

REVIEW

Coloniality, clonality, and modularity in animals: The elephant in the room

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Abstract

Nearly half of the animal phyla contain species that propagate asexually via agametic reproduction, often forming colonies of genetically identical modules, that is, ramets, zooids, or polyps. Clonal reproduction, colony formation, and modular organization have important consequences for many aspects of organismal biology. Theories in ecology, evolution, and development are often based on unitary and, mainly, strictly sexually reproducing organisms, and though colonial animals dominate many marine ecosystems and habitats, recognized concepts for the study of clonal species are often lacking. In this review, we present an overview of the study of colonial and clonal animals, from the historic interests in this subject to modern research in a range of topics, including immunology, stem cell biology, aging, biogeography, and ecology. We attempt to portray the fundamental questions lying behind the biology of colonial animals, focusing on how colonial animals challenge several dogmas in biology as well as the remaining puzzles still to be answered, of which there are many.

KEYWORDS

agametic development, allorecognition, immortality, individuality, major evolutionary transitions, polymorphism, superorganism, units of selection

1 | INTRODUCTION

Most living animals reproduce sexually, a strategy that is regarded as evolutionary advantageous in allowing rapid adaptation to constantly changing environments by providing new gene combinations and removal of deleterious mutations (reviewed by West, Lively, & Read, 1999). However, other reproductive modes coexist and at least half of all animal phyla contain species that can propagate asexually via agametic reproduction (Blackstone & Jasker, 2003; Buss, 1983a; R. N. Hughes, 1989; Sköld, Obst, Sköld, & Åkesson, 2009). Agametic reproduction differs from parthenogenesis in which unfertilized eggs develop. Instead, agametic cloning occurs when a species propagates asexually, by budding, fission, autofragmentation with subsequent rejuvenation, or production of resting bodies, forming a set of genetically identical modules. The modular units are termed zooids (e.g., in tunicates and bryozoans),

ramets, or polyps (e.g., in cnidarians). These units can either remain connected physically and physiologically to one another forming temporary or permanent colonies (Beklemishev, 1969; Blackstone & Jasker, 2003; Boardman, Cheetham, & Oliver, 1973; R. N. Hughes, 1989; Mackie, Harper, Rosen, & White, 1986; Rosen, 1979), or stay nearby each other but lose their reciprocal connection forming clones or clonal aggregates (Buss, 1983a). The genetically identical colony or aggregate is often referred to as a genet (R. N. Hughes, 1989).

Though clonal and colonial animals are a major component of global biodiversity (Jackson, 1977), "...so much of the study of ecology and evolution has been based on the behavior of unitary organisms" (Harper, 1985). Thus, animals that adopt clonal reproduction or colony formation challenge ecological and evolutionary theories often developed to implicitly fit populations of sexually reproducing organisms (Harper, 1985; Williams, 1986). The biology of colonial organisms

tests the notion of individuality itself and concepts like kin selection, and the inheritance of somatic mutations, extending the hierarchy of units of selection. Asexual ontogenesis hardly fits text-book definitions and categories coined for embryonic development such as the very existence of germ layers or mosaic and regulative development. By replacing (or repairing) modules, colonial organisms can delay senescence and this leads to virtually indefinite growth, defying current evolutionary theories of aging (R. N. Hughes, 1989; Winston, 2010). In this review, we start by presenting an excerpt from the historical perspective of issues raised by animal coloniality. Then, we provide a bird's-eye view of the main aspects of the biology of colonial and clonally-aggregating metazoans and their challenges for ecology, developmental, and evolutionary biology.

2 | SOME HISTORICAL QUANDARIES ON COLONIALITY

Despite their underrepresented presence in modern biology, fascination for colonial organisms dates back centuries, and the philosophical debate consequently raised is surprisingly rich. Far from providing an exhaustive outline, we focus on selected facets of such debates. Early philosophers and zoologists (dating back to Aristotle's time) noted the similarities of corals, hydroids, bryozoans, and sponges, to the plants, both in terms of their appearance and mode of growth (e.g., Johnston, 1847; reviewed by Gibson, 2012), in fact, until not more than a century ago colonial animals were grouped together as "zoophytes", a term that emphasizes the uncertainty of their affiliation with either animals or plants or even their chimeras. A. Trembley (1710–1784) and J. Ellis (1710–1776), among others, worked on cnidarians ("animal-flowers") and sponges and offered arguably convincing evidence that these species were "compound animals" (Ellis, 1767; Trembley, 1986). This body of zoological studies was later reviewed in popular natural history volumes to help to establish the zoophytes as animals in the minds of naturalists (Buffon, 1804, 1749; Goldsmith, 1774; reviewed by Gibson, 2012).

In the Victorian era "compound individuality" became a major philosophical issue (reviewed by Nyhart & Lidgard, 2011). At the center of this debate was how to define an individual in the context of a colony or in the context of a lifecycle that included alterations in form between generations (T. H. Huxley, 1852; Owen, 1856). On one side of the debate, were the supporters of the idea that "the individual animal is the sum of the phenomena presented by a single life, in other words, all those animal forms which proceed from a single egg taken together" (T. H. Huxley, 1852, p 188). Thus, according to this so-called "poly-organ" theory, a colony would be considered one individual and the parts that arise as buds as mere organs (W. B. Carpenter, 1848; T. H. Huxley, 1852). On the other side were supporters of the "poly-person" theory—the idea that each member of the colony is like a separate individual living in a society (Leuckart, 1851; Vogt, 1847). The debate ran into the late 19th century when cell theory was being developed. Some believed that a multicellular organism could be considered a colony of cells

(e.g., Perrier, 1881). This conception led to the organization of individuality into hierarchical levels, from cells to organs to organisms to what Haeckel called a "cormus", (i.e., a colony; Haeckel, 1866) and what Spencer called a "superorganic" aggregate (i.e., a society; Spencer, 1904). It was suggested that as evolution progresses toward higher levels of this hierarchy, the lower levels individuals lose "rights" to the higher levels (Haeckel, 1904).

Animal coloniality came back into the spotlight in the middle of the 20th century, partly because colonial organisms did not neatly fit into the models of population biology developed around solitary organisms as part of the Modern Synthesis. Beklemishev's (1950, 1969) work and set the stage for modern ideas on animal colonies. First, he defined a colony as consisting of individual members that arise asexually from a founder and remain in connection, allowing for the life-long exchange of substances and for the coordination of behavior and growth (Beklemishev, 1950, p 93). Beklemishev also devised a series of evolutionary stages involved in "the weakening of the individuality of zooids" and in the "intensification of the individuality of the colony" eventually reaching "individuals of a higher order" (Beklemishev, 1969).

Harper's (1977) book on plant ecology introduced the concept of modularity in plant forms, which was later extended to colonial animals. Harper used the term module, "a repeated unit of a multicellular structure normally arranged in a branch system," to describe the products of the apical meristem (Harper, 1980). Barrington (1967) and Boardman et al. (1973) helped solidify the modern definition of colonial animals as those whose members are physically connected and who possess common ancestry through asexual reproduction. A 1985 book (Jackson, Buss, Cook, & Ashmun, 1985), based on a conference on coloniality, emphasized that "the way that a clonal organism occupies space, as connected or disconnected ramets, is fundamental to its prosperity in different situations, both in terms of its functional integration and chance of survival against different forms of adversity." This book also reiterated that "nowhere else do notions of what is an individual, or what are the fundamental units of selection, become more clouded than for clonal organisms." Units of selection was a major topic during this time as group selection was being reinvented in the late 1980s. This brought along the revival of the term "superorganisms", which was used by Wheeler (1911) to describe social insects. The concept was later applied to colonial animals with a superorganism being defined as "a collection of single creatures that together possess the functional organization implicit in the formal definition of organism" (Wilson & Sober, 1989, p 339). Thus, the ideas related to hierarchy in individuality and evolution reemerged.

3 | DEVELOPMENT WITHOUT AN EMBRYO

Most colonial and clonal animals reproduce both sexually and asexually and have a disparate array of complex life cycles. Still, during sexual reproduction, the development of the body begins with a fertilized egg, and processes such as cell-fate choice, symmetry

breaking, and axis formation occur in the context of embryogenesis. However, during asexual propagation, an adult body is built through nonembryonic development (Alié et al., 2018), and the “originator,” that is, the cellular source of the emerging new body, is not the fusion of two gametes but somatic cells. Note that this does not include polyembryony, which while constituting clonal reproduction, is a type of embryonic development.

Clonal development necessitates population(s) of somatic stem cells that display different degrees of potency, or by fully differentiated somatic tissues with the ability to dedifferentiate or transdifferentiate, or through the combination of these two mechanisms (e.g., Cartwright, 2003; Kürn, Rendulic, Tiozzo, & Lauzon, 2011; Reinhardt, Broun, Blitz, & Bode, 2004; Sköld et al., 2009).

New modules arise by fission/laceration in a variety of taxa. This includes, but is not limited to, some anthozoans, a number of larval and adult echinoderms, some polychaetes, some nemerteans, xenoturbellids, and some ctenophores (R. N. Hughes, 1989; Sköld et al., 2009). In a number of these species, such as many echinoderms, subsequent regeneration involves the recruitment of undifferentiated cell types (Candia Carnevali, 2006).

New modules may arise by budding to form temporary colonies, such as in phoronids, cyclophorans, some turbellarian flatworms, and trematodes, among others (R. N. Hughes, 1989). In cyclophorans, buds arise from undifferentiated mesenchymal cells in the trunk. In the case of phoronids and many others, the source of the differentiating tissue of the bud is unknown (Zimmer, 1991).

Tissue/cell sources underlying budding in true colonies have only been investigated in a few species. In some hydrozoans (e.g., *Hydractinia*), the interstitial cells (i-cells) have the potential to give rise to all tissues of the developing polyp (Frank, Plickert, & Müller, 2009). Blood-borne circulating stem cells have also been documented to contribute to body tissues in some species of colonial ascidian (e.g., *Perophora viridis* and *Botrylloides leachi*; Freeman, 1964; Kassmer, Langenbacher, & de Tomaso, 2019). In other species of colonial ascidians, such as *Polyandrocarpa misakiensis*, a new zooid arises mostly from the folding of a parental fully differentiated epithelium that undergoes transdifferentiation (Kawamura & Fujiwara, 1995). In the hydrozoan *Podocoryne*, both stem cells and transdifferentiating somatic cells contribute to the formation of the new module (Schmid, Wydler, & Alder, 1982). Totipotent archeocytes have been documented in demosponges (Alié et al., 2018; Funayama, 2013), although whether sponges can be considered true colonies is unclear (Lanna et al., in review). Whether rhizocephalan barnacles should be defined as colonies is also unclear (Blackstone & Jasker, 2003), but it has been reported that totipotent stem cells are involved in asexual budding of the interna of the parasitic stage (Shukalyuk, Isaeva, Kizilova, & Baiborodin, 2005).

Interestingly, despite the nature of the originator, somatic mutations can propagate within the colony to the next asexual generation through the budding tissues or even disseminate through the production of propagules (see review by Gill, Chao, Perkins, & Wolf, 1995). In addition, in several colonial animals, populations of long-lived germline precursors can persist throughout asexual

propagation and are also subject to heritable somatic mutations (see Section 6, Brown & Swalla, 2012; Buss, 1982, 1987; Whittle & Extavour, 2017). In this sense, nonembryonic development challenges Weismann's paradigm that asserts that heritable variation can only be passed through the germline (Buss, 1987), raising questions about the nature and level of the unit of selection in these organisms.

This dilemma has recently been investigated phenotypically in the bryozoan genus *Stylopoma*, using quantitative genetic techniques (Simpson, Herrera-Cubilla, & Jackson, 2020). Surprisingly, asexually-produced mother and daughter zooids are not morphometrically similar. In other words, the phenotypic heritability among asexual members is effectively zero. This result is interpreted as an adaptation to prevent colonies from evolving in response to what is likely to be ubiquitous selection among zooid lineages as the colonies grow and compete ecologically. Moreover, colony-level traits, those traits that consist of geometries among and numbers of polymorphic zooids are shown to be heritable among generations of sexually produced colonies. Consequently, *Stylopoma* preserves Weismann's paradigm but does so at the level of the colony, not the member animal.

Nonembryonic development also circumvents the concepts of determinative or regulative development, common to embryology and undertakes completely different ontogenetic pathways, sometimes skipping intermediate stages, that is, larvae and metamorphosis and often, but not always, leading to adult bodies almost indistinguishable from the sexually derived ones (O'Dea, 2006).

The underlying regulatory mechanisms for cell specification and morphogenesis in asexual development appear to have coopted signaling pathways and regulatory modules from their respective embryonic developments (Prünster, Ricci, Brown, & Tiozzo, 2019a, 2019b; Ricci et al., 2016). For instance, in the ascidian *Botryllus schlosseri*, young buds reuse “germ layer markers” during a phase of tissue specification, cell type diversification, and spatial rearrangement that may be compared to the drastic cellular and structural changes that occur during embryonic gastrulation. By disrupting the embryonic anteroposterior axis signals, retinoic acid and wnt pathway, axis formation is impaired during cnidarian (Nawrocki & Cartwright, 2013; Philipp et al., 2009) and ascidian (Di Maio, Setar, Tiozzo, & de Tomaso, 2015) budding. Genes cassettes that regulate left-right symmetries (Tiozzo & de Tomaso, 2009; Tiozzo et al., 2005), myogenesis, and neurogenesis (Prünster et al., 2019a, 2019b) have also been shown to be redeployed during budding of some ascidians. For regeneration and fission in some cnidarians, the gene modules from embryogenesis, such as those for cell proliferation, have been shown to be redeployed (Warner, Amiel, Johnston, & Röttinger, 2019). Even in cnidarian species with true colony-production, such as *Hydractinia*, some genes originally known from embryogenesis are involved in polyp formation and in the differentiation of polymorphic polyp types (Sanders, Shcheglovitova, & Cartwright, 2014). Embryonic developmental genes have also been reported in bryozoan budding (Treibergs, 2019) and in siphonophores (Siebert et al., 2011).

Interestingly, the species that stand out as having the ability to regenerate the entire bodies from minute numbers of cells (i.e., those

capable of “whole-body regeneration”, including *Hydra*, planarians, and some colonial ascidians) are also capable of asexual propagation. In some cases, the results of these two ontogeneses are indistinguishable except for the triggering cause, that is, injury versus asexual lifecycle (Hand and Uhlinger, 1995). Some authors hypothesized that various forms of regeneration could have been originated via the cooption of asexual reproductive processes (Alvarado, 2000). Whole-body regeneration also coopts embryonic regulative mechanisms (Ricci et al., 2016; Tiozzo & Copley, 2015; Warner et al., 2019) suggesting that both asexual development and regeneration are likely epiphenomena of embryonic development (Tiozzo & Copley, 2015). Studying nonembryonic development, that is, asexual development and whole-body regeneration, and particularly the cooption of embryonic modules and their rewiring in completely different morphological contexts, are very promising and potentially informative to understand the evolution and the plasticity of the animal developmental program, and perhaps to uncover mechanisms of tissues and organ regeneration (Tiozzo & Copley, 2015).

4 | SETTING BACK AGING: UNDETERMINED GROWTH AND DELAYED SENESENCE

Aging, namely the progressive loss of physiological integrity, is different in colonial animals as compared with the aging of unitary animals (Nilsson Sköld & Obst, 2011; Orive, 1995). Colonial animals constantly add, replace, and repair their modules. Though the lifespan of each ramet is generally constrained, the whole colony ages at a slower rate (Reichard, 2017). Thus, the development, growth, and death of the modules can be considered part of colony homeostasis. Such “extended homeostasis” allows single genotypes to survive for decades or even millennia, like in the case of Caribbean brain coral and some deep-sea corals (Roark, Guilderson, Dunbar, Fallon, & Mucciarone, 2009) and Antarctic sponges (Dayton, Robilliard, Paine, & Dayton, 1974).

Colonial animals may undergo cyclical replacement and/or retrogression of functional modules, interfering with the progressive accumulation of somatic problems (mutation, oxidative stress, telomere shortening, accumulation of waste products, etc.) that typically cause aging of unitary organisms (Kirkwood & Austad, 2000; López-Otín, Blasco, Partridge, Serrano, & Kroemer, 2013). For example, some colonial ascidians undergo “takeover,” whereby old zooids undergo cell death and are replaced by newly-formed buds (Lauzon, Rinkevich, Patton, & Weissman, 2000). Bryozoans also undergo cyclical regression of the polypides (brown body formation) and renewal (reviewed by Gordon, 1977). Brown body formation, that is, degenerating zooids, has also been observed in colonial hemichordates (Stebbing, 1970). Thecate hydrozoans also have cycles of degeneration and regeneration and entoprocts periodically renew their calyx (Crowell, 1953; Harmer, 1886). Cycles of replacement and renewal are also found in nonaggregating clonal species such as some cnidarians and flatworms (Bosch, 2009; Saló, 2006).

Further contribution to the longevity of a colony comes from the ability of many species to go dormant, that is, modules or whole colonies enter a state of physiological and morphological inactivity usually by structurally simplifying their body and enriching them with population(s) of undifferentiated cells (Cáceres, 1997; Coma, Ribes, Gili, & Zabala, 2000). Other processes of structural simplification that contribute to extend the lifespan and to delay senescence of the genet occurs during cyclic retrogression to “younger” developmental stages. It is the case of hydrozoan known as “immortal jellyfish” (*Turritopsis*; Piraino, Boero, Aeschbach, & Schmid, 1996), in which the mature reproducing medusa can degenerate, undergo cellular reorganization, and form a new larval polyp. Some scyphozoans show similar simplification processes (He, Zheng, Zhang, & Lin, 2015), which have been described as “tissue saving” (Silveira, Jarms, & Morandini, 2002) or “reverse development” (Piraino, de Vito, Schmich, Bouillon, & Boero, 2004).

One of the basic assumptions of the classic evolutionary theories of aging is the early separation between somatic cells and germline (Kirkwood, 1977; Medawar, 1952; Weismann, 1893). The trade-off between germline protection versus somatic cell repair is the main hypothesis for functional and reproductive aging (Maklakov & Immler, 2016). As introduced in the previous chapter, in clonal animals this distinction is not always straightforward (Blackstone & Jasker, 2003; Siebert et al., 2015; Simpson, 2011): modules may keep recruiting germline precursors in their body and somatic cells can retain toti/multipotency (see Section 3, Buss, 1983b; Extavour & Akam, 2003). One consequence is an altered balance between soma and germline (Buss, 1983b). It is important to point out that the germ soma distinction emerges at the colony level in species that are polymorphic (Simpson, 2012). Across polymorphic species, sexual zooids tend to become increasingly rare as the number of other polymorph types increases. In light of the germline hypothesis of aging, it would be interesting to know whether or not highly polymorphic species age differently than less polymorphic species. If not, this result at the whole-colony level may in turn shed light on the evolutionary role of the germline at the cellular level.

Telomerase attrition, stem cell exhaustion, and other hallmarks of aging (López-Otín et al., 2013) are mainly studied in unitary organisms. However, the molecular and cellular mechanisms that lie behind the longevity and the extended senescence of colonial and modular organisms are being uncovered in a few clonal species (Nilsson Sköld & Obst, 2011; Orive, 1995). Stem cell exhaustion is bypassed by a modification to cell cycle (G2 pausing, promoting DNA repair) and spatially-restricting the location of stem cells in *Hydra* (Buzgariu, Crescenzi, & Galliot, 2014). *Hydra* also relies on insulin and autophagy pathways to regulate nutrient-sensing to maintain the lifespan. *Hydra* has mechanisms to bypass mitochondrial dysfunction as well via constant activation of DNA repair pathways (reviewed by Schenkelaars et al., 2017). In two colonial ascidians telomerase activity, which is usually low in adult tissues, increases both in developing buds and in putative stem cells (Laird & Weissman, 2004; Nilsson Sköld & Obst, 2011). High telomerase activity has also been found in two marine demosponges, *Hydra*, and asexual, but not sexual planarians (Kozioł, Borojevic, Steffen, & Müller, 1998; Tan et al., 2012). Epigenetic alterations are limited in the stem cells of *Hydra* and high

cell turnover limits the accumulation of misfolded proteins (loss of protein homeostasis). However, telomerase activity and telomere length were found to be lower in one ascidian species propagated for years in the laboratory compared to their offspring, suggesting that molecular senescence does occur during agametic growth (Sköld, Asplund, Wood, & Bishop, 2011). But this is a species that sexually produces dormant eggs that allow for the survival of the winter, suggesting that selection pressure for maintaining telomerase activity beyond a year might not be present in the natural population. Indeed, models show a trade-off between sexual versus clonal reproduction that may or may not result in selection for clonal senescence (Gardner & Mangel, 1997). A better understanding of the genetic, epigenetic, and cellular processes involved in the diversity of colonial/clonal life cycles may provide breakthroughs in the science of aging, rejuvenation, and developmental biology in general (Nilsson Sköld & Obst, 2011).

5 | FUNCTIONAL SPECIALIZATION OF MODULES: THE RISE OF POLYMORPHISMS

Many, but not all, groups of colonial animals possess phenotypically distinct body types termed polymorphs. Polymorphs in colonial animals presumably evolve through similar evolutionary processes as the castes in eusocial insects and the cell types in multicellular organisms (Harvell, 1994; Simpson, 2012).

The benefits of polymorphism are likely to be profound because, through their diversity of functions, they allow an organism to operate efficiently (Beklemishev, 1969; J. Huxley, 1912; Weismann, 1893). The ecology of species that lack polymorphism must either adjust their physiology to accommodate changing environments or remain simple. Nevertheless, most group-living animals (including social insects and vertebrates along with colonial marine invertebrates) lack polymorphism—of the 226 independent origins of group-living, 172 lack polymorphism of any kind (Simpson, 2012).

Polymorphism has evolved in at least 10 phyla of animals (Beklemishev, 1969; Costa, 2006; Harvell, 1994; Wilson, 1975). Extreme polymorphism, with three or more polymorph types occurring within the same colony, is common in cnidarians, particularly in siphonophores (Dunn, 2009; Mackie et al., 1986; Munro et al., 2018; Pugh, 2003) and other hydrozoans (Cartwright & Nawrocki, 2010), bryozoans, especially the cheilostomes (D. J. Hughes & Jackson, 1990; Lidgard, Carter, Dick, Gordon, & Ostrovsky, 2012; Schack, Gordon, & Ryan, 2019; Silén, 1977; Simpson, Jackson, & Herrera-Cubilla, 2017), and in doliolid tunicates (Deibel & Lowen, 2012; Harvell, 1994). Schack et al. (2019) provides a wonderful recent review of the variety of polymorph types in marine invertebrates.

The independent origins of polymorphism in different phyla surprisingly share many general features (Beklemishev, 1969; Harvell, 1994; Lidgard et al., 2012; McShea, 2001; Simpson, 2012; Wilson, 1975). These similarities arise as convergent solutions to shared evolutionary problems. And in some cases, the rate at which

novelties originate may reflect group-specific constraints (Jablonski, Lidgard, & Taylor, 1997).

Polymorph types in fossil and living colonial invertebrates tend to exhibit discrete differences (Carter, Gordon, & Gardner, 2010a; Lidgard et al., 2012). In bryozoans, the conceptual model for the origin of polymorphism is a gradualistic divergence (Banta, 1973; Cheetham, 1973; Silén, 1977). The cheilostome genus *Steganoporella* possess morphologically similar A- and B-zooids and serves as an exemplar of this possible mode of evolution (Banta, 1973; McKinney & Jackson, 1989; Silén, 1977), but surprisingly there are few other examples (another possibility is the apical polyp in acroporan corals which is a little taller than other polyps).

The paucity of slight and gradualistic differentiation may, in fact, be informative. Inheriting multiple polymorph types across a colonial lifecycle is likely to be difficult and the first step is incorporating a unicellular stage in the lifecycle (Grosberg & Strathmann, 1998; Simpson, 2011, 2012). Furthermore, the evolution of inheritance may underpin the empirical observation that when polymorphism first evolves in a species the first division of labor is always reproductive. One of the polymorph types maintains sexual competency and functions as the reproductive specialist, whereas the remainder of polymorph types lack sexual ability (Simpson, 2012). Intriguingly, all phyla exhibit the pattern that the rarity of the sexual specialists decline in frequency as additional polymorph types evolve (Simpson, 2012). Although, why and how polymorphism evolves remains a mystery, it involves the evolution of colonial life cycles and the packaging of inheritance of the suite of polymorphism through a restricted number of reproductive specialists. Despite the similar evolutionary function among sexual polymorphs, at least in bryozoans, there is a remarkable diversity of forms that the sexual specialists take on including specialized structures that evolved from complexes of polymorphs that allow patterns of convergence to be identified (Ostrovsky, 2013; Ostrovsky & Taylor, 2005).

Given that colonial marine invertebrates are clonal, their polymorphism represents a crystallization of one of the most vexing problems in evolution and developmental biology—how do extreme phenotypic differences evolve with a minimum of genotypic change (Gould, 1977). The expression of many phenotypes with one (clonal) genotype must involve some sort of phenotypic plasticity. Evo-devo work on siphonophore polymorphism has highlighted the role of cell-level developmental processes in colony-level phenotypes (Dunn, 2005; Dunn & Wagner, 2006). Of particular importance are localized growth zones and the maintenance of populations of undifferentiated i-cells within them (Siebert et al., 2015), which likely permits differences in polymorphic body types to evolve just as modular characters within an organism do.

Many polymorph types are also facultative (Harvell, 1991) and colonies may be coordinated by decentralized mechanisms at unity of modules level, particularly in bryozoans. In some bryozoan genera such as genera within the Candidae (Vieira, Spencer Jones, Winston, Migotto, & Marques, 2014), both facultative and obligatory polymorphs may be present in the same colony. Lang (1921) points out the implausibility of inducible polymorphism being an evolutionary

path towards stable polymorphism because the simplest colonies phenotypically will need to be the most complex in terms of genetic regulation. What facultative and inducible polymorphism show, is that polymorphs are expensive to maintain given their inability to feed.

For any phenotypic trait to evolve, it requires preexisting variation for the selection to act. This is true for polymorphism as well. The initial origin of reproductive specialization may provide a clue as to where the phenotypic variation that polymorphism evolves from initially arose. All organisms possess a juvenile phase in which they lack reproductive capacity and additionally phenotypic variation over ontogeny can be extreme, especially with allometric growth. The stunting of juvenile development provides a possible mechanism for increasing phenotypic variation and introducing a reproductive division of labor. In this way, it is possible to conceive of doliolids or siphonophores as consisting of many parts of a complex lifecycle cooccurring together.

Ontogenetic truncation is similar but not strictly identical to heterochrony. Moreover, allometry, norms of reaction, and other expressions of the ability for a genotype to produce multiple phenotypes are likely to be involved in the evolution of polymorphism. Additional processes, such as the complexity drain, where organisms within hierarchical wholes (cells in a multicellular organism or animals within a colony) are less complex than their free-living counterparts (McShea, 2002; McShea & Changizi, 2003), are likely to be involved. One example of this in colonial invertebrates involves the modified function and simplification observed among different types of polymorphic avicularia in cheilostome bryozoans. Here, the polypide (food-gathering apparatus associated with a gut) in avicularia are reduced and feeding and other abilities are lost compared with the ancestral autozooid form (Carter, Gordon, & Gardner, 2010b).

In polymorphic species, the polymorphic animals within a colony lack much of the functionality of their solitary ancestors. This extreme phenotypic modification is possible only by virtue of the connectivity of animals within a colony, where other members of the colony can sustain the life of their reduced and modified colony mates.

6 | ECOLOGICAL SIGNIFICANCE OF COLONIALITY

The modular organization, physical connectivity, and clonal nature have important ecological consequences for the evolutionary potential of colonial animals (Burgess et al., 2017; R. N. Hughes, 2005). Often, colonial animals are constructed out of autonomous modules that can survive independently as well as connected. Because of this functionally autonomous modularity, colonial animals escape a number of constraints on growth and shape relative to their solitary counterparts. The release of these constraints allows for extensive morphological plasticity and flexibility (Kim & Lasker, 1998; Marfenin, 1997). For example, colonies can grow in various directions and even compete/overtake other sessile species that do not have such expansive capacity (Jackson, 1977). The capacity for directional growth allows for

exploitation of patchy resources and for the selection of spatial refuges, away from predators, competitors, and physical disturbances (Buss, 1979). Colony-level morphological plasticity also allows colonial forms to survive after partial predation, death, or damage (Berning, 2008; Hiebert, Vieira, Dias, Tiozzo, & Brown, 2019). However, regeneration comes with a potential cost—sponges and corals show reduced somatic growth, reduced sexual reproduction, and impaired ecological interactions after regeneration (Henry & Hart, 2005).

Reduced constraints on growth of colonies allow for an increase in biomass, and may even permit indeterminate growth. As modular animals can take up food across their whole surface and have the potential for sharing resources between members, their overall mass does not necessarily scale with their metabolic rate, unlike most solitary animals (Burgess et al., 2017).

With extensive plasticity in their morphology, colonial animals can make colony-level adjustments in response to the environment (Jackson & Coates, 1986). For example, a colony can adjust reproductive allocation (favoring asexual or sexual) with changing conditions or seasons (Nekliudova et al., 2019). Modular organisms may also adjust budding and branching patterns based on the local environment (Harper, 1977). Colonies with polymorphic zooid types may change the proportion of each morph to meet the needs of the living conditions, increasing defensive morphs if predators are abundant, for example (Harvell, 1990).

Many colonial species can undergo dormancy during unfavorable conditions. For example, freshwater bryozoans possess asexually derived structures called statoblasts that are able to withstand desiccation and other extremes that are common in freshwater systems. In some species, individual modular units in a colony undergo cycles of degeneration and regeneration (see Section 4), a process termed modular senescence (Palumbi & Jackson, 1983). In other cases, whole colonies seasonally degenerate and develop into resistance forms that survive to regenerate when conditions improve (Jackson & Coates, 1986).

Although colonial animals are widely distributed and present in a range of habitat types, they are found much more frequently, and with higher diversity, in some regions than others. For example, colonial forms may be rare in the intertidal and soft-sediment marine habitats (Jackson, 1977), although this is not true for all colonial species, such as bryozoans (Ryland, 1976). Colonial species are a dominant and highly diverse component of hard-substratum marine communities. Colonial tunicates appear to be more diverse in tropical and subtropical waters than in temperate and polar regions. It is possible that these latitudinal trends in diversity and abundance may be driven by the ability of colonial forms to withstand predation, their high competitive abilities, and their low susceptibility to fouling and overgrowth—all are traits favored in the highly diverse low latitudes, where substrata is limited and predation is high (Hiebert et al., 2019; Jackson, 1977; Kott, 1981). Scleractinian corals are also highly diverse in the tropics (Veron, Stafford-Smith, DeVantier, & Turak, 2015). However, polar bryozoans are very diverse and abundant (Hayward, 1995; Kluge, 1975). The diversity of many other colonial taxa remains understudied.

Parental care of offspring occurs more often in colonial species than in solitary (Ramirez, 2002). For example, most colonial tunicates brood embryos while most solitary tunicates are free-spawners. Brooding is also common in hydrozoans and octocorals (Bouillon, Gravili, Pagès, Gili, & Boero, 2006; Coelho & Lasker, 2014) and the vast majority of bryozoans incubate their young (Ostrovsky, 2013). Larvae of brooding colonial animals are often developmentally advanced at the time of release and often settle nearby (Jackson & Coates, 1986). Other modes of dispersal such as colony fragmentation also permit short-distance dispersal (O'Dea, 2006; O'Dea, Jackson, Taylor, & Rodriguez, 2008; O'Dea, Ostrovsky, & Rodriguez, 2010). Such modes of dispersal might be advantageous for colonial forms that are already adapted to take advantage of patchy resources, as larvae or colony fragments with long dispersal abilities that wander too far would be selected against. In likes of Baker's law (Baker, 1955; Stebbins, 1957), uniparental asexual reproduction, is expected to provide selective advantageous in colonizing situations for example, along an invasion front, or when colonizing disturbed habitats (Pannell et al., 2015). Yet, this strategy is expected to have the long-term effect of increasing extinction rates (Goldberg et al., 2010; Jackson & Coates, 1986). O'Dea and Jackson (2009) found that environmental changes that occurred during the closure of the isthmus of Panama lead to a shift in the dominant reproductive strategy (sexual founding or asexual fragmentation) within the cupuladriid bryozoans.

Another consequence of limited dispersal is that siblings, their parents, and even clonal-twins are often living side-by-side (Jackson & Coates, 1986). Thus, recognition of self versus non-self (and close relative) is likely useful in natural conditions (see next session).

7 | WHEN COLONY MEET COLONY: PUZZLING ASPECTS OF ALLORECOGNITION

Most colonial invertebrates such as many cnidarians, bryozoans, and ascidians are sessile and encrust benthic environments. While growing and competing for space they often encounter conspecifics with either no, or some degree of kinship. Once they come into contact, two (or more) colonies can maintain their physically separate identities either by activating an "aggressive" response or by coexisting peacefully and neighboring each other. Occasionally, colonies can undergo somatic fusion, sharing resources and forming genetic chimeras. Though aggressive rejection can put the colony at risk, the cost is balanced by the potential benefit of competition for space. In some cases, colony formation occurs by the fusion of nonclonal (sexually derived) individuals such as in the case of some hydrozoans (Chang, Orive, & Cartwright, 2018; Nawrocki & Cartwright, 2012).

Somatic fusion also has consequences on the fitness of each of the encountering partners. As mentioned in the previous chapter, from an ecological perspective an immediate benefit of fusion is an increase of size: larger colonies have better foraging capacity, produce more gametes, and are more likely to survive predation, physical damage, or diseases (Grosberg, 1988). A larger colony can also more efficiently colonize spatially separated substrates (Buss, 1982).

It has also been suggested that fusion of non-genetically identical colonies can produce "chimeric vigor" via increasing genetic diversity, which could be advantageous for adaptation to rapidly changing environments (M. A. Carpenter et al., 2011; Grosberg, Hedgecock, & Nelson, 2012). On the contrary, if the sharing is not equitable for both genets the fusion could represent a compelling cost for the loser. For instance, we have outlined in Sections 3 and 4 that some colonial species retain both somatic toti/multipotent stem cells, which are responsible for their asexual developments, and long-lived germline precursors (Brown et al., 2009). During fusion, these cell populations can circulate between two colonies and compete for establishing the germline and the soma throughout the life of the colony (Cadavid, 2005; Stoner, Rinkevich, & Weissman, 1999). In other words, through parasitic stem cells, one colony can force another one to produce its own gametes or change its soma. Indeed, this represents another cost of fusion.

The occurrence of fusion or rejection depends on the degree of compatibility between colonies, which is mediated by allorecognition systems that ultimately gives the colony the ability to distinguish between self and non-self (Grosberg, 1988). The molecular mechanisms of allorecognition have been mostly studied in colonial ascidians (de Tomaso, 2006; Voskoboinik & Weissman, 2015), *Hydractinia* (Grosberg, Levitan, & Cameron, 1996), and the sponge *Amphimedon queenslandica* (Grice et al., 2017) but have also been reported in other cnidarians and bryozoans (Hughes, Manríquez, Morley, Craig, & Bishop, 2004). Allorecognition is generally controlled by one locus, which allows somatic fusion only if the alleles are shared (de Tomaso et al., 2005; Grosberg et al., 1996; McKittrick & de Tomaso, 2010). The strategy works because allorecognition loci are extremely polymorphic, making it unlikely that completely unrelated genets fuse together. The genes at these loci are known to code for cell-surface proteins or extracellular proteins, but the nature of the binding partners of those proteins, and thus, how one colony actually recognizes another, is not fully resolved. The evolution and maintenance of highly polymorphic allorecognition systems in colonial animals is also not fully clear but is probably the outcome of a complex network of selective pressures highlighted by the many costs and benefits linked to somatic fusion as well as to the presence of somatic and germline parasitism (Brusini, Robin, & Franc, 2013; de Tomaso, 2006).

The homology of the allodeterminant genes and downstream signaling pathway is also unclear. More information about these pathways in the current models and the allorecognition systems in additional taxa may provide evidence for the evolutionary origins of the polymorphic loci involved in invertebrate allorecognition and possible links with the vertebrate immune system (Nicotra, 2019; Rosengarten & Nicotra, 2011; Rosental et al., 2018).

8 | EVO-DEVO AND THE RETURN OF THE INDIVIDUALITY PROBLEM?

Recent work on the developmental mechanisms underlying clonal propagation shows that tissues and cells that drive budding

("originators") are widely divergent between clades (see Section 3). This supports the view that agametic development evolved convergently many times across the animal phylogeny. On the basis of the distribution of agametic developmental modes, coloniality and clonal aggregation are likely to have evolved independently within many separate phyla: once at the base of bryozoans (Schwaha, Ostrovsky, & Wanninger, 2020), at least four times in cnidarians (and was lost and gained many times; Barbeitos, Romano, & Lasker, 2010; Kayal et al., 2018), six or seven times in tunicates (Alié, Hiebert, Scelzo, & Tiozzo, 2020), once within kamptozoans, and once or twice within hemichordates. Two families of rotifers are also known to form clonal aggregates (Wallace, 1987). This suggests that agametic cloning is a highly evolvable trait with a possible selective advantage. Some true colonies have relatives who form temporary colonies or aggregates. It is intriguing to consider whether some block to the separation mechanism or the emergence of a skeleton/tunic may have contributed to the origins of true colonies from temporary ones. However, many colonial taxa have no clonal relatives, hinting that coloniality may not always be preceded by a form of clonality. Either way, both coloniality and clonality within the animals are often found in taxa with high regenerative capacity, suggesting that mechanisms for regeneration may have been recruited/modified in the origins of agametic development (Nilsson Sköld & Obst, 2011).

It appears that asexual species have mostly appeared recently in the fossil record, suggesting that they may be more susceptible to extinction (Maynard-Smith, 1978). The true number of gains and losses of coloniality and clonality, the underlying developmental and evolutionary mechanisms responsible, as well as speciation and extinction rates linked to these life histories, are poorly understood. Future work will help elucidate how colonial forms evolved from solitary ancestors repeatedly in evolutionary history.

The evolution of polymorphism is a further mystery with developmental underpinnings. The phenotypes of many polymorph types seem to be allometric modifications of the body type from which they are derived (Banta, 1973; Harvell, 1994). Moreover, the spatial distribution of polymorphism is more often nonrandom than random, especially in siphonophores (Siebert et al., 2015) and erect bryozoans (Hageman, 2001). In branching colonies, including bryozoans and siphonophores, the patterns of polymorphism seem to be structured into repeated modular units, each containing several polymorph types, in a way that is reminiscent of meristematic growth in plants.

Even early researchers saw similarities between plants and colonial animals. Erasmus Darwin wrote: "If a bud be torn from the branch of a tree and cut out and planted... or inserted in the bark of another tree, it will grow, and become a plant in every respect like its parent. This evinces that every bud of a tree is an individual vegetable being, like the polypus... or the branching cells of the coral-insect..." (Darwin, 1800). Each plant bud has the same potential as a bud in a colonial animal, yet we do not think of tree "colonies" arising evolutionarily from incomplete asexual reproduction. Instead, the origin of plant modularity is explained by the emergence of metamerism, with metameric growth underlined by stem cells and

growth zones (see Barlow, 1989). This is a remarkable degree of convergence between plants and branching colonial animals, which have similar growth modes (van Valen, 1978). The question is how colonial animals evolved the ability to grow in repeated units of hierarchically organized modules (Munro et al., 2018).

With polymorphism, and its packaging into cormidia or sets of polymorphs, modularity occurs at more than one level within a colony—the cell level, within a zooid, the zooid level, and at a hierarchically more inclusive level of sets of zooids (Lidgard et al., 2012). The dominant hierarchical level at which the modularity occurs has implications and consequences for evolutionary and developmental mechanisms. At one extreme is modularity at the tissue/organ/body-part level (just the organs, tissues, or set of cell types for example), which can occur in even the simplest colonial organisms. At the other extreme are siphonophores and some bryozoans, where sets of polymorphic zooids always occur and whole-colony differentiation arises to variation among these multizoidal sets across the colony. Therefore, it will be useful to know the level at which the modular units are repeated and whether or not they have distinct consequences for the evolvability of development and morphological complexity or if they impose constraints in development or evolution. This is a more concrete way to frame the units of selection problem. Instead of trying to identify the unit at which selection occurs the strongest, we instead suggest trying to understand the levels at which the evolutionary potential is the strongest. There are hints that more complex colonies tend to have increasingly rare reproductive members (Simpson, 2012) and that the patterns of evolutionary potential within different hierarchical levels within and among colonies do vary (Simpson, Herrera-Cubilla, & Jackson, 2020). Both observations imply that the macroevolution of coloniality is largely controlled by developmental processes. What these developmental processes are is still totally unknown.

9 | CONCLUSIONS

Colonial and clonal animals have received less attention than unitary, strictly sexually reproducing species in many fields of biological sciences. Nevertheless, it has long been apparent that the evolution of coloniality is at the locus of the major problems within evolutionary biology, ecology, and developmental biology. Clonality and coloniality have been gained and lost several times across different taxonomic ranks of metazoans. Their scattered distribution clearly shows how these traits have been independently acquired (Figure 1). Such events of convergence support the view that agametic development may have some adaptive value. Despite their widespread occurrence, impact on many ecosystems and habitats, and the influence on population dynamics, very little is known about how asexual propagation and coloniality have evolved and how their mechanisms are regulated at a genetic and molecular level.

The origin of cells, multicellularity, and eusociality (the evolution of "superorganisms") have all been prominent topics of evolutionary biology. These so-called "major evolutionary transitions" or "evolutionary

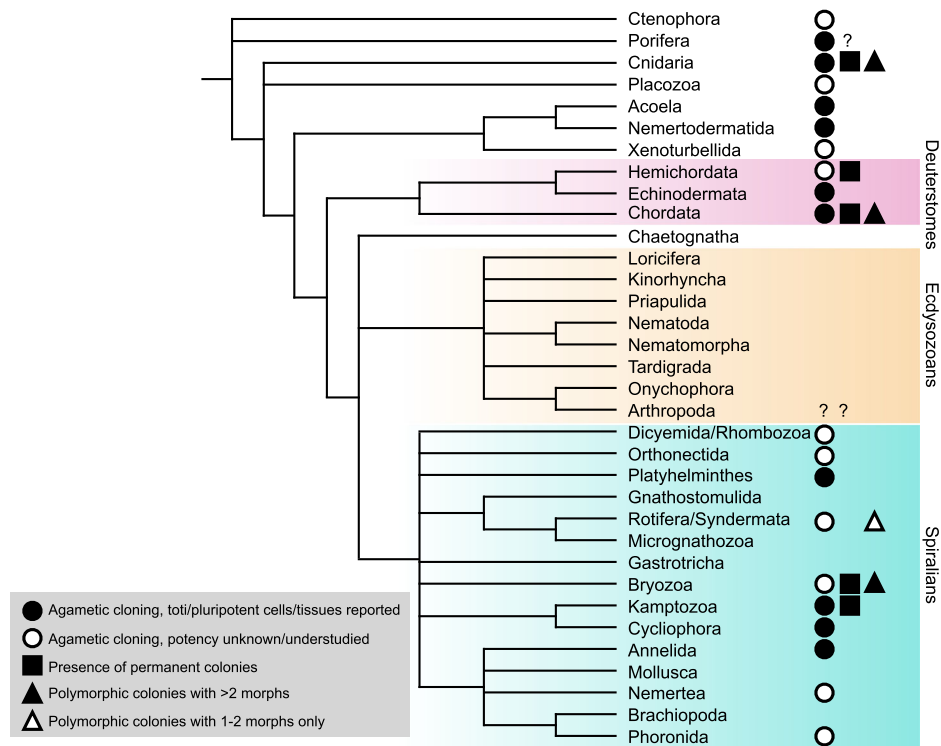


FIGURE 1 Phylogenetic distribution of colonial and clonal traits within the metazoans. Traits associated with coloniality and clonality are mapped on a summary tree of metazoan phyla. Agametic cloning (i.e., the ability to produce a new ramet/module by a nonembryonic asexual process) is indicated by a circle. The color of the circle indicates the source of tissue/cells from which the new modular body originates, at least partially (black—totipotent stem cells, or pluripotent cells or tissues, white—potency of the cells/tissues is unknown). The black square indicates the presence of permanent colonies. The triangle indicates groups that display species with polymorphism across modules within a colony (black—extreme polymorphism with three or more types, white—one to two types). Assignment of traits modified from Sköld and Obst (2011), Blackstone and Jasker (2003), and Harvell (1994). Question marks indicate cases where clonality and clonality are not certain—in sponges and in rhizocephalan barnacles. Insect polymorphism is omitted because insects do not form true colonies according to the definition used here [Color figure can be viewed at wileyonlinelibrary.com]

transitions in individuality” are transformations of previously independent entities into new higher-level wholes (Buss, 1987; Szathmáry & Smith, 1995). This conceptual framework has been used to understand how hierarchical complexity arose during the evolution of life on Earth and has been key to understanding the origins of cooperation and conflict, self-organization, the origins of modules at various levels, evolvability, multilevel selection, and many more fundamental concepts in biology. Transitions to coloniality and clonal aggregation can be treated in a similar way and may serve as useful models to understand how major evolutionary transitions occur. Thus, colonial animals may help address fundamental questions in the origins of life's hierarchy: how an individual at a higher-level emerges from a collection of lower levels individuals, and how those individual units become integrated and, possibly, specialized.

During the transition to coloniality, a number of emergent properties arose due to the higher level of organization. The fact that there is redundancy across the colony (i.e., multiple similar modules) allows for the release of certain constraints on growth and form that give colonies extreme plasticity in shape, size, age, and ecological niche. There is also a release of evolutionary constraints on single modules that allow for specialization to occur at the module level. A release of particular developmental constraints allows for the building of an adult

body without the need of sexual reproduction and thus, the colony exhibits exceptional regenerative capacity. Finally, the growth of encrusting colonies allows for the need of a self/non-self recognition system. All of these traits together form a set of evolutionary novelties of colonial animals and may in part underlie the transitions from unitary to colonial. However, which are the driving forces in this major transition and which are mere consequences is still uncertain.

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