Exceptionally preserved ammonites from the Charmouth Mudstone Formation (Lower Jurassic) and their significance for ammonite taphonomy

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Very rarely, examples of ammonites that are preserved in nodules from the Charmouth Mudstone Formation in Dorset, UK, retain some shell material attached to the internal mould of the shell. The shell material is always only a very thin, highly iridescent veneer of the innermost shell layer and only occurs at the rear of the body-chamber. Normally ammonites preserved in nodules part cleanly between the inner shell and the internal mould when the nodules are split. The body-chambers are filled with various amounts of sediment and diagenetic calcite, but the anterior boundaries of the iridescent veneer and of the diagenetic calcite fill do not coincide. Equally, nodules with several ammonites only one of which is iridescent indicate that the iridescence is not due to unusual preservation of a specific nodule. Thus, this exceptional preservation indicates an original difference in the shell microarchitecture between the rear and front of the ammonite body-chamber rather than a result of diagenesis. The small amount of sediment in the anterior body-chambers of most examples suggests these ammonites could retract their bodies a short distance into the shell when threatened.

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Introduction

Ammonites are common fossils in nodules within the Charmouth Mudstone Formation of Dorset (e.g. Cope, 1994; Curtis *et al*., 2000; Page, 2004, 2010 and references therein; Andrew *et al*., 2010). Most commonly, the nodules are split open to reveal perfectly preserved, uncrushed ammonites within (e.g. Cope 1994, pls 1, 2; Andrew *et al*., 2010, figs 2, 5, 11, 12). When the nodule is split, normally the ammonite shell parts from the internal mould along its smooth inner surface, thus revealing the fill of sedimentary rock and diagenetic calcite that makes up the internal mould. In uncrushed ammonites from within nodules the phragmocone chambers are almost always undamaged and filled with diagenetic calcite. In contrast, the body-chambers usually contain some original sediment, which may fill the entire body-chamber or be confined to variable amounts of the anterior portion only. The preservation of these clean internal moulds also allows study of the ammonite suture lines, which help determine whether or not the ammonites are fully grown.

Very rarely (perhaps one in 500-1000 specimens) the ammonites preserved in nodules are iridescent. Cope (1994, p. 58) mentioned that "*Occasionally iridescent aragonite is preserved as a thin layer on these internal moulds*", but did not specify where on the ammonites the thin layer occurred. In the examples described herein the iridescent veneer of presumed aragonite is very thin and confined to the rear of the body-chamber; it does not extend back onto the phragmocone, nor forward into the anterior of the body-chamber. In these exceptionally preserved ammonites the boundaries between the iridescent and 'normal' parts of the body-chamber and those between the diagenetic calcite-filled and sediment-filled parts do not coincide. Thus, it would seem the presence of the iridescence is unrelated to the fill of the body-chamber. This is especially true of a small number of examples in which the sediment preserves a geopetal fill. Thus, one side of the body-chamber is sediment-filled and the other side calcite-filled. Furthermore, we have seen several examples of nodules with more than one ammonite preserved within, only one or in one case (LYMPH 2015/21) two of which show the unusual iridescence. So, again, it would seem this is not the result of some unusual diagenetic reaction within a specific nodule. Close inspection shows that the iridescence is due to a very thin veneer of the original ammonite shell remaining attached to the internal mould and showing the pearly lustre characteristic of the inner layers of all molluscan shells. The question then arises, 'why should only the rear part of the body-chamber split within the shell layers to allow the veneer to remain attached to the internal mould, when the other parts of the shell split from the internal mould along the inner shell surface?' Most of the ammonites belong to the genus *Promicroceras* Spath, 1926, the commonest ammonite genus at the stratigraphic interval from which most of our specimens originate, but we have also seen rare examples of iridescent *Asteroceras* Hyatt, 1867, *Xipheroceras* Buckman, 1911 and even one Upper Liassic *Dactylioceras* Hyatt, 1867, from Yorkshire. *Promicroceras* and *Xipheroceras* may be microconch and macroconch, respectively, of the same biological taxon (Cope, 1994; Howarth, 2013, p. 40), although Kevin Page doubts this (*in lit* 5 June 2015).

Iridescent ammonite shells preserved in clays and shales are not particularly rare and it is usually assumed that the iridescence results from the original aragonite being preserved. We have no mineralogical information to confirm this assumption, but what is undoubtedly clear is that the iridescence requires the original layered structure of the shell to be preserved, as in the examples of *Promicroceras* from the Marston 'Marble' (Andrew *et al*., 2015). Ammonites preserved in neomorphic calcite do not split parallel to the original shell layers and so are not iridescent. However, when the original layering is preserved in ammonite shells, they often appear to be iridescent throughout, from the external surface down through any layers that adhere to the internal mould. Hence, the entire ammonite may appear to be iridescent. In addition, such layered shells are usually white and the iridescence is weak (see, for example, the specimen of *Promicroceras* illustrated at *www.fossilwalks.com/ammonites/pages/promicro.htm*). The unusual feature of the ammonites we discuss herein, which we cannot fully explain, is that they are brightly iridescent, especially when fresh and the iridescence is confined to the rear of the body-chamber. This paper aims to describe these unusual iridescent ammonites to draw attention to their existence in the hope of stimulating discussion of their significance and identifying other examples. Specimens are preserved in the Lyme Regis Philpot Museum (LYMPH) and in the J. F. Jackson collection, National Museum of Wales, Cardiff (NMW) and we have seen further examples in private collections.

Material and methods

The specimens were all collected loose in nodules weathered out from the Charmouth Mudstone Formation either just west of Lyme Regis or below Black Ven east of Lyme Regis, Dorset and below Stonebarrow Hill, east of Charmouth (Figure 1). Thus, determining the precise horizon of the nodules is a matter of experience and not all examples can be localized. J. F. Jackson collected specimens prior to 1960, when his collection was acquired by the National Museum of Wales (NMW). The specimens in the Lyme Regis Museum were collected over the past decade or so. Most of the ammonites originated from nodule horizons within Lang's bed 83 in the Black Ven Marl Member of the Charmouth Mudstone Formation (Figure 2; see Lang and Spath, 1926; Simms, 2004, fig. 2.8, p. 67), which corresponds to the *semicostatoides* and *cf. confusum* biohorizons of Page (1992) in the Obtusum Subzone. Some of the Jackson collection specimens originated from Lang's bed 85, Stellare Subzone *margaritoides* biohorizon. In addition, we suspect that the few specimens collected west of Lyme Regis came from lower down in the succession high in the Shales-with-Beef Member of the Charmouth Mudstone Formation, but we cannot confirm their precise horizon.

Nodules were split open to reveal any included fossils and those showing iridescent ammonites kept to one side and further prepared with an airpen. Specimens were photographed using a Nikon D300 camera and proprietary software (Zerene Stacker) to produce greater depth of field. To describe the extent of the iridescence and of any sediment fill in the body-chambers the measurements shown in Figure 3 were taken from camera lucida drawings or photographs.

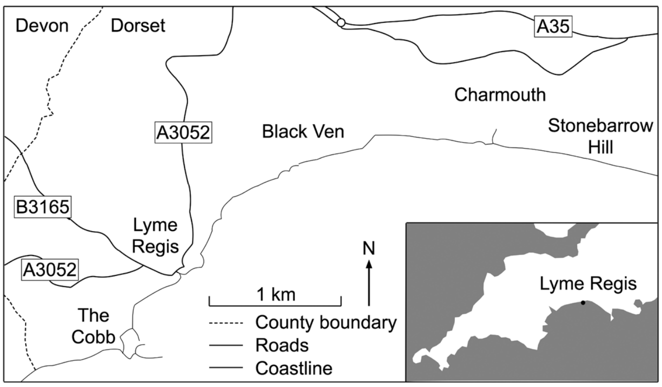

Figure 1. *Location of the sites mentioned in the text. Most of the ammonites described herein came from the foreshore below Black Ven.*

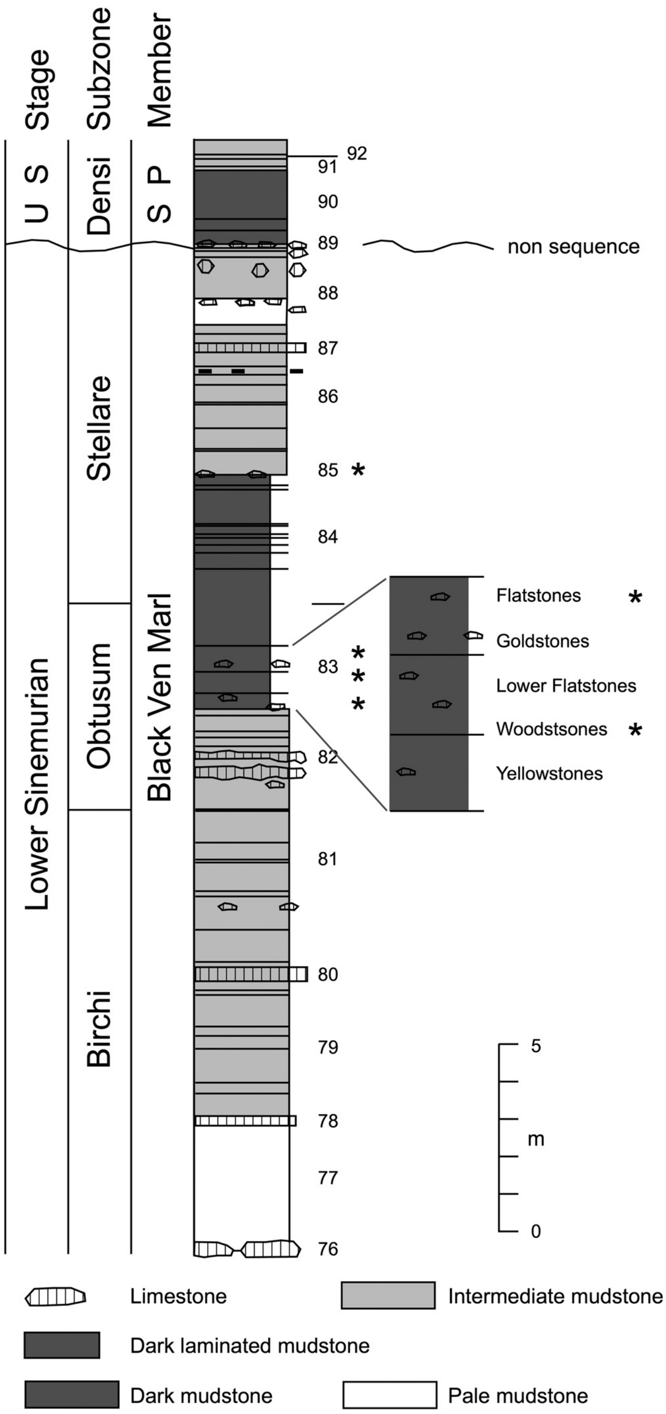

Figure 2. *Stratigraphy of the Charmouth Mudstone Formation to show levels where iridescent ammonites have been collected (*). Note that all lie within Lang's beds 83 and 85 (Lang and Spath, 1926). U S = Upper Sinemurian, Densi = Densinodulum Subzone, S P = Stonebarrow Pyritic Member. Based on Lang and Spath (1926, fig. 1), Hesselbo and Jenkyns (1995, figs 9, 10) and Simms (2004, fig. 2.8).*

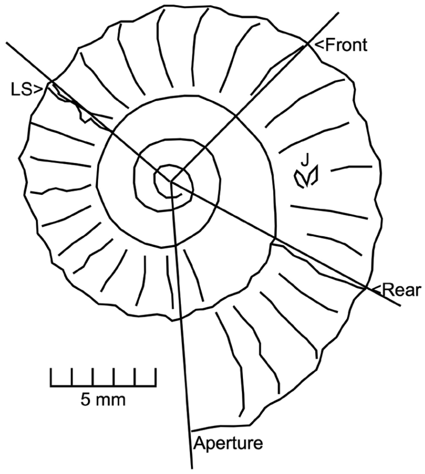

Figure 3. *Camera lucida drawing of LYMPH 2015/12 to show the measurements made on iridescent* Promicroceras. *(Aperture) line from origin to aperture, (LS) line to last suture, (Front) line to anterior of iridescence, (J) jaw, (Rear) line to posterior limit of sediment penetration into body-chamber.*

Results

Results are summarized in Table 1. Twelve iridescent examples have been seen recently, nine of which are preserved in the Lyme Regis Museum, Registration numbers LYMPH 2015/7-12 and 2015/20-21 (Figures 4 and 5). A further 22 iridescent ammonites are preserved in the Jackson collection in Cardiff (Figure 6). Many of the ammonites remain within the nodules, so only one side is visible. Most of the *Promicroceras* have the last two or three suture lines approximated (e.g. LYMPH 2015/7 and 2015/12, Figures 4b, f) indicating they were fully-grown, despite averaging only 26 mm diameter. The adult body-chamber averaged 209°, but as two individuals gave values below 180° they were probably incomplete and so the average is an underestimate. The phragmocone consists of more than five whorls in the best-preserved examples (e.g. LYMPH 2015/9, Figure 4c). The extent of the iridescent veneer ranged from 42° (LYMPH 2015/12, Figure 4f) to 147° (NMW 60.510.G4490, Figure 6d) in front of the last suture line. However, the average was 88.9° and in most examples the veneer did not extend into the anterior half of the body-chamber. The outline of the iridescent areas is apparently controlled by the attachment of the thin veneer to the internal mould. In the two examples where we have both parts of the

Specimen	Side	Diameter (mm)	Body chamber (°)	Extent of veneer (°)	Extent of sediment (°)
Private collection	Right	27.0	225	115	31
LYMPH 2015/7	Right	23.5	221	89	
LYMPH 2015/8	Right	27.1	233	82	57
LYMPH 2015/9	Left	25.0	219	114	52
LYMPH 2015/10	Left	22.5	228	96	58
LYMPH 2015/11	Right	21.25	193	94	70
LYMPH 2015/12	Left	32.1	200	42	70
Private collection	Left		235	92	77
LYMPH 2015/20	Right	21.7	198	81	
LYMPH 2015/21	Left	23.3	208	107	
NMW 60.510.G74	Left	32.0	221	72	
NMW 60.510.G78	Left	23.0	199	52	
NMW 60.510.G82	Right	34.0	206	112	73
NMW 60.510.G85	Left	27.0	204	85	
NMW 60.510.G86	Left	28.0	185	79	31
NMW 60.510.G595	Left	28.0	245	125	55
NMW 60.510.G596	Right	25.0	199	74	53
NMW 60.510.G597	Right	25.0	213	90	
NMW 60.510.G598	Both	28.0	214	68	75
NMW 60.510.G599	Both	27.0	220	86	42
NMW 60.510.G600	Right	29.0	190	114	
NMW 60.510.G601	Both	25.0	207	58	31.5
NMW 60.510.G606	Left	29.0	177	64	55
NMW 60.510.G608	Right	25.0	167	78	
NMW 60.510.G4490	Left	28.0	230	147	
NMW 65.510.G87	Right	22.0	203	96	52
Mean	11 Right	26.34	209.23	88.92	55.16
Standard deviation	12 Left	3.35	18.56	23.71	15.42
Coefficient of variation	3 Both	12.72%	8.87%	26.67%	27.92 %
N	26	25	26	26	16

Table 1. *Measurements of extent of iridescent veneer and of sediment penetration into body chambers of* Promicroceras *from the Charmouth Mudstone Formation, near Lyme Regis, Dorset.*

Figure 4. Promicroceras *from the Charmouth Mudstone Formation, Lyme Regis, showing extent of iridescent veneers and sediment penetration into body-chambers.* ***(a)*** *LYMPH 2015/8 with limited veneer and sediment.* ***(b)*** *LYMPH 2015/7 with sharp, sloping anterior margin to veneer and extensive sediment fill.* ***(c)*** *LYMPH 2015/9 with sloping anterior margin to veneer and little sediment.* ***(d)*** *LYMPH 2015/10 with sloping anterior margin to veneer, jaws preserved (J) and apparently little sediment.* ***(e)*** *LYMPH 2015/11 with moderately large veneer and sediment.* ***(f)*** *LYMPH 2015/12 with poorly preserved veneer and gradual boundary to penetrating sediment. Scale bars = 5 mm. White arrows indicate position of last suture.*

Figure 5. *Specimen LYMPH 2015/21 from the Charmouth Mudstone Formation, west of Lyme Regis, showing two iridescent ammonites (arrowed) in the same nodule. Scale bar = 5 mm.*

nodule (e.g. LYMPH 2015/7, Figure 4b, LYMPH 2015/21, Figure 5) some of the iridescent veneer remained attached to the shell in the external mould as well. Thus, the outlines of the iridescence are usually irregular and do not seem to reflect any obvious, internal anatomical boundary, but are probably incomplete. In LYMPH 2015/7 the anterior margin of the veneer is an obvious, gently sloping line that is more anterior at the venter than the dorsum (Figure 4b). A similar, but more subtle, gently sloping anterior margin occurs in LYMPH 2015/9 (Figure 4c) and a more irregular sloping line in LYMPH 2015/10 (Figure 4d). In addition, NMW 60.510.G85, G86, G600 (Figure 6b) and G608 (Figure 6a) show similar sloping anterior margins. These sloping margins are at a variety of angles to the umbilical seam and the ventral margin of the shell, and almost all extend further towards the aperture ventrally (Figure 7). They occur over a narrow range at about 90° anterior to the last suture. Thus, they may represent a consistent original anterior margin to the iridescent veneer. However, NMW 60.510.G82 (Figure 5c) apparently has an anterior sloping margin that extends further towards the aperture dorsally, not ventrally.

Similarly, in LYMPH 2015/7 and 2015/10 the posterior margin of the iridescent veneer follows the last suture quite closely, including an extension into the lateral lobe (Figure 8). This is also true of the only example we have seen of iridescent *Asteroceras obtusum* (NMW 60.510.G3518, Figure 9). LYMPH 2015/10 is unusual in showing two minute areas of iridescence attached to the last and antepenultimate chambers of the phragmocone (arrows in Figure 8b). In other specimens, except LYMPH 2015/12 where the iridescence is minimal, the posterior limit is either at the last suture or at the rib immediately in front of the last suture. Thus, we think the

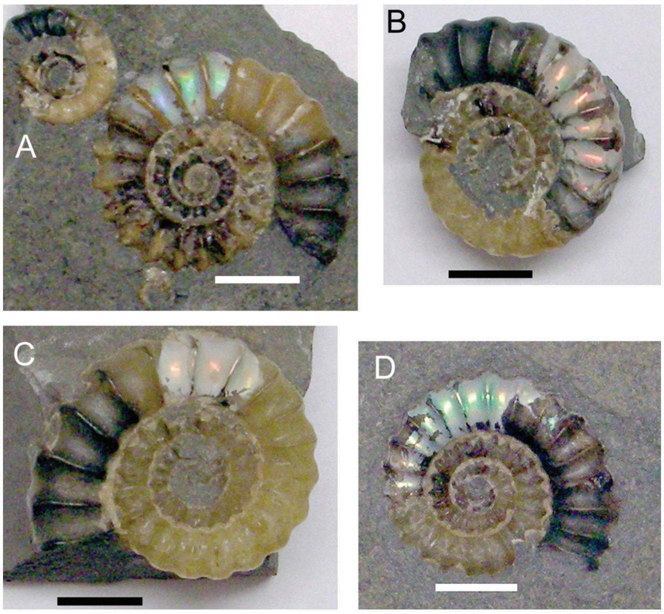

Figure 6. Promicroceras *from the Charmouth Mudstone Formation, Lyme Regis, showing extent of iridescent veneers and sediment penetration into body-chambers. (**a**) NMW 60.510.G606 showing curved anterior margin to iridescent veneer and moderate sediment penetration, plus two other non-iridescent ammonites. (**b**) NMW 60.510.G600 showing curved anterior margin to veneer extending over sediment fill. (**c**) NMW 60.510.G82 showing anterior margin that curves backwards towards the venter. (**d**) NMW 60.510.G4490 showing extensive veneer with irregular anterior margin extending over sediment filled body-chamber. Scale bars = 10 mm.*

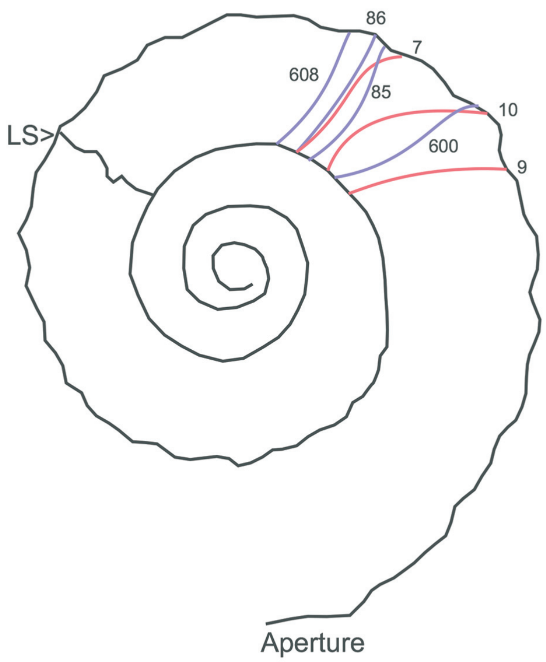

Figure 7. *Diagrammatic outline of* Promicroceras *with anterior margins of iridescent veneers of seven specimens superimposed. Note that the anterior margins tend to extend further towards the aperture as they approach the venter and that they coincide quite closely in position. Blue indicates NMW specimens, red LYMPH specimens. (LS) last suture. Numbers refer to the last part of the registration number. So, 7 = LYMPH 2015/7, 608 = NMW 60.510.G608.*

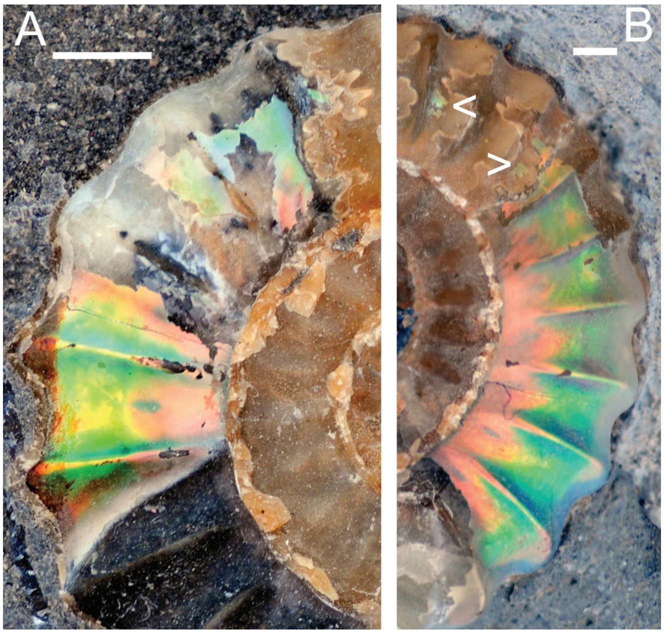

Figure 8. *Detail of veneers in* Promicroceras *from the Charmouth Mudstone Formation, Lyme Regis. (**a**) LYMPH 2015/7 to show the sharp anterior junction (below) and posterior limit within lobes of the last suture (above right). (**b**) LYMPH 2015/10 showing an irregularly curved anterior margin (below) and posterior margin following last suture (above). Note two minute patches of veneer on the phragmocone (arrowed). Scale bars = 5 mm.*

Figure 9. *A specimen of* Asteroceras obtusum *from the Charmouth Mudstone Formation, Lyme Regis, with a short, iridescent veneer (NMW 60.510.G3518). Scale bar = 10 mm.*

original posterior limit was probably at the last suture. Where one can see it, the veneer extended over the venter of the ammonite (e.g. LYMPH 2015/12, Figure 4f) and it is present on both sides. This is also true of several examples in the Jackson collection (e.g. NMW 60.510.G598-601, G608), which are largely or entirely free of matrix.

Sediment penetrated back into the body-chamber from the aperture by as little as 31° (NMW 60.510.G86, Table 1) to 100% of the body-chamber (e.g., NMW 60.510.G600, Figure 6b), although in many specimens it did not exceed 77° (Table 1). Nevertheless, in at least three examples (LYMPH 2015/7, Figure 4b; NMW 60.510.G85 and G600, Figure 6b) the sediment continues beneath the iridescent veneer, so the nature of the fill did not affect the presence of the iridescent veneer. The boundary between the calcite-filled and sediment-filled parts of the body-chambers may be sharp (e.g. LYMPH 2015/10, Figure 4d) or quite diffuse (e.g. LYMPH 2015/12, Figure 4f). LYMPH 2015/10 appears to preserve part of the jaw (j in Figure 4d), which lies 85-90° behind the aperture and 30-35° behind the rear margin of the sediment fill in the body-chamber. This position is very similar to the position of the upper jaw (anaptychus) of another specimen of *Promicroceras* from the Lower Lias of Dorset illustrated by Cope and Sole (2000, fig. 1f). LYMPH 2015/12 occurs in a large nodule, 120 mm long, with at least seven other, normally preserved ammonites, at least one bivalve shell (*Parainoceramus* ?), a minute, high-spired gastropod (0.75 mm high) preserved within an ammonite body-chamber, as well as a large piece of wood at least 50 mm across and running the length of the nodule as now preserved. Similarly, NMW 60.510.G74 and G635 are Woodstones nodules (Lang's bed 83f, Lang and Spath, 1926, p. 160) with at least six and a dozen ammonites preserved, respectively, but only one showing iridescence. At least two Flatstones nodules (Lang's bed 83h, Lang and Spath, 1926, p. 160) in the Jackson collection also show multiple ammonites, but only one iridescent example. LYMPH 2015/21 is part and counterpart of a small Woodstones nodule (bed 83f) with about 10 small ammonites preserved, two of which show an iridescent veneer (Figure 5). This is the only example we have seen with more than one iridescent ammonite within the same nodule.

INTERPRETATION

The iridescence in these exceptionally preserved *Promicroceras* and *Asteroceras* is due to a thin veneer of the original shell remaining attached to the internal mould. This suggests that the shell retained its original layered structure with the layers composed of small crystallites lying parallel to the internal surface of the shell (see, for example, Doguzhaeva *et al.*, 2007, fig. 11.2b). The iridescence is not an original colour pattern, but results from the interference of the crystallites with incident light. Precisely which colour one sees depends on the orientation of the incident light and it changes when the shells are re-orientated, especially when viewed under a microscope. This also suggests that the shell material in these exceptionally preserved ammonites is still aragonite, but we have no definite confirmation of the crystallography. Aragonite is known to be preserved in other ammonites buried in clay-grade sediments (e.g. see Mychaluk *et al.* 2001). Cope (1994, p. 58) also interpreted iridescence as due to a thin layer of aragonitic shell. Whatever the shell mineralogy, there still remains the question of why the iridescent veneer of shell is confined to the rear half of the body-chamber.

Presumably, when a nodule splits adjacent to an ammonite shell the rock parts along the weakest surface. Usually this is the smooth surface between the internal mould, whether calcite or sedimentary rock, and the internal surface of the shell. In the original living ammonite the internal surface would have been smooth and lined with aragonite crystallites. On the other hand, the external surface of the shell would have been much rougher, with growth lines, possibly damage caused by attachment of epibiota and/or boring organisms and, in many species, external ornament of ribs and spines. Thus, it is likely that in most ammonites the bonding between the sedimentary rock and the external surface of the shell would have been considerably stronger than that between the internal surface of the shell and the internal mould. Even if the bonding was equally strong, the internal surface area is smaller than the external surface area, again making it likely that the weaker surface would have been between the inner shell surface and the internal mould. Hence, the restriction of the veneer of iridescent shell material to the rear of the body-chamber suggests that there was a difference between the bonding of the shell to the internal mould at the rear of the body-chamber compared with the front and with the phragmocone. We do not think this reflects the fact that most of the rear of the body-chambers in these exceptional ammonites is filled with diagenetic calcite because we have seen specimens with both types of fill and in some cases both types of fill on opposite sides of the same body-chamber. Furthermore, this would not explain the absence of the veneer on the phragmocone, which is almost always filled with diagenetic calcite. So, we think it is possible that the restriction of the veneer to the rear of the body-chamber reflects some original difference in the shell structure in that part of the shell. Two possibilities exist. One is that the attachment of the mantle to the shell differed between the front and rear of the body-chamber. The other is that the growth increments of the shell differed in their orientation between the front and rear of the body-chamber.

Muscle attachment areas in molluscs are frequently much rougher than other parts of the internal surface and are likely to produce locally stronger bonds between the shell and the internal mould. So, one possibility is that the rear of the body-chamber had a lining of muscle attachment for the mantle, which was absent in the front of the body-chamber. If so, we would expect the margins of the veneer to be gently curved revealing the limit of the different mantle attachment, analogous to the lateral muscle scars found in modern *Nautilus* (see Ward, 1987, fig. 1.13). It is true that LYMPH 2015/7, in particular, has an obvious, gently curved, anterior margin to the visible side of iridescent veneer (Figure 4b), and other specimens show a similar anterior margin to their veneers (Figures 4c, d, 7). However, in most specimens the distance from the last suture to the anterior margin of the veneer is nearly half the entire body-chamber and this is much larger than any reported muscle scar in ammonites or *Nautilus*. Furthermore, Doguzhaeva and Mutvei (1996) have discussed the attachment of ammonites to their shells and they described nothing as extensive as the veneers in these exceptionally preserved *Promicroceras* and *Asteroceras*.

Nevertheless, recently Mironenko (2013) has described much more extensive lateral attachment scars in two genera of Late Jurassic ammonites, which also have iridescent veneers attached to their internal moulds. In both genera some examples show muscle scars running from the last suture to a definite anterior margin still within the posterior part of the body-chamber, just as in our examples (e.g., Mironenko, 2013, fig. 2b, c, e). However, all Mironenko's many examples differ in having more or less sharp anterior margins that are convex towards the aperture laterally and hence have an obvious ventral sinus concave towards the aperture (Figure 10). In addition, some examples also had sharp posterior margins (facing the last suture) that were almost mirror images of the anterior margin (Figure 10), with convex lateral margins and a deep ventral sinus (e.g. Mironenko, 2013, fig. 2a, f). Others lacked any definite posterior margin, but clearly did not reach the last suture (e.g. Mironenko, 2013, fig. 2d). Mironenko (2013, fig. 2) also illustrated 'anterior lateral sinuses' that resemble fine growth lines, but concave towards the aperture laterally (Figure 10). We have seen no trace of such lateral sinuses in our iridescent ammonites.

In our examples the posterior margin appears to be defined by the last suture and the anterior margin apparently slopes sinuously from a posterior limit at the umbilical seam to its most anterior point at the venter. Thus, the structures we describe differ in their posterior margins from some of those described by Mironenko and in their anterior margins from all of Mironenko's examples. It would seem the structures we describe and those described by Mironenko are not the same.

Alternatively, ammonite shells grew by the addition of thin, annular increments to the shell at the aperture, the margins of which were slightly oblique to the shell surface. Thus, the growing shell was thinnest at the aperture and thickened posteriorly, eventually reaching its full thickness. Behind the point where the growing shell reached its full thickness, the mantle added a very thin inner layer parallel to the shell margins. Thus, the limits of the iridescent veneers in these exceptionally preserved *Promicroceras* could indicate the point where the shell reached its full thickness. However, this seems unlikely on two grounds. First these *Promicroceras* appear to be fully-grown. Generally, ammonites modified their apertures, often by thickening them, when they became mature. Thus, in mature ammonites one would not expect to find a point where the shell reached its full thickness. Such a point would be at the aperture. Secondly, the annular increments of a growing shell only extend a short distance behind the aperture, whereas the anterior margin of the iridescent veneers in these *Promicroceras* is at the minimum just under half way back from the aperture and in several specimens considerably further back. Thus, even in juvenile *Promicroceras* the rear margin of the growth increments would have been much closer to the aperture than the front margin of the iridescent veneers on these specimens.

However, Landman *et al*. (1999) described four different types of markings on pachydiscid ammonites from the Upper Cretaceous of the Western Interior Basin, USA, one of which may be relevant to our specimens. These markings consist of regularly spaced transverse lines on the surface of the inner shell layer that cross the venter with a marked adoral projection, as in the anterior limit of our iridescent veneers. They do not follow the shapes of external growth lines of the shells and they only extend as far as the middle of the body-chamber. Landman *et al*. (1999, p. 2) suggested that these "*transverse lines formed at the adoral margin of the zone of nacreous secretion in the middle of the body-chamber*". Thus, they thought the transverse lines marked a change in the shell structure of the internal layer of the shell, which presumably moved forward repeatedly as the shell grew. We do not see these growth increments in the iridescent veneers on our shells, but the sloping anterior that projects over the venter and the position more or less in the middle of the body-chamber coincide with the anterior margin of the transverse lines that Landman *et al*. described. In addition, our specimens show variations in the shape of the anterior margins of their veneers, whereas the specimens Landman *et al*. described have much more regular outlines. Another difference is that the transverse lines Landman *et al*. described appeared on the phragmocone as well as the body-chamber, whereas the iridescent veneers we

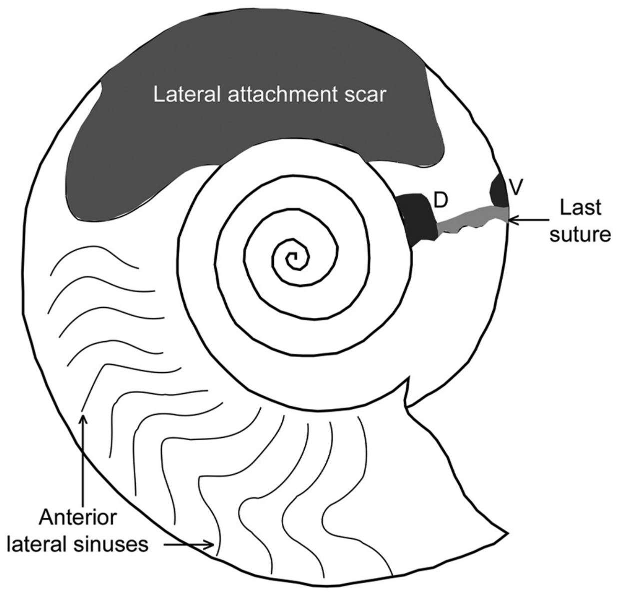

Figure 10. *Diagrammatic illustration of the 'lateral attachment scar' and 'anterior lateral sinuses' as preserved in the Late Jurassic ammonite* Kachpurites. *(D) right dorsal muscle scar. (V) unpaired ventral muscle scar. Note that the lateral attachment scar has a ventral sinus in front and behind. Redrawn from Mironenko (2013, fig. 2f).*

describe do not extend behind the last suture. Thus, it is difficult to judge whether the similarities between the lines Landman *et al*. (1999) described and the iridescent veneers on our specimens indicate a similar origin or are merely coincidental.

One possibility, which is highly speculative, is that ammonites probably had mantle cavities that occupied at least the anterior half of the body-chamber. For example, Paul (2014) has described changes in the position of thin patches of diagenetic calcite thought to represent remains of the mantle and a change in the sediment fill of the body-chamber in a specimen of *Dactylioceras* at about one third the body-chamber length from the last suture. It was thought that these changes might represent the posterior limit of the mantle cavity. *Dactylioceras* has a body-chamber just over one whorl in extent, whereas in these *Promicroceras* the body-chamber is less than three quarters of a whorl. It is possible that the anterior limit of the iridescent veneer of these exceptional *Promicroceras* coincides with the posterior limit of the mantle cavity, but why this should be and how it could be preserved are unknown.

All the specimens have some sediment penetrating the body-chamber from the aperture. In some the sediment did not penetrate very far and has a sharp contact with the diagenetic calcite filling most of the body-chamber (e.g. LYMPH 2015/9, Figure 4c). However, in LYMPH 2015/7 the sediment penetrated at least to the anterior margin of the iridescent veneer and probably much further (Figure 4b). We assume that in all the ammonites the sediment was unable to penetrate all the way to the last suture because at least some of the ammonite body still occupied the posterior part of the body-chamber. In LYMPH 2015/7 (Figure 4b) it seems likely that the ammonite had died and much of its body had been removed by a predator or scavenger, so that sediment was able to penetrate most of the body-chamber. In other examples with only a small amount of sediment near the aperture we think the ammonite body may have been essentially complete. We suspect that *Promicroceras* could withdraw its body a short distance into the shell when threatened. LYMPH 2015/10 (Figure 4d), which apparently preserves the jaw, supports this idea. It is possible that the ammonite body might have shrunk after death, although we think this is unlikely. A body saturated in seawater might be expected to swell rather than shrink as it decayed. Either way, these ammonites apparently did not have any structure analogous to the hood of *Nautilus* that prevented the body from withdrawing into the body-chamber, pre- or post-mortem.

Interestingly Monks (2000) has described two types of damage to Cretaceous heteromorph ammonites. In the first type the shell margin had chips removed from it, which Monks interpreted as unsuccessful attempts at predation by crustaceans. Although some shell material had been removed, when the missing parts had been repaired the ammonite was able to continue secreting a shell with the normal ornament of ribs. Monks argued that this suggested only the shell was damaged. However, in the second type of damage not only were chips removed from the shell, but after repair a permanent change to the normal shell ornament continued as the shell grew. In this second case Monks argued that the predator had managed not only to damage the shell, but the mantle as well. He concluded that the heteromorph ammonites were probably able to withdraw their bodies a short distance into the shell, thus in some cases avoiding permanent damage when attacked. Monks' idea is consistent with the preservation of small amounts of sediment in the apertures of these iridescent (and other) *Promicroceras*.

Summary

Rare examples of ammonites preserved in nodules from the Charmouth Mudstone Formation near Lyme Regis have thin, iridescent veneers of the shell attached to the internal moulds. The veneers are confined to the rear part of the body-chambers. Their posterior limit appears to have been the last suture and the anterior limit extended anteriorly over the venter. The veneers are not related to the fill of the body-chamber, nor to any unusual preservation history of individual nodules. Several examples occur of nodules with many ammonites preserved inside, only one of which has an iridescent veneer. Coincidence of the occurrence of anterior margins suggests that the veneers reflect an original difference in the shell structure between the rear and front of the body-chamber. However, whether this represents soft tissue attachment or another type of original difference in shell structure is uncertain.

In most of the ammonites some sediment penetrated the anterior part of the body-chamber, but most of the body-chamber is now filled with diagenetic calcite. We interpret examples with a sharp contact between the sediment fill and the diagenetic calcite as having had the body still within the shell when they were buried. Thus, the body prevented the sediment from penetrating far into the body-chamber. We suspect that this indicates that ammonites were able to withdraw their bodies a short way into the shell when threatened, unlike modern *Nautilus*.

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References

ANDREW, C., HOWE, P., PAUL, C.R.C. and DONOVAN, S.K. 2010. Fatally bitten ammonites from the Lower Lias Group (Lower Jurassic) of Lyme Regis, Dorset. *Proceedings of the Yorkshire Geological Society,* **58**, 81-94.

ANDREW, C., HOWE, P. and PAUL, C.R.C. 2015. Fatally bitten ammonites from septarian concretions in the 'Marston Marble' (Lower Jurassic, Sinemurian), Somerset, UK, and their taphonomy. *Proceedings of the Geologists' Association,* **126**, 119-129.

BUCKMAN, S.S. 1911. *Yorkshire Type Ammonites*, vol. 1, parts 3-5. Wheldon Wesley, London, 23-44.

COPE, J.C.W. 1994. Preservation, sexual dimorphism and mode of life of some Sinemurian ammonites. In: PALLINI, G. (Ed.), Proceedings of the 3rd Pergola International Symposium "Fossili, Evoluzione, Ambiente". *Palaeopelagos Special Publication,* **1**, 57-66.

COPE, J.C.W. and SOLE, D.T.C. 2000. Ammonite jaw apparatuses from the Sinemurian (Lower Jurassic) of Dorset and their taphonomic relevance. *Journal of the Geological Society, London,* **157**, 201-205.

CURTIS, C.D., COPE, J.C.W., PLANT, D. and MACQUAKER, J.H.S. 2000. 'Instantaneous' sedimentation, early microbial sediment strengthening and a lengthy record of chemical diagenesis preserved in Lower Jurassic ammonitiferous concretions from Dorset. *Journal of the Geological Society, London,* **157**, 165-172.

DOGUZHAEVA, L. and MUTVEI, H. 1996. Attachment of the body to the shell in ammonoids. In: LANDMAN, N.H., TANABE, K. and DAVIS, R.A. (Eds), *Ammonoid Paleobiology*. Plenum Press, New York, 43-63.

DOGUZHAEVA, L., MAPES, R.H., SUMMESBERGER, H. and MUTVEI, H. 2007. The preservation of body tissues, shell, and mandibles in the ceratitid ammonoid *Austrotrachyceras* (Late Triassic), Austria. In: LANDMAN, N.H., DAVIS, R.A. and MAPES, R.H. (Eds.), *Cephalopods Present and Past: New Insights and Fresh Perspectives*. Springer, Dordrecht, 221-238.

HESSELBO, S.P. and JENKYNS, H.C. 1995. A comparison of the Hettangian to Bajocian successions of Dorset and Yorkshire. In: TAYLOR, P.D. (Ed.), *Field Geology of the British Jurassic*. Geological Society, London, 105-150.

HOWARTH, M.K. 2013. *Treatise Online, No. 57. Part L, Revised, Volume 3B, Chapter 4: Psiloceratoidea, Eoderoceratoidea, Hildoceratoidea*, 1-139.

HYATT, A. 1867. The fossil Cephalopoda of the Museum of Comparative Zoology. *Bulletin of the Museum of Comparative Zoology,* **5**, 71-102.

LANDMAN, N.H., LANE, J., COBBAN, W.A., JORGENSEN, S.D., KENNEDY, W.J. and LARSON, N.L. 1999. Impressions of the attachment of the soft body to the shell in Late Cretaceous pachydiscid ammonites from the Western Interior Basin of the Unites States. *American Museum Novitates,* **3273**, 1-31.

LANG, W.D. and SPATH, L.F. 1926. The black marl of Black Ven and Stonebarrow, in the Lias of the Dorset Coast. *Quarterly Journal of the Geological Society of London,* **84**, 144-187.

MIRONENKO, A.A. 2013. The soft-tissue attachment scars in Late Jurassic ammonites from Central Russia. *Acta Palaeontologica Polonica, DOI 10.4202/app.00041.2013.*

MONKS, N. 2000. Mid-Cretaceous heteromorph ammonite shell damage. *Journal of Molluscan Studies,* **66**, 283-285.

MYCHALUK, K.A., LEVINSON, A.A. and HALL, R.L. 2001. Ammolite: iridescent fossilized ammonite from southern Alberta, Canada. *Gems and Gemmology,* **37**, 4-25.

PAGE, K.N. 1992. The sequence of ammonite correlatable horizons in the British Sinemurian (Lower Jurassic). *Newsletters on Stratigraphy,* **27**, 129-156.

PAGE, K.N. 2004. The establishment of the Jurassic System and the stages of the Lower Jurassic Series. In: SIMMS, M.J., CHIDLAW, N., MORTON, N. and PAGE, K.N. (Eds), British Lower Jurassic Stratigraphy. *Geological Conservation Review Series* **30**. Joint Nature Conservation Committee, Peterborough, 5-16.

PAGE, K.N. 2009. High resolution ammonite stratigraphy of the Charmouth Mudstone Formation (Lower Jurassic: Sinemurian-Lower Pliensbachian) in south-west England, UK. *Volumina Jurassica,* **7**, 19-29.

PAUL, C.R.C. 2014. Did *Dactylioceras* eat fish? *Proceedings of the Yorkshire Geological Society,* **60**, 9-17.

SIMMS, M.J. 2004. Pinhay Bay to Fault Corner and East Cliff. In: SIMMS, M.J., CHIDLAW, N., MORTON, N. and PAGE, K.N. (Eds), British Lower Jurassic Stratigraphy. *Geological Conservation Review Series* **30**. Joint Nature Conservation Committee, Peterborough, 60-82.

SPATH, L.F. 1926. Notes on Yorkshire ammonites. *The Naturalist, Hull* (**1926**), 299-306. [Not seen]

WARD, P.D. 1987. *The Natural History of Nautilus.* Allen & Unwin, London.