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Invited review

Early evolution of colonial animals (Ediacaran Evolutionary Radiation–Cambrian Evolutionary Radiation–Great Ordovician Biodiversification Interval)

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ABSTRACT

Re-evaluation of eumetazoan modular coloniality gives a new perspective to Ediacaran–Ordovician animal diversification. Highly integrated eumetazoan colonies (porpitids [“chondrophorines”], pennatulacean octocorals, anthozoans) prove to be unknown in the Ediacaran. Ediacaran Evolutionary Radiation (EER, new term) fossils include macroscopic and multicellular remains that cannot be compellingly related to any modern group. Claims of eumetazoan coloniality in the Ediacaran are questionable. The subsequent Cambrian Evolutionary Radiation (CER, terminal Ediacaran–late early Cambrian) records appearance and diversification of deep burrowers and a relatively abrupt development of biomineralization. The CER began in a transition zone that spans the Ediacaran–Cambrian boundary and includes the final few million years of the Ediacaran. The early CER has pseudocolonial(?) *Corumbella* that may be related to some Phanerozoic taxa (conulariids) and records appearance of the first macroscopic biomineralised organisms (*Cloudina*, *Namacalathus*, *Namapoikea*), which may not be eumetazoans. Modular eumetazoans dominate and define many Ordovician and younger habitats (coral, bryozoan, sabellitid reefs; pelagic larvaceans, salps, early–middle Palaeozoic graptolites), but eumetazoan coloniality largely “missed” the EER and CER. All purported Ediacaran–Ordovician porpitids (“chondophorines”) and pennatulaceans are not colonial eumetazoans. Only in the late early Cambrian (late CER) or early middle Cambrian do a few modular colonial eumetazoans first occur as fossils. These include *Sphenothallus* (available evidence precludes *Torellella* coloniality), some corals (colonial “coralomorphs”), and lower middle Cambrian graptolithoids. Modular eumetazoan colonies (corals, graptolithoids) in the late early and early middle Cambrian (late Epoch 2–early Epoch 3) and appearance of mid-water predators (cephalopods, euconodonts) and bryozoans in the late Cambrian–earliest Ordovician (late Furongian–early Tremadocian) are the root for the Great Ordovician Biodiversification Interval (GOBI, new term) and diverse later Phanerozoic communities.

1. Introduction

The history of life on Earth records the repeated evolution of colonial associations in many high-level taxonomic groups. These groups include procaryotes, fungi, protists, multicellular algae and higher plants, sponges (including archaeocyaths and stromatoporoids), and a number of eumetazoan clades. The oldest interpreted record of coloniality includes cm-sized, disk-like structures produced by apparent colonial procaryotes from the 2.1 Ga Franceville “Series” of Gabon, western Africa (El Albani et al., 2014). This report summarizes the fossil record, as well as the numerous incorrectly identified forms, of marine colonial organisms from the Ediacaran Period, through the Cambrian, and into the Ordovician Period. [See Fig. 1 and caption for definitions of informal early, middle, and terminal Ediacaran Period and proposed early–late Cambrian subperiods. The division of the Ordovician into epochs/series (Early/Lower, Middle/Middle, Late/Upper) follows

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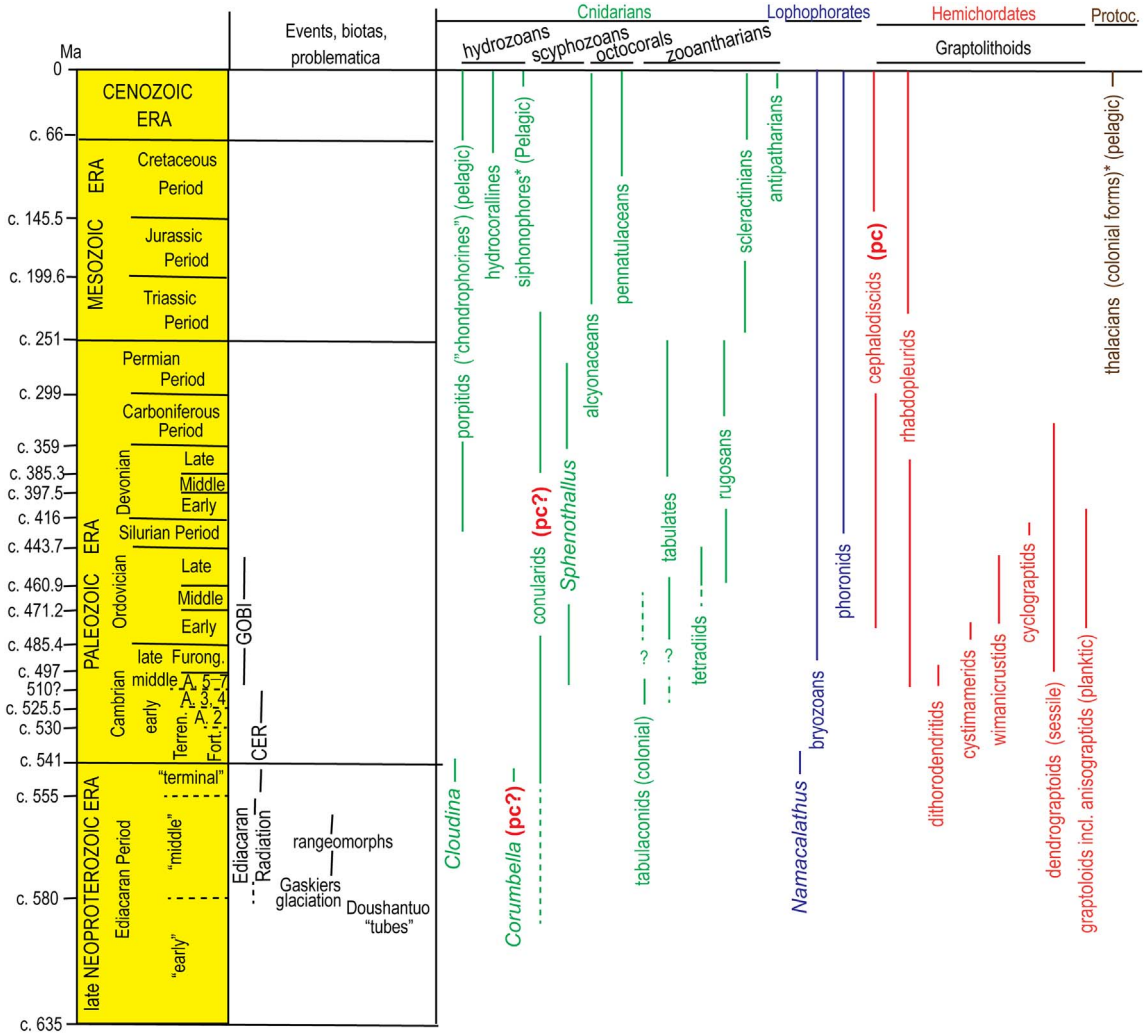

Fig. 1. Modular coloniality in eumetazoans through time. *Cloudina*, *Corumbella*, and *Namacalathus* included in figure although available evidence strongly suggests they may not be eumetazoans or animals (see text); tetratiids may be modular colonial rhodophytes. Carrera et al. (2017) report tabulate-like coralomorphs as high as the lowest Ordovician and a coralomorph genus in the Middle Ordovician. Graptolithoids include graptolithines and pterobranchs (see text). Asterisk (*) indicates group presently only known from Recent. Geochronology from Ogg et al. (2008); late Cambrian–Early Ordovician dates from Landing et al. (2015). Divisions of Ediacaran Period are informal with "early" including pre-Gaskiers glaciation interval, 'middle' bracketing deep- and shallow-water vendobiont associations (e.g., Avalonia faunas of Mistaken Point and Fermeuse formations, Charnwood Forest), and "terminal" Ediacaran including Nama-type macrofaunas of Namibia, Brazil, and Wood Canyon of Nevada with ca. 549–c. 540 Ma age (e.g., Brasier et al., 2012). Cambrian chronostratigraphic and geochronologic subdivisions in figure and text are proposed subseries of the Cambrian; lower/early Cambrian = Terreneuvian Series/Epoch + Series/Epoch 2, middle/middle Cambrian = Series/Epoch 3, upper/late Cambrian = Furongian Series/Epoch (Landing, 1998a, 1998b; Landing et al., 2010; Landing, 2012a, 2012b; Landing et al., 2013, 2015). Abbreviations: A., Age; CER, Cambrian Evolutionary Radiation; EER, Ediacaran Evolutionary Radiation; Fort., Fortunian Age; Furong., Furongian Epoch; GOBI, Great Ordovician Diversification Interval; pc, pseudocolonial; pc?, possibly pseudocolonial; Protoc., protochordates; Terran., Terraneuvian Epoch.

global, International Stratigraphic Commission definitions (e.g., Webby et al., 2004b, 2004a).] One key theme of this report is that regular and repeated appearances of probable and definite coloniality in "advanced animals" (i.e., eumetazoans, see below) likely reflects strategies for optimization or control of habitat space and food and increased reproductive success with greater biomass (e.g., Hayward and Ryland, 1975). As also discussed below, the repeated appearance of coloniality in distantly related eumetazoan groups reflects an evolutionary convergence. By this apparent convergence, higher level taxa that originated as individuals subsequently began to bud and form integrated colonies of genetically related individuals that ultimately came to function as integrated multi-individual, ecological associations.

2. Multicellular animals

Animals, or the Metazoa Haeckel, 1874, are multicellular heterotrophs that are always motile at some point in their life cycle. Metazoa almost always pass through an embryonic stage called the blastula where the embryo consists of a hollow ball of cells (e.g., Valentine, 2004).

The total group of animals includes a basal monophyletic grouping of all sponges, as well as primitive basal groups such as the Placozoa, and more complex animals usually grouped into the sub-kingdom Eumetazoa. The relationship between these groups is controversial and has excited much recent debate (Philippe et al., 2009, 2011; Srivastava et al., 2010; Pick et al., 2010). However, now it seems nearly certain that the sponges are a coherent biological grouping and are the most basal of all the animal groups (Wörheide et al., 2012; Antcliffe et al., 2014). It is also clear that the Eumetazoa are a monophyletic group which contains the Cnidaria as well as the monophyletic Bilateria (Simion et al., 2017). The Eumetazoa are distinguished from the more primitive members of the Metazoa (sponges, placozoans etc) by the presence of true tissue organized in germ layers, as well as embryos that are capable of gastrulation. The presence of neurons, muscles, and embryo gastrulation are usually used to allow assignment to the sub-kingdom Eumetazoa Bütschli, 1910. Eumetazoans include such clades