7. WHITM:2011/44. Aptychus preserved within the living chamber of the ammonite *Tiltoniceras antiquum*. Scale bar = 6 cm.

small fraction of the aptychus is preserved, perhaps presenting the apical edge or terminal point. It is possible that some of the aptychus may have been eroded away, but the rest is primarily covered by the shell of the ammonite which makes it difficult to identify the exact genus. Determination of the specimen as *Cornaptychus* sp. is discussed further below.

3.7. DONMG:ZG425

DONMG:ZG425 consists of an undescribed skull and partial rostrum of the marine crocodyliform *Steneosaurus* cf. *bollensis*. It was collected from the Whitby area, but very little collection information was recorded with the specimen. Close inspection of

Fig. 8. DONMG:ZG425. A single *Cornaptychus* valve preserved within the supratemporal fenestra of *Steneosaurus* cf. *bollensis*. Scale bar = 1 cm.

the crocodilian skull revealed the presence of an isolated, single aptychus within the supratemporal fenestra. The aptychus represents the underside of the right valve, and measures 20 mm long and 7.5 mm wide. It is preserved as a whole specimen, apart from the umbilical projection and the apical edge which have either not been preserved or are covered by matrix. The lateral margin is complete with no constrictions. The symphysis is also complete and tapers towards the apical point; this is in the opposite direction of the tapering seen in specimen WHITM:2011/16.2, but the same as that in WHITM:2011/16.3. The aptychus, identified as *Cornaptychus*, is well preserved, presenting the inner surface, and is comparable to the *Cornaptychus* specimens collected from Port Mulgrave (Fig. 8).

3.8. Comparison of specimens

The specimens assigned to *Cornaptychus* above are very similar to one another. There are slight differences between WHITM: 2011/16.1, WHITM:2011/16.2, WHITM:2011/16.3, WHITM: 2011/44 and DONMG:ZG425, specifically in the fine striations and general shape, but the variability seen is encompassed within that of *Cornaptychus* (see Fig. 9). In comparison, the strong, coarse ribbing pattern of WHITM:2011/16.4 identifies this specimen as belonging to a separate genus.

Each specimen assigned to *Cornaptychus* displays a pronounced symphysis that extends dorsoventrally along the centre line of the specimen. It increases in size and width towards the growing edge (terminal point), apart from specimen WHITM:2011/16.2 in which the opposite is apparent. That specimen, however, is incompletely preserved and so may give a false impression of its true morphology. The general shape of each specimen is quite elongate, each curving gradually, tapering to a rounded end with a V-shaped notch where the two valves would join to form the complete diaptychus, as seen in WHITM:2011/16.4. The tapering is also marked by a slight constriction where the symphysis becomes markedly smaller in medium to larger specimens. The growth lines of WHITM:2011/44 are slightly more widely spaced and show similarities with the growth lines seen at the apical edge of WHITM:2011/16.3. This might indicate that the fragment of the aptychus seen in WHITM:2011/44 is the apical edge of the aptychus, as opposed to the terminal point. When compared with the other specimens under discussion and those seen in Riegraf *et al*. (1984, fig. 41), WHITM:2011/44 shows similarities with *Cornaptychus* and likely belongs to that genus.

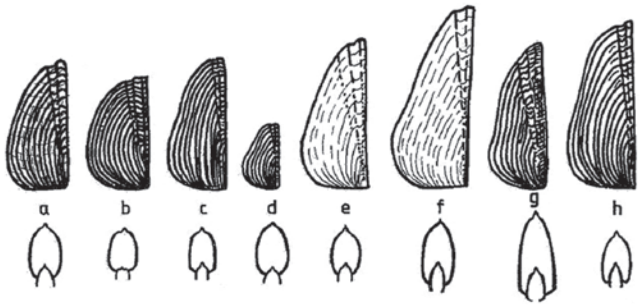

Fig. 9. Comparison of the aptychus different morphologies of *Cornaptychus* found associated with ammonites from the Toarcian Posidonia Shale, Germany. (**a**) *Protogrammoceras paltum*. (**b**) *Hildoceras levisoni*. (**c**) *Hildoceras serpentinum*. (**d**) *Hildoceras subserpentinum*. (**e**) *Harpoceras antiquum*. (**f**) *Harpoceras elegantulum*. (**g**) *Harpoceras elegans*. (**h**) *Harpoceras falciferum*. Taken and slightly modified from Riegraf *et al*. 1984, fig 41.

3.9. Faunal associations and provenance

Specimen WHITM:2011/44 was collected *in situ* from the Grey Shale Member at Port Mulgrave and is associated with the ammonite *Tiltoniceras antiquum* (Wright) and crushed specimens of the bivalve *Bositra radiata*. Specimens WHITM:2011/16.2 and WHITM:2011/16.3 were collected loose on the foreshore at Port Mulgrave, but are also associated with ammonites identified as *Tiltoniceras antiquum* (Wright), which suggests that they probably derived from the Grey Shale Member also.

In contrast, the occurrence of crushed specimens of the inoceramid bivalve *Pseudomytiloides dubius* in the matrix of the blocks containing WHITM:2011/16.1 and WHITM:2011/16.4 suggests a possible different origin for these two specimens. *Pseudomytiloides* is common in the Mulgrave Shale Member, and thus both WHITM:2011/16.1 and WHITM:2011/16.4 might have been derived from that member.

4. RESULTS OF THE ESEM STUDY AND THEIR IMPLICATIONS

The aptychi were preserved as impressions, usually with a prominent dark layer. The chemistry of the dark layer was analysed using an EDAX Environmental Scanning Electron

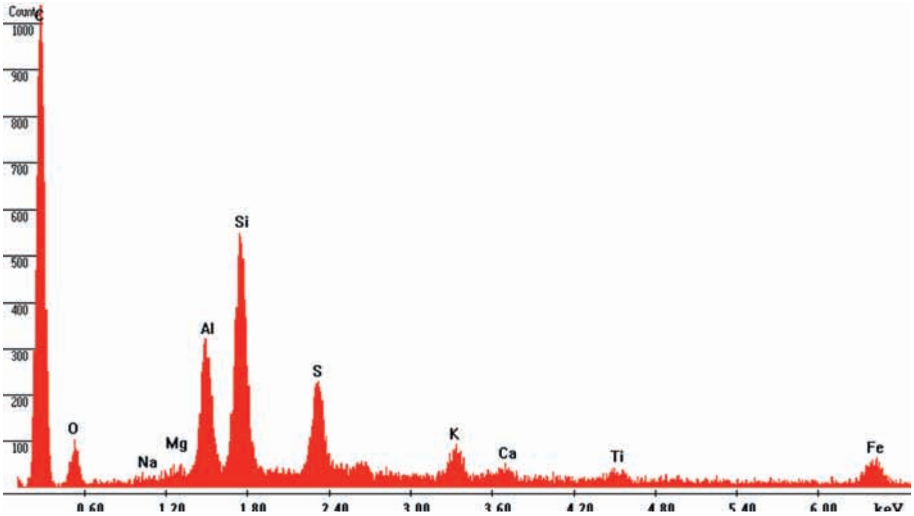

Fig. 10. ESEM. analysis of WHITM:2011/16.1 showing a high C peak. This is interpreted to indicate that the aptychus is overlain by a carbon-rich film, probably due to the organic carbon present in the original chitin that composed the aptychus. Other peaks include Ca, S, O, K and Ti, probably from clay minerals in the matrix.

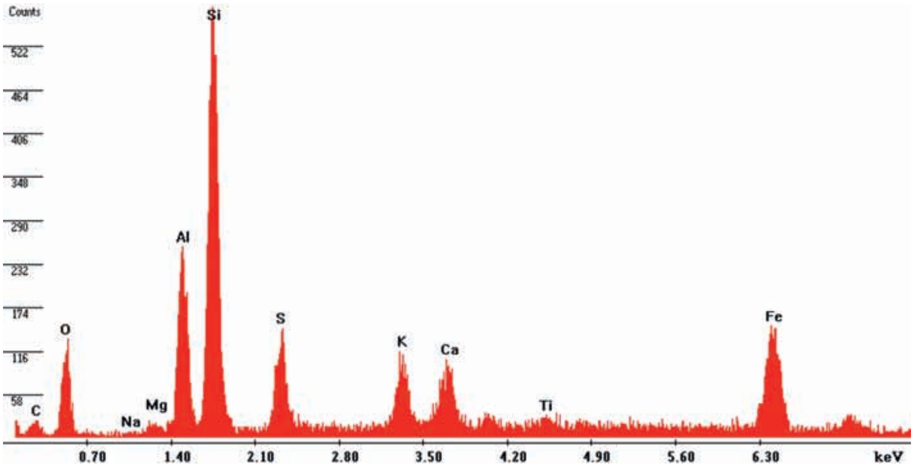

Fig. 11. ESEM. analysis of the matrix of WHITM:2011/16.1. Peaks indicate the relative amounts of each element present.

Microscope (ESEM), which enabled analysis of uncoated specimens. Analysis of uncoated material allowed calculation of the relative concentrations of elements present from the surface back scatter of electrons, and provided information on the abundance of elements such as carbon and calcium. The dark layers of the aptychi are composed primarily of carbon (Fig. 10), most probably due to a layer of thick chitin.

In contrast, the amount of calcium carbonate in the matrix, as indicated by the relatively low abundance of Ca (Fig. 11), suggests that any fossil composed of calcium carbonate would have had very low preservation potential, except as impressions or moulds. It also suggests that aptychi preserved as carbon films might have had a higher preservation potential than the aragonitic ammonite shells, and might also explain why most of the aptychi have only their carbonised parts preserved, showing growth lines rather than the ridges of their outer layers which would have been composed of calcite (Měchová *et al*. 2010). Dissolution of ammonite shells combined with post-mortem decay of soft parts makes it difficult to find ammonite aptychi associations, though they are still present as seen in WHITM:2011/44 (see fig. 7). Post-mortem decay probably also explains why so many aptychi described in this paper comprise single isolated valves.

5. DISCUSSION

All the aptychi described in this paper were preserved within shale beds rather than in nodules. No aptychi, complete or fragmented, were found in nodules.

5.1. Ammonite-aptychus co-occurrences

Three of the specimens discussed in this paper are specimens of *Cornaptychus* that are associated with ammonites belonging to the Subfamily Harpoceratinae of the Family Hildoceratidae. The appearance of each aptychus varies in size, structure and preservation style, although the variability is encompassed within that of *Cornaptychus*, the size varying between 12 and 46 mm in length. The association of *Cornaptychus* with Harpoceratid ammonites has been discussed by several authors, including Trauth (1930), Arkell (1957), Lehmann (1972), Riegraf *et al*. (1984), Lehmann & Kulicki (1990) and Hirano *et al*. (1990). A number of Harpoceratid genera, including *Harpoceras, Tiltoniceras, Eleganticeras* and *Hildoceras*, have been found associated with *Cornaptychus*, an association that was reported in the mid 19th century by Quenstedt (1856-1858) and later by Riegraf *et al*. (1984).

Ammonite-aptychus associations are rare, but are more likely to occur under better preservational conditions such as those of the Toarcian Posidonia Shale of Holzmaden, Germany, which is a conservation Lagerstätte. Ammonite-aptychus associations are common in the Posidonia Shale. Ammonites such as *Harpoceras, Tiltoniceras* and *Eleganticeras* have all been found with aptychi in the Posidonia Shale, and it has been estimated that 25 percent of all *Harpoceras* and *Hildoceras* specimens from the Posidonia Shale are preserved with aptychi (Fraaye & Jäger 1995). The aptychi associated with ammonites from the Posidonia Shale bear close similarities to those discussed in this paper (Fig. 9). The aptychi discussed by Riegraf *et al*. (1984) and labelled e, f, g and h in Figure 9 are of particular interest as they are associated with the genus *Harpoceras*. In particular, the aptychus labelled 'e' (Fig. 9) is associated with *Harpoceras antiquum*, which is a synonym of *Tiltoniceras* (Howarth 1992*a*), and specimens WHITM:2011/16.3 and WHITM:2011/44 are both associated with *Tiltoniceras antiquum*. Each specimen discussed and illustrated by Riegraf *et al*. (1984) is closely comparable in terms of striations and the shape and positioning of the symphysis with WHITM:2011/16.1, WHITM:2011/16.2, WHITM:2011/16.3 and DONMG:ZG425.

The discussion above highlights the association of *Cornaptychus* with Harpoceratid ammonites. Other instances have been documented in which a particular type of aptychus is associated with a particular family of ammonites. Thus, Thomson (1972, fig. 3) showed that *Lamellaptychus* was found closely associated with oppeliid ammonites preserved as negative moulds and stated that *Lamellaptychus* had been found widely elsewhere in the conches of oppeliid ammonites.

5.2. Other aptychi from the Lower Jurassic of the Yorkshire coast

Lehmann (1971, 1979) has reported aptychi from the Lower Jurassic of the Yorkshire Coast, but associated with ammonites other than Harpoceratids and anaptychi rather than diaptychi or isolated valves. Thus, Lehmann (1971) sectioned several specimens of *Arnioceras* from the lower Lias Group of the Yorkshire Coast and found them to be associated with the anaptychus type of jaw. A further study by Lehmann (1979) discussed anaptychi within the living chambers of two ammonites, *Dactylioceras tenuicostatum* and *Dactylioceras semicelatum*, from the Grey Shale Member of Port Mulgrave. The ammonites investigated were cut along their median plane, and the anaptychi were removed and sectioned by grinding, being photographed at each stage (Lehmann 1979).

5.3. Taphonomy

As discussed above, most aptychi recorded from Port Mulgrave consist of a dark carbonaceous film overlying the impression of the aptychus within the shale, although WHITM:2011/16.4 consists of just the impression with no film, suggesting that the latter may have eroded away or stayed attached to the counterpart. The aptychi were probably composed originally of chitin with varying amounts of calcium carbonate within both the chitin structure and as layers, as exemplified by fossil coleoids (Doguzhaeva *et al*. 2007), modern coleoids (Kear *et al*. 1995) and modern nautiloids (Saunders *et al*. 1978). If the calcium carbonate were to dissolve, the tough chitin structure of the aptychi can still enable their preservation, thus broadening their preservation potential when separated from the ammonite shell. Separation of aptychi from the ammonite shell could be due to either dissolution of shell material or to post-mortem decay of soft parts and disassociation of the shell material and aptychi. Variations in the pore fluids and sediment could allow acidic fluids to remove calcium carbonate and therefore remove some shelly fossils, or alternatively allow neutral and calcium carbonate bearing fluids to preserve calcium carbonate based fossils (Martill 1987, 1993). However, evidence for aptychi separation due to decay rather than ammonite dissolution during the initial stage of taphonomy is supported by specimen DONMG:ZG425. This specimen shows that calcium carbonate was never completely dissolved within the area around the crocodyliform, as the crocodyliform is preserved in calcium carbonate with excess calcium carbonate infilling cracks. If any ammonite had been present, its preservation potential would not have been affected by calcium carbonate dissolution in the area.

6. CONCLUSIONS

The aptychus *Cornaptychus* has not been reported previously in association with any ammonite family from the Lower Jurassic of North Yorkshire, but three specimens of *Cornaptychus* are reported in this paper to be associated with ammonites of the Subfamily Harpoceratinae from Toarcian shales near Whitby. WHITM:2011/16.3 is found closely associated with *Tiltoniceras antiquum* and WHITM:2011/16.2 is also found in close association with a Harpoceratid, tentatively identified as cf. *Harpoceras* sp. or cf. *Eleganticeras* sp. Additionally the aptychus of WHITM:2011/44 is preserved in the chamber of the ammonite *Tiltoniceras antiquum*. The preservation of the aptychi is through impression overlain by a film of organic carbon, originally composed of chitin, whose preservation potential has been increased most probably through the local enrichment of organic carbon as indicated by the results of the ESEM study (Fig. 10).

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