Marine oxygenation, lithistid sponges, and the early history of Paleozoic skeletal reefs

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ABSTRACT

Microbial carbonates were major components of early Paleozoic reefs until coral-stromatoporoid-bryozoan reefs appeared in the mid-Ordovician. Microbial reefs were augmented by archaeocyath sponges for ~15 Myr in the early Cambrian, by lithistid sponges for the remaining ~25 Myr of the Cambrian, and then by lithistid, calathiid and pulchrilaminid sponges for the first ~25 Myr of the Ordovician. The factors responsible for mid–late Cambrian microbial-lithistid sponge reef dominance remain unclear. Although oxygen increase appears to have significantly contributed to the early Cambrian 'Explosion' of marine animal life, it was followed by a prolonged period dominated by 'greenhouse' conditions, as sea-level rose and CO_2 increased. The mid–late Cambrian was unusually warm, and these elevated temperatures can be expected to have lowered oxygen solubility, and to have promoted widespread thermal stratification resulting in marine dysoxia and hypoxia. Greenhouse conditions would also have stimulated carbonate platform development, locally further limiting shallow-water circulation. Low marine oxygenation has been linked to episodic extinctions of phytoplankton, trilobites and other metazoans during the mid–late Cambrian. We propose that this tendency to dysoxia-hypoxia in shallow marine environments also limited many metazoan reef-builders. In contrast, during the mid–late Cambrian, the ability of lithistid sponges to withstand low oxygen levels allowed them to create a benthic association with microbial carbonates that dominated global reefs. These conditions ameliorated during the Ordovician, as temperature decline promoted ocean ventilation. The prolonged time gap occupied by low diversity reefs between the 'Cambrian Explosion' and the 'Great Ordovician Biodiversification Event' reflects elevated temperatures and reduced marine oxygenation that limited metazoan diversification in shallow marine environments.

1. Introduction

The early Paleozoic radiation of marine animals, commonly referred to as the 'Cambrian Explosion' (Cloud, 1948; Bowring et al., 1993; Conway Morris, 2006), stalled in the mid-Cambrian and did not regain impetus until the mid-Ordovician (Sepkoski Jr., 1981; Webby, 2002; Bambach et al., 2004) during the 'Great Ordovician Biodiversitification Event' (Webby et al., 2004). Reef development shows a similar pattern, leading to the observation that mid–late Cambrian reef communities were dominantly microbial (Fagerstrom, 1987; Zhuravlev, 1996; Rowland and Shapiro, 2002). As a result, the prolonged interval between late early Cambrian extinction of archaeocyath sponges and the Early Ordovician rise of lithistid sponge-microbial-calathiid reef communities came to be regarded as a "reef gap" (Sheehan, 1985; Zhuravlev, 1996; Rowland and Shapiro, 2002; Kiessling, 2009). Challenges to this view first emerged in the report of early Furongian (late Cambrian) lithistid sponge-microbial (LSM) reefs in Iran (Hamdi et al.,

1995). Additional examples of mid–late Cambrian LSM reefs have since been recognized throughout Laurentia and Gondwana (Mrozek et al., 2003; Shapiro and Rigby, 2004; Johns et al., 2007; Kruse and Zhuravlev, 2008; Hong et al., 2012, 2016; Kruse and Reitner, 2014; Adachi et al., 2015; Lee et al., 2016a). It is now clear that LSM reef communities were globally distributed for ~25 Myr during the mid–late Cambrian. This community was augmented in the Early Ordovician by a variety of skeletal organisms, such as *Calathium*, *Pulchrilamina*, *Amsassia*, bryozoans, stromatoporoids, and *Lichenaria*, but reef diversification remained relatively slow until bryozoans, corals and stromatoporoids became common in the mid-Ordovician, ~460 Ma (Fagerstrom, 1987; Webby, 2002; Servais et al., 2009). Numerical ages used here accord with those of the International Chronostratigraphic Chart (Cohen et al., 2013). Recognition of mid–late Cambrian LSM reefs closes the "reef gap" (Lee et al., 2016a and references therein) but also raises questions. What factors contributed to lithistid success following archaeocyath decline, why did LSM reefs dominate the remainder of the

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Cambrian, and why did it take so long for the bryozoan-coral-stromatoporoid community to emerge in the Ordovician? Explanations for these aspects of reef developments could shed light on broader patterns of change that continue to be debated, particularly the seemingly slow overall pace of mid–late Cambrian animal diversification (Sepkoski Jr., 1981; Pruss et al., 2010; Knoll and Fischer, 2011; McKenzie et al., 2014; Saltzman et al., 2015).

Here we explore the possibility that prolonged low levels of marine oxygenation significantly influenced the relative success and development of reef communities during the mid–late Cambrian and Early Ordovician (Webby, 2002; Saltzman et al., 2015; Lee and Riding, 2016). High mid–late Cambrian sea-level and elevated atmospheric CO_2 promoted 'greenhouse' conditions with elevated temperatures (Berner, 1990, 2009; McKenzie et al., 2014). Higher temperatures decrease oxygen solubility in seawater, increase thermal stratification of the ocean, and favor marine productivity, while simultaneously stimulating carbonate platform development that restricts shallow-water circulation. Collectively, these factors tend to induce episodic marine dysoxia-hypoxia (Saltzman, 2005; Gill et al., 2011) that has been linked to repeated extinctions of phytoplankton, trilobites and other metazoans during the mid–late Cambrian (e.g., Bambach et al., 2004).

We propose that lithistid sponges, along with microbes, were predisposed to tolerate low oxygen levels, and that this was a central factor in their development and persistence during the mid–late Cambrian. These conditions began to change in the Early Ordovician as temperature decline (Trotter et al., 2008) promoted ocean ventilation (Thompson et al., 2012; Kah et al., 2016; Young et al., 2016). In the mid-Ordovician the bryozoan-coral-stromatoporoid community established itself as the next major phase of Paleozoic reef development (Pitcher, 1964; Fagerstrom, 1987). From this perspective, the relationship between reef community evolution and dysoxia-hypoxia is a key to understanding not only the Cambrian "reef gap", but also the relatively slow progress of animal radiation in mid-Cambrian to mid-Ordovician shallow marine environments.

2. Cambrian–Ordovician marine diversity

Marine animal generic diversity shows a plateau in the late Cambrian (Furongian Epoch; Paibian and Jiangshanian ages) (~510–485 Ma) (Sepkoski Jr., 1979, 1981), before recovering near the Cambrian–Ordovician transition (Na and Kiessling, 2015). This interval of depressed diversity largely reflects archaeocyath extinctions, followed by trilobite extinctions and low levels of origination (Bambach et al., 2004). Mid–late Cambrian and Early Ordovician trilobite extinctions define "biomere" boundaries (Palmer, 1984; Taylor, 2006) that, as in the case of the late Cambrian Age 3 Sinsk Event (Zhuravlev and Wood, 1996), have been linked to influxes of anoxic and/or cold basinal waters onto shallow shelves (Stitt, 1975; Palmer, 1984; Westrop and Ludvigsen, 1987). This is consistent with survival of trilobites adapted to reduced oxygen availability at biomere boundaries (Palmer, 1984; Taylor, 2006; McKenzie et al., 2014; Saltzman et al., 2015). In addition, dysoxia-tolerant arthropod groups such as olenids (Fortey, 2000) and phosphatocopids (Williams et al., 2011) increased in diversity in the late Cambrian (Fig. 1).

Biomere and other Cambrian biotic turnovers/extinctions have in turn been linked to carbon isotope excursions (Taylor, 2006; Zhu et al., 2006; Peng et al., 2012; Saltzman et al., 2015). In addition to the ~510 Ma Sinsk Event, these include the early Paibian Marjumiid–Pterocephaliid biomere boundary and the early Jiangshanian Pterocephaliid–Ptychaspid biomere boundary, which approximately correspond with the lower and upper boundaries respectively of the Steptoean positive carbon isotope excursion (SPICE) event (Saltzman et al., 1995, 2000; Perfetta et al., 1999; Saltzman, 1999; Montañez et al., 2000; Lee et al., 2015a; Gerhardt and Gill, 2016) (for correlations see Taylor et al., 2012, fig. 1) (Fig. 1). We infer, along with others, that mid–late Cambrian extinctions occurred as poorly oxygenated basinal

water encroached onto carbonate platforms, stressing shallow-water communities (Palmer, 1984; Berry et al., 1989; Taylor, 2006; Gill et al., 2011; Landing, 2012a, 2012b; Saltzman et al., 2015). Similar effects have been invoked to account for extinction of carbonate platform communities in Jurassic–Cretaceous Oceanic Anoxic Events (Schlanger and Jenkyns, 1976; Jenkyns, 1991, 2010; Parente et al., 2008).

Marine diversity greatly increased during the Ordovician (Sepkoski Jr., 1981). The Great Ordovician Biodiversification Event (GOBE) (Webby et al., 2004) was a diachronous and extended event, initiated in the Furongian and accelerating in the Darriwilian, that continued until almost the end of the Ordovician (Sepkoski Jr., 1981; Webby et al., 2004; Harper, 2006; Servais et al., 2010, 2016). Significant increases in animal biodiversity at family, genus and species level resulted in the rise of the 'Paleozoic Evolutionary Fauna', dominated by suspension-feeding organisms such as brachiopods, rugose and tabulate corals, crinoids, bryozoans, and stromatoporoids (Sepkoski Jr., 1979; Bambach et al., 2002). This community developed throughout the Early Ordovician, and by the late Darriwilian had a radical affect on reef building (Pitcher, 1964; Fagerstrom, 1987; Webby, 2002; Webby et al., 2004). In addition, global increase in phytoplankton (acritarch) diversity, broadly paralleling that of animals, occurred in the Furongian and Early Ordovician (Servais et al., 2008, 2016; Nowak et al., 2015). These Ordovician upturns in diversity have been broadly related to increase in atmospheric O_2 (Servais et al., 2008, 2010, 2016; Saltzman et al., 2011; Edwards et al., 2017) and decline in global temperature (Trotter et al., 2008).

3. Late Ediacaran–mid-Ordovician eukaryote reef development

Microbial carbonates (stromatolites, thrombolites and associated calcimicrobes) generally dominated reefs from the Ediacaran to the Early Ordovician. The earliest skeletal reefs involved Ediacaran calcified sessile benthic eukaryotes (*Cloudina*, *Namacalathus*, *Namapoikia*) and early Cambrian "*Ladatheca*". Archaeocyaths, and locally radiocyaths and coralomorphs, are conspicuous in early Cambrian reefs. Archaeocyaths and coralomorphs continued – although much reduced – during the mid–late Cambrian, when lithistid sponges were the most prominent components of skeletal reefs. Large lithistids (*Archaeoscyphia*) appeared in the Early Ordovician, augmented by calathiids, pulchrilaminids, and the first undisputed tabulate corals, bryozoans and stromatoporoids. These latter appearances set the scene for the mid-Ordovician diversification of stromatoporoids, tabulates and bryozoans, that created reefs dominated by encrusting and massive skeletons at the end of the Darriwilian.

The affinities of many Ediacaran–Ordovician skeletons remain problematic. *Namapoikia* may be a chaetetid sponge or simple colonial cnidarian (Wood et al., 2002; Wood, 2017). Archaeocyaths and lithistids are sponges. Radiocyath skeletal structure resembles that of *Calathium*, which is sponge-like (Church, 1991; Rowland, 2001), and also that of cyclocrinitids (Beadle, 1988); but these groups have also been compared with green algae (e.g., Nitecki and Debrenne, 1979). Coralomorphs comprise a heterogeneous semi-formal group encompassing massive as well as cuplike skeletons; some of them are considered real corals (e.g., Scrutton, 1997; Hicks, 2006). Pulchrilaminids are stromatoporoid-like, but regarded as a separate group of hypercalcified sponges (Webby, 2015).

Based on their eukaryote skeletal components, we distinguish six reef intervals during this ~100 Myr period (~550–444 Ma), when reefs evolved from mainly microbial into mainly skeletal structures. Time scales are based on Peng et al. (2012), Cohen et al. (2013), and Ogg et al. (2016). These main reef intervals are: I, late Ediacaran (~550–541 Ma): microbial-*Cloudina*; II, Fortunian–mid-Age 2 (541–525 Ma): microbial-"*Ladatheca*"; III, mid-Age 2/late Age 4 (525–510 Ma): microbial-archaeocyath; IV, late Age 4/end Age 10 (510–485 Ma): microbial-lithistid; V, Tremadocian–middle Darriwilian (485–460 Ma): microbial-lithistid-calathiid-pulchrilaminid; VI, late Darriwilian–end-Ordovician (460 Ma–444 Ma): stromatoporoid-bryozoan-tabulate-receptaculitid-microbial.
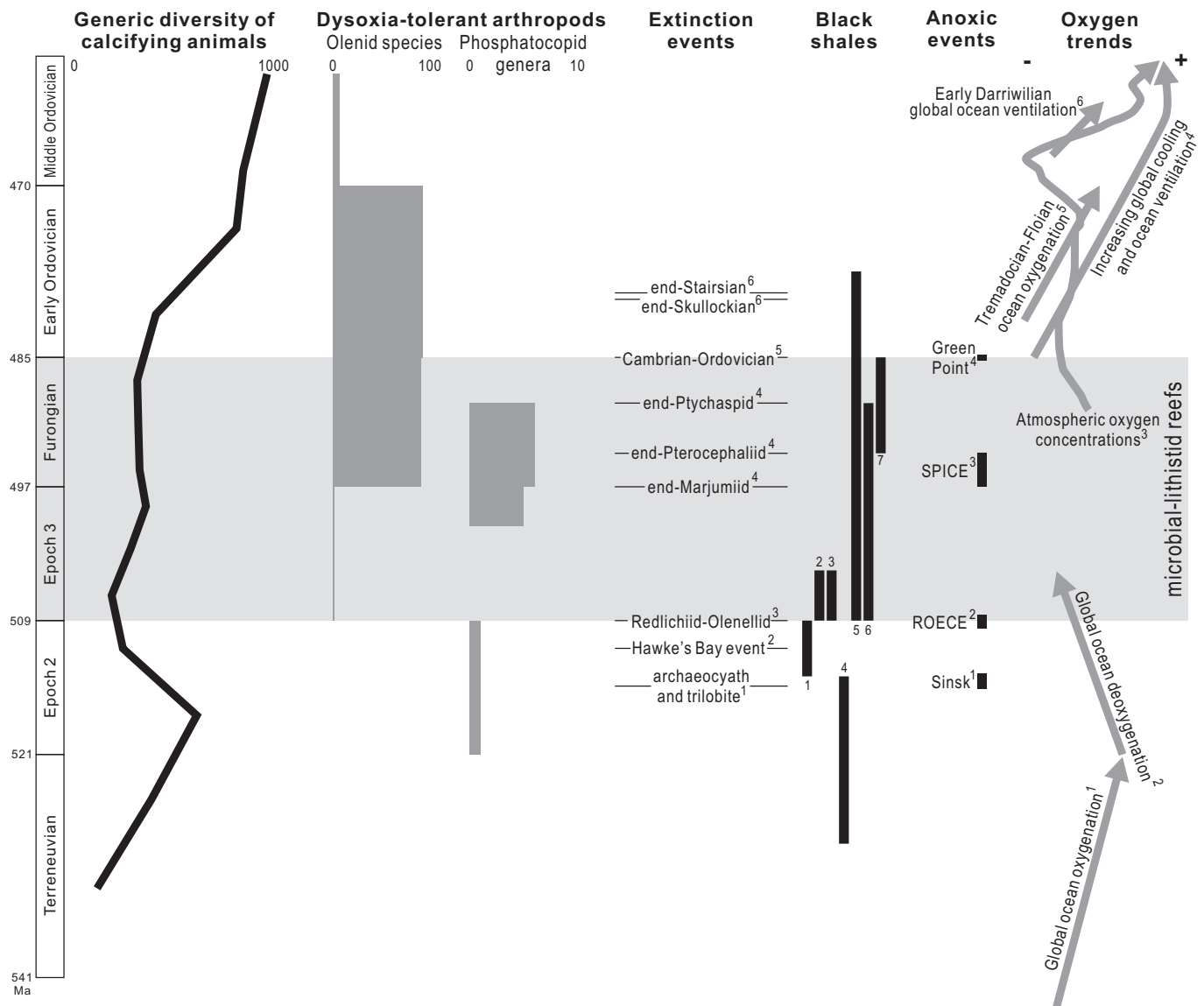
Fig. 1. Cambrian to Middle Ordovician oxygen level indicators and associated changes in biotic diversity. Generic diversity of calcifying animal groups (Anthozoa, Archaeocyathida, Articulata, Bryozoa, Demospongia, Echinodermata, Mollusca, Ostracoda, and Trilobita) after Pruss et al. (2010). Olenid trilobite diversity from http://fossilworks.org/ (accessed 22nd Dec. 2017). Bivalved arthropod phosphatocopid diversity from Williams et al. (2011). Extinction events adapted from: 1. Zhuravlev and Wood (1996), 2. Palmer and James (1979), 3. Peng et al. (2012), 4. Palmer (1984), 5. Loch et al. (1993), 6. Adrain et al. (2009). Examples of black shale deposits from Babcock et al. (2015): 1. Pestrotsvet Fm., Russia, 2. Spence Shale, Utah and Idaho, USA, 3. Burgess Shale, British Columbia, Canada, 4. Niutitang Fm., South China, 5. Alum Shale, Scandinavia, 6. Huaqiao Fm., South China, 7. White-leaved Oak Shale, England. Global anoxic events: 1. Sinsk (Zhuravlev and Wood, 1996), 2. Redlichiid-Olenellid Extinction Carbon isotope Excursion (ROECE) (Zhu et al., 2006; Faggetter et al., 2017), 3. Steptoean Positive Carbon Isotope Excursion (SPICE) (Saltzman et al., 2000), 4. Reducing condition across the Cambro-Ordovician boundary at Green Point GSSP section (Tripathy et al., 2014). Oxygenation trends: 1. Global ocean oxygenation across the Ediacaran–Cambrian boundary indicated by Mo isotopes (Chen et al., 2015), 2. Global ocean deoxygenation indicated by bioturbation, Mo isotopes, TOC and U (Boyle et al., 2014), 3. Atmospheric oxygen levels calculated by Edwards et al. (2017). 4. Ordovician sea-surface temperatures based on conodont thermometry (Trotter et al., 2008). 5. Tremadocian-Floian ocean oxygenation (Saltzman et al., 2015). 6. Early Darriwilian global ocean ventilation (Kah et al., 2016).

3.1. Late Ediacaran (~550–541 Ma): microbial-Cloudina

Calcified sessile problematic metazoans contributed to and locally constructed reefs in the late Ediacaran (~550–541 Ma) (Germs, 1972; Conway Morris et al., 1990; Seilacher, 1999; Grotzinger et al., 2000; Hofmann and Mountjoy, 2001; Penny et al., 2014, 2017; Wood, 2017). Masses of narrow conical calcified *Cloudina* tubes (annelid or cnidarian, Vinn and Zatoń, 2012; Pacheco et al., 2015), individually up to 8 mm wide and 15 cm long, constructed reefs up to 7 m wide and 3 m high (Wood, 2017). *Cloudina* also often occurs in stromatolite and thrombolite reefs, locally in association with stalked cups of the calcified, but very thin-walled problematic *Namacalathus* (lophophorate? Zhuravlev et al., 2015) up to 35 mm in size (Grotzinger et al., 2000; Hofmann and Mountjoy, 2001; Zhuravlev et al., 2015; Wood, 2017). *Cloudina* and *Namacalathus* locally mutually attached (Penny et al., 2014, 2017). *Namapoikia*, another early metazoan in late Ediacaran microbial reefs, is tabular crustose and chaetetid-like (see 3.3.4. Chaetetids, below) (Wood et al., 2002), composed of millimetric labyrinthine tubules, and in cavities locally forms sheet-like crusts up to 1 m in extent (Wood, 2017). *Cloudina*, *Namacalathus* and *Namapoikia* are not known to have survived into the Cambrian (Amthor et al., 2003).

3.2. Earliest Cambrian, Fortunian/mid-Age 2 (541–525 Ma): microbial-"Ladatheca"

Early Cambrian (Terreneuvian) reefs, like those of the Ediacaran, are predominantly stromatolitic and calcimicrobial (Drosdova, 1980; Riding and Voronova, 1984; Kruse et al., 1996). Among the shelly fossils that appeared in the Fortunian (Bengston, 2004), a single example of a 'worm reef' formed by operculate tubular "Ladatheca", individually up to 15 cm long and 6 mm wide, occurs in the late Fortunian (Landing, 1993), and is reminiscent of *Cloudina* reefs.

3.3. Early Cambrian, mid-Age 2/late Age 4 (525–510 Ma): microbial-archaeocyath

3.3.1. Archaeocyaths

Archaeocyaths, previously considered a distinct phylum or compared with coelenterates and algae, are now regarded as sponges (Debrenne et al., 2015b). These distinctive and often heavily calcified skeletons, typically conical with porous walls partitioned and supported by septa, appeared in the lower Tommotian Stage of Siberia (mid-Age 2, ~525 Ma, Ogg et al., 2016) in the zone named after the archaeocyath *Nochoroicyathus sunnaginicus* (Fig. 2). Most archaeocyath cups are < 15 mm in diameter and several centimeters in height, but examples 1.5 m in size are reported, and some show mutual attachment that favored reef-construction (Hill, 1964; Wood et al., 1993; Debrenne et al., 2015b). They were long regarded as the first animals to attain a global reef-building role (Fagerstrom, 1987; Rowland and Gangloff, 1988; Wood, 1999; Knoll, 2003; Gandin and Debrenne, 2010), and some early Cambrian reefs are dominated by archaeocyath frameworks (Rowland, 1984; Riding and Zhuravlev, 1995). However, they are usually also closely associated with abundant calcimicrobes (Pratt et al., 2001; Riding, 2001; Lee et al., 2014b) that diversified in the early Cambrian (Riding and Voronova, 1984; Zhuravlev, 1996), and less commonly with coralomorphs and radiocyaths (Jell, 1984; Kruse et al., 1995, 1996; Zhuravlev and Wood, 1995; Zhuravlev, 2001a; Zhuravlev et al., 2015) (Fig. 3). The peak of archaeocyath diversity in Age 3 (~518 Ma) coincided with that of marine animal genera as a whole (Na and Kiessling, 2015), but the group declined rapidly ~510 Ma (Peng et al., 2012). Archaeocyath decline, sometimes considered the first significant extinction of the Phanerozoic (Newell, 1972; Signor, 1992; Zhuravlev, 1996, 2001a; Bambach et al., 2002; Bambach, 2006), was linked to the Hawke's Bay Regression in the lower Toyonian Stage of Siberia (middle Age 4) by Palmer and James (1979), but Zhuravlev and Wood (1996) suggested that the anoxic Sinsk Event, in the Botomian Stage of Siberia (late Age 3), may have been more important in reducing archaeocyath diversity. Hyoliths, inarticulate brachiopods, and trilobites also show reduced levels of originations in the Botomian (Bambach et al., 2004) (Fig. 1).

3.3.2. Cribricyaths, radiocyaths

During Cambrian Epoch 2, the diverse archaeocyath reef community was augmented by other, mostly problematic, calcified skeletal organisms of various shapes and sizes, such as cribricyaths, radiocyaths and coralomorphs. Cribricyatha (Vologdin, 1961) are small (< 1 cm long), locally abundant, calcareous conical Problematica (Zhuravlev, 2001b) that contributed to reef formation (Wood et al., 1993) in the
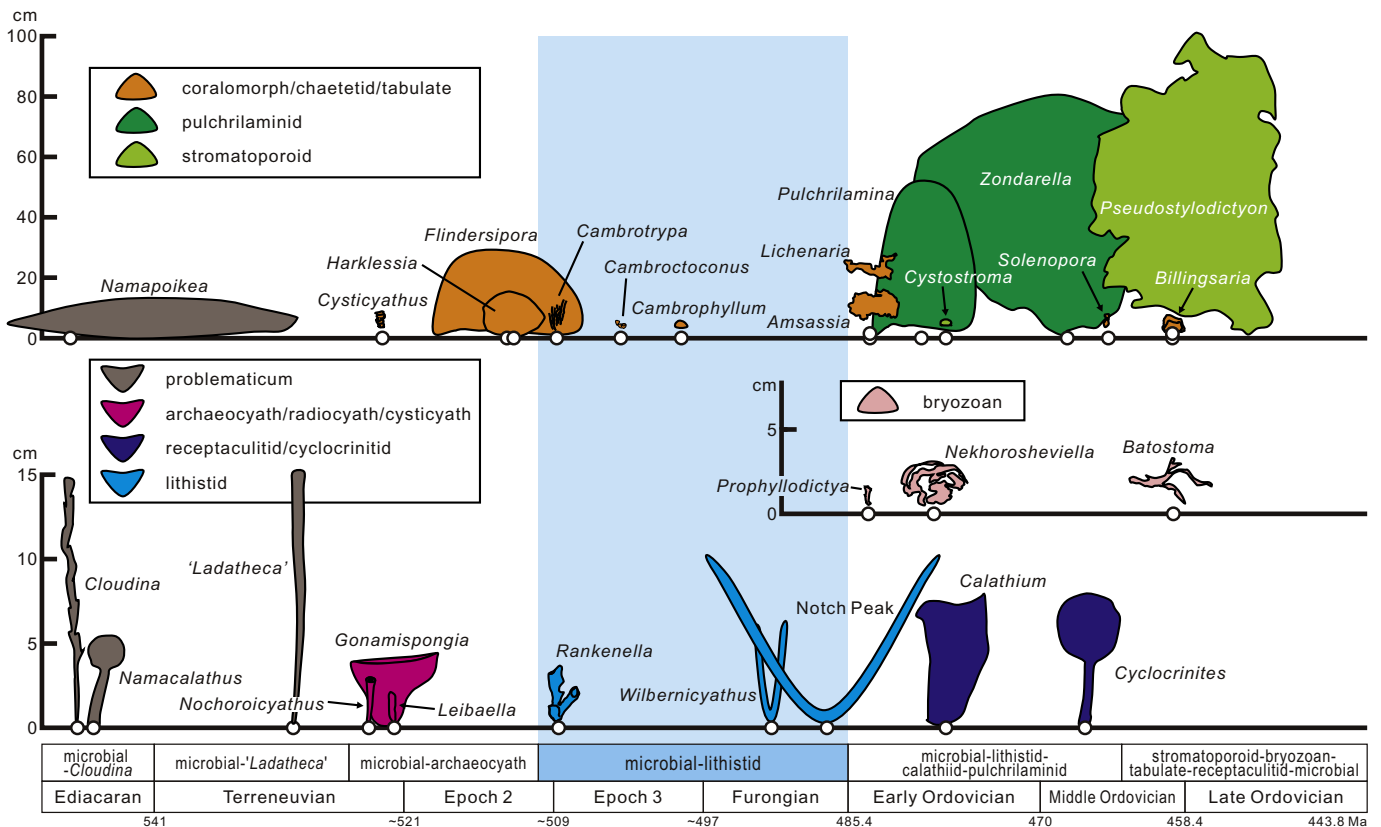

Fig. 2. Schematic size, shape, and age summary of reef-building skeletal organisms from late Ediacaran to early Late Ordovician. Time scales from Peng et al. (2012), Cohen et al. (2013), and Ogg et al. (2016). Six reef intervals are recognized: I, Late Ediacaran (~550–541 Ma) microbial reefs with *Cloudina*, *Namacalathus*, and *Namapoikia*. II, Earliest Cambrian (Fortunian–mid-Age 2) microbial reefs with rare "*Ladatheca*". III, Microbial-archaeocyath sponge reefs with radiocyaths, coralomorphs, etc. from mid-Age 2 to Age 4. IV, Microbial-lithistid sponge reefs in the mid–late Cambrian. V, Microbial-lithistid sponge reefs augmented by *Calathium*, pulchrilaminids, bryozoans, *Lichenaria*, *Amsassia*, and *Cystostroma* in the Early and early Middle Ordovician. VI, Skeletal-dominant reefs mainly constructed by stromatoporoids, corals, and bryozoans together with microbial carbonates in the late Darriwilian and Late Ordovician.
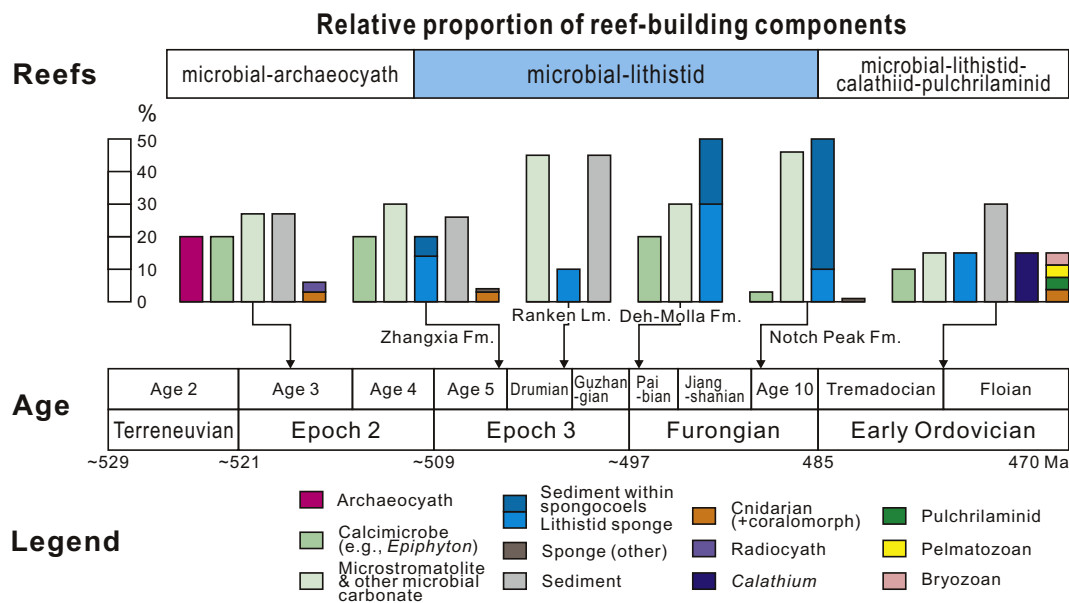
Fig. 3. Relative proportions of main reef components during the Cambrian and Early Ordovician. Early Cambrian microbial-archaeocyath reefs from Gandin and Debrenne (2010), Early Ordovician microbial-lithistid-calathiid reefs from Hong et al. (2015), Li et al. (2015) and references therein. Proportions of mid–late Cambrian reef-building components based on examples in Table 1.

early Cambrian (Tommotian–Botomian) (Debrenne et al., 2015a). An early cribricyath is *Leibaella* (late Tommotian, late Age 2) (Wood et al., 1993). Radiocyaths are similar in size and shape to archaeocyaths, with which they were often confused (Kruse et al., 2015), but were distinguished as a distinct group (Radiocyatha) by Debrenne et al. (1970). An early example is *Gonamispongia* (late Tommotian, late Age 2). Radiocyaths have globular to pear-shaped skeletons, with outer walls composed of distinctive plates (nesasters) and more closely resemble receptaculitids than archaeocyaths (Nitecki and Debrenne, 1979), although receptaculitids are not common until the Ordovician (see Section 3.5.1. Receptaculitids, radiocyaths, cyclocrinitids, below). However, the largest skeletal additions to early Cambrian reef communities were locally made by coralomorphs, such as *Flindersipora* (Fuller and Jenkins, 2007).

3.3.3. Early Cambrian coralomorphs

Tabulate-like phosphatic fossils (e.g., *Ramitubus*) occur in the mid-Ediacaran (~585 Ma) Doushantuo Formation (Van Iten et al., 2014), and *Namapoikia* may be a cnidarian (Wood et al., 2002). Coral-like calcified fossils are diverse in the early Cambrian (Zhuravlev et al., 1993; Wrona and Zhuravlev, 1996; Scrutton, 1999; Debrenne and Reitner, 2001; Hicks, 2006; Fuller and Jenkins, 2007), but are difficult to relate to Tabulata or Rugosa, neither of which is confidently recognized until the Ordovician (Scrutton, 1992; Oliver, 1996; Scrutton, 1997). Jell (1984) placed coral-like early Cambrian fossils within the Coralomorpha. This highly heterogeneous semi-formal group encompasses chaetetids and early "tabulates", with or without septa and tabulae, as well as cuplike skeletons.

Early coralomorphs are best known from calcimicrobial-archaeocyath reefs in the early Cambrian. They exhibit two contrasting morphotypes: small cup-like and large massive domical. Scrutton (1997) recognized two orders of Cambrian zoantharian corals (Tabulaconida, Debrenne et al., 1987; Cothoniida, Oliver and Coates, 1987) and suggested that calcified early–early middle Cambrian corals represent 'a series of short-lived calcification episodes among contemporary anemones' (Scrutton, 1999). Middle Tommotian (523 Ma) *Cysticyathus*, previously included in archaeocyaths, is an early cup-like coralomorph in calcimicrobial-archaeocyath reefs (Debrenne and Reitner, 2001, fig. 14.6b). Somewhat younger cup-like forms include Age 5–Drumian

Cambroctoconus (Park et al., 2011; Peel, 2017b), Age 4 *Cothonion* (Peel, 2011) and *Lipopora* (see Park et al., 2016. Some of these formed mid-Cambrian reefs, e.g., *Cambroctoconus* (Lee et al., 2016a), which has been described as a stem-group cnidarian based on its octoradial symmetry (Park et al., 2011).

Much larger domical forms in the late Botomian (~513 Ma) include *Flindersipora* (Lafuste et al., 1991; Savarese et al., 1993; Debrenne and Reitner, 2001; Fuller and Jenkins, 2007), *Yaworipora* (Zhuravlev, 1999), *Moorowipora* (Sorauf and Savarese, 1995), *Arrowipora* and *Blinmanipora* (Scrutton, 1992, 1997; Fuller and Jenkins, 2007). *Flindersipora* is up to 70 cm tall (Fuller and Jenkins, 2007). *Moorowipora* and *Arrowipora,* cerioid forms with short septal spines and tabulae, resemble tabulates (Fuller and Jenkins, 1994, 1995; Sorauf and Savarese, 1995). Contemporaneous *Harklessia* (Botomian–Toyonian = ~512.5 Ma) lacks both septa and tabulae (Hicks, 2006). These domical coralomorphs declined at the end-early Cambrian, and only a few middle and late Cambrian examples are known (Debrenne and Reitner, 2001).

3.3.4. Chaetetids

In addition to coralomorphs, modular calcified skeletons occur in chaetetid sponges. In general, chaetetids have tabulae but poorly developed - or no - septa, whereas tabulate corals possess tabulae and may or may not have well-developed septa (Scrutton, 1979, 1997; West, 2012). Ediacaran *Namapoikia* has been compared with both chaetetids and coralomorphs (Wood et al., 2002). Botomian *Labyrinthus* (Kobluk, 1979) and *Rosellatana* (Kobluk, 1984), which attached to archaeocyaths, were regarded as coralomorphs by Debrenne and Reitner (2001). However, their mode of increase, similar to longitudinal fission, suggests affinities with chaetetids more than corals (Scrutton, 1997; Pratt et al., 2001). *Cambrophyllum* (Fritz and Howell, 1955) from the lower Dresbachian Stage of North America (Guzhangian Age, ~499 Ma), 30 mm wide and 15 mm high, with septa-like processes within the 'corallites' (Scrutton, 1979; Jell, 1984; Kobluk, 1984) has also been compared with chaetetids (Scrutton, 1997). *Solenopora* (Riding, 2004), first known in the early Darriwilian (~465 Ma) (Klappa and James, 1980) and common in the late Darriwilian (Kröger et al., 2017) and early Late Ordovician (Opalinski and Harland, 1981), may be the first abundant rock-forming chaetetid.

3.3.5. Pelmatozoans

Pelmatozoans (stem-bearing echinoderms) appear in Cambrian Epoch 2 (Zamora et al., 2013; Peel, 2017a). The eocrinoid *Kinzercystis* from early Epoch 2 (~519 Ma) is an early example (Zamora et al., 2013, fig. 13.3). Echinoderms declined in the Guzhangian–Paibian and then recovered in the mid–late Furongian (Zamora et al., 2013). Echinoderms attached to firm substrates in the mid–late Cambrian (Brett et al., 1983; Zamora et al., 2010, 2017), but within Cambrian reefs they mostly occur as scattered fragments (James and Kobluk, 1978; Pruss and Knoll, 2017) and may have been passive filter feeders restricted to low-velocity currents (Smith, 1990). Only locally did they form reef fabric, e.g., in the basal parts of some late Cambrian LSM reefs (Spincer, 1996; Johns et al., 2007). Nonetheless, together with bryozoans, their holdfasts created reef substrates in the late Tremadocian (~480 Ma) (Adachi et al., 2011, fig. 6), Darriwilian (Pratt, 1989) and Late Ordovician (e.g., *Hemicosmites*, Kröger et al., 2014).

3.4. Mid–late Cambrian ("reef gap") late Age 4/end Age 10 (510–485 Ma): microbial-lithistid

Mid–late Cambrian reefs have long been known to be dominantly microbial (Fagerstrom, 1987; Rowland and Shapiro, 2002; Riding, 2006). Lithistid sponges had been recognized in the mid–late Cambrian, but were often considered too small, too simple, and too scarce to be effective reef-builders (Fagerstrom, 1987; Pratt et al., 2001; Rowland and Shapiro, 2002). Consequently, the interval between archaeocyath decline at the end of the early Cambrian and the appearance of large skeletal reefs in the mid-Ordovician came to be regarded as a major 'reef gap', the longest of the Phanerozoic (Copper, 2001; Stanley, 2001; Rowland and Shapiro, 2002; Kiessling, 2009; James and Wood, 2010). This view also tended to overlook the Early Ordovician reefs documented by Toomey (1970), Copper (1974), Toomey and Nitecki (1979) and others, that contain large domes and columns of *Pulchrilamina* as well as conspicuous conical lithistids (*Archaeoscyphia*) and calathiids (*Calathium*). Lithistid sponges as a whole constitute a long-ranging polyphyletic group of calcified demosponges (Pisera, 2002; Pisera and Lévi, 2002; Morrow and Cárdenas, 2015; Schuster et al., 2015) and continue to build reefs at the present-day (Maldonado et al., 2015). All known Cambrian lithistids, however, belong to the Family Anthaspidellidae, characterized by conical morphology and a distinctive ladder-like spicule structure. In overall shape and size, anthaspidellids broadly resemble archaeocyaths, and this similarity can extend to their reef-building role (Hong et al., 2016; Lee et al., 2016a). Both are commonly closely associated with, and volumetrically subordinate to, calcimicrobes and other microbial carbonates in reefs (Kruse and Zhuravlev, 2008; Kruse and Reitner, 2014; Adachi et al., 2015; Lee et al., 2016a).

For 25 Myr, throughout the mid–late Cambrian, skeletal reefs were dominated by cuplike lithistid sponges, always in association with microbial carbonates. The earliest known lithistid is *Rankenella* from near the Age 4/5 boundary (Kruse, 1983, 1996). A series of studies, beginning with Hamdi et al. (1995) (Lee et al., 2016a and references therein) (Fig. 1; Table 1), recognized lithistid contributions to mid–late Cambrian reefs. Lithistids were supported by their cemented basal attachments and interlocking spicules, and they could develop external ridged ornamentation that may have increased nutrient intake (Church, 2017). In Section 4 below, we summarize well-described mid–late Cambrian lithistid reefs, and in Fig. 2 show examples of lithistids. In addition to lithistids, mid–late Cambrian reefs also locally contain abundant siliceous sponges that have not yet been identified, but appear to resemble keratose sponges (cf. Luo and Reitner, 2014), and create maze-like "maceriate" structures (Lee et al., 2014a, 2015a, 2016c; Coulson and Brand, 2016).

Most early Cambrian skeletal reef-builders declined in the mid–late Cambrian. Radiocyaths disappeared in late Epoch 2 (middle Toyonian) (Kruse et al., 2015). Archaeocyaths and coralomorphs declined

Table 1
Examples of mid–late Cambrian lithistid sponge-microbial reefs.

Location	Age	Environment	Reef description	References
Dedebulak Formation, Kyrgyzstan	Stage 5?	Unknown	Lithistid sponge *Ortinocyathus-Epiphyton* reef	Teslenko et al. (1983)
Zhangxia Fm., Shandong Province, China	Upper Stage 5–lower Guzhangian	Shallow subtidal	Lithistid sponge (*Rankenella*)-calcimicrobe (*Epiphyton*)-stem-group cnidarian (*Cambroctoconus*) reef, meter-scale lens embedded within microbial-dominant reef; framework formed by mutual attachment of *Rankenella* and *Cambroctoconus* with *Epiphyton*; encrusted by microstromatolite	Woo (2009); Adachi et al. (2015), Lee et al. (2016a)
Daegi Fm., Taebaeksan Basin, Korea	Drumian	Shallow subtidal inner platform	Thrombolite-sponge reef; sponges mostly Anthaspidellidae; constructed primarily by *Epiphyton* and microbial clots; sponges occur between mesoclots	Hong et al. (2012, 2016)
Ranken Limestone, Georgina Basin, Australia	Upper Drumian	Bioclast-rich ramp debris	*Angusticellularia-Taninia*-lithistid sponge (*Rankenella*) reef; extent uncertain, possibly a few decimeters; sponges mainly passive reef builders within matrix formed by *Angusticellularia* and *Taninia*	Kruse and Reitner (2014)
Deh-Molla Formation, Iran	Lower Paibian	Subtidal, platform margin	Lithistid sponge (*Rankenella*)-*Girvanella* reef; sponges occupy up to 50% of reef volume and form framework by their mutual attachment; frameworks encrusted by *Girvanella* and/or ministromatolite	Hamdi et al. (1995), Kruse and Zhuravlev (2008)
Bonanza King Formation, Nevada and California, USA	Lower Paibian	Tidal channel within shallow subtidal ramp	Lithistid sponge (*Gallatinospongia*)-dendrolite reef; sponges in situ and enclosed by dendrolite; sponges occupy up to 30% in area	Shapiro and Rigby (2004)
Wilberns Formation, Texas, USA	Jiangshanian	Shallow marine	Lithistid sponge (*Wilbernicyathus*)-*Girvanella*-*Tarthinia* meter-scale reef; minor *Tarthinia*, *Epiphyton*, *Renalcis*; sponges constitute up to 30% of reef volume	Johns et al. (2007)
Notch Peak Formation, Nevada, USA	Lower Stage 10	Shallow subtidal	Anthaspidellid sponge-microbial reef; sponges form framework; pendent *Angusticellularia* grew beneath sponges; microstromatolites fill the interspaces between sponge frameworks and sometimes occur within spongocoels	Mrozek et al. (2003); Lee et al. (in prep.).
Dotsero Formation, Colorado, USA	Upper Stage 10	Shallow marine	*Girvanella-Tarthinia*-lithistid sponge (*Wilbernicyathus*) reef; thin veneer over *Girvanella* stromatolite	Johns et al. (2007)

substantially (Zhuravlev et al., 1993; Scrutton, 1997), but both groups persisted. Two examples of archaeocyaths occur in the Drumian (Wood et al., 1992; ~500–504 Ma, Bassett-Butt, 2016) and late Cambrian (Furongian) (Debrenne et al., 1984) of Antarctica, but the group did not regain its former prominence or form reefs (Bambach et al., 2002) and is not known in the Ordovician. Mid–late Cambrian conical coralomorphs include *Cothonian* and *Lipopora* in Age 4 and *Tretocylichne* in Age 5 (Park et al., 2016, figs. 4, 5), and the similar genus *Cambroctoconus* in late Age 5/early Drumian (~504 Ma) (Park et al., 2011) which was a reef-building component (Lee et al., 2016a). *Cambrotrypa* (Fritz and Howell, 1959; Bolton and Copeland, 1963; Scrutton, 1979; Jell, 1984), from the middle Cambrian of North America, could be a recumbent cerioid to phaceloid coral (Scrutton, 1997). In contrast to archaeocyaths, coralomorphs (e.g., *Amsassia*) recovered in the Early Ordovician.

3.5. Early–Middle Ordovician (485–460 Ma): microbial-lithistid-calathiid-pulchrilaminid

Early Ordovician lithistid-microbial reefs broadly resemble those of the mid–late Cambrian, but the lithistids are larger (e.g., *Archaeoscyphia*) (Fig. 4) and an additional cuplike group, the calathiids, appeared, exemplified by *Calathium* from the late Tremadocian/early Floian (Church, 1974). The major change at this time, however, was the appearance of a variety of encrusting-domical forms that included pulchrilaminids, coralomorphs (*Amsassia*), and the first definite appearances of tabulate corals (*Lichenaria*), bryozoans (*Nekhorosheviella*) and stromatoporoids (*Cystostroma*). These encrusting skeletons progressively transformed reef structure (Kröger et al., 2017). Pulchrilaminids (*Pulchrilamina*, *Zondarella*) can be up to 1 m in size, half as large again as early Cambrian *Flindersipora*. These reefs locally formed skeletal frameworks and hosted cryptic benthic organisms (Hong et al., 2014, 2015; Li et al., 2017b) (Fig. 4). This significant increase in

skeletal reef-builders has been regarded as an initial phase of the GOBE, foreshadowing the subsequent importance of reef-building stromatoporoids and tabulate corals (Webby, 2002; Webby et al., 2004; Adachi et al., 2011).

3.5.1. Receptaculitids, radiocyaths, cyclocrinitids

These calcified cup-like, pear-shaped, or globular macrofossils differ in age, and their affinities (generally suggested to be sponge or algal) continue to be debated. Radiocyaths are restricted to the early Cambrian (Kruse et al., 2015), where they are generally minor reef components. They were initially compared with archaeocyaths (Bedford and Bedford, 1934), with which they are associated in reef construction; but they differ in structure (Debrenne et al., 1970). Receptaculitids appear ~478 Ma (Tremadocian/Floian) and *Calathium* is a common frame-builder in Early Ordovician reefs (Church, 1974, 2009; Toomey and Nitecki, 1979; Cañas and Carrera, 1993; Li et al., 2014, 2015; Shen and Neuweiler, 2018). Ordovician receptaculitids are diverse and have been subdivided into three main groups: ischaditids, receptaculitids, soanitids (or calathiids) (Nitecki et al., 2004, fig. 31.1). They are locally important in later Ordovician reefs (e.g., Kröger et al., 2014), and range to the late Paleozoic. Cyclocrinitids mainly occur in the mid–late Ordovician and were diverse (e.g., *Apidium*, *Coelosphaeridium*, *Cyclocrinites*) near the Sandbian–Katian transition (Nitecki et al., 2004).

Receptaculitids, radiocyaths and cyclocrinitids have been compared because their walls are composed of numerous small plates that create a distinctively patterned external surface and bear internal rods. These structural similarities are greatest between radiocyaths and receptaculitids (Nitecki and Debrenne, 1979), and more superficial in cyclocrinitids (Beadle, 1988). Cyclocrinitids have long been compared with dasycladalean algae (Stolley, 1896), whereas receptaculitids (Austin, 1845; Billings, 1865) and radiocyaths (Bedford and Bedford, 1934) were both initially regarded as sponges. This long-established
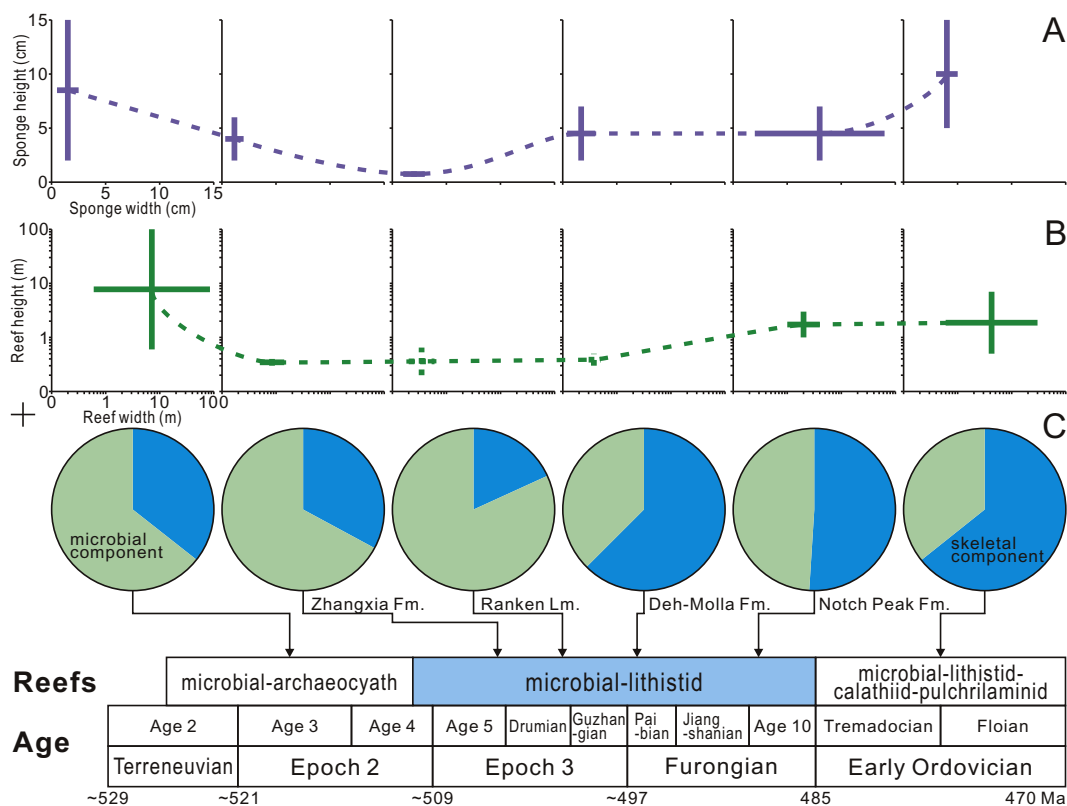

Fig. 4. Summary of Cambrian and Early Ordovician reefs. (A) Size of reef-building sponges. (B) Size of reefs in log-scale. (C) Pie diagrams of main reef-building components (microbial vs. skeletal). See Table 1 for data sources.

distinction was challenged by the proposal that the receptaculitid *Ischadites* is - like cyclocrinitids - a dasycladalean alga (Kesling and Graham, 1962; Byrnes, 1968). Support for this view not only resulted in it being applied to receptaculitids in general, but also in cyclocrinitids being regarded as receptaculitids (Nitecki, 1970, 1972; Nitecki and Debrenne, 1979; Rietschel and Nitecki, 1984).

Such sweeping interpretations attracted some opposition. Rietschel (1977) agreed that receptaculitids are algae but considered that they are not dasycladaleans. Beadle (1988) argued that receptaculitids and dasycladaleans are 'entirely unrelated'. These discussions were often complicated by being a part of the parallel debate about archaeocyath affinities (Rowland, 2001). Nitecki et al. (1999, 2004) suggested that cyclocrinitids are algae similar to dasyclads, but that receptaculitids are neither algae nor sponges. This latter view was also often considered for archaeocyaths (Vologdin and Zhuravleva, 1947; Zhuravleva and Myagkova, 1987) before they became generally regarded as sponges (Debrenne et al., 2015b).

One of the difficulties in determining receptaculitid affinities is the morphological heterogeneity of the group, ranging from enclosed pyriform to bowl-shaped bodies (Byrnes, 1968). Calathiids including *Calathium/Soanites* are clearly conical or cup-like (Myagkova, 1966; Church, 1991). This morphology, common in filter-feeding organisms (Billings, 1865; Myagkova, 1966; Li et al., 2015, 2017b), supports Billings' (1865) early view that *Calathium* is a sponge. A parsimonious view might be that radiocyaths (and cuplike receptaculitids, i.e., calathiids) are sponges, and that cyclocrinitids (perhaps together with enclosed receptaculitids) are algae. If radiocyaths and receptaculitids are related, then radiocyath decline at the end of the early Cambrian, followed by the Early Ordovician appearance of the calathiids, could be a further example of a group that was reduced in diversity and abundance during the mid–late Cambrian but recovered in the Early Ordovician. More information is required to elucidate these possibilities.

3.5.2. Bryozoans

The early history of bryozoans is problematic. The affinity of Dresbachian (Fritz, 1948) (~499 Ma) *Archaeotrypa* (Fritz, 1947) is uncertain; it may be a bryozoan or echinoderm (see Scrutton, 1979; Jell, 1984; Kobluk, 1984; Rozanov and Zhuravlev, 1992; Zhuravlev et al., 1993). *Pywackia*, reported by Landing et al. (2010) from Cambrian Stage 10 of Mexico has been compared with octocorals (Taylor et al., 2013; but see Landing et al., 2015). The earliest currently unquestioned bryozoan is *Prophyllodictya* from lower Tremadocian wackestones of South China (Ma et al., 2015), and the earliest reef-building bryozoan is late Tremadocian (~479 Ma) laminar *Nekhorosheviella semisphaerica*, also from South China (Cuffey and Zhu, 2010; Adachi et al., 2012; Cuffey et al., 2013, fig. 2.4a). *Nekhorosheviella* mutually encrusts, can occur on lithistids, and together with crinoid holdfasts forms small mounds 30 cm wide and 10 cm high, similar to Middle Ordovician pelmatozoan patch reefs (Pratt, 1989; Adachi et al., 2011). Larger bryozoan reefs appear in the late Darriwilian (Pitcher, 1964).

3.5.3. Pulchrilaminids

Late Tremadocian (~480 Ma) *Pulchrilamina* (Toomey and Ham, 1967) and Dapingian *Zondarella* (Keller and Flügel, 1996) are by far the largest Early Ordovician skeletons, although they often enclose or are interlayered with sediment. Pulchrilaminids share similarities with stromatoporoids, but their characteristic features such as very thin latilaminae and 'more loosely aggregated meshwork of skeletal elements, including slender, upwardly tapering, spinose rods that are spiculelike' suggest they are an independent group (Webby, 2015).

3.5.4. Corals

Lichenaria, generally considered the earliest tabulate coral (Scrutton, 1997; Elias et al., 2008), is recorded from the early Tremadocian (Pratt and James, 1982) (their Green Head Mound occurs in the lower Tremadocian Watts Bight Formation. See Knight et al., 2008, p.

118). However, Laub (1984) regarded the earliest *Lichenaria* as Darriwilian, and therefore contemporaneous with other tabulates such as *Billingsaria* and *Eofletcheria* (Desrochers and James, 1989; Pickett and Percival, 2001; Kröger et al., 2017). The coralomorph *Amsassia* (Carrera et al., 2017) may have been confused with *Lichenaria*, but differs in growth mode and has been suggested to be an alga (Sun et al., 2014).

3.6. Late Middle–Late Ordovician (460–444 Ma): stromatoporoid-bryozoan-tabulate-receptaculitid-microbial

Stromatoporoids appear in the Early Ordovician (early Floian) as small specimens of the labechiid *Cystostroma* attached to *Calathium* (Li et al., 2017b). Much larger labechiids (*Labechia, Pachystylostroma*) and also clathrodictyiids (*Pseudostylodictyon*) appear in the late Darriwilian ~460 Ma (Pitcher, 1964). Together with bryozoans (*Batostoma*) and tabulate corals (*Billingsaria*), as well as the chaetetid *Solenopora*, they constructed large Darriwilian/Sandbian reefs, such as the classic Chazy examples in Vermont (Pitcher, 1964; Finks and Toomey, 1969; Kapp, 1975), and the upper Sandbian Carters Formation of Tennessee (Alberstadt et al., 1974). In addition to their size and abundance, mid-Ordovician stromatoporoids, bryozoans and tabulates are also notable for their laminar and domical shapes (Copper, 1974; Fagerstrom, 1987; Webby, 2002; Webby et al., 2004; Adachi et al., 2011) which transformed substrate colonization and vertical succession in reefs (Pitcher, 1964; Finks and Toomey, 1969; Alberstadt et al., 1974; Copper, 1974; Hong et al., 2017, 2018; Kröger et al., 2017). Rugose corals also appear in the late Darriwilian, but did not become common until the Sandbian–Katian (Baars et al., 2012). All these groups diversified further in the Late Ordovician, together with encrusting echinoderms, cuplike receptaculitids, and globular cyclocrinitids. Skeletal reefs with bivalves, siliceous sponges, and the coralomorph *Amsassia*, also occur during this time interval (Lee et al., 2014c, 2016b; Sun et al., 2014). These developments were part of continued GOBE diversification in the Middle to Late Ordovician that resulted in complex and well-structured benthic communities (Droser and Sheehan, 1997; Webby, 2002; Harper, 2006). Lithistids, often in association with *Calathium* and microbial carbonates continued to be locally abundant in late Darriwilian reefs (Alberstadt et al., 1974; Klappa and James, 1980; Desrochers and James, 1989; Brunton and Dixon, 1994; Liu et al., 2003; Li et al., 2017c), but the volumetric importance of these components appears to have declined by the Late Ordovician as stromatoporoids, corals and bryozoans increased (Webby, 2002; Adachi et al., 2011).

4. Mid–late Cambrian lithistid sponge-microbial reefs

The nature and distribution of lithistid sponge-microbial reefs are central to our discussion of mid–late Cambrian environments and biotas. Following their discovery in lower Furongian strata of Iran (Hamdi et al., 1995), mid–late Cambrian LSM reefs have been recognized worldwide (Mrozek et al., 2003; Shapiro and Rigby, 2004; Johns et al., 2007; Kruse and Zhuravlev, 2008; Hong et al., 2012, 2016; Kruse and Reitner, 2014; Adachi et al., 2015; Lee et al., 2016a) (Table 1). In contrast to early Cambrian archaeocyath-microbial reefs and Early Ordovician lithistid sponge-microbial reefs, which have been studied in detail for more than 100 years, middle–late Cambrian LSM reefs remain much less well-known. Here we briefly summarize the composition and structure of four relatively well-described examples.

4.1. Zhangxia Formation (upper Stage 5, Cambrian Series 3), Shandong, China

The oldest LSM reefs currently known occur in the lower part of the Zhangxia Formation (Shandong Province, China) (Woo, 2009; Adachi et al., 2015) where they form lenses ~150 cm thick within microbial mounds (Lee et al., 2016a). Based on the trilobite biozone *Lioparia*, they belong to the upper part of Stage 5 of Cambrian Series 3. At this level,
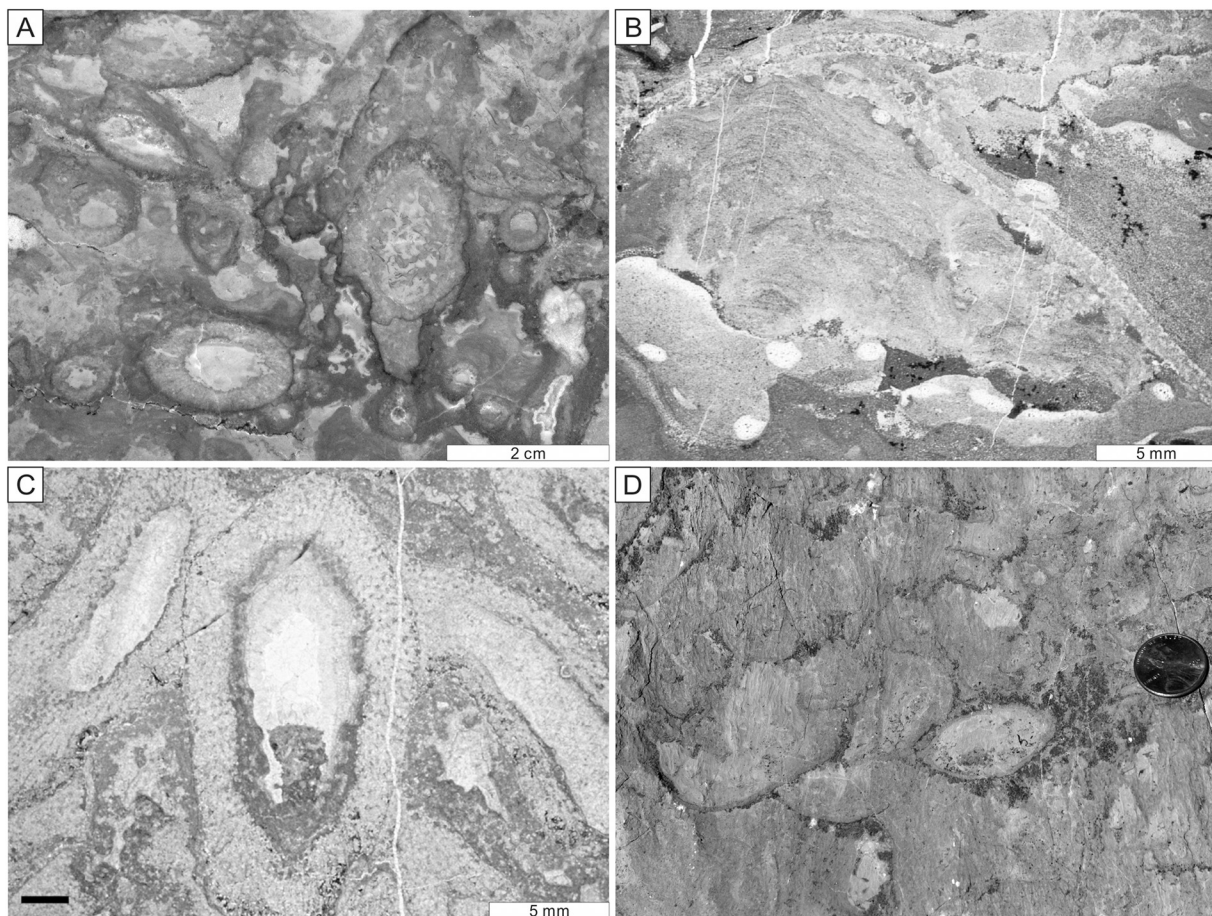
Fig. 5. Examples of mid–late Cambrian reef-building sponges. (A) *Rankenella zhangxianensis* (upper Stage 5; Zhangxia Formation), Beiquanzi section, Shandong Province, China. (B) *R. mors* (upper Drumian; Ranken Limestone), locality NTGS4648, Georgina Basin, Australia (after Kruse and Reitner, 2014, fig. 5A). (C) *R. hamdii* (lower Paibian; Deh-Molla Formation), Shahmirzad section, northern Iran (after Kruse and Zhuravlev, 2008, fig. 7D). (D) Unidentified anthaspidellid sponge (Stage 10; Notch Peak Formation), Arrow Canyon section, Nevada, USA. Coin is 19 mm in diameter.

the Zhangxia Formation is mainly composed of bioturbated wackestone and oolitic, skeletal, and peloidal packstone-grainstone, deposited on a shallow subtidal carbonate platform (Woo, 2009; Lee et al., 2015b). Metazoans include the lithistid sponge *Rankenella zhangxianensis* Lee et al., 2016d (Family Anthaspidellidae, Order Orchocladina), the stem-group cnidarian *Cambroctoconus orientalis* Park et al., 2011, and unidentified siliceous sponges (Fig. 5A). Microbial components include *Epiphyton*, microstromatolite, and undifferentiated microbialite (Lee et al., 2016a) (Fig. 6A, B). *R. zhangxianensis* occupies up to 20% of the reef volume, is mostly conical in shape with smooth outlines, and is 3–21 mm in diameter and up to 610 mm in length. *C. orientalis* (8–11 mm in diameter, 11–13 mm in length; Park et al., 2011) is shaped like an octagonal cone and occupies < 3% of the reef volume. The unidentified siliceous sponges (~1% of reef volume) consist of irregularly shaped spicule networks resembling keratose sponges (cf. Luo and Reitner, 2014). Small dendritic calcified epiphytaceans are a major component, up to 20% of the reef volume. Microstromatolites are characterized by thin convex-up laminae of alternating dark and light gray micrite. Undifferentiated microbialite, composed of clotted-peloidal fabric with faint laminae, possibly represents poorly preserved microstromatolite. The main framework builders are the lithistids, *Epiphyton* and stem-group cnidarians (Lee et al., 2016a). The lithistids and stem-group cnidarians locally mutually attach (Fig. 5A), whereas *Epiphyton* is either mutually attached or attached to the sponges. These metazoan-calcimicrobial frameworks were encrusted and stabilized by microstromatolite (Fig. 6A, B), and probably created at least a few centimeters of synsedimentary relief.

4.2. Ranken Limestone (upper Drumian, Cambrian Series 3), Georgina Basin, Australia

Reef fabrics formed by lithistid sponges and microbes in the Ranken Limestone are only known from loose blocks described by Kruse and Reitner (2014) who supposed that the individual reefs would not have exceeded a few decimeters in size. The Ranken Limestone consists of cross-bedded bioclast-ooid-intraclast grainstone and subordinate bioclastic wackestone and appears to be a ramp deposit. Biostratigraphic control is poor, but relationships with adjacent deposits suggest a late Drumian age (Kruse and Reitner, 2014). The reef fabric mainly consists of microstromatolite and the anthaspidellid sponge *Rankenella mors* Kruse, 1983 (Kruse and Reitner, 2014) (Fig. 5B), which is mostly explanate in shape and only about 1 mm thick, although conical examples are also present. Domical or locally columnar masses of microstromatolite, up to 11 mm thick and 26 mm across, consist of light and dark laminae with patches of calcified microbes (*Angusticellularia*, *Tania*). The Ranken reef is therefore mainly microbial and the role of *R. mors* appears to have been subordinate, mainly providing a substrate for stromatolite growth. Elsewhere in the Georgina Basin, *R. mors* inhabited low-energy anaerobic mudstone environments in the mid-Cambrian Arthur Creek Formation (Kruse, 1996; Debrenne and Reitner, 2001).

4.3. Deh-Molla Formation (lower Paibian, Furongian), northern Iran

These generally small LSM reefs, less than a few tens of centimeters
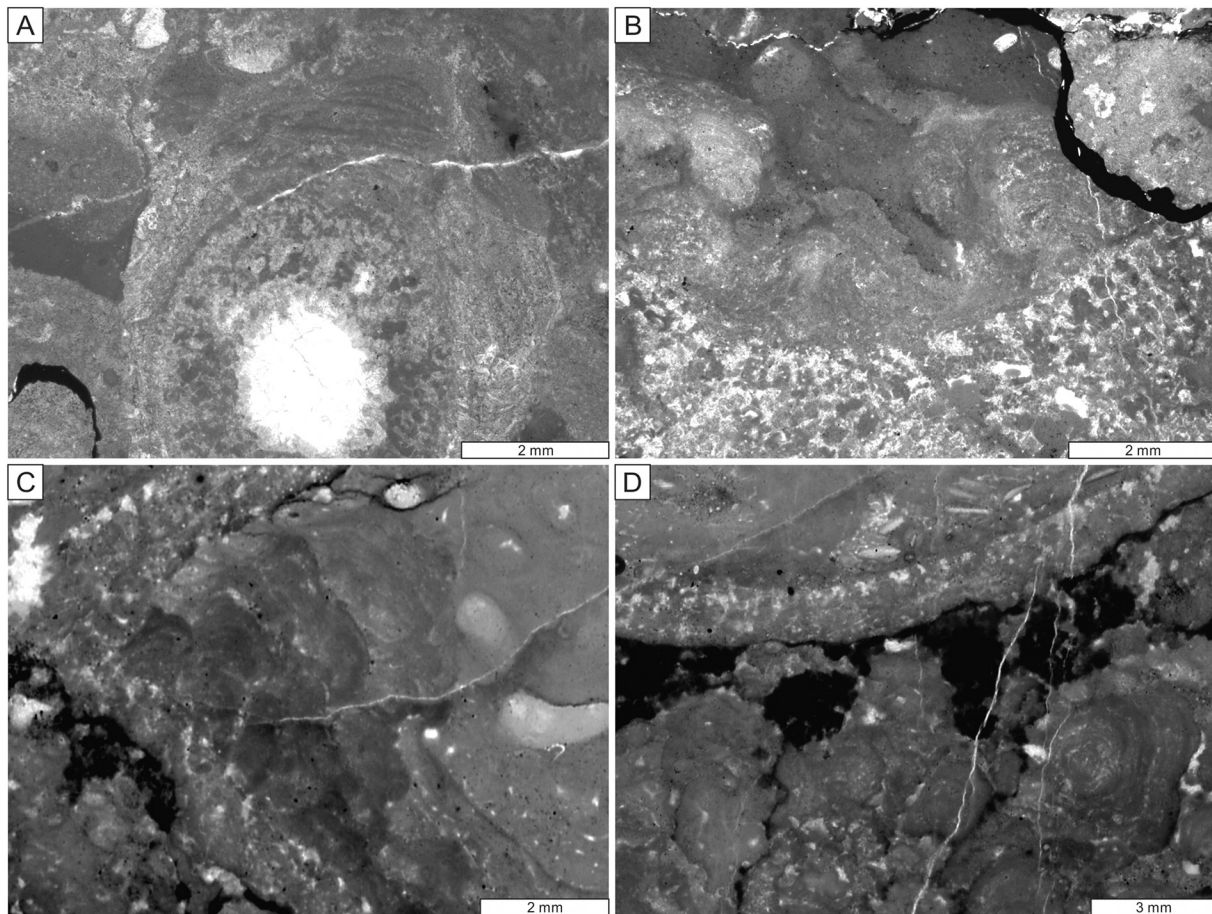
Fig. 6. Photomicrographs of lithistid sponges and microstromatolites in mid–late Cambrian reefs. (A, B) *Rankenella zhangxianensis-Epiphyton-Cambroctoconus orientalis* reef (upper Stage 5; Zhangxia Formation), Beiquanzi section, Shandong Province, China. (C, D) Anthaspidellid sponge-microbial reef (Stage 10; Notch Peak Formation), Arrow Canyon section, Nevada, USA.

in height and width (Hamdi et al., 1995; Kruse and Zhuravlev, 2008), occur in the Mila (renamed Deh-Molla) Formation (Geyer et al., 2014). The reef-bearing interval overlies the *Prochuangia* trilobite biozone, suggesting an early Furongian (Paibian) age (Peng et al., 1999). The platform margin on which it developed preserves microbial boundstone/floatstone with abundant demosponges (Geyer et al., 2014). The main reef components are *Rankenella hamdii* (anthaspidellid sponge) and *Girvanella* (calcified cyanobacterium). *R. hamdii* occupies up to 50% of the reef volume (Hamdi et al., 1995). It is conical, bowl or digitate in shape (Fig. 5C), 4–31 mm in diameter, and up to 80 mm in height and mutually attaches, forming frameworks that are commonly thickly encrusted by *Girvanella*, columnar microstromatolites and clotted-peloidal fabric. These encrustations mainly occur on the dermal surfaces of the sponges, but sometimes also on the gastral surfaces (Fig. 5C).

4.4. Notch Peak Formation (Stage 10, Furongian), Nevada, USA

Anthaspidellid sponge-microbialite reefs occur in the upper part of Notch Peak Formation (Mrozek et al., 2003). Oolitic and bioclastic packstone-grainstone and flat-pebble conglomerates, as well as stromatolites and the lithistid sponge-microbial reefs, are locally well-preserved within an otherwise dolomitized succession. The facies association suggests a shallow subtidal environment. The reefs are domical and a few meters thick, commonly occurring with columnar stromatolites (Mrozek et al., 2003). They contain the *Eoconodontus notchpeakensis* conodont fauna, suggesting a late Furongian (Age 10) age (Mrozek et al., 2003; Dattilo et al., 2004). Three main components of

these LSM reef are unidentified lithistid sponge, microstromatolite, and the calcified microbe *Angusticellularia* (Mrozek et al., 2003; J-H.L., personal observation) (Figs. 5D and 6C, D). The lithistids are mainly thin walled (~5 mm) upward widening cups (often 3 cm, but up to 14 cm, in diameter). They do not appear to closely resemble any described lithistid genus, but display typical anthaspidellid-type spicule networks (J-H.L., personal observation). The microstromatolites consist of thin alternating light-dark laminae, grading to faintly clotted/laminated fabric. Dark pendent *Angusticellularia* is common on the lower surfaces of the sponges. Keratose-like siliceous sponges occur rarely within the lithistid spongocoels. The main frame-builders of these Notch Peak reefs are lithistids, which appear to have been firmly mutually attached. The downward growing *Angusticellularia*, although forming only very thin crusts, suggests sediment-free space beneath the growing sponges. Bioturbated micrite, skeletal fragments and unidentified siliceous sponges fill the spongocoels. Microstromatolites occupy much of the space between sponges (Fig. 6C), and thin microstromatolite layers locally encrust sponge dermal surfaces within spongocoels (Fig. 6D).

4.5. Summary

Although much further research is required, in structure and composition these mid–late Cambrian LSM reefs quite closely resemble Early Ordovician examples built by microbes and the lithistid *Archaeoscyphia*. The above examples suggest several general characteristics of late Cambrian LSM reefs: 1. Decimeter- to meter-scale lensoid to domal shape. 2. Co-occurrence with, and often within,

microbial reefs. 3. Mutually attached frameworks formed by sponges. 4. Microstromatolites encrusting and stabilizing the sponge frameworks. 5. Formation in shallow subtidal packstone-grainstone environments.

5. Mid–late Cambrian dysoxia-hypoxia and sponge-microbial reefs

5.1. Evidence for low-oxygen conditions

A minimum level of oxygen required to maintain aerobic metabolism has long been linked to animal diversification during the Proterozoic–Cambrian transition (Berkner and Marshall, 1965; Rhoads and Morse, 1971; Knoll and Carroll, 1999; Canfield et al., 2007; Payne et al., 2009, 2011; Dahl et al., 2010; Maloof et al., 2010a; Knoll, 2011; Sperling et al., 2013; Ader et al., 2014; Mills and Canfield, 2014; Xiao, 2014; Zhang et al., 2014, 2018; Chen et al., 2015; Li et al., 2017a; Shields, 2017). It has been suggested that ocean oxygenation promoted animal diversification in the early Ediacaran ~630 Ma (Sahoo et al., 2012) and early–mid (541–509 Ma) Cambrian (Li et al., 2017a) and that 'modern-like oxygen levels' appeared by ~521 Myr ago (Chen et al., 2015). However, evidence from iron speciation (Sperling et al., 2015a), Mo-isotopes (Dahl et al., 2010) and alteration of deep sea basalts (Stolper and Keller, 2018) provide compelling evidence that persistent elevated oxygen levels are likely a later Paleozoic phenomenon. It seems that oxygenation of the oceans during the Ediacaran-Cambrian transition was likely a protracted and fluctuating series of oxic-anoxic/euxinic phases (Fike et al., 2006; Canfield et al., 2007, 2008; Shen et al., 2008; Jiang et al., 2009; Halverson et al., 2010; Wood et al., 2015; Zhang et al., 2018; Wood and Erwin, 2018). This secular pattern was further complicated by local variations in basinal and shelf anoxia (Goldberg et al., 2005; Schröder and Grotzinger, 2007; Canfield et al., 2008; Kendall et al., 2015; Sperling et al., 2015a; Jin et al., 2016; Och et al., 2016; Cheng et al., 2017). Moreover, the tendency toward low seawater oxygen concentrations subsequently appears to have increased during the Cambrian (Boyle et al., 2014; Cremonese et al., 2014), and persisted into the Ordovician (Railsback et al., 1990; Strauss, 2006; Kah and Bartley, 2011; Thompson and Kah, 2012; Wallace et al., 2017) (Fig. 1). Based on extensive black shale occurrences, Berry and Wilde (1978) inferred widespread and recurrent episodes of marine hypoxia during the mid–late Cambrian and Early Ordovician. They compared these conditions with those of the Cretaceous, attributed them to elevated temperatures, and suggested that they did not decline until cooling promoted mid-Ordovician ocean ventilation (Fig. 1). Black (or dark-colored) shales have been widely recognized in lower Paleozoic strata worldwide (e.g., Leggett, 1980; Wilde and Berry, 1984; Berry et al., 1986, 1989; Wilde et al., 1989; Fyffe and Pickerill, 1993; Saltzman et al., 2000; Egenhoff et al., 2015). The Chengjiang (ca. 520 Ma), Burgess Shale (ca. 508 Ma) and Fezouata (ca. 480 Ma) biotas, as well as other Burgess-Shale type biotas, which record a large proportion of early animal taxa, are preserved in organic-rich shales that are thought to reflect low-oxygen conditions (Conway Morris, 1986; Gaines et al., 2005; Gaines and Droser, 2010; Van Roy et al., 2010), even though other factors could have been necessary to preserve these fossils (Gaines, 2014). Some of these shales are significant sources of petroleum (e.g., Buchardt and Lewan, 1990; Mi et al., 2007; Ryder et al., 2014), and gas (e.g., Yu et al., 2009; Schovsbo et al., 2011; Huang et al., 2012; Pashin et al., 2012; Pool et al., 2012). Preservation of abundant organic matter in these shales suggests that low-oxygen conditions were prevalent throughout their deposition. Extinctions of archaeocyaths (Zhuravlev and Wood, 1996) and trilobites (Palmer, 1984; Westrop and Ludvigsen, 1987) in the Cambrian have been linked to anoxia.

This broad interpretation of a tendency to low oxygen marine conditions during the interval between the early Cambrian and mid-Ordovician has received support from studies of biogeochemically cycled redox-sensitive elements (C, N, S, U isotopic values; and Zn/Fe, Mo, Ce/Ce*, Th/U abundances), particularly for the mid–late Cambrian

(Perfetta et al., 1999; Saltzman et al., 2000; Gill et al., 2011; Dahl et al., 2014; Saltzman et al., 2015). Well documented examples of correspondence between black shale deposition, faunal change, and geochemical indicators of hypoxia include the ~510 Ma Sinsk and ~500 Ma SPICE events. Incursions of anoxic water onto shelves at ~510 Ma have been inferred from negative carbon isotope (Montañez et al., 2000; Guo et al., 2010) and positive $\delta^{34}S$ (Hough et al., 2006) values. Similar age $\delta^{15}N$ values, among the lowest of the Phanerozoic, may suggest low-oxygen photic zone conditions (Algeo et al., 2014, fig. 1). Interpretation of the ~500 Ma Steptoean Positive Carbon Isotope Excursion (SPICE) as reflecting low-oxygen conditions in shelf waters (Saltzman et al., 2000) is supported by coeval positive $\delta^{34}S$ sulfate excursions (Gill et al., 2007, 2011; Hurtgen et al., 2009), decreased Mo enrichment (Gill et al., 2011), and negative $\delta^{238}U$ excursion (Dahl et al., 2014). In addition, the Drumian (middle Cambrian) negative carbon isotope excursion (DICE) (~505 Ma) and associated Mo, U, and V values have been linked to euxinic conditions that extended into the photic zone (Pagès and Schmid, 2016). Cambrian–Ordovician boundary (~485 Ma) slope carbonates in Newfoundland have Ce/Ce* and Th/U ratios and N and U-isotope values consistent with dysoxic conditions (Azmy et al., 2014, 2015). The inference of Berry and Wilde (1978), that the tendency for shelf biotas to experience influxes of low-oxygen waters only diminished in the mid-Ordovician as ocean circulation improved, is supported by oxygen (Railsback et al., 1990) and sulfur (Kah et al., 2016) isotope studies as well as Th/U ratios in carbonates (Marenco et al., 2016), and has been linked to global cooling (Trotter et al., 2008) (Fig. 1).

These changes are widely considered to have been important in ushering in the GOBE (McKenzie et al., 2014; Saltzman et al., 2015). Edwards et al. (2017) suggest that atmospheric oxygen concentrations were low (~12%) during the Early Ordovician and doubled to about 25% by the Darriwilian, coinciding with increased biodiversity. Based on sea-surface temperature (Trotter et al., 2008, fig. 3) and modeled estimates of atmospheric oxygen (Edwards et al., 2017, fig. 2), we calculated the dissolved oxygen concentrations in seawater during the Ordovician (Fig. 7). These values are generally near 100 μM during the Early Ordovician, approximately one third of present-day seawater. They begin to rise ~465 Ma (early Darriwilian) and reach a peak at 451 Ma (early Katian), before declining steeply to 446 Ma (late Katian). This overall trend broadly corresponds with that of marine invertebrate diversity (Sepkoski Jr., 1995, fig. 1; Webby et al., 2004, fig. 1.1). Our calculated dissolved oxygen values (Fig. 7) from Edwards et al. (2017, fig. 2) are mainly for the Ordovician, but also indicate ~12% atmospheric oxygen in the late Cambrian. Based on the minimum requirements of animals (lower value) and pervasive subsurface anoxia (upper value), Sperling et al. (2015b, fig. 3) (also Stolper and Keller, 2018) estimated overall Cambrian atmospheric oxygen levels to have been even lower, in the range 15–40% of present atmospheric level (= 3–8% oxygen). These average values can be expected to have resulted in much lower levels of dissolved oxygen, seasonally and locally. Even in the present-day ocean, under 21% atmospheric O_2, hypoxia commonly develops (Rabalais et al., 2010) and oxygen-deficient waters threaten coral reefs (Altieri et al., 2017). There is evidence for early to middle Cambrian oxygen-minimum zones (Guilbaud et al., 2018). It is therefore likely that localized and seasonal conditions resulted in fluctuations well below the average level of dissolved oxygen (~100–115 μM/L) that we calculated (Fig. 7) for the Early Ordovician, and which is already hypoxic according to the definition of Tyson and Pearson (1991).

Terms commonly used to describe dissolved oxygen levels include anoxic, suboxic, dysoxic/hypoxic, oxic/normoxic (e.g., Tyson and Pearson, 1991; Middleburg and Levin, 2009; Rabalais et al., 2010; Sperling et al., 2015a). These terms, the thresholds defining them, and the units used to measure them (e.g., mg/L, μM/kg, mL/L, μM/L) often differ according to author and research field. Tyson and Pearson (1991, table 2) pointed out that terms such as dysoxic, dysaerobic and hypoxic
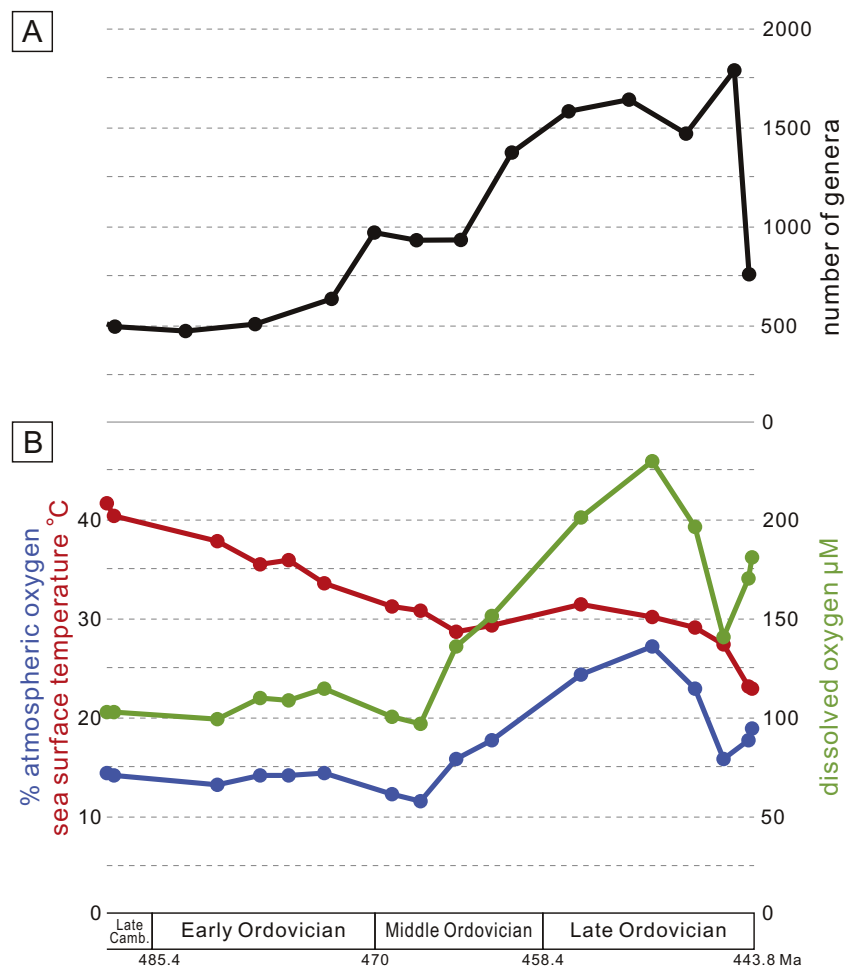
Fig. 7. (A) Ordovician marine invertebrate diversity (Sepkoski Jr., 1995, fig. 1). (B) Dissolved oxygen concentrations in seawater calculated from sea-surface temperature (Trotter et al., 2008, fig. 3) and atmospheric oxygen (Edwards et al., 2017, fig. 2) data (see Supplementary Oxygen and Temperature Data).

had been applied to environment, biofacies and physiology respectively. Over time, however, some of these distinctions have become blurred. The following terms (for environments, facies, oxygenation levels) and thresholds were recommended by Tyson and Pearson (1991, table 2) in mL/L, at 10 °C, 1 atm pressure, with 1.029 density of seawater (conversions to other widely used units are shown in brackets):

oxic: 8.0–2.0 mL/L (= 12.03–3.01 mg/L, 376–94 µM/L, 365.4–91.35 µM/kg, 11.69–2.92 ppm)

dysoxic: 2.0–0.2 mL/L (= 3.01–0.30 mg/L, 94–9.4 µM/L, 91.35–9.14 µM/kg, 2.92–0.29 ppm)

suboxic: 0.2–0.0 mL/L (= 0.30–0 mg/L, 9.4–0 µM/L, 9.14–0 µM/kg, 0.29–0 ppm)

anoxic: ≥ 0.0 mL/L (= ≥ 0 in all cases)

Unlike reef-builders, mobile organisms can move to avoid localized environmental changes. Furongian and Early Ordovician reefs in Newfoundland, for example, occur in close association with skeletons of trilobites and cephalopods (see Pruss and Knoll, 2017). Several present-day groups, including shrimps and crabs, can detect and avoid oxygen deficient sea water (Renaud, 1986). Mobile nekton on the northern Gulf of Mexico continental shelf avoids oxygen levels < 2 mg/L (1.4 mL/L) (Pavela et al., 1983; Renaud, 1986), and fish avoidance generally occurs at oxygen concentrations 0.5 to 2 mg/L (0.35 to 1.4 mL/L) (Levin et al., 2009). Similarly, various motile organisms, including ctenophores, crustaceans, and cephalopods, can tolerate low oxygen levels (Ekau et al., 2010, table 2). Variability in oxygen concentrations can be more limiting than the absolute value (Matabos et al., 2012). There is evidence that late Cambrian groups such as olenids (Fortey, 2000) and

phosphatocopids (Williams et al., 2011) were dysoxia-tolerant. Large present-day arthropods, such as lobsters, are relatively tolerant of oxygen levels as low as 2 ppm, though 4 ppm is generally considered to be the minimum (Bayer et al., 1998). Our calculation of ~100 µM oxygen (3.2 ppm) in the Early Ordovician is approaching the upper limit of dysoxic (2.92 ppm) based on Tyson and Pearson (1991, table 2). This suggests that average oxygen levels in Early Ordovician seawater could have supported large arthropods but that seasonal and local variations could readily have resulted in oxygen limitation.

5.2. Factors promoting low-oxygen conditions in shallow marine environments

Interrelated factors generally contributing to shallow marine deoxygenation include global warming, increased marine productivity, thermal stratification, and expansion of shallow platform areas (Schmittner et al., 2008; Keeling et al., 2010; Praetorius et al., 2015). Global warmth, that characterized the mid-Cambrian to mid-Ordovician (Frakes et al., 1992, p. 14) and promoted low-oxygen conditions, has been linked to high sea-level and high CO_2 “greenhouse” conditions during commencement of the first Phanerozoic supercycle (Fischer, 1984; Landing, 2012b; Nance and Murphy, 2013). Modeled estimates suggest that CO_2 (Berner, 2009) and temperature (Royer et al., 2004, fig. 4) peaked in the mid-Cambrian. Oxygen isotope thermometry indicates earliest Ordovician sea-surface temperatures (Shields et al., 2003; Kasting et al., 2006) in excess of 40 °C (Trotter et al., 2008). Earlier additional episodic warming due to CO_2 increase has been

attributed to extensive continental flood basalt volcanism, such as the late Cambrian Age 4 Kalkarindji Large Igneous Province in Australia (510.7 ± 0.6 Ma, Jourdan et al., 2014) (Glass and Phillips, 2006; Hough et al., 2006). As shown by Mesozoic Ocean Anoxic Events (OAEs), clear links can exist between anoxia and Large Igneous Provinces (LIPs). However, further studies are needed to identify Paleozoic LIPs (Percival et al., 2015, fig. 1) and disparities in timing between early Botomian anoxia (> 514 Ma; Peng et al., 2012), the Hawke's Bay regression (~511 Ma), and the Kalkarindji eruption (~510 Ma) recommend caution in linking these events.

Low oxygen areas develop or persist seasonally or continuously beneath upwelling regions, associated with the upper parts of oxygen minimum zones, and in warm oceans that are more stratified, hold less oxygen and experience greater advection of oxygen-poor source waters (Levin et al., 2009). In addition to lowering oxygen solubility, higher temperatures make water less dense, promoting thermal stratification that in turn reduces ventilation (Erbacher et al., 2001). Warming also favors biological productivity in the water column (e.g., phytoplankton blooms) which increases carbon burial, and thus the likelihood of bottom-water hypoxia (Pedersen and Calvert, 1990; Sen Gupta et al., 1996). Global Cambrian sea-level rise (Miller et al., 2005) promoted development of extensive, shallow epeiric carbonate platforms (Peters and Gaines, 2012), that tend to limit shallow-water circulation (Irwin, 1965) and expand the environments subject to thermal stratification (Allison and Wright, 2005; Allison and Wells, 2006). In Laurentia, mid-Cambrian sea-level rise established extensive platforms that locally persisted into the Late Ordovician (Bond et al., 1989; Morgan, 2012). This 'Great American Carbonate Bank' enclosed intrashelf basins (e.g., Markello and Read, 1981) prone to dysoxia-anoxia, and black mudstones accumulated on its slopes during eustatic highs (Landing, 2012a, 2012b; Lavoie et al., 2012; Miller et al., 2012; Peters and Gaines, 2012). These conditions ameliorated by the mid-Ordovician, as indicated by early Darriwilian sulfur isotope values consistent with ocean ventilation that appear to coincide with lower sea-surface temperatures (Kah et al., 2016), as well as with decrease in strontium isotope values (Edwards et al., 2015). Ordovician cooling and oxygenation, coincident with diversification of the "Paleozoic" and "Modern" faunas (Trotter et al., 2008), also marked the end of sponge-microbial reef dominance in the early Paleozoic (Brunton and Dixon, 1994). This trend continued until widespread oxygenation of the deep ocean occurred in the mid-Paleozoic (Dahl et al., 2010).

5.3. Low oxygen levels and lithistid sponges

Lithistids are a polyphyletic group of demosponges with interlocked siliceous spicules (desmas) that form a rigid skeleton (Hinde, 1883; Lévi, 1991; Debrenne and Reitner, 2001; Pisera, 2002; Pisera and Lévi, 2002; Hill et al., 2013). They are represented by about 46 extant genera (Maldonado et al., 2016). Present-day lithistids can dominate benthic faunas at depths of ~150–1800 m (Kelly, 2007), and locally aggregate into reefs (Conway et al., 1991) similar to ancient examples (Brunton and Dixon, 1994). Dense intertwined clusters of the lithistid *Leiodermatium pfeifferae*, with thin (3–9 mm) erect foliose branches up to ~80 cm high and 1 m wide, at depths of ~750 m in the western Mediterranean, have been compared with Mesozoic lithistid reefs (Maldonado et al., 2015, 2016). However, since the anthaspidellid lithistids that dominated Cambrian–Ordovician reefs went extinct in the Permian, caution is required when comparing lithistid reefs of different ages (Pisera, 2002).

Data concerning the oxygen requirements of present-day lithistids are limited; more information is available concerning other demosponges and also hexactinellids. Many sponges survive periods of anoxia. In experiments, demosponges not only tolerate hypoxia, but appear to have higher survival rates under hypoxic conditions than under normoxia (Gunda and Janapala, 2009). *Halichondria panicea*, for example, grows under oxygen in the range 0.5–4% of present atmospheric level

(Mills et al., 2014). Similar examples are documented from the wild. For example, in Saanich Inlet, western Canada, hexactinellids survive anoxia (oxygen concentrations < 0.2 mL/L) (Tunnicliffe, 1981), readily tolerate hypoxia (< 1.4 mL/L) (Chu and Tunnicliffe, 2015), and generally appear to do well in oxygen as low as 0.5 mL/L (i.e., severe hypoxia) (Jackson Chu, pers. comm, 2016). Thus, overall, at least some sponges dominate hypoxic systems and tolerate periodic anoxia (Hoffmann and Schläppy, 2011; Steckbauer et al., 2011; Riedel et al., 2014).

Sponge cells together with their associated symbiotic microbes often experience anaerobic conditions when pumping activity stops, and can maintain internal suboxic and locally hypoxic conditions (Hoffmann and Schläppy, 2011; Lavy et al., 2016). Sponges typically use only a small fraction of available oxygen for respiration (Hoffmann et al., 2005) and their ability to tolerate low oxygen levels may be linked to facultatively anaerobic mitochondria (Mentel et al., 2014). Some sponges, including lithistids (Brück et al., 2012) harbor large numbers of bacterial symbionts (Imhoff and Trüper, 1976; Fan et al., 2012) that can constitute up to 40% of sponge biomass (Taylor et al., 2007; Schmitt et al., 2012) and provide significant nutrition. These include anaerobic bacteria that occupy "anoxic niches" (Schläppy et al., 2010). The complex lithistid microbiome (Hentschel et al., 2012) is a source of pharmaceutical metabolites (Thomas et al., 2010).

Molds of sponges (Gehling and Rigby, 1996) and phosphatized sponges (Li et al., 1998; Yin et al., 2015) occur in the Ediacaran. Spicules that have been reported (Brasier et al., 1997) may have been misidentified (Antcliffe et al., 2014; Muscente et al., 2015). Biomarkers (Love et al., 2009; Sperling et al., 2010) suggest that demosponges and weakly calcified sponge-grade metazoans (Maloof et al., 2010b) appeared even earlier (Erwin et al., 2011), consistent with sponges having low oxygen requirements (Mills and Canfield, 2014). Oxygen increase during the Ediacaran–Cambrian transition (Fike et al., 2006; Chen et al., 2015) does not appear to have been sustained (see Section 5.1). The appearance of archaeocyaths in the early Cambrian, and their relatively abrupt decline coincident with the anoxic Sinsk Event (Zhuravlev and Wood, 1996) suggests that they may have been less tolerant than lithistids to low oxygen conditions. In contrast, lithistids appear unaffected by mid–late Cambrian and Early Ordovician extinction events attributed to anoxia (Saltzman et al., 2015). The only gradual increase observed in sponge size through the mid-Cambrian to early Ordovician (Fig. 3) could reflect the need to maintain the advantage of small body size under low-oxygen conditions (Payne et al., 2011).

Stromatoporoids and corals were important reef-builders from the mid-Ordovician to Late Devonian (Fagerstrom, 1987; Wood, 1999; James and Wood, 2010). The lithistid-microbial association reappeared sporadically; e.g., in the Late Ordovician (Brunton and Dixon, 1994; Leinfelder et al., 2002, p. 185), Late Silurian (de Freitas et al., 1999), and in Early Carboniferous reefs (e.g., Mundy, 1994; Webb, 1999) following Late Devonian stromatoporoid extinction. Similarly, a variety of sponges together with microbes occurs in reefs following the end-Permian extinction (Brayard et al., 2011). Probably the most conspicuous Mesozoic development of lithistid-microbial reefs was in the mid–late Jurassic, together with hexactinellid sponges (Leinfelder et al., 2002). Lithistid-microbial reefs are common in poorly oxygenated environments in the Upper Jurassic of Germany and Middle to Upper Jurassic of Spain and Portugal (Leinfelder et al., 1994, 1996) at depths of 30–90 m, coeval with shallower water coral-sponge-microbial reefs (Leinfelder, 2001, fig. 18). This was a period of relatively warm conditions (Jenkyns et al., 2012) when reduced oceanic circulation is inferred to have promoted black shale formations and dysaerobic reefs (Leinfelder et al., 1994, 1996). Lithistid-microbial reefs could therefore represent a default "low oxygen" Phanerozoic reef community.

Stromatoporoids may have had different oxygen requirements from lithistids. Present-day hypercalcified sponges (sclerosponges), considered to be relict stromatoporoids (Stearn, 2015b), preferentially

occur in shallow water (~20 m) with corals (Reitner, 1993; Quinn and Kojis, 1999). Together with light dependence in Paleozoic stromatoporoids (Kershaw, 2015; Stearn, 2015a) and the depth-dependent occurrence of hypercalcified sponges in Jurassic reefs (e.g., their dominance in shallow marine reefs and absence in deep, poorly oxygenated Jurassic lithistid-microbial reefs) (Fürsich and Werner, 1991; Werner et al., 1994), it can be postulated that stromatoporoids preferred shallow, oxygen-rich environments.

5.4. Mid-Cambrian to Early Ordovician reef development

It is now apparent that the mid–late Cambrian "reef gap" was occupied by LSM reefs, and that early Cambrian archaeocyath-microbial reefs and Early Ordovician LSM reefs were broadly similar in structure to those of the mid–late Cambrian. Cambrian to Early Ordovician reef development prompts a number of key questions: why did archaeocyaths decline; why were lithistids the only significant metazoan reef builders during the mid–late Cambrian; what factors could have limited other reef builders during this period; and what prompted the rise of new skeletal reef-builders in the Early Ordovician?

Archaeocyath decline has been linked to one or more of sea-level fall (Palmer and James, 1979), anoxia (Zhuravlev and Wood, 1996; Zhuravlev, 2001b), and ocean acidification (Knoll and Fischer, 2011); all of which have also tentatively been related to the Kalkarindji flood basalt eruptions (Glass and Phillips, 2006; Hough et al., 2006). The subsequent mid–late Cambrian interval, with reefs largely dominated by calcimicrobes and microbial carbonates, has been regarded as a post-extinction phase following archaeocyath demise, in which microbes represent a "disaster flora" (Fagerstrom, 1987; Zhuravlev, 1996; Wood, 1999). Although it has been speculated that the microbes may have outcompeted metazoan reef-builders during this interval (Riding and Zhuravlev, 1994; Zhuravlev, 1996; Rowland and Shapiro, 2002), this alone would not account for its ~25 Myr duration, which far exceeds recovery from much larger subsequent extinctions. For example, the end-Permian extinction event aftermath is not generally thought to have exceeded 5 Myr, and was significantly less in the case of metazoan-rich reefs which appeared within 1.5 Myr (Brayard et al., 2011).

In reviewing factors to explain the prolonged 'resurgence of microbialites and the absence of reef-building metazoans' during the mid-Cambrian to early Ordovician, Rowland and Shapiro (2002, p. 116–120) concluded that nutrient deficiency, elevated levels of CO_2 and temperature (including associated reduction in oxygen availability), and lower levels of Mg/Ca ratio in seawater could have been involved. Webby (2002) recognized that Ordovician low oxygen prolonged microbial carbonates and slowed metazoan diversification until the Late Ordovician. Increased bioturbation has been related to the return of widespread anoxic and sometimes euxinic conditions in the early–mid Paleozoic ocean (Boyle et al., 2014; Lenton et al., 2014), and Saltzman et al. (2015) noted that the Cambrian and Ordovician radiations are separated by persistent oceanic anoxia and elevated extinction rates. Pruss et al. (2010) linked the scarcity of calcified skeletons in Furongian–Tremadocian seas, in which subsurface water masses were 'commonly dysoxic to anoxic', to reduction in carbonate saturation. This interpretation of lowered saturation for $CaCO_3$ minerals in surface waters during episodes of anoxia stems from efforts to account for the scarcity of "robust skeletons" during the Early Triassic (Fischer et al., 2007; Knoll et al., 2007). Since anaerobic microbial processes can increase alkalinity, it has been suggested that times when deep anoxic seawater was geologically widespread could have had higher carbonate saturation (Ω) that promoted seafloor precipitation of $CaCO_3$ minerals, and that under these conditions of increased subsurface alkalinity 'the Ω of overlying surface waters should be reduced' (Higgins et al., 2009). Accordingly, Knoll and Fischer (2011, pp. 75, 78) suggested that the limited quantity of hypercalcified organisms ('massively calcifying sponges and cnidarians, and calcareous algae') and metazoan reefs in late Cambrian and earliest Ordovician oceans may, at least in part,

reflect depressed carbonate saturation in surface seawater. A difficulty with this interpretation is that such low carbonate saturation in shallow water should also have inhibited the formation of microbial carbonates and oolites, yet these deposits dominate many late Cambrian–early Ordovician successions, including those examined by Pruss et al. (2010).

Widespread and protracted hypoxia can critically affect the physiology of marine animals. We suggest that lithistids were more tolerant of low oxygen conditions than archaeocyaths, and also than most of the skeletal reef builders that flourished in the Middle to Late Ordovician, consistent with the mid-Cambrian to early Ordovician persistence of lithistid sponges. Subsequent invertebrate diversification and microbial carbonate decline during the Ordovician reflect the effects of progressive temperature reduction (Trotter et al., 2008; Rasmussen et al., 2016) and increased ocean ventilation (Young et al., 2016; Edwards et al., 2017) and oxygenation on metazoan diversification (Figs. 1, 3, 4, 7). Tolerance of hypoxia by lithistids and microbes, could therefore account for the LSM community's persistence during the greenhouse period of the early Paleozoic.

5.5. Overview

The pattern of early skeletal reef development outlined here commenced with *Cloudina* ~550 Ma in the late Ediacaran and continued until large stromatoporoid-coral reefs appeared ~465 Ma in the Darriwilian. We recognize six reef intervals during this time (Fig. 8). I: Late Ediacaran (~550–541 Ma) reefs contain *Cloudina* up to 15 cm in size, *Namacalathus* up to 3.5 cm and *Namapoikia* (although apparently limited to fissures) up to 1 m in extent. These organisms have not been recognized in the Paleozoic. II: So far as is known, reefs of the earliest Cambrian (Fortunian–mid-Age 2) lack skeletal metazoans except for "*Ladatheca*" worms. III: Archaeocyath sponges, from mid-Age 2 to within Age 4, commonly up to 15 cm in size, locally constructed relatively large frameworks (Fig. 4). IV: Late Age 4 to Age 10 lithistid sponges and the reefs they constructed were both initially relatively small (Figs. 4, 5), but increased in size in the late Cambrian (Age 10). V: Additions to lithistids in Early Ordovician reefs include cup-like calathiids, bryozoans, *Amsassia*, *Lichenaria*, *Cystostroma* and *Pulchrilamina*. With the possible exception of *Namapoikia*, the latter four may represent the earliest massive laminar-domical skeletal reef-builders. Thus, from mid–late Cambrian to early Ordovician, lithistid-microbial reefs, appear to show progressive increase (Figs. 3, 4) in sponge size and reef size, as well as in diversity with the addition of non-lithistid reef-builders. VI: This interval commenced in the late Darriwilian with the appearance of stromatoporoid-coral-bryozoan reefs (Webby, 2002).

These various Ediacaran–Ordovician reefs are all potentially frame-reefs in the sense of Riding (2002). Their metazoan skeletons are tubular, coniform, globular, domical, and laminar in outline, and all appear to have been capable, at least partially, of mutual attachment (Pitcher, 1964; Rowland, 1984; Riding and Zhuravlev, 1995; Penny et al., 2014; Hong et al., 2015; Li et al., 2015; Lee et al., 2016a). Nonetheless, vertical-oriented forms (tubular, coniform, globular) require either mutual support or matrix (including microbial carbonate) support, whereas laminar to domical forms are more able to create their own stability (Kröger et al., 2017). Thus, Ediacaran–Ordovician reef building skeletons shift from dependence on matrix and/or framework support (erect tubular, globular, coniform) prior to the Early Ordovician, to self-stabilizing, encrusting laminar-domical forms (tabulate corals, bryozoans, stromatoporoids) in the mid-Ordovician.

Numerous areas for investigation arise from this overview of early Phanerozoic skeletal reef-building organisms. Much remains to be discovered concerning the affinities, ecology and history of Ediacaran organisms such as *Cloudina*, *Namacalathus* and *Namapoikia*. These appear to have suffered end-Ediacaran extinction (Amthor et al., 2003), but the apparent scarcity of reef-building animals in the earliest Cambrian requires confirmation. Similar questions of affinity and history
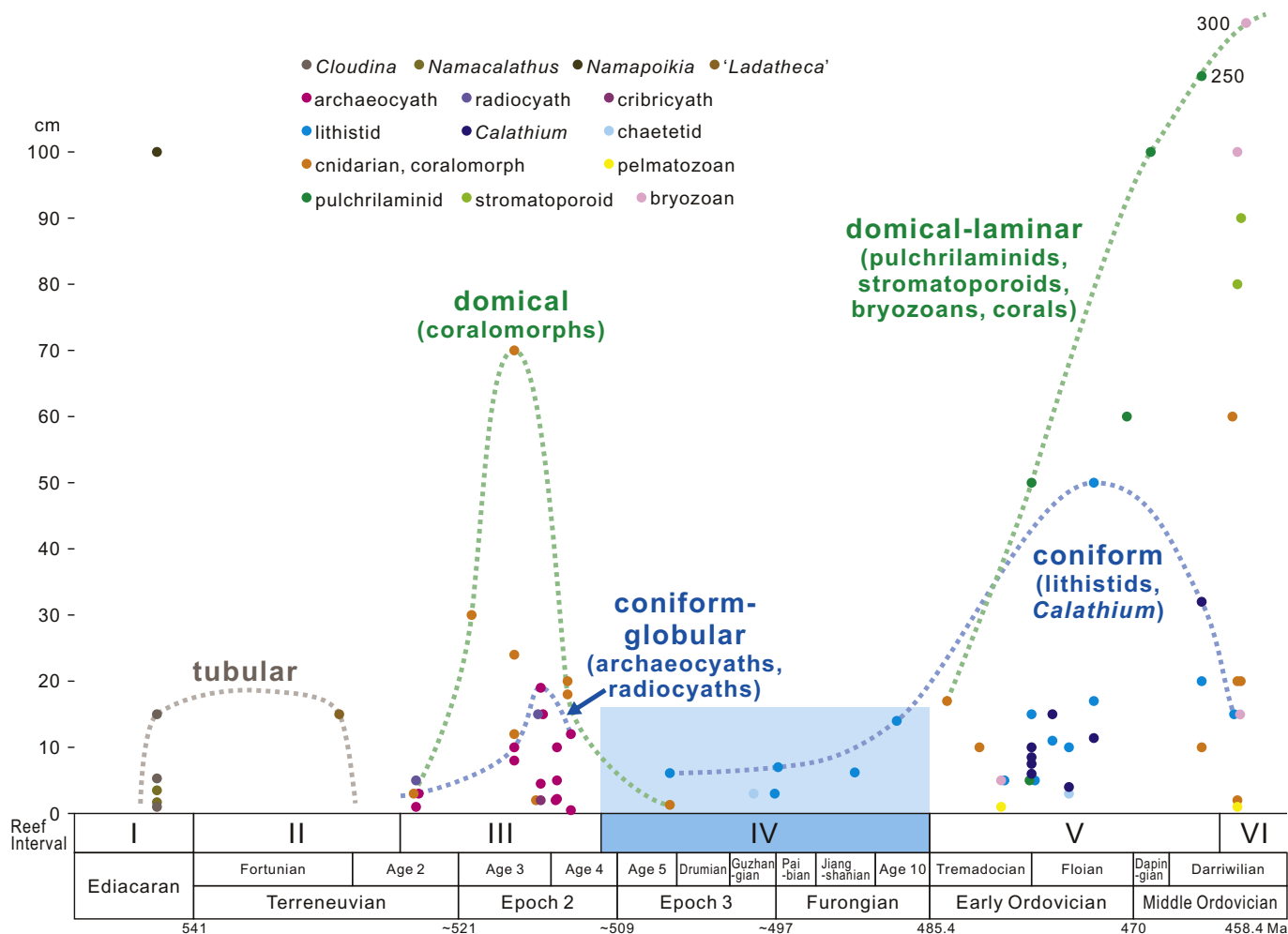
Fig. 8. Size patterns of late Ediacaran to Middle Ordovician reef-building skeletal organisms based on examples in Supplementary Table 1. Three major morphotypes are emphasized: tubular, coniform-globular, domical-laminar. Tubular *Cloudina* and "*Ladatheca*" occur in the late Ediacaran and early Cambrian, respectively. Coniform sponges (archaeocyaths, lithistids, *Calathium*), augmented by globular radiocyaths, are locally conspicuous in Cambrian and Early Ordovician reefs. Domical-laminar forms are represented by coralomorphs in Cambrian Age 2–4, and by pulchrilaminids, stromatoporoids, bryozoans and corals in the Ordovician. These data suggest peaks in skeletal reef-builder size in Reef Interval III and in Reef Intervals V and VI, with smaller skeletons during Reef Interval IV. Reef intervals: I, microbial-*Cloudina*; II, microbial-"*Ladatheca*"; III, microbial-archaeocyath; IV, microbial-lithistid; V, microbial-lithistid-calathiid-pulchrilaminid; VI, stromatoporoid-bryozoan-tabulate-receptaculitid-microbial.

surround Cambrian coralomorphs, and the early history of lithistids is also unclear. The earliest recorded lithistid, *Rankenella* from near the early–middle Cambrian boundary (Kruse, 1996), does not appear to be reefal. The earliest known reef-building lithistid is *Rankenella zhangxianensis* in the upper part of Stage 5 of Cambrian Series 3 (Lee et al., 2016a). Our focus on the mid–late Cambrian draws attention to environmental changes associated with archaeocyath decline in late Epoch 2, as well as those linked to reef diversification in the Tremadocian. It also directs attention toward lithistid reef abundance within the last 25 Myrs of the Cambrian. Most of the examples we emphasize here have been discovered or described since 2003 (Table 1). Certainly, many more remain to be discovered and will provide new insights into this neglected group and their reef-building abilities. Similarly, recent progress in understanding coralomorphs, bryozoans, tabulates, pulchrilaminids and stromatoporoids is important in assessing how laminar/domical morphotypes contributed to and changed reefs during the Ordovician. Commonly overlooked groups, such as radiocyaths, receptaculitids and cyclocrinitids, are locally probably more significant reef components than is generally realized and deserve more attention. In this review we have often mentioned, but not emphasized, the significant role of microbial carbonates as major reef components associated with these skeletal organisms throughout the late Ediacaran to

mid-Ordovician. Competitive and mutualistic relationships between these closely associated but very different components provide fertile ground for research to elucidate substrate evolution and reef-building strategies at the dawn of the Phanerozoic. Not least, our emphasis of the significance of marine oxygenation, and its spatial and temporal patterns during this interval, raises numerous unresolved and tempting questions at the interfaces of geochemistry, geobiology and sedimentology.

6. Conclusions

Cambrian reefs were dominated by microbial carbonates (stromatolites, dendrolites, thrombolites), together with either calcareous (archaeocyath) or siliceous (lithistid) sponges capable of constructing interconnected skeletal frameworks. Heavily calcified archaeocyaths are relatively conspicuous in early Cambrian reefs. Following their decline, microbial carbonates continued to dominate reefs and the mid–late Cambrian was regarded as a significant gap in metazoan reef development. However, it is now recognized that lithistid sponges are widespread in mid–late Cambrian reefs. Although easy to overlook and often subordinate to microbial carbonates, lithistids built frameworks similar to archaeocyaths. This lithistid-microbial reef consortium
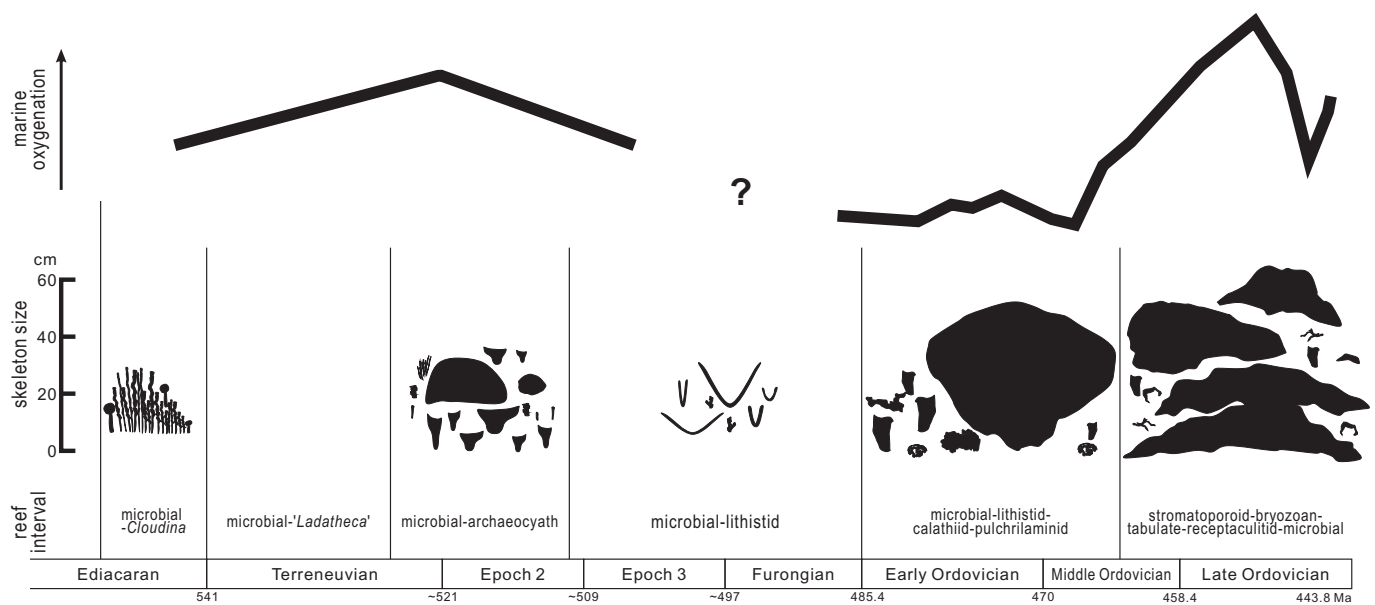
Fig. 9. Schematic patterns of Ediacaran–Ordovician skeletal reef structure and marine oxygenation based on data summarized here (see Figs. 1, 2, 7). Microbial-archaeocyath reefs include domical coralomorphs. Marine oxygenation is inferred to have stimulated reef diversification into and including the early Cambrian, whereas reduced oxygen availability in mid–late Cambrian reef environments is reflected by development of lithistid-microbial reefs. This continued, with addition of calathiids and pulchrilaminids, into the early Ordovician. Increased marine oxygenation in the mid–late Ordovician stimulated further and significant diversification of reef organisms, setting the scene for much of the Silurian and Devonian.

continued into the Early Ordovician, when lithistids became more diverse and reef-building was significantly augmented by bryozoans, tabulate corals, and sponges such as the archaeocyath-like *Calathium* and stromatoporoid-like *Pulchrilamina*. This Early Ordovician reef association can be seen as a transition from Cambrian lithistid-microbial reefs to the bryozoan-tabulate coral-stromatoporoid reefs that flourished in the late Darriwilian, ~460 Ma. Subsequently, these relatively large and heavily calcified skeletons, many of which are laminar to domical in overall morphology, continued to dominate reef-building for ~100 Myr, until the Late Devonian.

Geochemical evidence suggests that rise in marine oxygenation during the Ediacaran–Cambrian transition was not maintained, and was followed during the mid–late Cambrian by a widespread tendency to marine hypoxia-dysoxia. This supports the long-established inference that black shale intervals, linked to episodes of Cambrian trilobite extinction, reflect widespread anoxia. It is also consistent with the view that mid–late Cambrian "greenhouse" conditions, with temperatures increased by elevated CO_2, led to marine stratification that reduced oxygen availability. Extensive carbonate platforms that developed in response to increased CO_2, temperature and sea-level, are likely to have further restricted shallow-marine circulation in the mid–late Cambrian and Early Ordovician.

Many present-day silicified sponges, including lithistids, are well-adapted to low oxygen conditions, as are microbes; whereas corals and bryozoans generally are not. The mid–late Cambrian development and persistence of lithistid-microbial reefs could therefore reflect a prolonged tendency to low oxygen conditions in shallow marine environments. Oxygen limitation may have caused the decline of late early Cambrian archaeocyaths and also hindered their subsequent recovery. It is likely to have delayed the diversification of reef builders such as bryozoans and corals. The tendency toward marine hypoxia continued for at least 25 Myr, until the end of the Cambrian. Its gradual amelioration in the Early Ordovician can be linked to decline in sea-surface temperatures that promoted ocean ventilation. The addition of bryozoans, tabulates and stromatoporoids to lithistid-microbial reefs in the Early Ordovician reflects progressive marine oxygenation. Lithistid-microbial reefs did not disappear, but their period of early Paleozoic dominance was at an end by the late Darriwilian. Nonetheless, nearly

300 Myr later, during the Middle to Late Jurassic, a similar lithistid-microbial reef community reappeared in low-oxygen marine environments.

Marine oxygenation likely stimulated Ediacaran–Cambrian diversification, but "greenhouse" conditions subsequently reduced oxygen availability in shallow reefal environments, delaying mid–late Cambrian metazoan diversification, and prolonging development of lithistid-microbial reefs (Fig. 9). Marine oxygen level could therefore have been a key factor that initially facilitated early Cambrian diversification, and then – as oxygenation declined – restrained its subsequent advance until the Ordovician. This two-step tempo, paralleling that of coeval animal evolution in general, could account for the prolonged pause between the Cambrian Explosion and the GOBE.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.earscirev.2018.04.003.

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