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Division of labor and recurrent evolution of polymorphisms in a group of colonial animals

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Abstract Rendering developmental and ecological processes into macroevolutionary events and trends has proved to be a difficult undertaking, not least because processes and outcomes occur at different scales. Here we attempt to integrate comparative analyses that bear on this problem, drawing from a system that has seldom been used in this way: the co-occurrence of alternate phenotypes within genetic individuals, and repeated evolution of distinct categories of these phenotypes. In cheilostome bryozoans, zooid polymorphs (avicularia) and some skeletal structures (several frontal shield types and brood chambers) that evolved from polymorphs have arisen convergently at different times in evolutionary history, apparently reflecting evolvability inherent in modular organization of their colonial bodies. We suggest that division of labor evident in the morphology and functional capacity of polymorphs and other structural modules likely evolved, at least in part,

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in response to the persistent, diffuse selective influence of predation by small motile invertebrate epibionts.

Introduction

Does ecology matter? This was the title of a review written over two decades ago, when certain prominent critics disbelieved that ecological interactions among different taxa were important determinants of major evolutionary patterns, especially patterns allied to biodiversity (Jackson 1988). Evolutionary ecology has responded since then to criticisms of overly smug adaptationist explanations (Jablonski and Sepkoski 1996; Rose and Lauder 1996; Glor 2010). Nevertheless, certain fundamentals of Jackson's question and response are as germane now as then. Developmental and ecological processes studied in the living world are scarcely discernible by direct means at the macroevolutionary scale. Conversely, the unfolding outcomes of such processes, such as morphological diversification or the dynamics of large clades, are inaccessible by direct observation without recourse to the imperfect fossil record (Jablonski 2005; Jackson and Erwin 2006) or by indirect inference via phylogenetic reconstruction, which may introduce its own ambiguities (Cunningham et al. 1998; Losos 2010). We lack a manifest theory and mechanism to render developmental and ecological processes into macroevolutionary events and trends. Thus there is a need for integration of approaches across different temporal scales and hierarchical levels of biological organization, and empirical data that can inform this integration (Jablonski 2007, 2008; Gavrilets and Losos 2009).

Here we attempt to synthesize evidence that has seldom been used to integrate relevant patterns at morphological, ecological and macroevolutionary scales: the co-occurrence of alternate phenotypes *within* genetic individuals, and repeated evolution of distinct categories of these phenotypes. We focus on a clade of wholly colonial animals, cheilostome bryozoans. Unlike familiar solitary animals, physiologically contiguous colonial animals and most plants are decentralized organisms. The colonial body of a single genetic individual results from morphogenesis of reiterated units (modules and groups of modules) that are semiautonomous in their development, physiology, and structural architecture (White 1979; Mackie 1986; Vuorisalo and Tuomi 1986; Watson 1986; Hageman 2003). Also unlike solitary animals, this additional level of organization yields a distinct component of phenotypic variation at this unit level (Cheetham et al. 1993; Hageman et al. 1999; Herrera 2009). Developmental selection has a hierarchical causal structure on phenotypic effects—at this unit level, at an intermediate level(s) of groups of primary modules (in at least some modular organisms), and at the whole-organism level (Tuomi and Vuorisalo 1989; Hageman 2003; de Kroon et al. 2005; Herrera 2009; Clarke 2011). This in turn creates an opportunity for adaptive responses, or evolvability, at this unit level *as well as* higher levels across environmental backgrounds and changing backgrounds through time.

We first describe the nature of structural modularity in bryozoan colonies, in which zooids are the focal units. We then consider evidence for repeated evolutionary transitions to complex frontal shields, skeletal brood chambers (ovicells), and the peculiar zooidal polymorphs called avicularia. Each of these structural categories was involved with or has itself been interpreted as a key innovation that decisively amplified the diversification of cheilostomes (Schopf 1973; Taylor 1988; McKinney and Jackson 1989; Ostrovsky and

Taylor 2005). We contend that this interplay of plasticity and selection at the zooid level can potentially mediate ecological interactions, the evolution of alternate phenotypes, and small- to large-scale species diversification, not unlike mediation at the level of genetic individuals (Miner et al. 2005; Pfennig et al. 2010). In all of these cases, ecological and paleontological evidence is consistent with the view that division of labor evident in the morphology and functional capacity of polymorphic zooids likely evolved—at least in part—in response to a persistent, diffuse selective force: predation by small invertebrate epibionts. Complementary perspectives at developmental, ecological and macroevolutionary scales are not incommensurate; rather, they help to better illuminate ways that these modular animals have evolved. Additionally, the force of our inferences is not carried by any one example, but by the consistency of apparently similar, repeated patterns among different polymorph categories and different bryozoan lineages.

Modularity and zooid budding in cheilostome bryozoans

Biological modularity is frequently considered in a hierarchy of levels, according to attributes of structure, process, function, or relationship to Darwinian fitness. Interactions occurring within modules are greater than those among modules at the same or a different level, with varying degrees of integration. Thus modularity may also be perceived as a complex network. In bryozoans, each zooid is a structural and developmental module, some of which serve a limited range of functional needs of the colony as an integrated whole. All zooids are themselves developmentally and functionally integrated entities (*sensu* Young and Badyaev 2006). Zooid morphological polymorphism is present when zooid modules of two or more distinct categories co-occur in a colony. As a rule, the morphological difference between categories is greater than that expressed by members within a category.

   With few exceptions, stereotypical autozooids capable of feeding (though having diverse types of frontal shields, ovicells, and avicularia) have long been considered one type among polymorphic zooids. Frontal shields (Fig. 1) are partial or nearly complete skeletal coverings that protect the outwardly facing (frontal) surface of the main zooid body cavity. Shields may be formed by one of several different morphogenetic patterns and sequences, or by a combination of these (Gordon and Voigt 1996). Composite frontal shields can consist of spines—considered by some workers as polymorphs or former polymorphs (e.g., Silén 1942, 1977)—or are inferred to have been derived from fusions of kenozooidal polymorphs. In contrast, gymnocystal shields (Fig. 1d) are the simple consequence of calcification of the frontal epithelium of the primary body cavity. Ovicells (Fig. 2), including their skeletal component (ooecia), are embryo brood chambers partly or wholly external to the main zooid body cavity (Ostrovsky 2008a). Avicularia (Fig. 3) are functionally specialized zooids with typically augmented muscles acting on a hinged mandible. There are four types of avicularia, three of which are defined by their budding position in the colony and the fourth by morphology (Ryland 1970; Schopf 1973; Silén 1977; Cheetham and Cook 1983; Carter et al. 2010a, b). Vicarious avicularia 'replace' an autozooid in the budding sequence (Fig. 3d). Interzooidal avicularia, which are smaller than their progenitor zooid, are squeezed in between autozooids (Fig. 3g). Adventitious avicularia develop on the lateral, frontal or basal walls of an autozooid (Fig. 3a–c, h). Vibracula are defined by their unique morphology and are considered highly specialized avicularia. They differ from other avicularia by the rotational ability of their hair-like mandibles, or setae, as opposed to movement in one plane in other avicularian types (Fig. 3f).
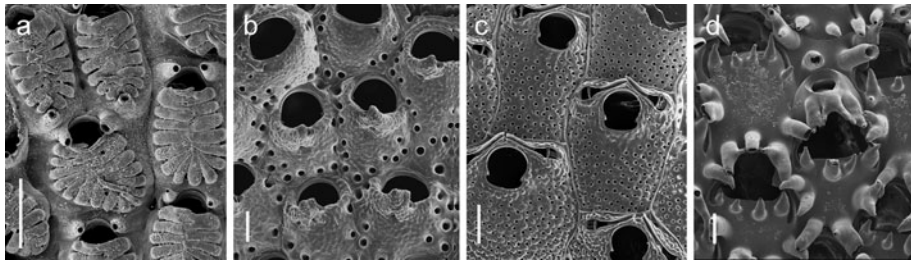
Fig. 1 Frontal shields. **a** Spinocystal shield in *Aspidelectra zhoushanica* (Wang, 1989), an anascan analogue of a cribrimorph. In many species, the developing spines can become fused distally, laterally, or both. **b** Umbonuloid shield in *Celleporaria pilaefera* (Canu & Bassler, 1929). The shield develops as an infolding beneath the frontal membrane, extending distally from the zooid proximal margin. Growth of the calcified shield separates an overlying hypostegal coelom from the water compensation sac (ascus) and the main coelomic cavity. Typically, pores with communication cells at the zooid margins connect the hypostegal and main cooeloms. **c** Leprarioid shield in *Hippopodina feegeensis* (Busk, 1884). The shield is formed as an internal partition (cryptocyst), overlain by a hypostegal coelom and underlain by the ascus and main coelomic chamber, respectively. Pores with communication cells connect to the main coelomic cavity. Less-complete internal partitions are also present in some cheilostomes with membranous frontal walls. **d** Gymnocystal shield in *Integripelta acanthus* Gordon & Rudman, 2006, wherein the shield itself merely includes the calcification of the frontal body wall, and has not been considered a polymorphic zooid, nor derived from one. Soft tissue removed from all specimens. *Scale bars* **a** 200 μm; **b** 100 μm; **c** 200 μm; **d** 100 μm

These zooid polymorphs, together with several others not considered here, have mostly been thought of as morphological categories based on structural and functional similarities (Silén 1977). Colonies of most cheilostome species possess one or more categories of zooid polymorph. In cheilostomes, polymorphs are readily discerned in fossil skeletal remains, in contrast to many other groups of colonial animals that lack such an accessible fossil history of polymorphism.

Growth of the colony body results from cyclic morphogenesis of zooid modules (Lidgard 1985; Reed 1991). Organs produced as parts of the autozooids—such as feeding and digestive organs—are often reduced or absent in other polymorphs. Within a species, incipient zooids tend to originate from specific loci on a parent zooid. At each budding locus, populations of cells (cell condensations) proliferate, differentiating into the form to be assumed by the daughter zooid module. The source of the bud is not so much the parent zooid as the parent body wall (cystid, see Silén 1977; Mukai et al. 1997). The cystid has the totipotency to produce structures to the inside (organs, musculature) and outside (surficial derivatives and new zooids). In non-calcified bryozoans it comprises an outer cuticle lined by the epithelium that secretes it, a peritoneum, and a sparse inter-module nerve net; in calcified bryozoans, skeletal carbonate is typically formed by the epithelial layer beneath the cuticle or by intussusception into a body chamber. The cystid is linked to the physiological unity of the zooid and colony as part of a dynamic, integrated system responsive not only to internal but also to external cues (Ryland 1977; Mukai et al. 1997). It appears to be the interaction of cell condensations in proximity to the cystid that, with the aid of cellular morphogenetic movements, results in differentiation of structures and subsequent zooid modules.

Aiding communication between parent and differentiating daughter modules is the funicular nutrient-transport system that is at least an analog of a blood vascular system (Carle and Ruppert 1983; Ruppert and Carle 1983). A colonial nerve network links all zooids (Mukai et al. 1997). Experimental work on nerve propagation (Thorpe et al. 1975a, b, 1982), feeding (Pratt 2004), resource translocation within colonies (Lutaud 1985;
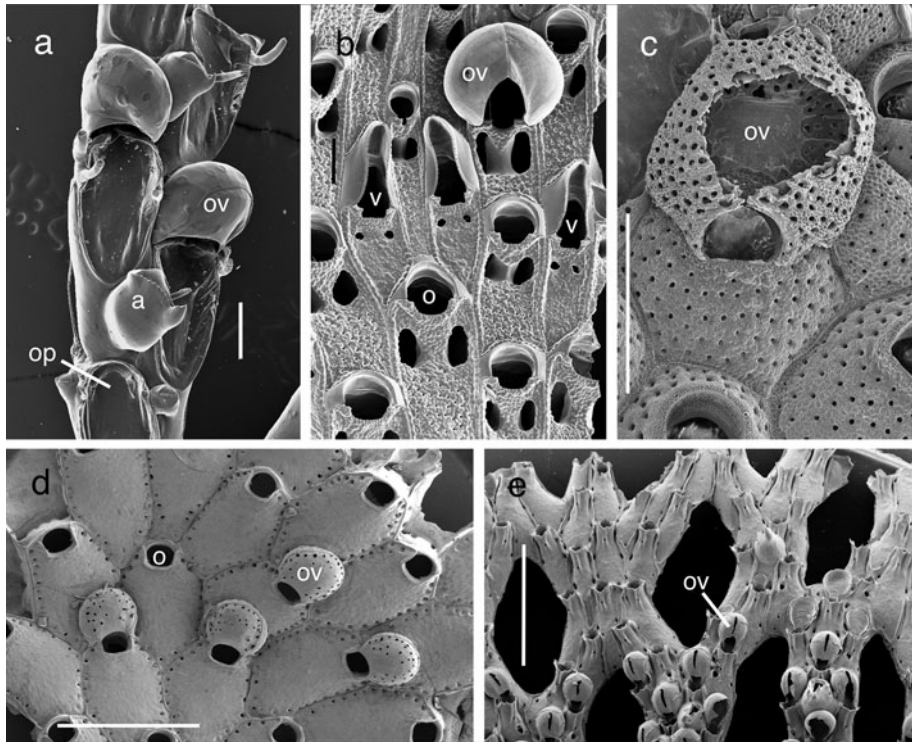
Fig. 2 Ovicells. **a** *Scrupocellaria* sp. has an erect colony and autozooids with simple membranous (anascan) frontal walls lacking a calcareous shield. Ovicells are distal to the zooid orifice and partly extend over the next distal zooid, the typical pattern for cheilostomes. Large adventitious avicularia are budded from zooid frontal surfaces. **b** *Thalamoporella* sp. is an anascan with a calcareous (cryptocystal) shelf beneath the membranous frontal wall; paired openings (opesiules) allow muscles to pass through the shelf and attach to the membrane. A large bipartite ovicell and several vicarious avicularia—taking the place of autozooids in the budding pattern—are shown. **c** *Macropora polymorpha* (Philipps, 1899) is also an anascan with a cryptocyst. A partly formed ovicell reveals its inner and outer calcareous wall architecture. The 'vicarious' ovicell appears to take the place of the next distal zooid. **d** An encrusting colony of the ascophoran *Hippomonavella gymnae* Gordon, 1984 has zooids with calcareous (lepralioid) frontal shields, and scattered ovicells. **e** A colony of the ascophoran *Reteporella aurantium* Gordon, 2009 is an erect meshwork formed by zooids with calcareous (lepralioid) frontal shields. Note the clustering of ovicells far proximal to the growing margin at top. Soft tissue removed from specimens (**b–e**). Annotations: a, adventitious avicularium; o, orifice; op, operculum; ov, ovicell; v, vicarious avicularium. *Scale bars* **a** 100 μm; **b** 200 μm; **c** 1 mm; **d** 1 mm; **e** 1 mm

Best and Thorpe 1985, 2002; Miles et al. 1995), timing of sexual maturity (Harvell and Grosberg 1988), and inducible defenses and reproduction (e.g., Harvell 1990; Harvell and Helling 1993), inter alia, gives ample evidence that the bryozoan zooid and colony are highly functionally integrated. This fact is important to the consideration of the evolution of zooidal polymorphism and of adaptive responses.

The lability of iterative zooidal budding in cheilostomes confers plasticity in the expression of zooid phenotypes. Ontogenetic heterochrony can affect the size of the bud and hence the contents of the ensuing zooid (Harvell 1994). Further, heterochrony expressed in zooid morphogenesis can affect parts of the bud as they differentiate, such that an operculum and/or its musculature, or the polypide, or gonads may be larger or
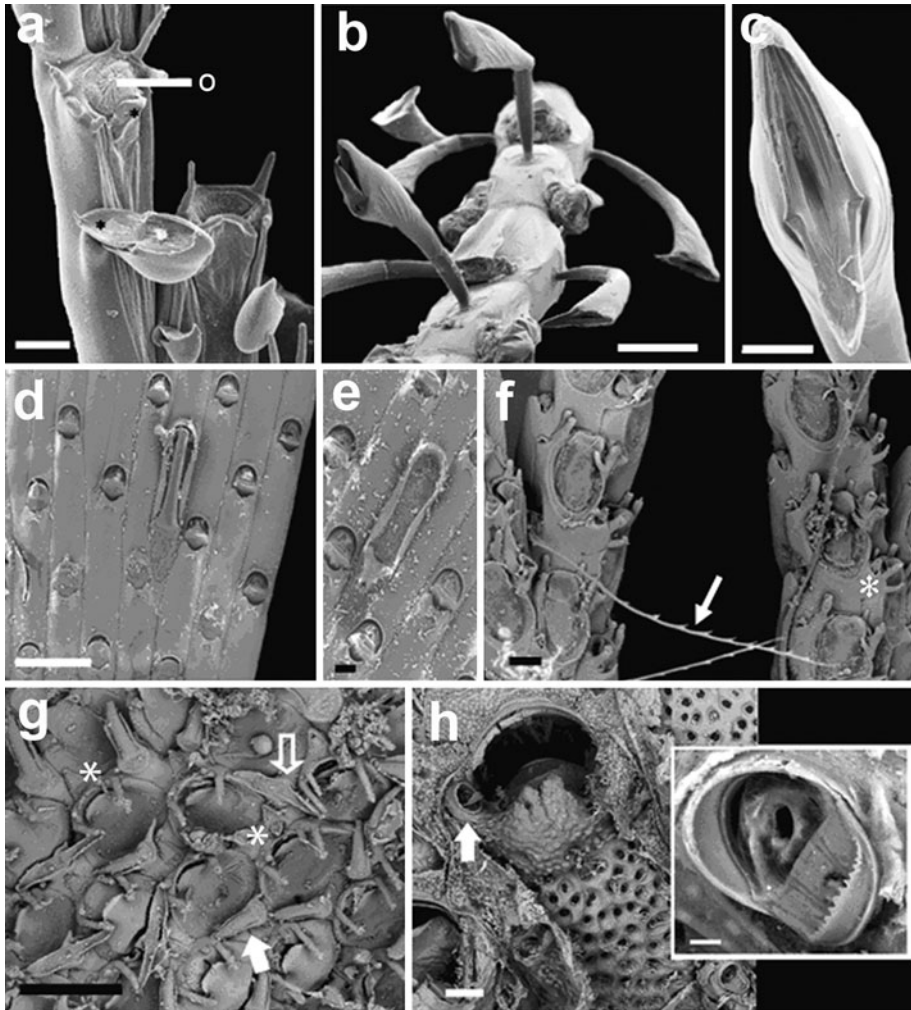
Fig. 3 Avicularia. **a** *Bugula flabellata* (Thompson in Gray, 1848) colony with autozooids and bird's-head form of adventitious avicularia. o, orifice of autozooid; *asterisks* (shown in black) denote the operculum of the autozooid and homologous structure in the avicularium, the mandible. *Scale bar*, 100 μm. **b** *Nordgaardia cornucopioides* d'Hondt, 1983 with autozooids and adventitious avicularia. *Scale bar*, 200 μm. **c** Adventitious avicularium of *N. cornucopioides*. *Scale bar*, 50 μm. **d** *Euthyroides jellyae* Levinsen, 1909 and closed vicarious avicularium. *Scale bar* 500 μm. **e** Opened vicarious avicularium of *E. jellyae*. *Scale bar*, 100 μm. **f** *Cabereaasterisks* sp. with vibracula (*arrow*, vibracular seta) and adventitious avicularium (*asterisk*), *scale bar*, 100 μm. **g** *Chaperiopsis* cf. *rubida* (Hincks, 1881) with adventitious (*asterisks*) and interzooidal avicularia (*open arrow*, mandible open; *filled arrow*, mandible closed). *Scale bar*, 500 μm. **h** *Mucropetraliella* sp. colony with small suboral adventitious avicularium. *Scale bar*, 100 μm. *Inset*, avicularium. *Scale bar* 10 μm. After Carter et al. (2010a). **a**–**c** Originally in Carter et al. (2008)

smaller relative to the size of the formed zooid. In contrast, heterochrony expressed at a higher colony level (astogeny: changes across multiple zooids) may affect the location of a bud within the colony. Harvell (1994) cites the example of the shift from an interzooidal (e.g., Fig. 3a) to adventitious (e.g., Fig. 3b) location of avicularia; the same can occur with

other polymorphs. Being decoupled, both ontogenetic and astogenetic transformations can potentially happen concurrently.

Many of the morphological changes observed in the evolution of polymorphism may be polyphenic, induced by external or internal environmental cues, resulting in extensive epigenetic variation in morphology. Polymorphs can be extremely uniform in some species, appearing with virtual certainty in the same locations on progenitor zooids and within the colony as a whole, while in other species polymorphs appear sporadically in different locations, suggesting variable responses to environmental cues. Alternate phenotypes as polyphenisms (Gilbert and Epel 2008) may eventually be shown to be as common as or more common than polymorphisms under strict genetic control. In a study of genetic variation and polymorphism in the inducible cuticular spines of a species of *Membranipora*, Harvell (1998) discovered that populations are a mix of genetic individuals, comprising non-spined (irrespective of a stimulus), inducibly spined (when exposed to an appropriate cue such as a water-borne predator extract), and constitutively spined (produced in the absence of the cue) phenotypes. Even inducible individuals showed high heritable variation. Hence, even in a phylogenetically less-derived taxon like *Membranipora*, the potential for morphological novelty is relatively well developed. Other work shows that potential autozooids can be inducibly transformed into kenozooids (non-feeding polymorphs lacking an aperture, lophophore, and certain internal organs), appearing as elongate non-feeding 'tower zooids' that may form at the contact zone between two different colonies or at the lateral margin of the algal frond on which a colony occurs, evidently to reduce abrasion (Xing and Qian 1999). Further, zooid damage is sometimes followed by regeneration of an alternate morphology. Figure 4a shows a series of adventitious avicularia that have been regenerated over time within the confines of previous avicularia that were presumably damaged. In contrast, Fig. 4b shows a miniature autozooid phenotype regenerated in a like manner within the cystid of an adventitious avicularium. These natural experiments in regeneration reveal prospective homologies, and the possibility of regulatory 'switches' in certain zooid developmental pathways.
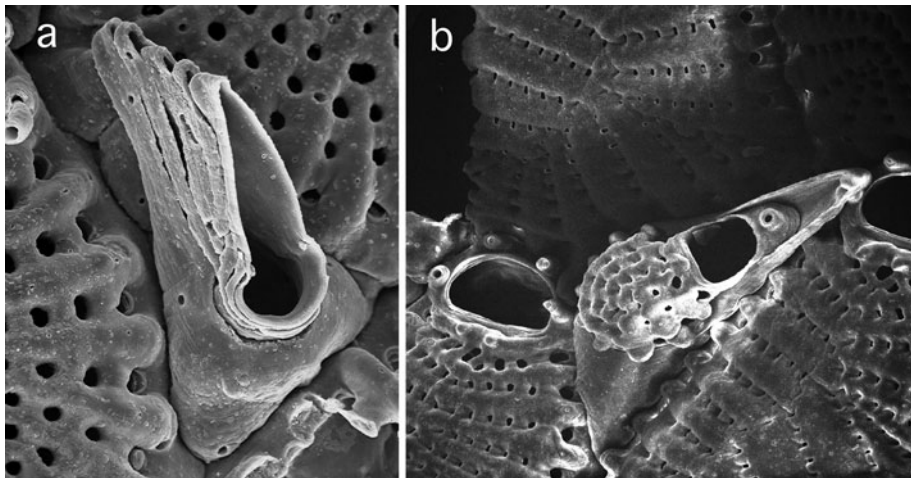

Fig. 4 **a** A succession of avicularia has been regenerated within the damaged cystids of preceding ones in *Puellina venusta* (Canu & Bassler, 1925). **b** A miniature autozooid phenotype with frontal (costal) shield, orifice, and a distal spine base has been regenerated into the cystid of an interzooidal avicularium of *Puellina radiata* (Moll, 1803). Soft tissue removed from these specimens

Zooid modules represent a joint interface with genotype, developmental pathway, function, and environment. Because "Selection can … act independently on individual zooids, creating the potential to explore independent body plans as variation in zooid form" (Davidson et al. 2004, p. 443), evolvability at the zooid level becomes possible, depending upon the mapping of genetic and epigenetic variation onto phenotypic variation. In this way, plasticity and variation are expressed at both the zooid and colony levels (Cheetham et al. 1993; Hageman et al. 1999). Any genetically structured zooid module can become heritably modified in future generations, just as arthropod segments or *Drosophila* bristles can. In cheilostomes, embryonic ontogeny from egg to histolysis of most larval organs at metamorphosis is decoupled (at least morphologically) from morphogenetic sequences of zooid budding that are then repeated over and over. Module phenotypes (and their reaction norms) that influence survival can be selected at this iterated zooid level (Tuomi and Vuorisalo 1989; de Kroon et al. 2005; Herrera 2009). However, while the developmental pathways leading to discontinuous variation among alternate zooid phenotypes in cheilostomes must have been drawn from a common genomic pool, their genetic and epigenetic bases are hardly known at this time.

A well-resolved, robust phylogenetic scaffolding encompassing most cheilostome genera or even families is similarly unavailable, despite significant progress toward this end (Fuchs et al. 2009; Tsyganov-Bodounov et al. 2009; Hausdorf et al. 2010; Knight et al. in press). Thus our overall approach is comparative and mainly morphological, drawing upon molecular phylogenetic studies where they are available. Our case studies also take a comparative approach to inferring adaptation rather than a population genetic or experimental one. We likewise draw on experimental studies where they are available, but studies concerning adaptation in physiologically contiguous animal colonies have mostly involved larvae, whole colonies, and populations of colonies (e.g., Grosberg and Patterson 1989; Karlson 2002; Okamura et al. 2002; Osman and Whitlatch 2004), rather than the polymorphic modules *within* colonies. From this perspective of modular growth, we turn now to three case studies bearing on distinct functions—the division of labor at the level of zooid modules within a colony—and the evolutionary history of cheilostome polymorphism.

Zooid costal shields

Appearing in the Late Jurassic, the earliest cheilostomes were of anascan grade, having simple box-like zooids with calcified vertical walls, but a non-calcified frontal wall (frontal membrane) that provided a flexible, depressible surface functioning in eversion of the feeding organ, or polypide lophophore. Zooids of these early cheilostomes were nearly monomorphic. The first elaboration of this monotonous zooid form appeared as spines around the opesia (Taylor et al. 2009), the area occupied by the frontal membrane. Spine scars in fossil specimens suggest that the ancient spines were similar to those in living cheilostomes: hollow and calcified, with a flexible cuticular joint at the base. Spines in living colonies may play roles in resisting overgrowth competition, reducing surface abrasion and, perhaps most importantly, deterring small predators from exposed, membranous portions of the colony surface (Cook 1985; Harvell 1984, 1990; Iyengar and Harvell 2002).

The cribrimorphs represent the next evolutionary advance in protecting the frontal membrane; the opesial spines lost the flexible basal joint and became rigid projections called costae. The costae were separate in the first cribrimorphs (the myagromorphs) but later became fused laterally and medially to form a rigid costal shield over the body cavity (Larwood 1969, 1985). The cribrimorph costal shield (Fig. 1a) was a key innovation, as it

subsequently provided a scaffold for overgrowth by marginally budded kenozooids, which led to more robust skeletonized frontal shields. This overgrowth likely produced a compound, two-layered wall, with the spinocystal layer (costal field), and perhaps its originating gymnocyst, overlain by the kenozooidal-wall component bounded externally by a hypostegal coelom—a flattened coelomic chamber overlying the frontal calcification—in physiological communication with the zooidal coelom of the main body cavity via marginal openings with pore-cell complexes (Gordon and Voigt 1996; Mukai et al. 1997). Now superfluous, the costal field underwent evolutionary reductions in size and/or in the number of costal elements, leading to umbonuloid- and lepralioid-type shields (Fig. 1b, c). Both these shield types provide similar calcified 'roofs' over the body cavity, but differ in the pattern and sequence of skeletal morphogenesis, and in geometric relationships to epithelia and coelomic chambers. Reductions in the area of the costal field, however, concomitantly reduced the size of the frontal membrane, limiting the vital function of this membrane in lophophore eversion. The origin of the ascus, or water compensation sac, beneath the frontal shield circumvented this functional constraint and defined a novel grade, ascophorans.

Although there was evidence that both the costal shield and ascus evolved independently several times in cheilostomes (Voigt 1991; Gordon 2000), the discovery of the parallel Neogene origin of these structures in closely related species within a single well-defined genus, *Cauloramphus*, in the large anascan family Calloporidae, forced a reassessment of the significance and pervasiveness of convergence in these structures (Dick et al. 2009, 2011). Several *Cauloramphus* species comprise a transition series, from a stereotypical anascan with an exposed frontal membrane surrounded by jointed opesial spines (Fig. 5a), to a myagromorph morphology with rigid (basally calcified) but separate spines (now costae) arched over the frontal membrane (Fig. 5b), to a cribrimorph species with a skeletal costal shield over an unmodified frontal membrane (Fig. 5c), to an ascophoran with a highly fused, reduced costal shield, skeletally defined orifice, and ascus (Fig. 5d). A COI molecular phylogeny showed that these species formed a clade well embedded within *Cauloramphus* and confirmed the order of the inferred transitions (Dick et al. 2009). The phylogeny also confirmed the Miocene origin of *Cauloramphus* indicated by the fossil record and suggested that the transitions from a stereotypical anascan to a cribrimorph occurred less than 12 Myr ago and were rapid, taking no more than an estimated 3.8 Myr. These transitions paralleled those inferred from fossils to have occurred in one or more Cretaceous lineages 85–95 Ma (Larwood 1969; Dick et al. 2009).

Costal shields have evolved independently multiple times, evidenced by diverse calloporid lineages that include both stereotypical anascan species and cribrimorphs; examples of these cribrimorphs include *Callopora rylandi* Bobin & Prenant 1965, *Membraniporella nitida* (Johnston 1838), *Valdemunitella spinea* (Brown, 1952), and the species of *Cauloramphus* mentioned above (Dick et al. 2009). Likewise, although the ascus was once viewed as too complex a structure to have evolved repeatedly (Silén 1942), a few cheilostome families (e.g., Calloporidae, Cribrilinidae, Catenicellidae, Petalostegidae) contain some living species with a costal shield overlying an unmodified frontal membrane, and others with a reduced or vestigal shield and an ascus, indicating multiple independent origins of the ascus. Ascus development has been examined in detail in only a few species (e.g., Tavener-Smith and Williams 1970), and previous interpretations predated the understanding that ascophoran frontal shields evolved through successive reductions in the spinocystal component and underlying frontal membrane. The conceptual framework now exists for elucidating the incremental evolution of the ascus and explaining how an apparently developmentally complex structure repeatedly evolved convergently.
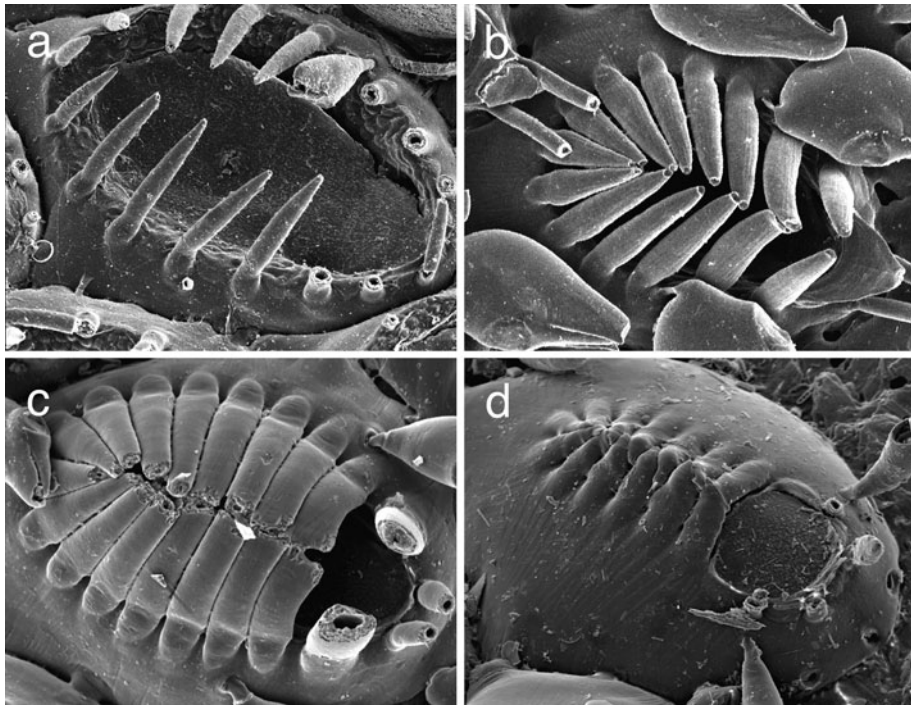
Fig. 5 Morphology of zooid frontal walls among inferred primitive and derived *Cauloramphus* species. **a** *C. ordinarius* Dick et al., 2011. **b** *C. cheliferoides* Dick et al., 2011. **c** *C. peltatus* Dick et al., 2011. **d** *C. ascofer* Dick et al., 2011

Ascophoran bryozoans have diversified extensively throughout the Cenozoic and are more successful than the cribrimorph and anascan grades (Gordon and Voigt 1996; Dick et al. 2009). Decisive new evidence of this diversification comes from the most complete phylogenetic analysis of Cheilostomata to date, based on five nuclear and mitochondrial loci across 91 species (Knight et al. in press). These authors demonstrate convincingly that gymnocystal, umbonuloid and lepralioid frontal shields (Fig. 1) have each evolved multiple times, and that infraorder Ascophorina is in fact not monophyletic. Two innovations key to the origin and radiation of ascophorans (excluding those with gymnocystal shields) both involved the integration of modular elements: first the costal shield, and then the new frontal layer produced by overgrowth by kenozooidal polymorphs. The hypostegal coelom and associated frontal-shield layer contributed to the sustained radiation of ascophorans by providing unprecedented opportunities for frontal budding, new defenses (e.g., elaboration of adventitious avicularia), and strengthening colonies for nodular and robust-erect growth (Gordon and Voigt 1996; McKinney and Jackson 1989), leading to significant adaptive evolution in colony form.

Skeletal ovicells

Living taxa that resemble the earliest anascan cheilostomes (Suborder Malacostegina) do not brood their larvae: these larvae feed and grow in the plankton over periods of days to

weeks—or even longer—prior to settlement. By contrast, the great majority of Recent and post-Early Cretaceous fossil cheilostomes are brooders. The evolution of brooding, signaled by the first skeletal brood chambers (ovicells), in the calloporid *Wilbertopora mutabilis* Cheetham, 1954 from the Upper Albian, was coincident with the onset of the first major radiation within the clade (Taylor and Larwood 1990; Cheetham et al. 2006). Relying in part on this evidence, Taylor (1988) proposed that the widespread fossil appearance of brood chambers evidenced the origin of poorly dispersing, non-feeding lecithotrophic larvae. This larval type could have provided a 'trigger' for the explosive Upper Cretaceous radiation of cheilostomes, as it may have increased population fragmentation and speciation rates. Subsequent work is consistent with this inference, considering the advent of brooded lecithotrophic larvae together with other evolutionary novelties such as frontal shields (e.g., Gordon and Voigt 1996).

Cheilostomes exhibit a variety of brooding patterns, ranging from outside the main body cavity in membranous sacs to intracoelomic (Ström 1977; Reed 1991; Ostrovsky 2008a, b, 2009). The vast majority of living taxa, however, accommodate developing embryos within specialized ovicells, within which non-feeding lecithotrophic larvae develop and, in matrotrophic species, grow. The larvae contain nutrients sufficient for a short free-swimming stage, settlement, and metamorphosis. In general, each ovicell is a two-walled hemispherical outfolding (ooecium) with a coelomic lumen between the walls. This lumen communicates with the visceral coelom of the zooid that constructs the outfold, either the maternal or next distal zooid.

Ovicells likely evolved from modified mural spines that may themselves represent polymorphic zooids (Silén 1942, 1977). This interpretation of ooecial origin dates back to works by Harmer (1902) and Levinsen (1902), and receives support from the fossil record. Authors of published descriptions of spinose ovicells in a number of fossil and Recent species from the families Calloporidae, Monoporellidae, Macroporidae and Cribrilinidae have interpreted this type of morphology as primitive (Taylor and McKinney 2002; Ostrovsky and Taylor 2004, 2005). Such ooecia are moderately common in the Upper Cretaceous, where they are known in 28 species, and also occur in one Paleocene, seven Eocene–Miocene and 11 Recent species. Ostrovsky and Taylor (2004, 2005) show that the most primitive cheilostome ovicells probably occurred in a mid-Cretaceous calloporid in which a group of mural spines belonging to the zooid distal to the maternal zooid evolved to form a cage-like structure for reception of the embryo through the maternal orifice. They argue that curvature or re-orientation of the proximal mural spines away from the frontal membrane of the distal zooid and towards the proximal, maternal zooid can be hypothesized as the first step towards the acquisition of a specialized brood chamber (Fig. 6a, b). Finally, these authors document a series of trends in early ovicell evolution: loss of basal spine articulation, spine flattening, closure of the gaps between spines, reduction in spine number (through loss or fusion), and development of a concave ovicell floor. The conventional 'unipartite' ovicells found in the majority of cheilostomes may have originated either by spine fusion, as seems likely in some cribrilinids, or through a progressive loss of spines via an intermediate stage (Fig. 6c, d), seen in some calloporids and in two monoporellids, where the ovicell comprises a pair of large flattened spines. The spinose ovicells of some monoporellids and macroporids subsequently evolved investments of hypostegal coelom (possibly of kenozooid origin) that allowed secretion of a surface layer of cryptocystal calcification (Ostrovsky 2009).

At an early stage in ovicell evolution, the main proximal entrance to spinose ovicells was probably open (Ostrovsky and Taylor 2005). Later in evolution this opening was closed by a non-calcified evagination of the maternal zooid frontal wall and, further, by the
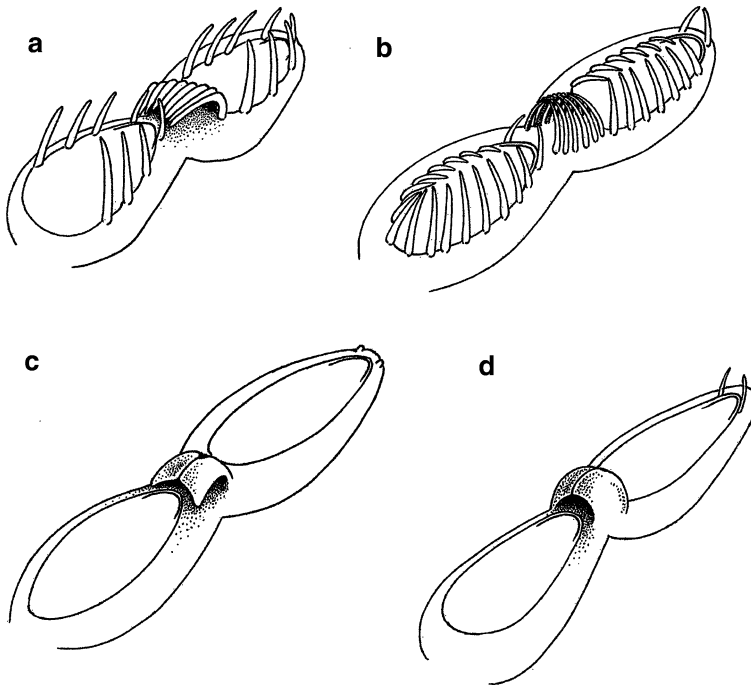
Fig. 6 Simplified reconstructions of some primitive cheilostome ovicells seen in oblique views of the maternal and distal zooids. **a** Multispinose ovicell in which the ooecial spine bases are arranged in a gently bowed row. **b** Multispinose ovicell with the ooecial spine bases arranged in a *semicircle*. **c** Bispinose ovicell. **d** More conventional bipartite ovicell (from Ostrovsky and Taylor 2004)

operculum of the maternal zooid. Thus, at least two zooids are involved in ovicell formation, and such complexes can be considered as colonial 'organs' or cormidia (according to terminology of Beklemishev 1969). Moreover, ovicells in *Monoporella* (Cheetham and Cook 1983, fig. 72.2) involve the maternal, distal and two lateral zooids, representing a "cluster of polymorphic autozooids forming [the] brooding structure" (Cheetham and Cook 1983, p. 166). Apart from the operculum of the maternal zooid that closes the main ovicell opening, the brooding cavity is isolated from the external medium by the frontal membranes of the two neighboring zooids closing lateral foramina.

The acanthostegous brood chambers found in the Recent family Tendridae provide one example of independent evolution of spinose brooding structures in Cheilostomata. These brood chambers, known only in *Tendra* and *Heteroecium,* represent another kind of spinose brood chamber that is not homologous with an ovicell. Whereas calloporid ovicells originated by the bending towards the maternal zooid of a small cluster of proximally situated mural spines belonging to the distal zooid, in tendrids all of the mural spines surrounding the opesia of the distal zooid contribute to brood-chamber formation. The brood-chamber floor in tendrids is formed by the frontal membrane of the distal zooid and is not calcified, in contrast to that of neocheilostome ovicells which is derived from the proximal gymnocyst of the distal zooid and is calcified. Another unique ooecium of the tentative cribrimorph *Bellulopora* consists of kenozooidal costae. Thus, the *Bellulopora* ovicell may not be homologous with those of other cribrimorphs, with the membranous floor originating from the frontal membrane of the reduced distal zooid in the same manner

as the acanthostegous brood-chambers of tendrids (Ostrovsky and Taylor 2005; Ostrovsky 2009).

The characteristic bivalved or multivalved ooecia originating from the maternal zooid and known in families Scrupariidae, Alysidiidae, and Thalamoporellidae may possibly represent additional independent evolutionary origins of brooding (Taylor 1988; Ostrovsky and Taylor 2004, 2005). The two ooecial valves, kenozooidal outgrowths of the maternal zooid frontal wall, fuse to form the completed structure, except in *Thalamoporella*, in which the ooecium is a hollow calcified hood with a medial suture formed by the fusion of two hollow lobate projections of the maternal zooid.

In Bryozoa, the evolution of chambers for embryo incubation was followed by and is inextricably linked with the acquisition of matrotrophy (extraembryonic nutrition). This phylum is unique among invertebrates in that extraembryonic nutrition occurs in all major classes (Ostrovsky et al. 2008, 2009a). Extraembryonic nutrition exists in at least 35 gymnolaemate (cheilostome plus ctenostome) genera among 26 families, and data from Harmer (1926), Cook (1985), and Kuklinski and Taylor (2006) suggest that there are likely to be more examples. Placental analogs occur within both ovicells and internal brooding sacs. If brood chambers evolved independently in all major bryozoan groups (classes and orders), then matrotrophy should have evolved independently too, as was first suggested by Reed (1991). All cheilostome families and genera with extant representatives having placental analogs are well nested within higher-level groups whose other constituent taxa have macrolecithal oogenesis, brooding, and lecithotrophic larvae, which is the more common pattern (Ostrovsky 2009; Ostrovsky et al. 2009a). Families and genera with living placental species also appear later in the fossil record than their non-placental brooding relatives. The occurrence of matrotrophy cannot be established definitively from cheilostome fossils, but what is presently known of cheilostome phylogeny supports multiple independent origins of matrotrophy. Also, the existence of different reproductive and especially brooding patterns that are 'adjacent' to one another within the same families and sometimes the same genera (Ostrovsky et al. 2009a) supports the idea that ovicells, extraembryonic nutrition, and placental analogs evolved multiple times within Cheilostomata.

Avicularia

Avicularia lack a fully developed functional feeding apparatus (gut and tentacle crown) but possess recognizable vestiges of autozooid organ structures. The highly varied morphology of these vestigial structures, and the diverse array of avicularian types—adventitious, interzooidal, vicarious, and vibracular—and of mandible morphologies (Fig. 3), strongly indicate that avicularia serve various functions across many taxa (Marcus 1939; Silén 1977; Winston 1984). Some avicularia can grasp and hold small motile invertebrates, often until death ensues (Nordmann 1840; Winston 1986, 1991, 2010; Carter et al. 2010a). Such behavior has led to the general consensus that many and perhaps most avicularia have a defensive function (Darwin 1872; Nordmann 1840; Johnston 1847; Kaufmann 1968, 1971; Winston 1984, 1986, 1991), yet their capacity for such a role and their impact on potential threats to the colony have not been rigorously examined (Carter et al. 2010b).

The earliest avicularia differentiated from ordinary feeding zooids through a series of morphological changes during the early Upper Cretaceous, just before the overall rapid radiation in cheilostome bryozoans. In an extensive analysis of the first known avicularia in the fossil record, Cheetham et al. (2006) constructed a phylogeny of species in *Wilbertopora*. They also studied the stratigraphic succession, meticulously demonstrating

stepwise transformations from autozooid to vicarious avicularium from species to species. Moreover, fully developed and vestigial ovicells found distally to avicularia in six of eight species studied indicate the presence of a polypide with ovary, probably functional in the less modified avicularia of *W. mutabilis*, and non-functional in later species. The occurrence of similar series of morphologically differentiated heterozooids in more recent stratigraphic collections implies that avicularia have evolved independently several times within the order (Cheetham et al. 2006).

The occurrence of transitional stages in polymorphism among living congeneric species has allowed the detection of structures homologous between autozooids and avicularia. Among living species of *Crassimarginatella* are polymorphs with a mosaic of avicularian and autozooidal elements (Cook 1968) that represent different stages of evolutionary transformation. The avicularia of *C. similis* Cook, 1968 lack the mandibular pivots (condyles), a characteristic feature of avicularia in general. These rudimentary vicarious avicularia are thus hardly differentiated from autozooids, are of comparable size, and possess a polypide. Other closely related species show clearer morphological differentiation between autozooids and avicularia, and the latter forms lack polypides. Among other genera, transitional stages are evident even in the same genetic individual (colony), with polymorphs co-occurring in apparently different stages of avicularian development. In *Akatopora leucocypha* (Marcus, 1937) there are two types of vicarious avicularia (Marcus 1939); one is hardly differentiated from autozooids but has a reduced polypide and augmented musculature, whereas the other is smaller, with a vestigial polypide.

Living *Bugula flabellata* (Thompson in Gray, 1848) colonies display a correlated array of soft tissue and exoskeleton homologies (ascertained by positional and morphological criteria) between autozooids and adventitious avicularia (Carter et al. in press). Individual parts of the bird's-head avicularia (Fig. 3a) have differentiated from autozooid homologues by vestigialization and augmentation, coincident with discrete functional innovations. Modification of the muscular system in avicularia has involved parallel augmentation and reduction (Fig. 7), with related co-variation in muscle development, allometric changes in avicularian architecture, and vestigialization of the entire feeding apparatus. In the avicularium, the adductor muscles are highly developed compared to the autozooid and are the dominant tissue mass. They insert into a heavily reinforced mandible via a ligament, and their contraction enables rapid closure of the mandible. In contrast, the retractor muscles, responsible for retraction of the polypide in the autozooid, are reduced to a couple of single fibers in the avicularium (Carter et al. in press). The vestigial polypide consists of a mass of ciliated cells, the remnant of the ciliated tentacles in autozooids (Carter et al. 2010a). When the mandible is open, a tuft of cilia everts through the avicularian palate and is exposed to the external environment (Fig. 7b). Like some of the cilia on feeding tentacles, the cilia in the bird's-head avicularium respond to tactile stimuli; for example, when the appendage of a small crustacean touches the cilia, the mandible rapidly closes on it (Fig. 8).

The taxonomic distribution of avicularia increased through several major pulses of cheilostome diversification, and most living species have at least one type. Species with only the vicarious type (the first to occur in the fossil record) have the lowest colony density of avicularia (0.04–2.0 per mm^2), whereas species with only adventitious types consistently have higher densities (>5 per mm^2). The combination of an adventitious avicularium with another type further increases the overall density. The bird's-head avicularia in *B. flabellata* occur in relatively high densities (10 per mm^2) and are actively involved in the immobilization of small motile epibionts, which can be more than 10 times the length of the avicularium (Fig. 8). This high density of avicularia enables more than one avicularium to grasp the same epibiont (Carter et al. 2010b).
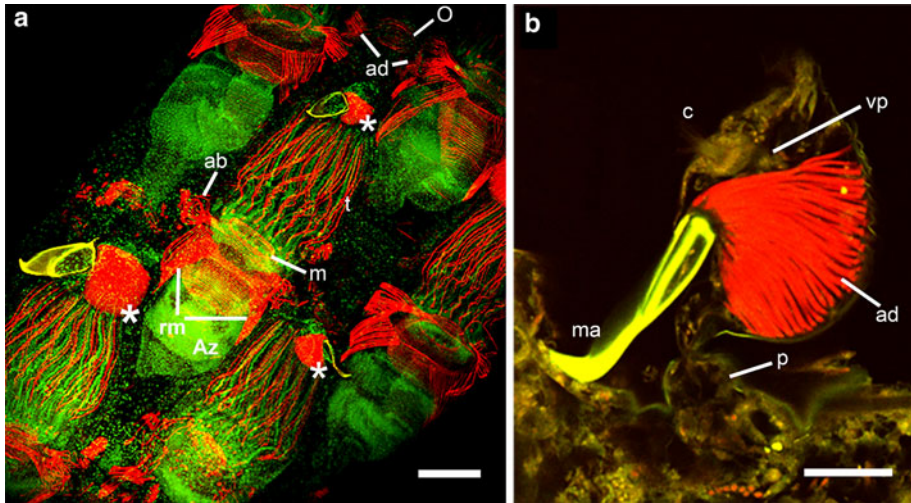
Fig. 7 Laser scanning confocal microscopic images of *Bugula flabellata* stained with phalloidin conjugated with an Alexa Fluor 568 fluorescent dye to target F-actin in muscles (*red*); other morphology (*green*) is the result of autofluorescence. **a** Colony with the gut muscular system (circular and retractor muscles) and opercular adductor muscles. *Asterisks* denote avicularia. *Scale bar* 75 μm. **b** Avicularium with mandible open. *ab* abductor muscles; *ad* adductor muscles; *Az* autozooid; *c* ciliary tuft; *m* mouth; *ma* mandible; *O* orifice; *p* peduncle; *rm* retractor muscles; *t* tentacles; *vp* vestigial polypide. *Scale bar* 50 μm

Adventitious avicularia occur in higher frequencies in natural populations relative to interzooidal, vibracular, and vicarious types (Hyman 1959; Carter et al. 2010b). Colony densities of adventitious avicularia are also higher (Carter et al. 2010b) and may represent an adaptive response with ecological and evolutionary implications for the division of labor within the colony, metabolic translocation to non-feeding polymorphs, and overall colony integration. Relegating adventitious avicularia to the level of the autozooid (by budding on the frontal wall) can potentially maximize integration and functional capacity throughout a colony (Carter et al. 2010b).

In summary, the occurrence of transitional stages of avicularia in the fossil record and developmental stages in Recent avicularia support the case for multiple originations of avicularia. Also, the co-occurrence of alternate phenotypes (i.e., autozooids and avicularia) within genetic individuals of cheilostome bryozoans has facilitated a redirection in colony functioning. The evolution of adventitious avicularia that was likely driven by persistent zooid-level predators can be considered an essential development in enhancing function.

Polymorphism and a diffuse, persistent selective force

Do ecological interactions among individual organisms matter in large-scale macroevolutionary trends? What salient factor or factors of natural selection could have led to the repeated evolution of forms within each of these three categories of structures, and in widely disparate lineages scattered over the ∼145 million year geologic history of cheilostomes? And how are these factors to be understood as operating in trends of diversification and persistence, sustained over such a long span of time? As Jackson pointed out (1988, p. 311), "most macroevolutionary trends … are diffuse", and if "ecological
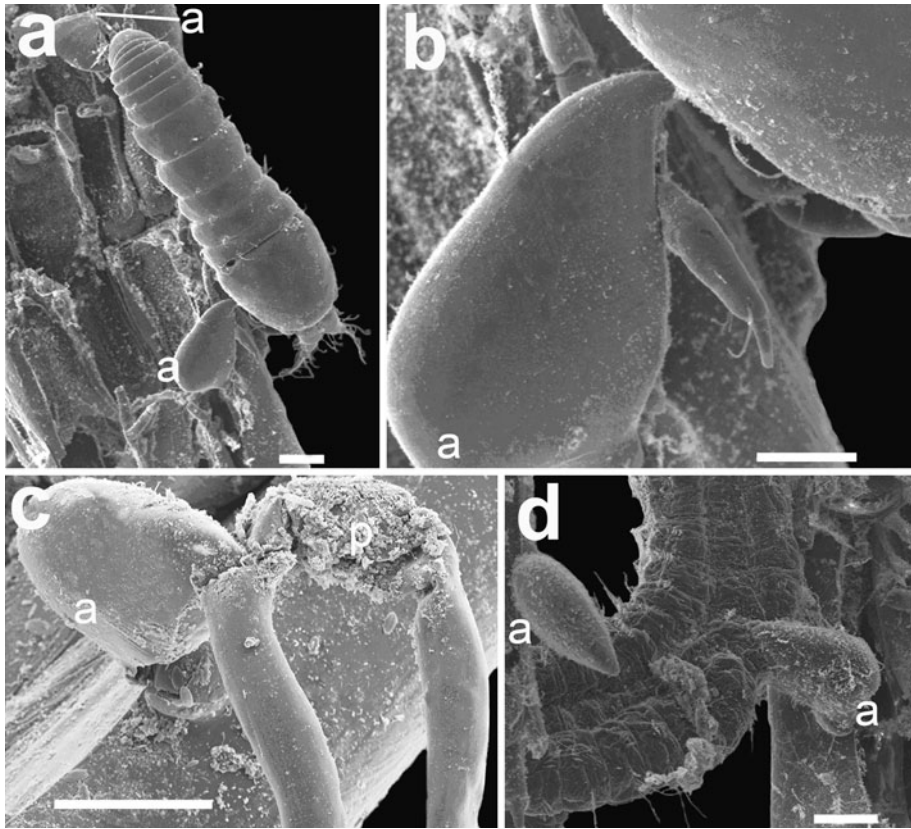
Fig. 8 Scanning electron micrographs of the bird's-head avicularia of *B. flabellata* and captured invertebrates. **a** Captured harpacticoid copepod. Scale bar 100 μm. **b** Enlargement from (**a**) showing an avicularium trapping one of the copepod's legs. *Scale bar* 50 μm. **c** Palp of a *Polydora* sp. (Spionidae) polychaete worm. *Scale bar* 100 μm. **d** Polychaete grasped by two avicularia. *Scale bar* 100 μm. *a* avicularia. After Carter et al. in press

interactions drive these patterns, then the interactions must be basic to macroevolution." We suggest that predation by small invertebrate epibionts has played a key role in the repeated evolutionary innovations in polymorphs (avicularia) and structures that evolved from polymorphs or other modules (brood chambers; costal, umbonuloid, and lepralioid autozooidal frontal shields) have a defensive function in many or most instances, sometimes in addition to other roles, reflecting a division of labor within colonies. The transitions in polymorph development and correlated trends in taxonomic diversification and persistence are undoubtedly due to a range of selective forces, but complementary ecological and paleontological evidence points us toward this hypothesis. We noted earlier that it is nearly always evolutionary outcomes or patterns, not processes, that are discernable in the fossil record.

In empirical testing of biotically driven trends in the fossil record, the mechanisms of selection are (and perhaps always will be) unobservable. They are inferred post-hoc from prey damage and repair, with actual predator types sometimes identifiable from traces such as the stellate gouges made by grazing echinoids (McKinney et al. 2003). These inferences

depend on an axiom that is essentially uniformitarian (an assumption that processes operating today have operated in much the same way in the distant past). It asserts that living predators and prey in the same (or similar) taxa are functionally analogous to fossil ones. This axiom and analogous ones underpin the inference of all biotic interactions as processes in the fossil record; this mode of inference appears to be one of the few means available for integration of approaches across different temporal scales. The fossil record and comparative morphology aid in piecing together a story about what *happened* and evolutionary ecology helps tell us about what *happens*.

Ecological evidence for the importance of epibiont predators is consistent with our hypothesis. One of the commonest fates of all organisms is to be eaten alive, in whole or in part, and species' interactions with enemies (*sensu* Vermeij 1994) are environmentally heterogeneous. A broad survey and analysis of bryozoan predators found that generalist consumers such as fishes and decapods remove significant portions of colony, while boring and suctorial predators including turbellarian flatworms, nematodes, syllid polychaetes, amphipods, copepods, pycnogonids, and both juvenile and adult prosobranch and opisthobranch gastropods generally damage one or a few zooids per attack (Lidgard 2008a, b). These smaller epibiont predators are extremely common on or near colonies, and most have low metabolic rates commensurate with the low caloric values of bryozoan prey; bryozoans typically constitute a large fraction or all of their diets by weight or volume. In contrast, bryozoans typically contribute a small to negligible fraction to the diets of their macro-scale predators, and these predators tend to have higher metabolic rates, unlikely to be sustained by bryozoan prey alone. Studies of the frequency of partial predation on bryozoans are lacking, but the consequences of injury for individual fitness and evolution of bryozoans and marine invertebrates in general are substantial and greatly under-appreciated (Vermeij 1982; Lidgard 2008a, b, 2010; Lindsay 2010).

The crushing or scraping mechanical forces exerted by macro-scale generalist predators greatly exceed the material strength of cheilostome skeletons (Best and Winston 1984), negating any passive or active defensive role of polymorphs. However, deterrence of small epibiont predators is supported by the available evidence (Lidgard 2008a). Active deterrence or protection is seen in the trapping of epibionts by avicularia, as described above. Passive protection is seen in the physical barriers provided by frontal shields and ovicells. Brooding within the main body cavity may be another evolutionary response to epibiont predators that feed on embryos held in the relatively exposed or acleithral ovicells (Ostrovsky et al. 2006, 2009b). Many epibiont predators feed preferentially on still-uncalcified zooid buds, and everted and unprotected polypides, or gain access to soft tissues and coelomic fluid through uncalcified opercula or membranous frontal walls (Best and Winston 1984; Lidgard 2008a). Experimental predation studies have shown that in *Membranipora*, with only a membranous frontal wall, simulated or controlled predation can induce the onset of colony reproduction, or the formation of spines that diminish zooid loss (Harvell 1984; Iyengar and Harvell 2002). Further, incomplete boreholes evincing unsuccessful epibiont predation attempts through frontal shields and ovicells are reported from both living and fossil colonies. Frequent regeneration of zooids within the confines of single damaged cystids—where surrounding zooids are undamaged—provides further evidence of the commonness of epibiont predation (Berning 2008), with attendant consequences for fitness. This zooid-scale regeneration is present even in the earliest cheilostomes with membranous frontal walls, and is part of a skeletal fossil record of successful and unsuccessful attacks that attests to a range of invertebrate predators as a continuous, environmentally heterogeneous, and diffuse selective force (McKinney et al. 2003). Our suggested corollaries are the broad secular increases from the Late Cretaceous onward of

calcified armament of the frontal wall of the zooid (frontal shields and ovicells), and of the occurrence of avicularia with defensive capabilities.

Finally, alternative hypotheses are unlikely to explain fully the repeated evolutionary patterns and diversity trends across the three polymorph categories. We acknowledge fully the likelihood that certain variants of ovicells and avicularia have additional functional roles, which implicates selective forces other than predation. For example, in certain species, different types of avicularia clear debris from the colony surface, permit colony movement or even locomotion, (possibly) permit chemosensory signaling or efficient flow of feeding currents, or fulfill other needs (Winston 1984, 2010). Yet these other functions do not account for trapping invertebrate epibionts and are not demonstrably of greater ecological significance than defense.

Similarly, differential maternal allocation to oocytes and embryos across the various cheilostome reproductive patterns involving brooding may be advantageous to species through fitness advantages of enhanced developmental plasticity and trans-generational effects in variable or unpredictable environments (Ostrovsky et al. 2009a). Where placental brooding occurs in ovicells, the calcareous structure also provides support for tissues that facilitate translocation of nutrients. Yet reinforced ovicells are most common in species with macrolecithal oocytes that develop into larvae without placentation.

Other than defense, we can offer no obvious alternative function for calcified frontal shields. The possibility that repeated evolutionary transitions to polymorphism and large-scale increase in the frequency of these polymorphs was driven by chance alone is rejected largely on the basis of costs. Division of labor by non-feeding polymorphs (or modular structures) for whole-colony efficiency exacts costs that must exist if nutritional resources are at all limiting (Gordon et al. 1987), with obvious implications for fitness. Calcification itself, and additional tissue needed to form and maintain these polymorphs, also incur metabolic expenses. In certain species, thickened calcification of frontal shields and ovicells exceeds the depth of the body chamber itself; while this phenomenon may contribute to breakage resistance in rigid erect colonies, it also occurs in encrusting ones. One possible alternative hypothesis, that calcification of tissues serves to balance or remove excess carbonate, explains neither the existence and ubiquity of avicularia, nor the abundance of polymorph-bearing taxa at great depths or in boreal-arctic regions where carbonate dissolution is the norm. Thus in response to Jackson's (1988) question, we hope that our empirical results and reasoning have shown that for the repeated evolution of cheilostome polymorphisms, ecology does matter.

Discussion

The association between division of labor and polymorphism in colonial animals and higher plants has deep roots that carry functional (adaptive) freight, and extend back to the mid-19th Century and even further. These concepts coincide with an underlying problem, the nature of biological individuality, and this problem also underlies modern concepts of biological modularity (Elwick 2007; Clarke 2011; Nyhart and Lidgard 2011). In the broad sense (Schlosser and Wagner 2004), "modular organisms" are understood primarily as plants and colonial animals whose bodies are formed by iteration of structural morphological units (Jackson et al. 1986; Vuorisalo and Tuomi 1986). Colonial protists and bacteria, as well as fungi, also are often regarded as modular. The rapid expansion of the modularity concept in evo-devo, molecular genetics, proteomics and elsewhere has led to different types of criteria for recognizing modular units: functional, developmental,

genetic, geometric, and structural, as well as foci of Darwinian selection. Similarly, polymorphism has taken on meanings beyond distinct morphological phenotypes within a colony. For geneticists, polymorphism connotes genetic polymorphism. Many other biologists regard 'polymorphisms' only as alternate phenotypes under strict genetic control, using 'polyphenisms' to describe alternate forms that develop in response to either internal or external environmental cues (Gilbert and Epel 2008). Bryozoan polymorphs as the term is used here almost certainly occur across taxa in a continuum of stages, from environmentally cued or directed polyphenism at one end to strictly programmed genetic polymorphism at the other. Knowledge of the genetic and developmental mechanisms producing these alternate phenotypes is lacking for bryozoans and most other modular organisms producing alternate phenotypes. Nonetheless, the patterns demonstrated here bear importantly on the origins of intra- and interspecific diversity, on transitions between environmental, genetic, and epigenetic control in phenotype development (Kalisz and Kramer 2008; Schwander and Leimar 2011), and on the interplay of adaptation, constraint and convergence (Losos 2011).

Partitioning organic wholes is hardly simple, and the distinction between zooid polymorph, module, and part is blurred by the use of different criteria for recognition. Even among the authors of this paper, there are slightly different views on what constitutes a "zooid polymorph," partly reflecting different weighting of criteria. Our use of the term "polymorph" is not necessarily the only one, nor the definitive one. For example, to this point we have presented a compromise view that through heterochrony and the reorganization of developmental pathways, evolutionary composite umbonuloid and lepralioid frontal shields (Fig. 1) are now (morphogenetically and functionally) simply components of autozooids. All ascophoran frontal shields are highly integrated with the ascus, without which the zooid would be wholly dysfunctional because it could not extrude the lophophore to feed, thus leading to the necessary interpretation of autozooid and shield together as a *functional* module. However, one could privilege the *morphological* criterion of the separation of coelomic cavities and communication between cavities via pore-cell complexes as the primary concept of a zooid polymorph. On this view, umbonuloid and lepralioid shield types would be considered independent kenozooid polymorphs. Further, the structural member of a colony that extrudes the polypide would thus be a composite of a kenozooidal and a feeding polymorph, or a cormidium (Beklemishev 1969). In a second example, Calvet (1900) and Silén (1942) argued that spines are zooidal polymorphs. In most, though not all of the Recent species where detailed anatomical work has been performed, spines are hollow outgrowths of the zooidal body wall. In such cases, pore-cell complexes between spine and zooidal coeloms are absent (Ostrovsky 1998), though they may have been present in ancestral forms. In a third example, ovicells (as ooecia) have been considered as polymorphic zooids since the mid-nineteenth century. Nonetheless, in most cases they lack a specialized pore-cell complex(es) in the ooecial communication pore(s) connecting them to the main zooid body cavity. It is conceivable that ancestral transitions may link some ovicells to ancestral kenozooids with communication pores. Species in a few Recent genera—*Cauloramphus, Scruparia, Bellulopora*, and in family Alysidiidae—do have pore-cell complexes that connect the coelomic chambers of ooecial lobes or costae with the main body coelom. These Recent taxa likely represent independent originations of ovicells.

From a rather different perspective, *any* polymorph category in bryozoans or other physiologically contiguous colonial animals could be regarded as a developmental module using a familiar criterion of differentiation from a cell condensation as a morphogenetic unit (Hall 2003). Looking beyond bryozoans, siphonophores are often considered as the most functionally integrated colonial group, with extremely high levels of polymorphism
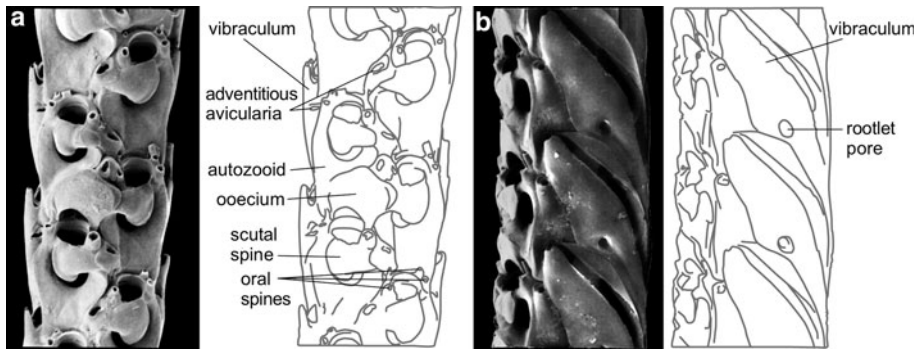
Fig. 9 Replicated cormidia forming part of a biserial branch of *Caberea solida* Gordon, 1986, shown in **a** frontal and **b** lateral views. The cormidia each comprise ten modules—autozooid, oecium, two adventious avicularia, three articulated oral-spine bases, flattened scutal spine, vibraculum, and rootlet [pore of origination evident in (**b**)]

among polyp-like modules. Siphonophores have a more or less confluent gastrovascular system. Here, pore cell complexes and body cavity partitions are not cited in delimiting modular polymorphs. Among plants, the descriptive terms 'phyton' and 'metamer,' referring to repeated units of plant structure combining leaf, node, internode, axillary bud, and so on, have been in use for over a century (Geddes and Mitchell 1911). They can now be understood in terms of iterated modules produced by differentiation of totipotent cells in an apical meristem (Barthélémy and Caraglio 2007). In a macroevolutionary pattern roughly analogous to the diversification of cheilostomes, there is significant evidence that modular structures such as roots and leaves have had multiple evolutionary origins (Boyce 2010), though their *morphological* and *physiological* partitioning is quite different from that of zooid or polyp modules in any colonial animal.

The modular concept can also apply to polymorphic clusters in cheilostomes. For example, a single autozooid of *Caberea* can support up to ten primary polymorphic modules (Fig. 9), depending on the species. Each autozooid and its subordinate modules constitute a cormidium, iterated in biserial fashion along each branch and exhibiting threshold levels of coordinated responses. The autozooid and all its polymorphic attachments could be considered a single developmental or structural module at a higher organizational level (Vuorisalo and Tuomi 1986; Hageman 2003). Dunn (2005) has shown that in some siphonophores, a single bud subdivides to form a sequence of zooids with alternate morphologies; different criteria could discern this as a single module or polymorph, or several. While the above considerations may appear to be mere semantic differences, in actuality they reflect complementary perspectives on the repeated evolution of polymorphisms. Exploring and comparing different criteria—functional, developmental, genetic, geometric, structural, focal units of Darwinian selection—for individuating modules within a living being may help develop not just a broader understanding of bryozoan evolution, but of parts, polymorphs, and hierarchies in other organisms as well.

Summary

Zooid budding is intrinsic to colony formation in modular organisms like bryozoans. Growth by iteration of units and variation among these units creates a space for

developmental selection at the zooid level of phenotypic traits and their developmental pathways. In cheilostomes, this apparent potential for evolvability has been realized in the repeated evolution of zooid polymorphs. In different types of zooidal polymorphs (avicularia) and skeletal structures that evolved from polymorphs or other modules (spinocystal, umbonuloid, and lepralioid frontal shields; ovicells), alternate phenotypes have arisen at different times in geologic history and among disparate lineages. While evidence of paleontological and ecological processes is incomplete, it is consistent with an hypothesis that division of labor evident in the morphology and functional capacity of polymorphic zooids likely evolved—at least in part—in response to a persistent, diffuse selective force: predation by small invertebrate epibionts.

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