Epizoic bryozoans on cephalopods through the Phanerozoic: a review

Patrick N. WYSE JACKSON[1*] & Marcus M. KEY, Jr. [2]

[1] Department of Geology, Trinity College, Dublin 2, Ireland
[2] Department of Earth Sciences, Dickinson College, Carlisle, PA 17013, USA
[*] Corresponding author e-mail: *wysjcknp@tcd.ie*

SUMMARY - *Epizoic bryozoans on cephalopods through the Phanerozoic: a review* - Cephalopods have a long geological record and have been utilised by many encrusting organisms as suitable substrates on which to settle and grow. Living cephalopods, dead floating shells, and those lying on the seabed have been encrusted by bryozoans since the Ordovician; these records are reviewed here. Encrustation by bryozoans declined through the Palaeozoic and into the Mesozoic, and few examples of encrustation of modern nautiloids and coleoids have been reported. The patterns of encrustation provides valuable information, firstly, on the palaeobiology of the hosts and the epizoan: some are obligate, but many appear accidental, and secondly, on the sedimentological conditions at the time of fouling of dead shells. Bryozoan-cephalopod interactions may additionally provide valuable data on present and past drifting patterns of shells, and on the palaeo- and biogeographic influences on bryozoan settlement on cephalopods.

RIASSUNTO - *Briozoi epizoici su cefalopodi attraverso il Fanerozoico: una rassegna* - I cefalopodi hanno una lunga documentazione geologica e sono stati utilizzati da molti organimi incrostanti come substrati disponibili su cui impiantarsi e crescere. I cefalopodi viventi, le conchiglie flottanti degli esemplari morti e quelle giacenti sui fondali marini sono state incrostate da briozoi fin dall'Ordoviciano; tutta questa documentazione è qui sintetizzata. I briozoi incrostanti hanno subito un declino durante il Paleozoico e nel Mesozoico, e sono pochi gli esempi di incrostazioni riportate su nautiloidi e coleoidi moderni. La disposizione delle incrostazioni fornisce utili informazioni prima di tutto sulla paeobiologia dell'ospite e dell'organismo epizoo (alcune associazioni sono obbligate ma molte sembrano accidentali) e in secondo luogo sulle condizioni sedimentologiche al momento della colonizzazione delle conchiglie degli esemplari morti. Le interazioni fra briozoi e cefalopodi possono fornire utili dati aggiuntivi sui modelli di trasporto, presenti e passati, da parte delle correnti e sull'influenza paleo- e bio-geografica sulla colonizzazione dei cefalopodi da parte dei briozoi.

Key words: bryozoan-cephalopod interactions
Parole chiave: interazioni briozoi-cefalopodi

1. INTRODUCTION

Cephalopods have a long geological history ranging from the Cambrian to the Recent (Holland 1987; Benton 1993; Kröger et al. 2011) and have provided substrates for many encrusting skeletobionts (see review in Taylor & Wilson 2003: 28-29) including bryozoans from their appearance in the Ordovician.

Cephalopods may be fouled while alive (e.g., Landman et al. 1987; Wyse Jackson et al. in press); on specimens that were necroplanktonic—dead floating shells (Davis et al. 1999; Taylor & Monks 1997); or encrustation may have been post-mortem (e.g., Mapes et al. 2010; Rakociński 2011). The distribution of fossil episkeletozoans (sensu Taylor & Wilson 2002) on their hosts can provide details of lifestyles of the host, their feeding habits as well as those of the encrusting organism, information on taphonomic processes, and as has been postulated recently to aid in our understanding of the post-mortem disperal of shells (Reyment 2008).

Settlement of bryozoan larvae on motile benthic or nektonic host substrates occurs much less frequently than on sessile epibenthic hosts or hardgrounds (Taylor 1990).

Bryozoan encrustation of motile hosts in the fossil record include those on trilobites (Key et al. 2010), cephalopods (Baird et al. 1989; Wyse Jackson et al. in press), and echinoderms (Schneider 2003). Motile hosts encrusted by modern bryozoans include cephalopods (Landman et al. 1987), sea snakes (Key et al. 1995), king or horseshoe crabs (Key et al. 1996a, 1996b, 2000), decapod crabs (Key et al. 1999), hermit crabs (Balazy & Kuklinski 2013), pycnogonids (Key et al. 2012), isopods (Key & Barnes 1999), and sea turtles (Frazier et aI. 1992).

Aside from bryozoans, numerous sessile organisms have encrusted cephalopods: brachiopods (Holland 1971; Gabbott 1999; Evans 2005), cornulitids (Evans 2005), crinoids/pelmatozoans (Prokop & Turek 1983; Evans 2005; Rakociński 2011; Evans et al. 2013), edrioasteroids (Baird et al. 1989), cystoids (Klug & Korn 2001), corals (Marek & Galle 1976; Baird et al. 1989), microconchids (Watkins 1981; Klug & Korn 2001; Evans 2005; Rakociński 2011), stromatoporoids (Ulrich, 1886), the hederelloid *Reptaria stolonifera* (Baird et al. 1989; Taylor & Wilson 2008), the problematica *Vinella radialis* (Ulrich 1893), and *Sphenothallus*, that forms black spots on the surfaces of Ordovician cephalopods from Ohio (Neal & Hannibal 2000).

This paper provides an in-depth review of bryozoan encrustation on cephalopods through time, documents the stratigraphic patterns of fouling of the hosts, and discusses geological and biological reasons to account for differences seen in the patterns of encrustation by bryozoans of Palaeozoic and post-Palaeozoic cephalopods.

Generally, encrustation of cephalopod shells is rare due to a number of factors (see below). Boring bryozoans are also known from cephalopod shells but these are not discussed here.

2.   BRYOZOANS ENCRUSTING CEPHALOPODS

2.1.   Ordovician

The association between skeletobiontic bryozoans and orthoconic nautiloids present in the Upper Ordovician (Katian, Cincinnatian) of the Cincinnati Arch Region of Ohio, Kentucky and Indiana in the USA has been recognised since Ulrich (1879). Bryozoans generally form thin encrusting sheets or runner-like expansions; the former were originally considered to be parasitic on the host (Ulrich 1882, 1883) but this relationship is certainly mutually beneficial to epizoan and host (see discussion in Wyse Jackson et al. in press, which also provides comprehensive details of the bryozoans involved and a discussion of the life habits and functions of both host and epizoans). The exceptional feature of this association is that coverage of the shells is often almost complete from the apex of the phragmocone to the anterior margin of the body chamber, and holoperipheral around shells and is considered to be *syn-vivo* encrustation (Baird et al. 1989; Wyse Jackson et al. in press). Fouling is almost always on orthoconic rather than cyrtoconic nautiloids but this may be simply a function of the abundance of the former in successions in the Cinncinatian (Frey 1989: Fig. 4). Trepostomes are the most abundant encrusting taxa present, with five genera represented of which *Spatiopora* Ulrich, 1882 is the most common; the cystoporate *Crepipora* Ulrich, 1882 also encrusts orthoconic nautiloids.

Spatiopora also occurs on orthoconic nautiloids from the Coburn Formation, Upper Ordovician of Pennsylvania (R.J. Cuffey, pers. comm. 19.7.2013). The genus has a widespread distribution in the Ordovician of the USA (Milne Edwards & Haime 1851; Nicholson 1874, 1875; Ulrich 1882, 1883, 1893; Witzke and Heathcote 1997), Canada (Foord 1883; Fritz 1928; Parks & Dyer 1922), Estonia (Bassler 1911) and Russia (Astrova 1965), the Silurian of the USA (Hall 1876; Bassler 1906), Sweden (Hennig 1908), Estonia (Astrova 1970), Bohemia (Barrande 1866, plate 216, fig. 1), and Mongolia (Kopajevich, 1984). Its range possibly extends into the Devonian of Russia (Schönmann 1926), although the age of this record is disputed by Astrova (1965) who suggested that it should be Ordovician.

Dead cephalopods provided hardgrounds on the seafloor for colonisation: the outer surfaces, or interiors of body chambers that furnished cryptic niches for the runner-like bryozoans *Cuffeyella* and *Corynotrypa* (Taylor & Wilson 1994: 251; Wilson et al. 1994), and many examples have been preserved on internal molds through lithoimmuration. Similarly post-mortem encrustation by *Spatiopora* occurred on internal molds of numerous cephalopods found

in a number of units in the Cincinnatian (Wyse Jackson in press 2014), as well as in the Kanosh Shale (Whiterockian, Lower Ordovician) of Utah (Wilson et al. 1992: 29).

From Britain, Evans (2005) noted a number of epibiontic bryozoans, some of which were encrusting internal surfaces of the phragmocone and septum, but also reported encrustation on the exterior surface of shells particularly from the Sholeshook Limestone (Katian) of Wales—these were usually small sheet-like expansions. Similarly Evans et al. (2013) noted rare encrustations of the exteriors of phragmocones in a fauna from Saudia Arabia as did Kröger et al. (2009) on dead animals from Estonia. The cystoporate *Ceramopora vadosa* (Počta, 1894) has been reported on just over 63% of the 321 orthoconic nautiloid shells sampled in the Zahorany Formation of the Prague Basin, Czech Republic. As bryozoan zoaria occur on all the surfaces of at least some conchs, the host was considered to have been alive when fouled, or if dead, when the shells were partially buried by their apical portions (Kácha & Šarič 2009).

2.2.   Silurian

In the Oslo district, classic successions of Lower Palaeozoic sequences crop out. In the Llandovery Solvik Formation the trepostome *Orbignyella* occurs on orthocones where it competed for space with colonial corals (Nakrem & Ernst 2013). In Bohemia, associations of Upper Silurian (Pridoli) episkeletozoans and nautiloids are moderately common, with six to eight cyclostome, trepostome and possible cystoporate species all found encrusting nautiloid shells or internal moulds (Turek 1987). The bulk of these associations featured dead cephalopods which it is suggested may have rolled around on the sediment-water interface and as a result were encrusted on both dorsal and ventral surfaces. Complete holoperipheral encrustation of a number of shells suggests that these animals were alive when encrusted (Turek 1987). The cephalopod assemblage is moderately diverse and consists of taxa with smooth to ornamented shells, both of which were equally populated by episkeletobionts.

2.3.   Devonian

From the Genesee Group of the Catskill Delta of New York, Thayer (1974) noted the occurrence of one example of an unidentified adnate bryozoan attached to an orthoconic nautiloid. In a Famennian suite of 50 cephalopods from the Holy Cross Mountains, Poland, Rakociński (2011) documented a post-mortem association dominated by crinoids and tubes of various affinities. The cephalopods were preserved as internal moulds and no external shell was present. Bryozoans were found on less than 3% of the shells with juvenile colonies showing a preference for goniatites and the trepostome *Paleschara* for orthoconic nautiloids.

2.4.   Mississippian to Permian

Klug & Korn (2001) reported on the occurrence of the worm *Serpularia* (probably a microconchid) on a Mississippian orthocone from the Anti-Atlas Mountains of Morocco, and Boston et al. (1988) noted the occurrence of epizoans on Pensylvanian coiled cephalopods from North

America, but as far as the current authors know, there have been no published records of bryozoans encrusting Mississippian and Permian cephalopods.

2.5. Triassic

Todd & Hagdorn (1993) reported on the oldest ctenostome bryozoan, which occurred preserved through bioimmuration by oysters from the Muschelkalk (Middle Triassic) of Germany. Similarly Klug & Lehmkuhl (2004) noted the identical mode of preservation of arachnidiid ctenostomes on the internal part of the body chamber preserved as steinkerns, of the nautiloid *Germanonautilus* from southern Germany. These had come to rest on the seabed and acted as isolated hardgrounds and were colonised by a broad range of organisms including foraminiferans, crinoids, brachiopods, bivalves, spirorbids, and some bryozoans.

2.6. Jurassic

The *Posidonia* Shales (Lower Jurassic) of Germany have yielded many exceptionally preserved fossils, particularly marine reptiles (Selden & Nudds 2012). Undoubtedly the shaly nature of the seabed and the stagant conditions reduced the availability for colonisation by an epibenthic community. However, Kauffman (1981) has reported that dead ammonite shells acted as centres for the settling of sessile benthic invertebrates including serpulids (although he didn't report any bryozoans), whereas Seilacher (1982) argued that large ammonites were certainly neckroplantonic while encrusted by bryozoans and other sessile organisms.

From the Catalan Basin of northeast Spain shallow-water basal Middle Jurassic condensed sections have yielded bryozoan-, and other epizoan-encrusted ammonites that were fouled after death of the hosts and the shells settled on the seabed, or on the internal molulds of shells. Ammonites collected from deeper water Lower Jurassic condensed sections from the Lusitanian Basin of western Portugal were much more sparsely encrusted (Fernández-Lopez et al. 2002).

2.7. Cretaceous

An early report of a Cretaceous ammonite-bryozoan commensal symbiosis was that of Dunbar (1928). Subsequently Casey (1961: 552) noted the occurrence of *Heteropora michelini* encrusting the outer and inner sides of (dead) ammonites from the Folkstone Beds of the Lower Greensand (Lower Cretaceous) of England.

Gill & Cobban (1966: A24-A25) recorded pyriporoid and membraniporid bryozoans inside the living chambers of dead baculititid ammonites of the Pierre Shale (Late Cretaceous) of the Red Bird section, Wyoming. Wilson & Taylor (2012) described a new ctenostome genus *Pierrella larsoni* that occurs on the steinkerns of baculititids from the same Pierre Shale. *Pierrella* is interpreted to have encrusted the internal surfaces of the body chambers while the dead shells were afloat where it formed runner-like expansions, and which were then preserved by the process of lithoimmuration by infilling sediment after the shell sank to the seabed. Subsequently the shell of the baculititid spalled away

revealing the steinkern and bryozoans. No bryozoans fouled the outer surfaces of conchs, and interestingly Landman et al. (1987, 2012) also found no bryozoans on the external surfaces of scaphitid ammonites from the same unit, but this was due to the scaphitids having a deep umbilicus and a rough surface ornament that apparently discouraged encrusting organisms from settling. The Late Cretaceous nautiloid *Eutrephoceras dekayi* from North America is encrusted by serpulids and bryzoans, but it displays a smoother shell and shallower umbilicus (similar to modern-day *Nautilus*), which could account for the presence of foulers (Landman et al. 1987).

Belemnites were an important group of coleoids that ranged from the Jurassic to Cretaceous. Although the skeleton is internal, this rostrum or guard could provide a hard substrate for encrustation after the animal had died and the soft tissue decayed. A number of encrusting bryozoans have been recorded on rostra: the Campanian cheilostomes *Herpetopora* from Hampshire, England (Taylor 1988: Text-Fig. 1) and *Hoeverella krauseae* from Hannover, Germany (Taylor & Voigt 1992), and the Maastrichtian cheilostome*Tecatia robusta* from Norfolk, England (Taylor et al. 1999). The latter etched the surfaces of the host producing the ichnogenus *Finichnus* [nom. nov. pro. *Leptichnus*] (Taylor et al. 2013).

2.8. Paleogene & Neogene

With the end-Cretaceous mass extinction event, ammonoids and belemnites disappeared and cephalopods were represented in the Paleogene and Neogene by only a few nautiloid genera and a number of coleoid taxa. The latter that include *Spirula* have internal shells, and these could become available for encrustation after host death. Modern-day nautiloid diversity today is low with only two genera *Nautilus* and *Allonautilus* extant (Ward & Saunders 1997).

A number of studies have investigated the drifting of dead external shelled cephalopods such as the nautiloid *Aturia* from the Palaeocene to Miocene that had a worldwide distribution (Chirat 2000), and or drifting of alive modern *Nautilus* and *Allonautilus* (Landman et al. 1987) and have attempted to use these records for palaeogeographic and water current reconstructions. *Aturia* had a dorsally-placed siphuncle with a narrow neck that resulted in the slow infilling of chambers by water after death, and so shells could be transported great distances (Chirat 2000). *Nautilus* and *Allonautilus* similarly could drift considerable distances after death as demonstrated by the distribution of encrusted shells far beyond the geographical limits of living animals (House 1987). On drifted shells of *N. pompilius* and *N. belauensis*, 11 bryozoan species were present on the former and three on the latter; distribution was random, on the surface and within the body chamber (Landman et al. 1987).

More recently, Mapes et al. (2010) argued that on naturally submerged *Nautilus* shells whose chambers became infilled with water, and most of which were recoved from deep water depths of up to 672 m, the length of time that shells were exposed on the seafloor did not control the degree of encrustation. In other words it was impossible to quantify the time shells spent on the seabed by the patterns of encrustation. Epizoans that included at least four bryozo-

an species were largely confined to the exteriors of shells, but some were noted on the interior wall of the body chamber and on the terminal septum. The low diversity of epizoans on the exterior of shells have led the authors to suggest that encrustation took place after the animals had died.

Live *Nautilus* and *Allonautilus* shells can also be encrusted by epizoans including bryozoans, but those shells washed up on beaches around the Indo-Pacific tended to lack epizoans as the outer shell has often been lost by erosion or dissolution (Landman et al. 1987). Encrustation cover by bryozoans also tended to be host species dependent: *N. pompilius* (0-3% shells encrusted by bryozoans), *A. scrobiculatus* (<1%) and *N. belauensis* (36%) (data from Landman et al. 1987, Fig. 1), and the highest diversity was recorded in the latter with eight bryozoan species present as against one on each of the two former taxa. Suzuki & Hayasaka (1988) noted that bryozoans were the only epizoans found on 60% of the 32 *Nautilus* shells collected from Fiji. It has been noted that live *Nautilus* shells from the Philippines were densely colonised by bryozoans and other epibionts (Hamada 1983) whereas those from New Caledonia were much cleaner (Suzuki & Hayasaka 1988) which may suggest that alternative hard substrates are more plentiful in New Caledonia. Clear quantification of coverage by epizoans is required as this finding appears to be in contrast to Landman et al. (1997) who suggested that encrustation on live shells is much less dense than on drifted shells. Clearly the factors that produce patterns of encrustation on drifting and living shells are difficult to interpret and further data is required, including detailed bryozoan taxonomic recording and analysis of skeletal mineralogy of the epizoans.

Internally-shelled cephalopods such as the coleoid *Spirula spirula* can provide pelagic substrates for encrusting bryozoans, but only become available following death of the animal and decay of the soft tissue. *Spirula* is a small coiled chambered shell that measures 1-2 cm in diameter and is frequently found washed ashore on beaches in central America, east Africa, and the southern Pacific (Taylor & Monks 1997). It has been suggested that it could float for a considerabe length of time on account of it*s* septal necks being macrochoanitic and calcified (Hewitt et al. 1991), and thus allow more time for encrustation. Donovan (1989) reported the occurrence of the cirriped *Lepas* on *Spirula*, and the bryozoan *Jellyella eburnea* is known from its association with floating *Spirula* shells (which are rarely encrusted by other bryozoans) and is thus pseudoplanktonic in lifestyle (Taylor & Monks 1997), a mode of life shared with the Ordovician genus *Spatiopora*.

3.   DECLINING BRYOZOAN-CEPHALOPOD
       ASSOCIATIONS THROUGH GEOLOGICAL
       HISTORY

The acme of orthoconic nautiloid bryozoan commensalism was undoubtedly during the Late Ordovician and was more common in the Cincinnati Arch region than elsewhere. In the end-Ordovician extinction event, nautiloid diversity crashed (Frey et al. 2004), and with it the nautiloid-bryozoan association became less common, and never recovered. Biological reasons could account for a decline in encrustation on cephalopods: if in later Palaeozoic faunas evolute coiled forms dominated, the outer final

whorl would have covered earlier encrustation. Alternatively, did later post-Ordovician nautiloids develop some chemical defence against larval settlement?

The *Spatiopora*-orthocone relationship is more commonly encountered in the Cincinnatian than elsewhere, and the reason for this must be that there was an environmental and sedimentological control on *Spatiopora* encrustation. Perhaps there were few suitable hard substrates at the sediment-water interface at times in the Cincinnatian seas and the nautiloids provided additional hard substrate space for colonisation. While much of the sediment being deposited at this time was muddy (Cuffey 1998: Figs 2.2, 2.4) which eventually became lithified as the shaly units, there are tens of ramose erect bryozoan species described from the Upper Ordovician of the region (see listing in Dalvé 1948) and settling larvae of these must have found a suitable hardground or hard substrate on which to settle and grow. For *Spatiopora* it appears that the association between orthocone and encrusting bryozoan was site specific and obligate (assuming that the genus holds up taxonomically), unlike other motile host-bryozoan associations such as that in sea snakes, for which encrustation by bryozoans is regarded as accidental (Frazier et al. 1992; Key et al. 1995). An alternative possibility is that some of the *Spatiopora* species are in fact other species of other genera with a propensity to plasticity of form, which attach to a variety of substrates and as a result develop a varied zoarial form. *Actatopora* and *Leptotrypa* for example are represented in the Cincinnatian as both ramose colonies and as encrusters on nautiloids. Similarly, *Leioclema* in the Mississippian of north Wales exhibits several zoarial forms that were contolled by various ecological parametres (Wyse Jackson et al. 1991).

Does the overall architecture of nautiloid shells influence the chances of encrustation by bryozoan larvae? In the Cincinnati Arch region the Late Ordovician cephalopod faunas are dominated by longiconic (orthoconic) forms, and cyrticonic nautiloids are rare. The former, and in particular *Treptoceras,* are the preferred host for *Spatiopora* and these two organisms developed a possible obligate relationship. Although *Treptoceras* survived the late Ordovican extinction event, Silurian forms in the Brassfield Formation of southwestern Ohio are not encrusted with *Spatiopora* (R.C. Frey, pers comm. 18.4.2013). The relative ratio of orthocones to curved and coiled nautiloids changed in the Silurian when curved forms became relatively more plentiful, but nevertheless were still very rare (C.H. Holland, pers comm. 15.4.2013) with cyrtoconic forms being more plentiful in reefal environments and longiconic forms more confined to open water, but neither are encrusted (R.C. Frey, pers comm. 18.4.2013). It would seem that the *Spatiopora*-orthoconic nautiloid association is largely confined to the Cincinnatian basin, where some environmental factors influenced increased bryozoan larval settlement. Perhaps the post-Ordovician larvae and their substrate preferences differed from those that evolved during the Ordovician.

From what is reported in the literature during the Mesozoic and Cenozoic it would appear that there is a lower incidence of encrustation of cephalopod shells by bryozoans than that observed during the Palaeozoic.

Through the Phanerozoic cephalopods have provided a niche for encrusting bryozoans either as hard substrates on the seafloor, or as motile or dead surfaces that al-

lowed a pseudoplanktonic lifestyle. Bryozoan-cephalopod interactions were at their greatest during the Ordovician but have decreased over the next 350 million years right up to the present day. Why might this be so? There are a number of possibilities that are briefly discussed below, a number of which are simply conjecture or speculation, but which we raise here in the hope that futher research into this question might be encouraged.

Generally encrustation of cephalopods by bryozoans as well as other organisms is rare, and this may be due to a number of factors that have been postulated to include the presence of an organic surface layer (periostracum) on some nautiloid and ammonoid conchs (Davis et al. 1999). Landman et al. (2012) noted that Upper Cretaceous scaphitid ammonites from the Pierre Shale of the USA were devoid of epizoans and suggested that this was due to the presence of a thin periostracum or the development of a mucus layer, or to the physical characteristics of the conchs. Another factor that could reduce infestation on shells is the ability of the cephalopod to 'clean' its shell surface, or have it cleaned by some symbiont (Boston et al. 1988; Donovan 1989; Davis et al. 1999), or to develop some chemical deterent (Boston et al. 1988). Rarity may also be due to the failure by researchers to recognize or simply report encrustation (Davis et al. 1999), their inability to satisfactorally identify epizoans when present, or for preparators and/or researchers to remove epizoans from the surface of good quality cephalopod fossils (Larson 2007).

Galle & Parsley (2005: 128) postulate that encrustation by epizoans was more prevalent in tropical and subtropical environments than in cooler water of higher latitudes during the Ordovician. Changes in palaeogeography during the Upper Palaeozoic may have contributed to a decline in an epiphytic mode of life.

Predation of cephalopods (see Tucker & Mapes 1978; Mapes & Chaffin 2003) may also play a part in the non-preservation of epizoans. In a recent study of Pennsylvanian cephalopods from Texas, Wani et al. (2012) discussed the phenonmen of 'predatory peeling' where the outer surface shell layer is removed by arthropods seeking organic material for nutrients. Though the precentages of affected shells in their study is low – 0.5% in nautiloids and 1.1% in ammonoids (based on observations on 2965 and 3515 specimens, respectively) such predatory action could affect recruitment and preservation of bryozoans on cephalopod shells. One wonders whether encrusted shells were less susceptible to predation than uninfested shells.

Nautiloids were most diverse during the Ordovician (Holland 1987), and as we have seen, the architecture of the host may influence bryozoan larval settlement preferences, and the decline in orthoconic forms after the Ordovician may have affected the ability of bryozoan larvae to settle. Taken further, by the Mississippian, orthoconic nautiloid stocks further declined relative to coiled goniatitic forms, which were ammonoid in structure. This turnover from nautiloid to ammonoid forms that commenced in the Lower Devonian but accelerated in the Mississippian and Pennsylvanian, resulted in the dominance during the Mesozoic of ammonoids. Perhaps aspects of the ammonoid life style together with skeletal mineralogy affected the ability of bryozoans to encrust or, if they did infest the shells, to be ultimately preserved in the fossil record. Lukender et al (2010) have shown from isotopic studies of shells that du-

ring ontogeny several depth distribution preferences were adopted by different groups of cephalopods. During ontogeny *Nautilus* and some Mesozoic ammonites were shown to migrate from shallow warm waters to deeper cooler waters and back to shallow environments as adults; wheras *Spirula* and different stocks of Mesozoic ammonites showd a pattern of migrating from cool to warm to cool waters during their development. This alteration of depth distribution would almost certainly affect the ability to be encrusted by bryozoans, or at least would be reflected in differences in bryozoan larvae that were encountered.

Organisms that encrust on external aragonitic shells are less likely to be preserved in the fossil record than those encrusting calcitic hosts due to the higher probability of the aragonite shell being lost due to dissolution. Equally those bryozoans with aragonite or high–magnesium calcite skeletons have a lower preservation potential to those with low-magnesium calcite or mixed mineralogy skeletons (Smith et al. 1992). In a study of bryozoan mineralogy, Smith et al (2006) showed that 17% of bryozoans analysed had skeletons composed of aragonite, 66% were calcitic, and the remainder of mixed mineralogy. The bulk of the extinct stenolaemates were calcitic, but the modern cheilostome bryozoans showed 21% being aragonic and 20% bimineralic, and this could lead to underrepresentation through taphonomic removal of these modern forms as epizoans on cephalopods.

4. BRYOZOANS ON CEPHALOPODS – BENEFITIAL OR DETRIMENTAL?

The filter feeders that spent their lives attached to living or floating shells benefitted in being lifted off the seafloor out of the bottom boundary layer and above the sediment-laden bottom layers that would have reduced feeding efficiency. Bryozoans being filter feeders that could generate their own incurrents that enhanced feeding, would have been subjected to different water regimes between those in their normal benthic position attached at the seabed as against those that adopted a pelagic mode of life attached to living motile cephalopods. Water movement is low at the sediment-water interface boundary layer (Caldwell & Chriss 1979), and so it may have been beneficial for benthic organisms to get into faster moving water where feeding may have been more efficient.

In such a suitation the bryozoan-cephalopod relationship could be seen to be commensal with the benefits of such a linkage being to the benefit of the encrusters only. Wyse Jackson et al (in press) have argued that there were mutual benefits to the cephalopods in having attached bryozoans, at least in the case from the Cincinnatian, and that the relationship is better classified as mutual.

Benefits to any encrusted cephalopod could be that bryozoans and episkeletozoans aided keeping the shells orientated correctly in the water column by adding some weight to the ventral side (although the additional weight provided would probably be minimal). Could the bryozoans have afforded greater camouflage to their hosts from predators and indeed prey?

Negative effects of fouling of cephalopods by bryozoans and other encrusters could include changes to the motility of the host if drag increased as a result while the

cephalopod was swimming, which would have resulted in reduced swimming speed for escaping predators and/or catching prey. In the cephalopod-*Spatiopora* association this is shown to have the opposite effect (Wyse Jackson et al. in press). The living animal might have modified its natural shell growth patterns or rates due to the presence of encrusters such as brachiopods, serpulids and cirripeds (Seilacher 1960; Checa et al. 2002; Rakociński 2011), although bryozoans have not been reported as causing such modifications which are also noted in the gastropod *Littorina* (Wahl 1996). Possibly, episkeletobionts may have affected buoyancy (Checa et al. 2002). It is equally possible that the bryozoan epicoles afforded their hosts neither benefit or disadvantage and was merely a phoretic relationship.

5.   CONCLUSIONS

Cephalopods have provided substrates for the encrustation by bryozoans since the Ordovician. Nautiloid and ammonoid cephalopods may be encrusted whist alive or after death, and various coleoids also provide surfaces for encrustation after death either while drifting (*Spirula*) or lying on the sediment-water interface (i.e., belemnites). The acme of the bryozoan-cephalopod association appears to be the Upper Ordovician, and it declined throughout the Mesozoic. Over time cephalopods may have developed biological habits or chemical defences to discourage encrustation. Modern-day cephalopods are rare, but nevertheless provide sites for encrustation.

Though most of the bryozoan-cephalopod associations are accidental–the epizoans simply utilising the available hard substrate, there is some evidence to suggest that some associations are obligate. The larvae of the trepostome *Spatiopora* in the Cincinnatian of North America are probably host specific to orthoconic nautiloids. Close examination of where on shells bryozoans preferentially encrust, may yield data on the life habits of both host and bryozoan.

The bryozoan-cephalopod association can reveal useful information in the fossil record regarding the availability of substrates and the sedimentological nature of the seafloor at the time of colonisation. It could also yield information on the palaeo-drifting and modern water current patterns of dead shells, but this is dependent on gathering adequate taxonomic identifications of the encrusting biota.

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