



Coevolution of post-Palaeozoic arthropod basibiont diversity and encrusting bryozoan epibiont diversity?

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We hypothesize that the diversification of motile marine arthropods with hard carapaces resulted in a concurrent increase in the diversity of encrusting marine bryozoans whose larvae exploited those substrates through the Mesozoic and Cenozoic. To test this, family-level data were tabulated from the literature on the post-Palaeozoic diversity of motile marine arthropod basibionts and sessile marine bryozoan epibionts. We found strong temporal correlation from general to more specific basibiont-epibiont relationships (i.e. arthropods and bryozoans in general to decapods and encrusting gymnolaemates to robust decapods and encrusting cheilostomes in particular). We compared the diversification of bryozoans to another common group of basibionts (i.e. molluscs) and found weaker correlations. This suggests that the diversification of motile arthropods with hard carapaces (e.g. brachyuran crabs) may have played a role in the diversification of sessile bryozoans (e.g. encrusting cheilostomes) in the post-Palaeozoic. □ *Arthropoda*, *Bryozoa*, *Cheilostomata*, *Chelicerata*, *coevolution*, *epibiosis*.

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Coevolution is the evolution of one clade in response to its interaction with another clade (Janzen 1980). The study of coevolution includes a long history of hypothesis testing with varied results (Ehrlich & Raven 1964; Nitecki 1983; Robinson & Clark 2018). One of the most studied types of coevolution is symbiotic relationships (Futuyma & Slatkin 1983). This is especially true of the concept of mutualism since Janzen's (1966) famous study of ants and acacia plants.

Arthropods have a rich fossil record of symbiotic relationships (Feldmann 2003a). These include epibionts such as limpets (Robin *et al.* 2017), barnacles (Glaessner 1969) and bryozoans (Aguirre-Urreta & Olivero 1992). While tabulating diversity data on arthropod basibionts and bryozoan epibionts (Schweitzer & Feldmann 2015; Key *et al.* 2017), we noticed a general similarity in the stratigraphical distribution of decapod arthropods and cheilostome bryozoans. The first occurrences of brachyuran decapods and encrusting cheilostomes are observed from the Jurassic with the majority of the diversification occurring from the Late Cretaceous to the Eocene. Could this apparent simultaneous timing in diversity be linked in a co-evolutionary basibiont-epibiont relationship?

A multilayer network that models the positive effect of mutualistic coevolution on diversity was

recently developed by Gracia-Lázaro *et al.* (2018). Their study suggests there could be a link between increased diversity of mutualistic organisms. Therefore, we hypothesize that the diversification of motile arthropods with hard carapaces should result in a concurrent increase in the diversity of encrusting bryozoans whose larvae exploit those substrates. The mutualistic positive feedback system could work by increased motile arthropod abundance triggering an increase in the number of substrates for encrusting bryozoans. This potentially benefits the bryozoans by increasing substrate space and reducing substrate competition, all while reducing predation and increasing feeding by living on a motile host. This potentially benefits the arthropods by increasing camouflage for the host and reducing predation (Wicksten 1979, 1993). These factors trigger an increase in diversity of both arthropods and bryozoans. These benefits (e.g. camouflage) and costs (e.g. living on a moulting host) resulting from arthropod-bryozoan relationships are well reviewed by Ross (1983) and Key *et al.* (1996a).

Bryozoans are one of the most common epibionts on arthropod exoskeletons (Ross 1983; Wahl 2009). Extant motile host basibionts, like arthropods, provide additional hard substrates for cheilostome bryozoan larvae to settle (Key *et al.* 1995, 1996a,b, 1999). Therefore, we hypothesize that the diversity of

arthropods with hard carapaces and encrusting bryozoans should co-vary through time. Hard substrate space is a limiting factor for bryozoans, especially encrusting bryozoans (Jackson 1977; Lidgard & Jackson 1989; McKinney 1995; Taylor 2016). Therefore, any increase in hard substrate space (e.g. motile host basibionts) should cause an increase in bryozoan diversity as documented by Balazy & Kuklinski (2013).

We follow the terminology of Wahl (1989) and refer to the motile arthropods as basibionts (i.e. the host substrate organisms) and the bryozoans as epibionts (i.e. the sessile organisms attached to the basibiont's outer surface without trophically depending on it). Following the terminology of Taylor & Wilson (2002), we will focus on epibionts as opposed to endosymbionts as the bryozoans are ectosymbionts or episkeletozoans inhabiting the exoskeleton of their host arthropod.

Arthropods in general have evolved multiple symbiotic relationships (Ross 1983). Crustaceans in particular have more symbiotic relationships than perhaps any major group of invertebrates (Ross 1983). Symbioses occur in all major groups of crustaceans, especially those with larger exoskeletons such as the isopods and decapods (Ross 1983). Of the marine animals, crustaceans are the most diverse group of basibionts and bryozoans are the most diverse group of epibionts (Wahl 2009, fig. 4.2). A classic example of extant decapod-bryozoan symbiosis includes decorator crabs using bryozoans as masking material (Parapar *et al.* 1997; Stachowicz & Hay 2000). Basibiont-epibiont relationships among fossilized decapod arthropods and cheilostome bryozoans have been recently reviewed by Key *et al.* (2017).

There are some limitations in using the fossil record of arthropod-bryozoan symbioses. First, some arthropod carapaces are weakly calcified and not likely to be fossilized (Plotnick 1986; Hof & Briggs 1997; Klompmaker *et al.* 2017). Second, some arthropods eat their exuviae following moulting (Skinner 1985; Wolcott & Hines 1990; Swift 1992; Jernakoff *et al.* 1993) which reduces the chance of fossilization. Third, the vagaries of fossilization of the host arthropod's epicuticle makes the preservation of any attached epibionts under-represented in the fossil record (Feldmann 2003a,b; Waugh *et al.* 2004). Fourth, some encrusting bryozoans lack biomineralization (i.e. Order Ctenostomata) so are less common in the fossil record. Fortunately, some ctenostomes can etch into substrates (Pohowsky 1978) or be preserved as a bioimmuration (Taylor 1990).

Studies often use temporal correlation of time series data to infer causality (e.g. anthropogenic greenhouse gas emissions and global warming). Studies on arthropods (Minelli *et al.* 2013; Klompmaker *et al.* 2015) and bryozoans (McKinney & Jackson 1989; Taylor & Waeschenbach 2015) often use biodiversity time series data to infer evolutionary causality. When trying to interpret biodiversity time series data, it is important to keep in mind that temporal correlation does not necessarily imply causation (Hannisdal & Liow 2018). The approach we take is to test for significant temporal correlation from general to more specific basibiont-epibiont relationships.

Materials and methods

We tabulated data from the literature on the diversity of motile marine arthropod basibionts and marine bryozoan epibionts through the Mesozoic and Cenozoic. We restricted this study to the post-Palaeozoic as decapod arthropods and cheilostome bryozoans are members of Class Malacostraca and Class Gymnolaemata which are both associated with Sepkoski's (1981, 1984) Modern Evolutionary Fauna. Members of this Modern fauna may have originated in the Palaeozoic but their diversification did not accelerate until the Mesozoic and Cenozoic.

Temporally, we used post-Palaeozoic stage-level bins except for the short stages of the Quaternary, where we used series. When there was a disagreement in the literature about a taxon's stratigraphical range, we used the greater range as the fossil record more often underestimates stratigraphical ranges (Marshall 1990; Donoghue & Benton 2007). For a geological time scale, we used the International Commission on Stratigraphy's 2018/08 version of the International Chronostratigraphic Chart (Cohen *et al.* 2013). We did not range families through unless there were occurrences in several epochs of the Cenozoic or if identifications were personally verified as recommended by Schweitzer & Feldmann (2014, 2015). To avoid the preservational bias of including Modern faunas, we followed standard practice (Foote & Miller 2007) and excluded the Holocene data. The stage-level bins ranged in duration from 0.70 (Induan) to 18.5 Myr (Norian) (mean = 5.2 Myr, standard deviation = 3.4 Myr). To correct for this variation, we used the number of families per million years for each stage in all the analyses.

Taxonomically, we used family-level data as family-level diversity and stratigraphical range are better constrained than at the genus- or species-levels. The costs and benefits of using higher taxa are well

known (Raup 1979), but the general diversity trends tend to be similar, although they have lower resolution at the higher taxonomic level (Alroy 2010). The nested structure of the taxonomic hierarchical classification system means that lower and higher taxa must always exhibit some degree of correlation (Gaston 2000), but it is minimized when the ratio of lower to higher taxa is less (Rosser 2017). This same pattern holds for bryozoans when comparing published genus (McKinney & Taylor 2001, fig. 2; Taylor & Waeschenbach 2015; fig. 8, 12) and family diversity curves (Boardman & Cheetham 1973, fig. 26; Taylor 1988, fig. 1; Lidgard *et al.* 1993, fig. 6; Taylor *et al.* 2009, fig. 8). The same pattern holds for arthropods which exhibit similar family- and genus-level diversity patterns (Sepkoski 2000, fig. 1; PBDB 2018).

We restricted this study to motile marine arthropod basibionts and sessile marine bryozoan epibionts. We excluded sessile marine arthropods (e.g. barnacles) because, even if they could provide three-dimensional attachment space, they do not provide the ecological benefit of a motile host for the bryozoans as discussed below. We chose from the following groups of motile marine arthropods with mineralized exoskeletons that can provide a viable substrate for a bryozoan larva. The malacostracans include Phyllocarida, Peracarida (amphipods, isopods, mysids), Hoplocarida (stomatopods, archaeostomatopods and paleostomatopods) and Eumalacostraca (Decapoda, euphausiids). We did not include phyllocarids, mysids and euphausiids because they generally are pelagic and have no records of fouling by bryozoans. We did not include amphipods due to their scant fossil record and no records of fouling by bryozoans. We did not include Archaeostomatopoda and Palaeostomatopoda as they are known only from the Palaeozoic (Schram *et al.* 2013).

Thus, the malacostracans were represented by the decapods (shrimp, crabs, lobsters, etc.), isopods (sea slaters) and stomatopods (mantis shrimp). The chelicerates were represented by the xiphosurids (horseshoe crabs) and pycnogonids (sea spiders). All five of these groups function today as basibionts for epibiont bryozoans. We excluded ostracods because of their different ecology (i.e. mostly planktonic and microscopic), which has precluded them being a host substrate for bryozoans in today's oceans.

The decapod basibiont-bryozoan epibiont relationships preserved in the fossil record are all from marine environments (Key *et al.* 2017). Therefore, we restricted this study to marine groups. The excluded freshwater arthropods included crayfish (four extant and two extinct families), shrimp (five families and one family inhabiting both marine and freshwater, all fossil freshwater representatives

excluded) and crabs (six families). We excluded the following eight exclusively freshwater bryozoans: all six families of phylactolaemates and two ctenostome families, Hislopiidae and Paludicellidae.

Post-Palaeozoic marine decapod families were tabulated per infraorder or in some cases, non-monophyletic groups of superficially similar organisms, into the following 12 groups. Shrimp were grouped into: (1) Dendrobranchiata (penaeid and related shrimp); (2) Pleocyemata (caridean and stenopodidean shrimp); (3) Axiidea; and, (4) Gebiidea, which include mud and ghost shrimp (the latter two often referred to as 'callianassids' in the fossil record). Crabs were grouped into: (5) Anomura (an array of crab and lobster-like decapods, including hermit crabs, squat lobsters and porcelain crabs); (6) Podotremes (a polyphyletic subset of Brachyura in which the genital openings are on the appendages, in several sections (Dromiacea 1833-1850; Homoloida De Haan, 1839; Tornyommidae Glaessner 1980; Etyoida Guinot & Tavares 2001; Raninoida Ahyong *et al.* 2007; Dakoticancroida Rathbun 1917; and Cyclodorippoida Ortmann 1892); (7) Heterotremata (a subset of Brachyura in which the genital openings are on the sternum (females) and appendages (males); and, (8) Thoracotremata (those brachyurans with genital openings on the sternum in both males and females). Lobsters were grouped into: (9) Glypheidea (a largely extinct group of clawed and pseudochelelate lobsters); (10) Homarida (a marine subset of Astacidea, which also includes freshwater crayfish); (11) Polychelida (mostly extinct lobsters with more than three sets of claws); and, (12) Achelata (lobster-like decapods such as spiny lobsters and slipper lobsters which lack claws but possess robust antennae such as palinurids and scyllarids).

Order Isopoda contributed eight families with a fossil record. Post-Palaeozoic Unipeltata stomatopods range from the Late Jurassic to Holocene. There are 17 extant families (Van Der Wal *et al.* 2017), of which we included the eight with a fossil record. Two additional families are extinct. Order Xiphosurida was represented by one horseshoe crab family. Order Pantopoda added three fossil sea spider families.

Extinct occurrences of decapods are based upon the compilation of Schweitzer *et al.* (2010) and their own updates to that list. The most current classification schemes to family level and extant family occurrences were culled from a variety of sources. Dendrobranchiata data were taken from De Grave & Fransen (2011) and Tavares & Martin (2010). Stenopodidea was taken from De Grave & Fransen (2011) and Goy (2010), and the caridean family

classification and occurrences were compiled from Wicksten (2010), De Grave & Fransen (2011), and De Grave *et al.* (2014, 2015). Anomura was compiled from Boyko & McLaughlin (2010), McLaughlin *et al.* (2010a,b), Osawa & McLaughlin (2010), and Tudge *et al.* (2012). Gebiidea and Axiidea occurrences were compiled from Dworschak *et al.* (2012), Poore & Dworschak (2017), and Dworschak & Poore (2018). Lobster classification follows Karasawa *et al.* (2013) and extant lobster occurrences were taken from Chan (2010). Podotreme crab classification follows Karasawa *et al.* (2011, 2014), Davie *et al.* (2015), and Schweitzer *et al.* (2016). Heterotremate crabs have received considerable attention in the past decade, and classification and occurrences were compiled from multiple sources, with Ng *et al.* (2008), De Grave *et al.* (2009) and Schweitzer *et al.* (2010) as base lines. Portunoidea family classification follows Evans (2018) with consultation of Karasawa *et al.* (2008), Ng *et al.* (2008), Spiridinov *et al.* (2014), and Davie *et al.* (2015). Classification of Trapezioidea follows Castro *et al.* (2004) and Davie *et al.* (2015). Classification for Xanthoidea follows Lai *et al.* (2011), Thoma *et al.* (2014), and Davie *et al.* (2015). For the classification and arrangement of superfamilies, families, subfamilies and genera within the Majoidea, we follow Guinot (2011, 2012) and Windsor & Felder (2014). Classification of Pinnotheroidea follows Davie *et al.* (2015) and Theil *et al.* (2016). Eriphioidea families are based upon Davie *et al.* (2015), and Pseudozioidea is based upon Naruse & Ng (2014).

The post-Palaeozoic stratigraphical distribution of isopod families was culled from Wieder & Feldmann (1992), Hyžný *et al.* (2013), Jones *et al.* (2014), Hessler (1969), Brandt *et al.* (1999) and Maguire *et al.* (2018). Isopod higher classification was based upon Ahyong *et al.* (2011) and generic occurrences in the World Register of Marine Species (WoRMS 2018). Stratigraphical ranges for stomatopods were compiled from several sources (Ahyong *et al.* 2007; Haug *et al.* 2010; Franțescu 2012; Schram *et al.* 2013; Charbonnier *et al.* 2017; and references therein). The stratigraphical distribution of horseshoe crab families was culled from Lamsdell (2016) and references therein. The stratigraphical distribution of sea spider families was culled from Arango & Wheeler (2007), Charbonnier *et al.* (2007) and Bamber (2011).

Post-Palaeozoic marine bryozoan families were tabulated per order into five groups following Bock & Gordon (2013): Order Cheilostomata and Order Ctenostomata in Class Gymnolaemata as well as Order Cryptostomata, Order Cyclostomata and Order Trepostomata in Class Stenolaemata. Despite lacking biomineralization, ctenostomes do have a

fossil record (Pohowsky 1978). Since they foul arthropods today (Key *et al.* 2017), we included Order Ctenostomata in this study. The families and their stratigraphical distributions were compiled from Taylor (1993), Bock & Gordon (2013), Bock (2018) and Gordon (2018).

To test for coevolution of the arthropods and bryozoans, we adopted the approach of Huntley & Kowalewski (2007) of using correlation coefficients to infer temporal coupling. Following their methodology, the data were corrected for autocorrelation by first differencing. We used the following four basibiont-epibiont pairs arranged from general to more specific subset relationships to test for time series correlations.

- 1 Arthropods and bryozoans. Arthropods include the post-Palaeozoic motile marine Decapoda, Isopoda, Stomatopoda, Pantopoda and Xiphosurida. Bryozoans include the post-Palaeozoic sessile marine Gymnolaemata and Stenolaemata;
- 2 Arthropods and encrusting bryozoans. Though erect bryozoans do occur on fossilized arthropods (Key *et al.* 2010) and many erect forms begin with a small encrusting base, by far the most common growth forms on arthropods are encrusting bryozoans (Key *et al.* 2017). Therefore, the bryozoan colony growth form was classified for each family using the simplified growth form classification of Nelson *et al.* (1988) as modified by Smith & Nelson (1994) and summarized in Smith *et al.* (1998). Each family was scored as either having at least one taxon that was encrusting or not, primarily based on Bock (2018) and augmented as needed by Bassler (1953) and the primary literature. In the encrusting colony growth form, we included the habit of etching into substrates by some ctenostomes and cheilostomes (Pohowsky 1978; Taylor *et al.* 1999, 2013);
- 3 Decapods and encrusting gymnolaemates. Among the arthropods, we focused on Order Decapoda as it is the most diverse group of arthropod basibionts in our data set. Among the bryozoans, we focused on Class Gymnolaemata as it contains the two most diverse extant epibiont bryozoan orders (Cheilostomata and Ctenostomata); and
- 4 Robust decapods and encrusting cheilostomes. Among the decapods, we excluded those that are rarely fouled by bryozoans such as the Anomura squat lobsters and porcelain crabs, the Thoracotremata brachyuran crabs that are often intertidal and burrowing, and those decapods that have thin exoskeletons such as burrowing and swimming shrimp. We included those decapods that provide firm substrates for fouling bryozoan larvae

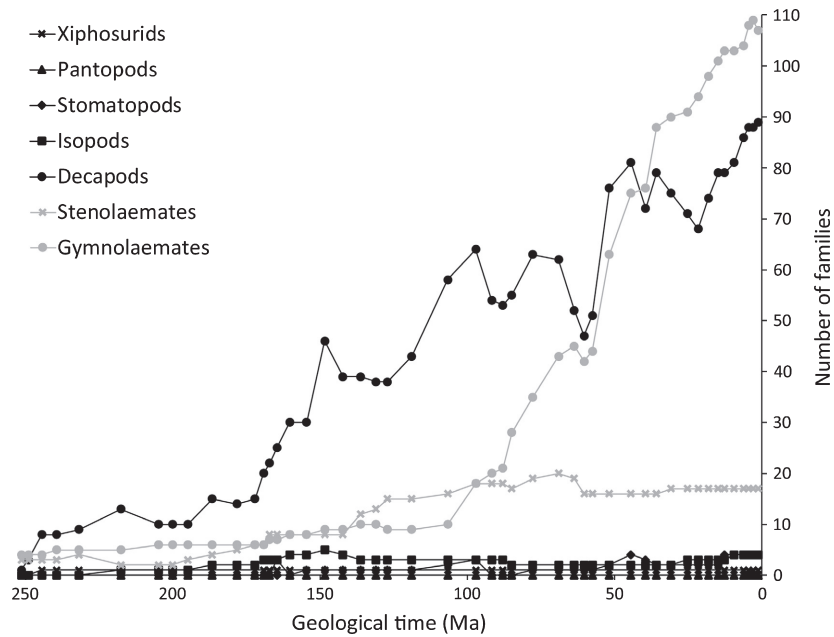


Fig. 1. Post-Palaeozoic family-level diversity of main groups of motile marine arthropods and sessile marine bryozoans used in this study. Raw data available in Table S1.

including the ubiquitous Heterotremata brachyuran crabs, the Podotremata brachyuran crabs which exhibit carrying behaviour and lobsters including Glypheidea, Homarida (i.e. marine Astacidea), Polychelida and Achelata (Giri & Wicksten 2001; Waugh *et al.* 2004; Key *et al.* 2017). Among the encrusting gymnolaemates, we focused on the cheilostomes as they dominate the fossil and extant bryozoan basibiont record (Key *et al.* 2017).

To test for similar correlations with our basibiont groups, we extracted stage-by-stage family-level molluscan diversity data from the Paleobiology Database (PBDB 2018) using the same range-through method for the arthropods and bryozoans. We chose molluscs as their robust shells are common substrates for bryozoans, and many are motile-like arthropods. Bivalves (Taylor 1979; Taylor & Wilson 2003), gastropods (Taylor *et al.* 1989; Taylor 1994) and cephalopods (Wyse Jackson & Key 2014; Wyse Jackson *et al.* 2014) all serve as basibionts for epibiont bryozoans and are well preserved in the fossil record.

To test for coevolution of the post-Palaeozoic bryozoans and molluscs, we used the following four basibiont-epibiont pairs arranged from general to more specific subset relationships to test for time series correlations: (1) all bryozoans and all molluscs; (2) encrusting bryozoans and all molluscs; (3) encrusting gymnolaemate bryozoans and motile molluscs most accessible to fouling bryozoans larvae (i.e. gastropods plus cephalopods but not bivalves which

often are infaunal); and, (4) encrusting cheilostome gymnolaemate bryozoans and gastropods plus cephalopods.

Results

At the most general level of correlation, the number of post-Palaeozoic motile marine arthropod families ranged from one in the Induan stage of the Lower Triassic to 98 in the Pleistocene Series of the Quaternary (Fig. 1; Table S1). The number of post-Palaeozoic sessile marine bryozoan families ranged from seven in the Induan to 126 in the Piacenzian stage of the Pliocene (Fig. 1; Table S1). After correcting for the different durations of the stage bins, this correlation produced a significant (i.e. $P < 0.001$) linear regression with an R^2 value of 0.969 (Fig. 2A, Table 1; Table S2) and when using first differences a significant (i.e. $P < 0.001$) R^2 value of 0.973 (Table 1; Table S3).

The number of post-Palaeozoic sessile marine encrusting bryozoan families ranged from 6 in the Induan to 78 in the Piacenzian (Fig. 3; Table S1). Correlating this time series with the number of post-Palaeozoic motile marine arthropod families (Fig. 3) produced a significant (i.e. $P < 0.001$) linear regression with an R^2 value of 0.970 (Fig. 2B) after correcting for the different durations of the stage bins (Table 1; Table S2). Using first differences yielded a significant (i.e. $P < 0.001$) R^2 value of 0.973 (Table 1; Table S3).

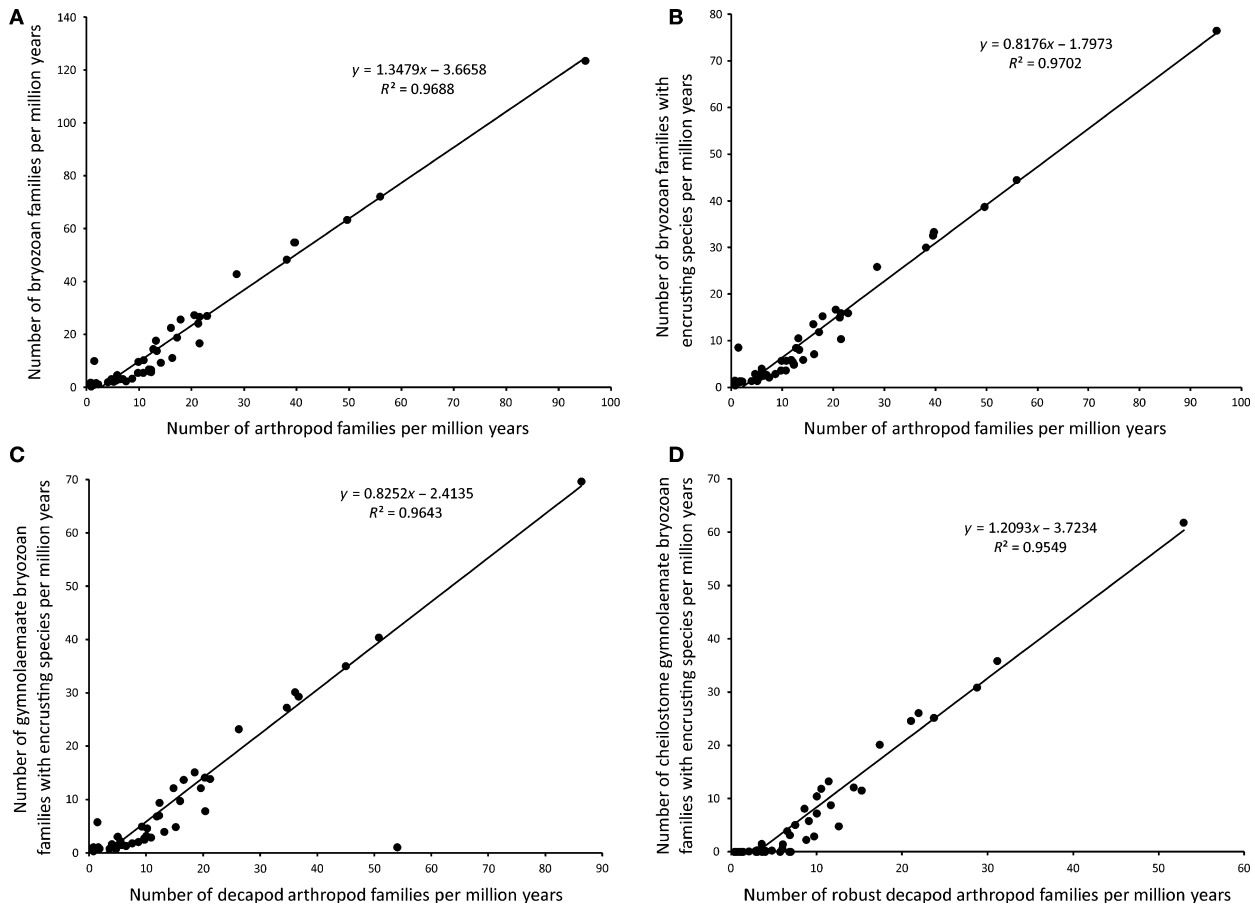


Fig. 2. Plots of post-Palaeozoic motile marine arthropod family-level diversity per million years versus post-Palaeozoic sessile marine bryozoan family-level diversity per million years. Correlations are in increasing specificity from all arthropods and all bryozoans (A), to all arthropods and encrusting bryozoans (B), to decapods and encrusting gymnolaemates (C), to robust decapods and encrusting cheilostomes (D). All R^2 values are significant to $P < 0.001$. Raw data available in Table S2.

The number of post-Palaeozoic motile marine decapod arthropod families ranged from 1 in the Induan to 89 in the Pleistocene (Fig. 4; Table S1). The number of post-Palaeozoic sessile marine encrusting gymnolaemate bryozoan families ranged from four in the Induan to 71 in the Piacenzian (Fig. 4; Table S1). After correcting for the different durations of the stage bins, this correlation produced a significant (i.e. $P < 0.001$) linear regression with an R^2 value of 0.964 (Fig. 2C) and when using first differences a significant (i.e. $P < 0.001$) R^2 value of 0.969 (Tables 1; Table S2).

The number of post-Palaeozoic motile marine robust decapod arthropod families ranged from 1 in the Induan to 60 in the Lutetian stage of the Eocene (Fig. 5; Table S1). The number of post-Palaeozoic sessile marine encrusting cheilostome gymnolaemate bryozoan families ranged from 1 in the Tithonian stage of the Upper Jurassic to 63 in the Pleistocene (Fig. 5; Table S1). After correcting for the different durations of the stage bins, this correlation produced

a significant (i.e. $P < 0.001$) linear regression with an R^2 value of 0.955 (Fig. 2D) and when using first differences a significant (i.e. $P < 0.001$) R^2 value of 0.940 (Table 1; Table S2).

In contrast to the bryozoan-arthropod correlations, the bryozoan-molluscan correlations (Fig. 6, Tables 1; Tables S4, S5) were on average significantly weaker (mean = 0.667; standard deviation = 0.060) than for bryozoans and arthropods (mean = 0.964; standard deviation = 0.014; t -test, $P = 0.004$).

Discussion

Our literature-based, family-level diversity tabulation is effective as a higher proportion of taxa can be incorporated than if working at the species- or genus-level as the latter data are not available for bryozoans. Additionally, most of the competing hypotheses for the diversification of cheilostome

Table 1. Correlation values for family-level diversity of basibiont–epibiont pairs using diversity per million years (Fig. 2), and diversity per million years corrected for autocorrelation by first differencing

Basibiont–Epibiont pair	R^2	
	Diversity per Myr	Diversity per Myr first differences
Arthropods–Bryozoans	0.969	0.973
Arthropods–Encrusting bryozoans	0.970	0.973
Decapods–Encrusting gymnolaemates	0.964	0.969
Robust decapods–Encrusting cheilostomes	0.955	0.940
Molluscs–Bryozoans	0.674	0.700
Molluscs–Encrusting bryozoans	0.705	0.732
Gastropod + cephalopod molluscs–Encrusting gymnolaemates	0.638	0.663
Gastropod + cephalopod molluscs–Encrusting cheilostomes	0.576	0.573

Linear regression P values are all <0.001 .

bryozoans discussed below were based on family-level data. This approach, though, is limited in four ways.

First, it requires the assumption that each family has the same cumulative surface area available for bryozoan larval settlement. This is not the case because intra-family diversity varies, intra-family population sizes vary and intra-family exoskeleton surface area varies. For example, the number of species per family in cheilostome bryozoans ranges from 1 to 336 (Bock & Gordon 2013).

Regarding the effect of intra-family population size variation, how well does family-level data reflect abundance in arthropods and bryozoans? Due to the difficulty of counting individuals in life and death assemblages (Lockwood & Chastant 2006), there are few studies comparing diversity and abundance to test how valid is our use of family-level diversity as a proxy for abundance. What studies there are, tend to be small scale and at the species level. Two studies in Panama using bryozoans (Taylor 2001) and arthropods (Abele 1976) suggest abundance and diversity tend to be positively correlated.

In regard to the effect of intra-family exoskeleton surface area variation, each arthropod basibiont does not provide the same target area for bryozoan larval settlement. Klompmaker *et al.* (2015) found that maximum, mean and median body size increased for crabs and lobsters over the course of the Mesozoic. They argued that this long-term increase in body size of crabs and lobsters, coupled with their increased diversity and abundance, suggests that their ecological impact may have increased over evolutionary time.

The Target Area Hypothesis (Lomolino 1990) of MacArthur & Wilson's (1967) Theory of Island Biogeography argues that larger targets (e.g. islands or the exoskeletons of decapod basibionts) should have more diversity simply because they are a larger target for 'propagules' (Stracey & Pimm 2009). The target area effect has been documented on a variety of basibionts fouled by bryozoans, including decapods (Key

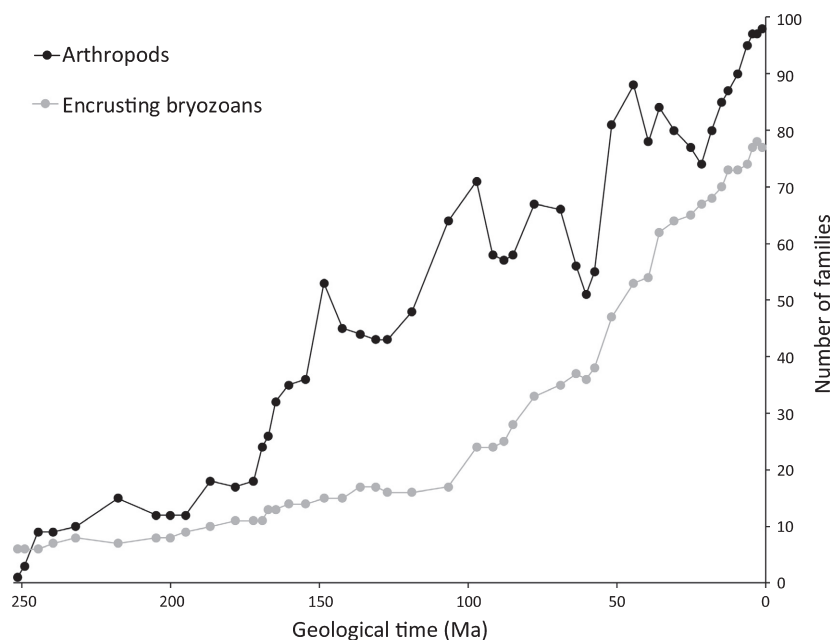


Fig. 3. Post-Palaeozoic family-level diversity of all motile marine arthropods and sessile marine encrusting bryozoans. Raw data available in Table S1.

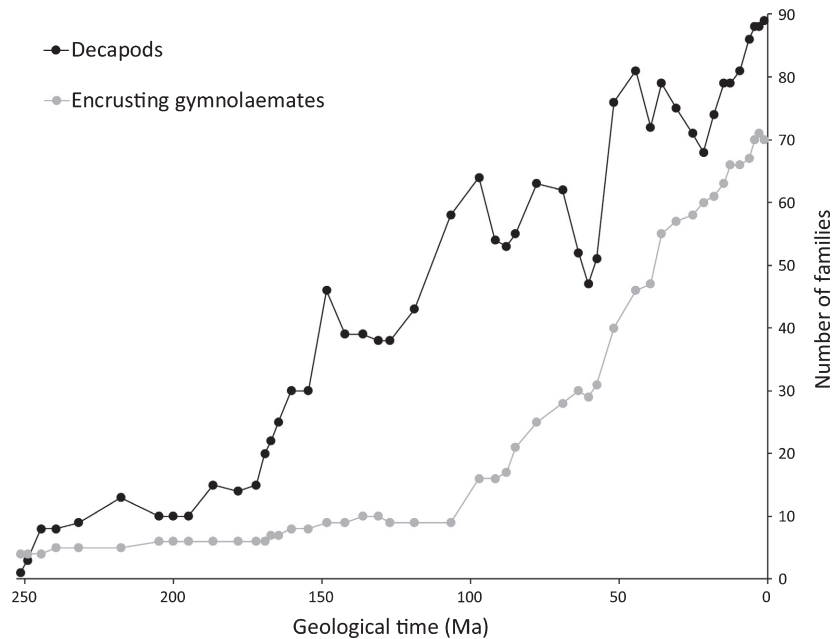


Fig. 4. Post-Palaeozoic family-level diversity of motile marine decapod arthropods and sessile marine encrusting gymnolaemate bryozoans. Raw data available in Table S1.

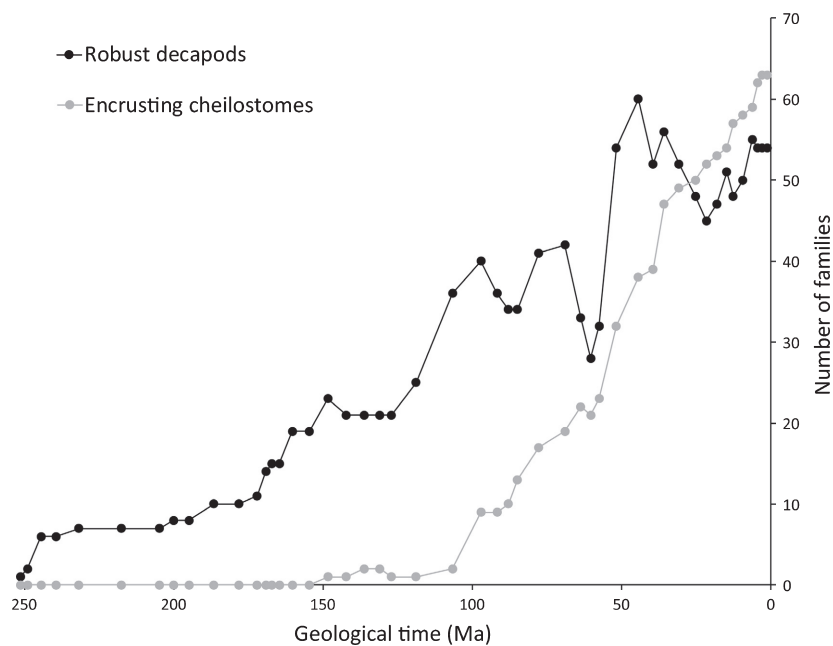


Fig. 5. Post-Palaeozoic family-level diversity of motile marine 'robust' decapod arthropods and sessile marine encrusting cheilostome gymnolaemate bryozoans. Raw data available in Table S1.

et al. 1996a, 2000, 2010, 2013, 2017; Key & Barnes 1999). Marine arthropods fouled by bryozoans vary in surface area by three orders of magnitude (Key *et al.* 2013, table 10.2). If the relative per cent cover of the host arthropod by the fouling bryozoan is low, then the potential benefit of camouflage is lost. If this is the case, then the relationship becomes more

commensal (i.e. the decapods are not harmed but not benefitted either).

Second, the approach requires the assumption that the prevalence of colony growth form is consistent within each bryozoan family. Colony growth form is quite ecophenotypically plastic and can vary within taxon (Hageman *et al.* 1997).

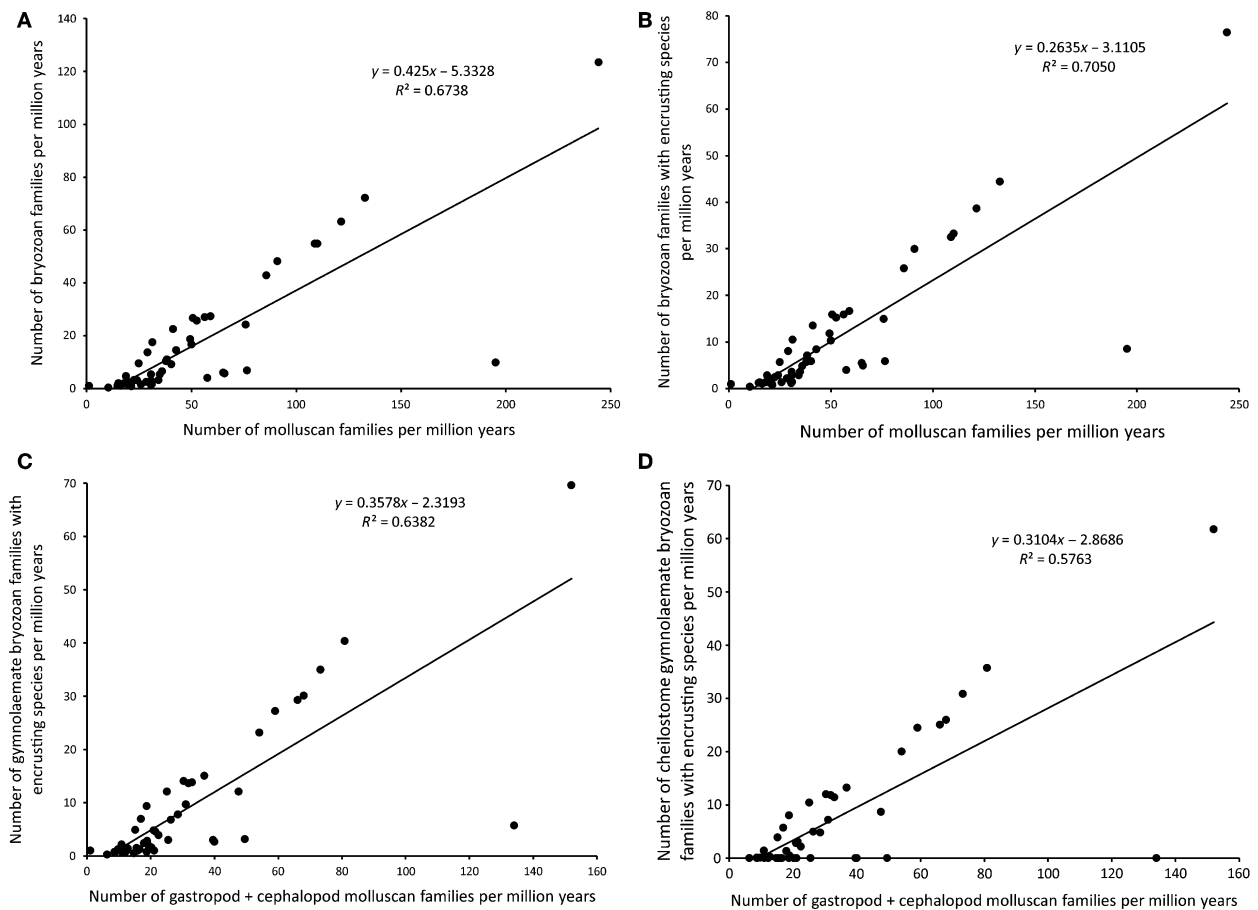


Fig. 6. Plots of post-Palaeozoic molluscan family-level diversity per million years versus post-Palaeozoic bryozoan family-level diversity per million years. Correlations are in increasing specificity from all molluscs and all bryozoans (A), to all molluscs and encrusting bryozoans (B), to gastropods + cephalopods and encrusting gymmolaemates (C), to gastropods + cephalopods and encrusting cheilostomes (D). All R^2 values are significant to $P < 0.001$. Raw data available in Table S4.

Third, this approach requires the assumption that bryozoan larval preference is equal among all arthropod basibionts. Bryozoan larvae often choose where to settle based on the composition of the biofilm community on the substrate (Dahms *et al.* 2004) and/or the mechanical properties of the surface on which bryozoan larvae settle (Gray *et al.* 2002).

Fourth, this approach requires the assumption that post-settlement bryozoan larval mortality is equal among all arthropod basibionts. While on the exoskeleton of the arthropod basibiont, bryozoan larvae and their resulting colonies are affected by differential abrasion from the substrate (Fernandez-Leborans 2010), host grooming (Bauer 1981; Tashman *et al.* 2018), predation (Key *et al.* 2013), food availability (Eggleston 1971) and subaerial exposure (Key *et al.* 1995).

Despite these required assumptions, we think the analysis is worthwhile as the data set includes hundreds of families ranging over hundreds of millions

of years that should still elucidate any general pattern present. Our approach of doing increasingly specific time series correlations revealed constant robust correlations. The R^2 values were all significant (i.e. $P < 0.001$), and using diversity per million years and first differences, ranged from 0.940 to 0.973 (mean = 0.964, standard deviation 0.014; Table 1). This suggests the diversification of arthropods is tightly correlated with the diversification of bryozoans. Despite the lowest diversity numbers of the four increasingly specific basibiont-epibiont correlations, the correlation between the decapods (and in particular robust ones like brachyuran crabs which are the most numerically abundant) and gymmolaemates (and in particular encrusting cheilostomes which are the most numerically abundant) was still strong with an R^2 of 0.940. This is supported by the fossil record of crabs where gymmolaemates dominate the literature reports of fouling bryozoans (83%, Key *et al.* 2017, table 4) and especially cheilostomes (78%, Key *et al.* 2017, table 4).

In order to determine whether this study would produce different results using genus-level taxonomy, we compared the family-level diversity plots (Figs 1, 3–5) with previously published genus-level plots. Published marine arthropod data at the genus-level show a general upward trend in diversity post-Palaeozoic (Sepkoski 2000). Our own data for decapods do as well, although with more peaks and troughs than the Sepkoski data, with peaks in the Tithonian, Albian-Cenomanian, Campanian-Maastrichtian, Lutetian and Priabonian and with troughs in the earliest Early Cretaceous, Turonian-Coniacian, Danian-Selandian, Bartonian and Oligocene. At least some of these peaks are due to collector bias (Schweitzer & Feldmann 2016).

Bryozoan genus-level data show similar patterns to family-level plots; however, plots exhibiting higher taxa data produce lower resolutions than do genus-level plots. Both McKinney & Taylor (2001, fig. 2) and Taylor & Waeschenbach (2015, figs 8, 12) show a post Palaeozoic switchover at ~75 Ma from more cyclostomes to more cheilostomes. Our family-level data suggest this happened at ~85 Ma. Our family-level data show similar trends with Lidgard *et al.*'s (1993, fig. 6) data on post-Triassic cyclostome and cheilostome diversity. Both the previously published genus and family-level data as well as our data show a general Cenozoic increase in cheilostome diversity. McKinney & Taylor (2001) attribute this increase in cheilostome diversity through the Cenozoic to lower extinction rates in encrusting as opposed to erect cheilostomes. This may be associated with increased diversity of arthropod basibiont substrates. Perhaps the coevolution of cheilostome epibionts and decapod basibionts contributed to the replacement of cyclostomes by cheilostomes in the Cenozoic (Lidgard *et al.* 1993; Sepkoski *et al.* 2000). Reports of cheilostomes fouling decapods today are three times more common than cyclostomes (Key *et al.* 2017, table 3) and five times more common in the fossil record (Key *et al.* 2017, table 4).

We suggest that the simultaneous timing of post-Palaeozoic marine arthropod and bryozoan diversification may be the result of co-evolutionary host substrate-fouling bryozoan relationships. But other potential causes were also undoubtedly operating during this time that may make this robust correlation simply a coincidence. For example, what is the temporal distribution of other hard substrates that we did not quantify? Encrusting bryozoans are also known to exploit abiotic hard substrates as well as dead biotic substrates (Taylor & Wilson 2003; Taylor *et al.* 2012; Taylor 2016), and carbonate hardgrounds increased in availability through the Jurassic and Cretaceous (Wilson & Palmer 1992). Competing

hypotheses for the radiation of cheilostomes include increasing colonial integration (Boardman & Cheetham 1973), the evolution of unilaminar erect growth forms (McKinney 1986), the evolution of zooidal and frontal budding (Lidgard 1986; Lidgard & Jackson 1989), the evolution of larval brooding (Taylor 1988), the advent of biomineralogical diversity (Taylor *et al.* 2009) and the evolution of features that protect the colony from micropredators (Lidgard *et al.* 2012; Taylor & Waeschenbach 2015). Perhaps increasing bryozoan fouling of motile marine 'robust' decapod arthropods allowed sessile marine encrusting cheilostome gymnolaemate bryozoans to diversify as well, in conjunction with these other drivers.

Adaptations for durophagy in decapods appeared in the early Mesozoic and were widespread by the Late Cretaceous, also coinciding with the radiation of Brachyura (Schweitzer & Feldmann 2010). Heterochely, which appeared in the early Triassic, confers numerous survival benefits beyond feeding (summarized in Schweitzer & Feldmann 2010). Many brachyuran lineages, including those extending into the Jurassic, exhibit multiple feeding strategies (Schweitzer & Feldmann 2010). Moreover, Decapoda includes some lineages exhibiting environmental preferences stable through time and some that inhabit a wide variety of environments at any given time (Schweitzer & Feldmann 2015). Lobster-like lineages exhibited niche partitioning through time, perhaps ensuring survival of more lineages (Schweitzer & Feldmann 2014). Major radiations within decapods coincide with reef-building through time (Klompaker *et al.* 2013). Perhaps this diversity of habitat preferences conferred survivability within the group. All of these factors may have driven diversification among decapods independent of cheilostomes.

It is possible that the correlation here between bryozoans and arthropods is caused by something extrinsic to either group or that affects each group in the same way. Both marine arthropods and bryozoans diversified post-Palaeozoic, and this could be due to factors that are favourable to each group. Perhaps lack of competition from other groups were favourable for both decapods and cheilostomes. For example, trilobite arthropods were replaced by malacostracan arthropods of the Modern Evolutionary Fauna (Sepkoski 1981) and cyclostomes were largely replaced by cheilostomes (McKinney & Taylor 2001; Taylor & Waeschenbach 2015). Extinction resistivity may be similar in each group so that the correlation seen here between arthropods and bryozoans simply parallels patterns of diversification seen in other marine groups of the Modern Evolutionary Fauna.

To address that, we tested for coevolution of the post-Palaeozoic bryozoans and molluscs, using the same methodology as for the bryozoans and arthropods. We used the following four basibiont-epibiont pairs arranged from general to more specific subset relationships to test for time series correlations: (1) all bryozoans and all molluscs; (2) encrusting bryozoans and all molluscs; (3) encrusting gymnolaemate bryozoans and motile molluscs most accessible to fouling bryozoans larvae (i.e. gastropods plus cephalopods but not bivalves which often are infaunal); and (4) encrusting cheilostome gymnolaemate bryozoans and gastropods plus cephalopods.

Using molluscs instead of arthropods requires the assumption that arthropods with sturdy skeletons and molluscs have similar relative abundances in living assemblages. Arthropod molts/carcasses can act as substrates for bryozoans (Key *et al.* 2017) which at least partially offsets the lower preservation potential of various arthropod clades relative to molluscs. Previous studies have suggested molluscs, especially robust gastropods, are more abundant in fossil assemblages than arthropods (Kidwell 2001; Pasch *et al.* 2010). Unfortunately, these studies also include infaunal and sessile taxa and are not restricted to epibenthic motile taxa as in our study. There is only one study directly comparing the relative abundance of epibenthic motile arthropods and molluscs in living assemblages (Merta 1980). Merta (1980) ingeniously examined surface trace fossils to focus on epibenthic motile taxa and inferred similar abundances of arthropods and molluscs. Unfortunately, Merta (1980) is not an ideal comparison as arthropods are more likely trace makers than molluscs.

Based on the literature, there are more reported cases of bryozoans encrusting molluscs than arthropods in modern faunas. This is probably in response to the greater diversity of marine molluscs than arthropods. What anecdotal evidence there is suggests that bivalves (Allen 1953; Ward & Thorpe 1991) and gastropods (Taylor *et al.* 1989; Schejter *et al.* 2011) are more commonly encrusted by bryozoans than arthropods (Key *et al.* 2017). Unfortunately, the molluscan data have not been analysed to exclude infaunal, sessile or dead hosts.

The bryozoan-molluscan correlations (Fig. 6, Table 1) were on average significantly weaker than for bryozoans and arthropods. The fact that the bryozoan-arthropod correlations are higher than those for the molluscs suggests any coevolution may have been more strongly coupled between the bryozoans and the arthropods than bryozoans and molluscs. This is despite the vagaries of fossilization of the host crab's epicuticle, which makes the preservation of any attached epibionts under-represented in the

fossil record (Feldmann 2003a,b; Waugh *et al.* 2004). The weaker correlation with the molluscs may also partly be a function of the post-Palaeozoic infaunalization of many siphonate bivalves in response to the Mesozoic Marine Revolution (Stanley 1977; Vermeij 1977; Buatois *et al.* 2016).

A similar arthropod-bryozoan co-evolutionary diversification may have also occurred in the Palaeozoic and played a role in the Great Ordovician Biodiversification Event (Webby *et al.* 2004). This co-evolutionary diversification would have involved different motile marine hosts and different sessile encrusting marine bryozoans than in this study. Trilobite arthropods, part of the Cambrian Evolutionary Fauna (Sepkoski 1981, 1984, 2000), were a common basibiont for stenolaemate bryozoans (Key *et al.* 2010). Nautiloid cephalopods, part of the Palaeozoic Evolutionary Fauna (Sepkoski 1981, 1984, 2000), were a common basibiont for stenolaemate bryozoans (Wyse Jackson & Key 2014; Wyse Jackson *et al.* 2014). The timing of the diversification of bryozoans through the Ordovician (Taylor & Ernst 2004; Ernst 2018) roughly coincides with the diversification of trilobites (Adrain *et al.* 2004) and nautiloid cephalopods (Frey *et al.* 2004). This apparent correlation merits more quantitative analysis.

Conclusions

The question addressed in this study is: Could the simultaneous timing in diversification of arthropods and bryozoans be linked in a co-evolutionary basibiont-epibiont relationship? Using family-level post-Palaeozoic stage-by-stage diversity of arthropods and bryozoans, we showed that the diversification of arthropods is tightly correlated with the diversification of bryozoans, especially those in the Modern Evolutionary Fauna (i.e. decapods and cheilostomes). The timing of diversification of molluscs, another viable basibiont and bryozoans is not as well correlated. This suggests that as decapod arthropods with robust exoskeletons diversified, they may have provided increased substrate space for encrusting cheilostome bryozoans to exploit and increasing camouflage for the hosts, thus leading to their subsequent coevolutionary diversification.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Post-Palaeozoic family-level diversity of main groups of motile marine arthropods and sessile marine bryozoans used in Figs 1, 3, 4 and 5 of this study.

Table S2. Post-Palaeozoic family-level diversity per million years of main groups of motile marine arthropods and sessile marine bryozoans used in Fig. 2 of this study.

Table S3. Post-Palaeozoic family-level diversity per million years using first differences of main groups of motile marine arthropods and sessile marine bryozoans.

Table S4. Post-Palaeozoic family-level diversity per million years of main groups of molluscs and sessile marine bryozoans used in Fig. 6 of this study.

Table S5. Post-Palaeozoic family-level diversity per million years using first differences of main groups of molluscs and sessile marine bryozoans.