Paleoecology of Pennsylvanian phylloid algal buildups in south Guizhou, China

Gong Enpu · Elias Samankassou · Guan Changqing · Zhang Yongli · Sun Baoliang

Abstract Pennsylvanian phylloid algal reefs are widespread and well exposed in south Guizhou, China. Here we report on reefs ranging from 2 to 8 m thickness and 30–50 m lateral extension. Algae, the main components, display a wide spectrum of growth forms, but are commonly cyathiform (cup-shaped) and leaf-like (undulate plates). The algal reef facies is dominated by boundstone. Algal thalli form a dense carpet whose framework pores are filled with marine cement and peloidal micrite. The peloidal matrix is dense, partly laminated or clotted with irregular surfaces and often gravity defying. Algal reefs in Guizhou differ from examples reported to date by the high biodiversity of organisms other than phylloids: e.g., the intergrowth of algae with corals (some of which are twice the size of algal thalli) and numerous large brachiopods. This contrasts to previous views that phylloid algal "meadows" dominated the actual seafloor, excluding other biota. Also, the pervasive marine cements (up to 50%) including botryoidal cement are noteworthy. Algal reefs developed at platform margins, a depositional environment similar to that of modern *Halimeda* mounds in Java, Australia and off Bahamas, and to that of time-equivalent examples reported from the Canadian Arctic Archipelago. Whereas nutrients appear decisive in the growth of *Halimeda* reefs, algal reefs reported herein seemingly grew under conditions of low nutrient levels. Overall, algal reefs in Guizhou challenge previous views on growth forms, diversity patterns, and depositional environments and add to the spectrum of these partly puzzling biogenic structures.
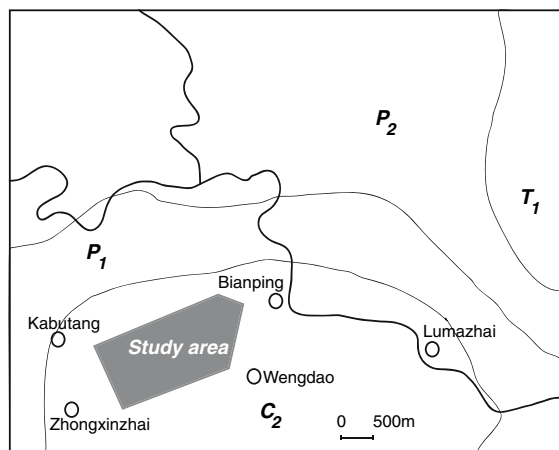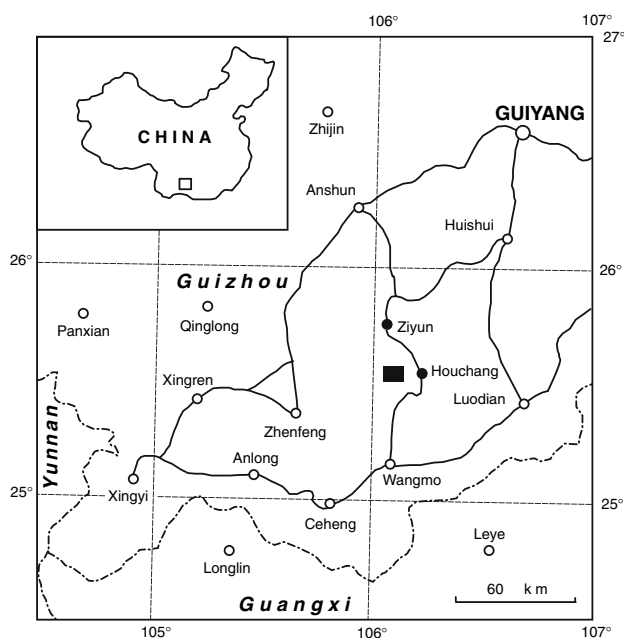
G. Enpu · G. Changqing · Z. Yongli · S. Baoliang
Department of Geology, Northeastern University,
Shenyang, 110004, China

E. Samankassou (✉)
Department of Geosciences, University of Fribourg,
Chemin du Musée 6, 1700 Fribourg, Switzerland
e-mail: elias.samankassou@unifr.ch

Introduction

Although numerous studies dealt with Pennsylvanian and Permian sequences in southern China (GGMRB 1987), Pennsylvanian algal buildups so widespread elsewhere—e.g., in Northern America (Pray and Wray 1963; Heckel and Cocke 1969; Toomey 1976, 1983; among others), the Arctic Canadian Archipelago (Beauchamp et al. 1989; Davies et al. 1989), the Carnic Alps in Austria and Italy (Flügel 1979; Samankassou 2003), and North Africa (Toomey 1991)—were surprisingly rarely reported from China, which is among the largest province for Late Paleozoic carbonate rocks (see Wahlman 2002). The short report of phylloid algal reefs by Fan and Rigby (1994) is the unique description to date.

The present study focuses on well-exposed phylloid algal reefs in south China, including those previously studied by Fan and Rigby (1994). The excellent exposure conditions and preservation allow the study of growth structures, internal features, accessory fossils associated with phylloid algae, and possible relationships between phylloid algae and these associated organisms.

The habit, growth mode, and ecology of phylloid algae have experienced new reports and models (e.g., Forsythe 2003; Samankassou and West 2002, 2003). The Chinese case thus represents a significant test for the extension of these emerging models. Field observation, and petrography of polished slabs and thin sections furnish the database for the interpretation and discussion in the present paper.

Setting and stratigraphy

Extended outcrops of Carboniferous and Permian carbonate rocks characterize the south Guizhou region, southern China. Due to the abundant fossils occurring in these rocks, the region has been a focus of research on Carboniferous stratigraphy. The Carboniferous sequences consist of the fossiliferous Weining and Maping Formations that include numerous carbonate buildups (GGMRB 1987).

Reefs crop out extensively close to the village Bianping, about 4 km west to the town Houchang, Ziyun County in the Guizhou province (Fig. 1). Reefs occur in a thick, cyclic appearing sequence of bedded and massive Pennsylvanian and Permian limestones. Stratigraphically, the algal reefs

belong to the Maping Formation (the Tricitites Zone, Gzhelian, uppermost Pennsylvanian) that overlies the Wining Formation (Fig. 2). The Maping Formation is part of the shallow-water carbonate record that filled the Ziyun-Yadu basin. The rock record of this basin can be traced back to Mid-Devonian (Qin et al. 1996). However, the basin is shallower and smaller during the deposition of the Maping Formation compared to that of the Weining Formation (Feng et al. 1998).

Reef description

Shape and size of reefs

Reefs vary in their size, ranging from 2 to 8 m thickness and 30–50 m lateral extension. They are isolated, lens-like (mound-shape) or, locally, superposed on each another to form composite bodies. Due to vegetation cover and agriculture, the size and forms are, however, partly difficult to trace accurately in the field.

Growth mode of algae

Algae in the studied reefs display a wide spectrum of growth forms. However, cyathiform (cup-shaped) and leaf-like (undulate plates) interpreted by Samankassou and West (2003) as constructional or accumulational growth forms, respectively, dominate (see also Baars and Torres 1991; Baars 1992; Torres et al. 1992; Torres 1995).

The often curled or undulating leaves are 0.8 mm thick and 10 cm long in average (Fig. 3). Thalli are overall obliterated by the pervasive recrystallization, precluding description of their internal structure. The rarely better-

Fig. 1 a Location of the studied area west of Houchang, South Guizhou Province. **b** C_2, P_1, P_2, and T_1 represent the Upper Pennsylvanian, Lower Permian, Upper Permian, and Lower Triassic rock series, respectively

Fig. 2 Stratigraphic scheme of Upper Pennsylvanian and Lower Permian rocks in the studied area, based on fusulinid and coral assemblages. The *dark bar* indicates the stratigraphic position of algal reefs
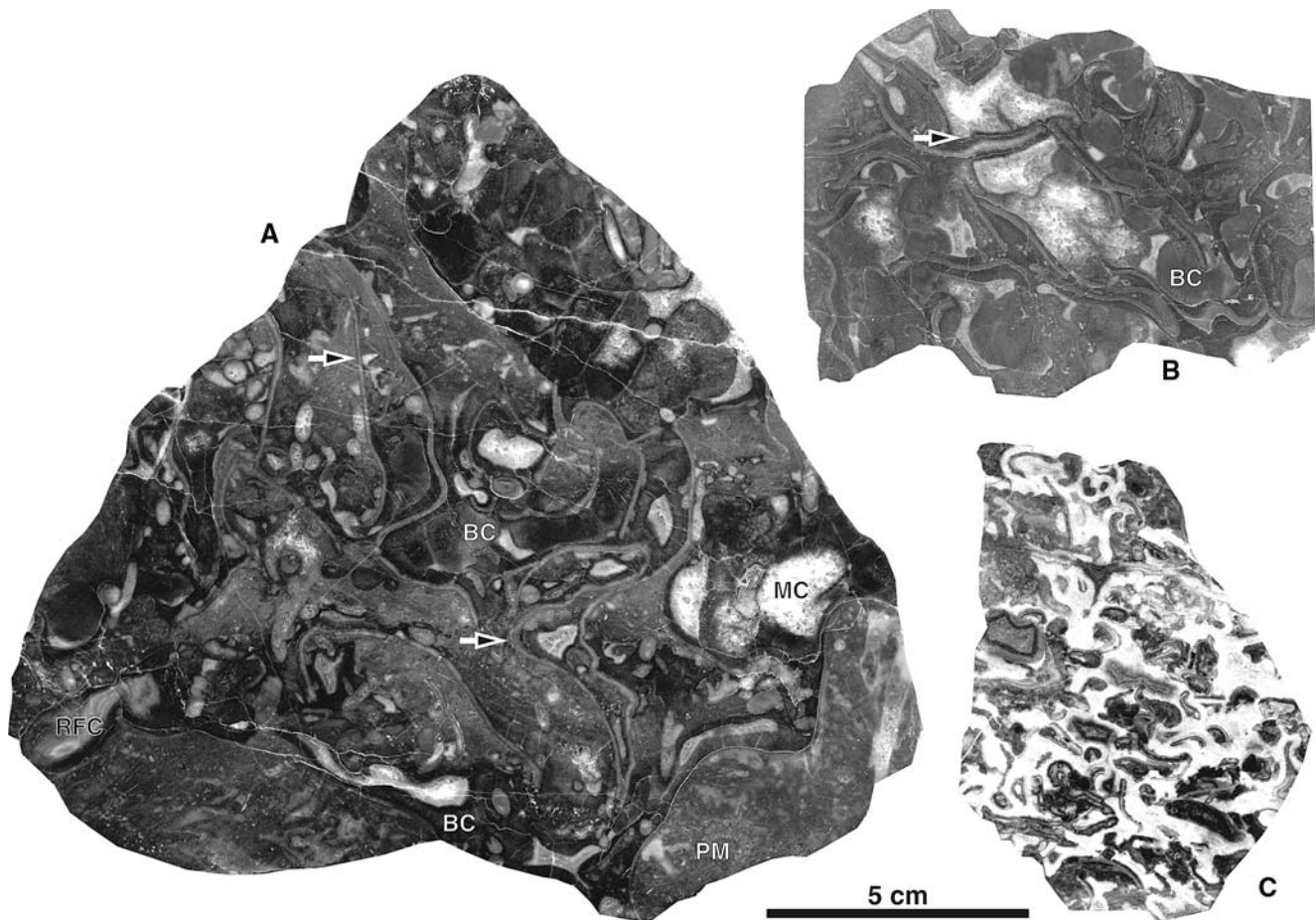
Fig. 3 Photographs of polished slabs of the reef facies. **a** Boundstone of large, curled phylloid algal thalli (*arrows*), botryoidal cement (*BC*), radiaxial fibrous cement (*RFC*), inhomogeneous peloidal micrite (*PM*), and voids filled with mosaic cement (*MC*). **b** Boundstone of phylloid algal thalli and multiple generations of cements (cements as in **a**). Note that the algal thalli were encrusted prior to marine cementation (*arrow*). **c** Cementstone including fragments of algal thalli. The latter are partly encrusted prior to precipitation of marine cements (see Figs. 5d, 7b)

preserved specimens showing cortical pores (Fig. 5c) suggest that some might belong to *Neoanchicodium* and *Eugonophyllum* (Konishi and Wray 1961; Kirkland et al. 1993). Some of the thalli are broken, but obviously not transported far from the life habitat because of their size (Fig. 3b, c) and the collapse brecciation indicated by thalli that are only slightly offset.

Reef substrate

The substrate of reefs consists of packstone and grainstone, passing over into clotted wackestone toward the reefs. Brachiopods, crinoids, fragments of algal thalli, fusulinids, and smaller foraminifers (calcitornellids, *Tuberitina* sp., *Bradyina* sp.) and peloids are common. Further components include bryozoan fragments and rare gastropods (Fig. 5a, b). Coating and micritization of algal thalli occur.

Reef composition

The algal reef facies is dominated by boundstone. Algal thalli form a dense carpet whose framework pores are filled with marine cement and peloidal micrite (Fig. 5a, b). The peloidal matrix is dense, partly laminated or clotted with irregular surfaces and often gravity defying. Individual peloids, some of which are surrounded by thin marine fibrous cements, are in average 0.1 mm in diameter. The peloidal matrix includes foraminifers, bryozoan fragments, *Tubiphytes/Shamovella*, and undefined tubes (0.2–0.3 mm long and 0.1 mm in diameter).

In distinct layers, algal thalli are draped by conspicuous marine cements (Fig. 3c) or encrusted prior to the precipitation of marine cements in interstitial space (Fig. 3b).

Secondary encrusters including *Tubiphytes* and smaller foraminifers (*Tuberitina* and endothyrids) commonly occur.
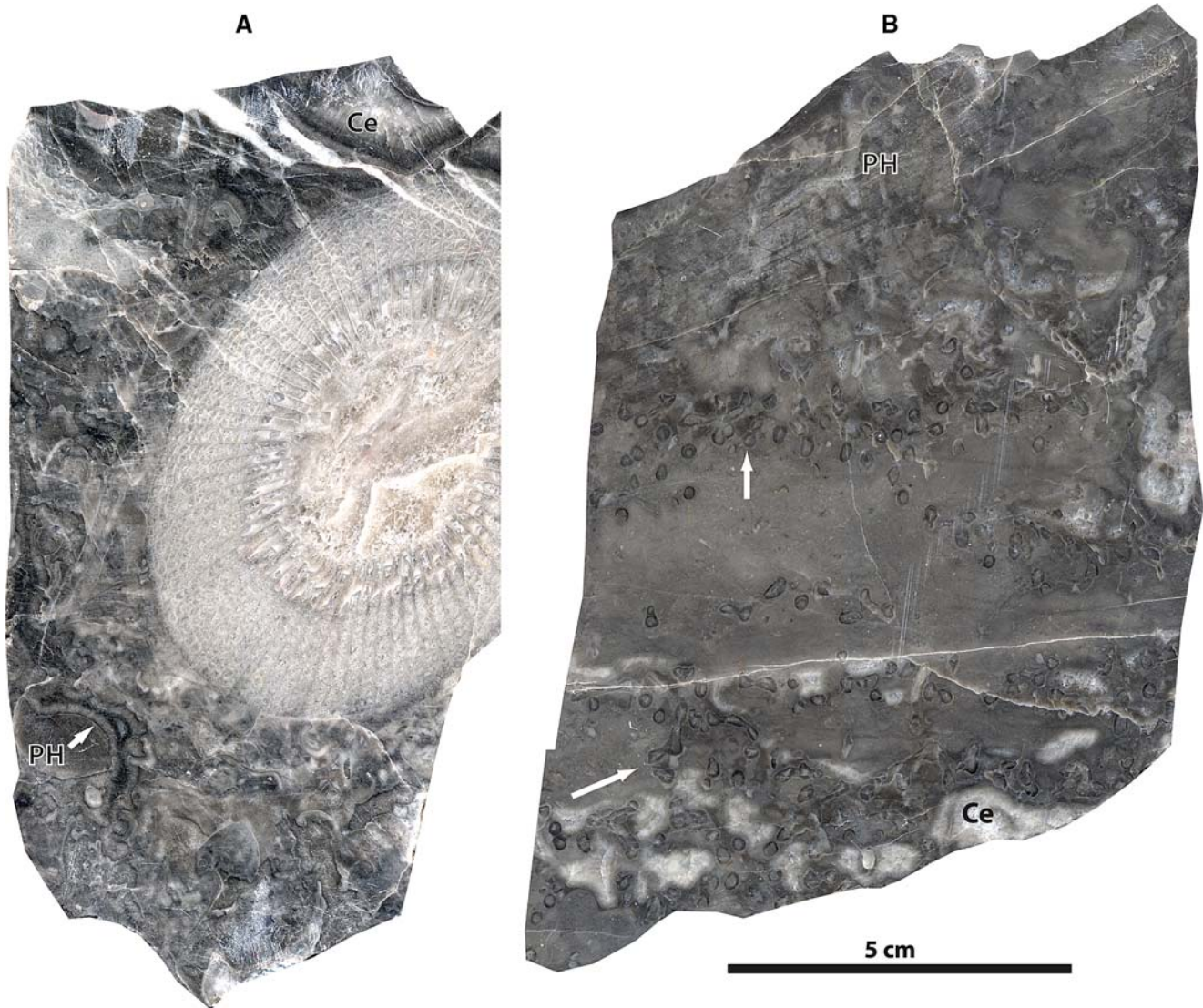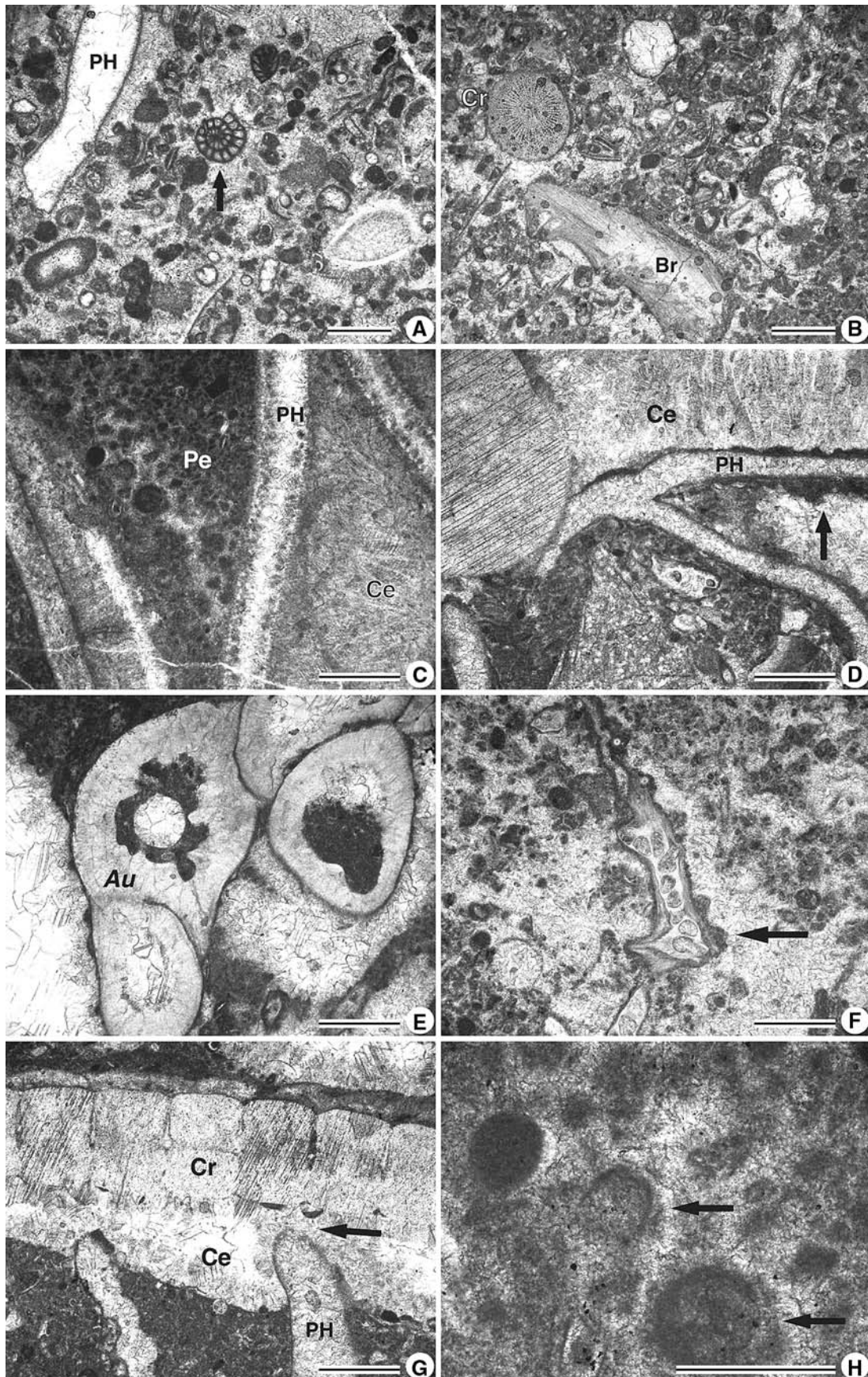
Fig. 4 Photographs of polished slabs of coral-dominated facies. **a** Section through a large solitary coral. Such corals, not confined to framework cavities of phyll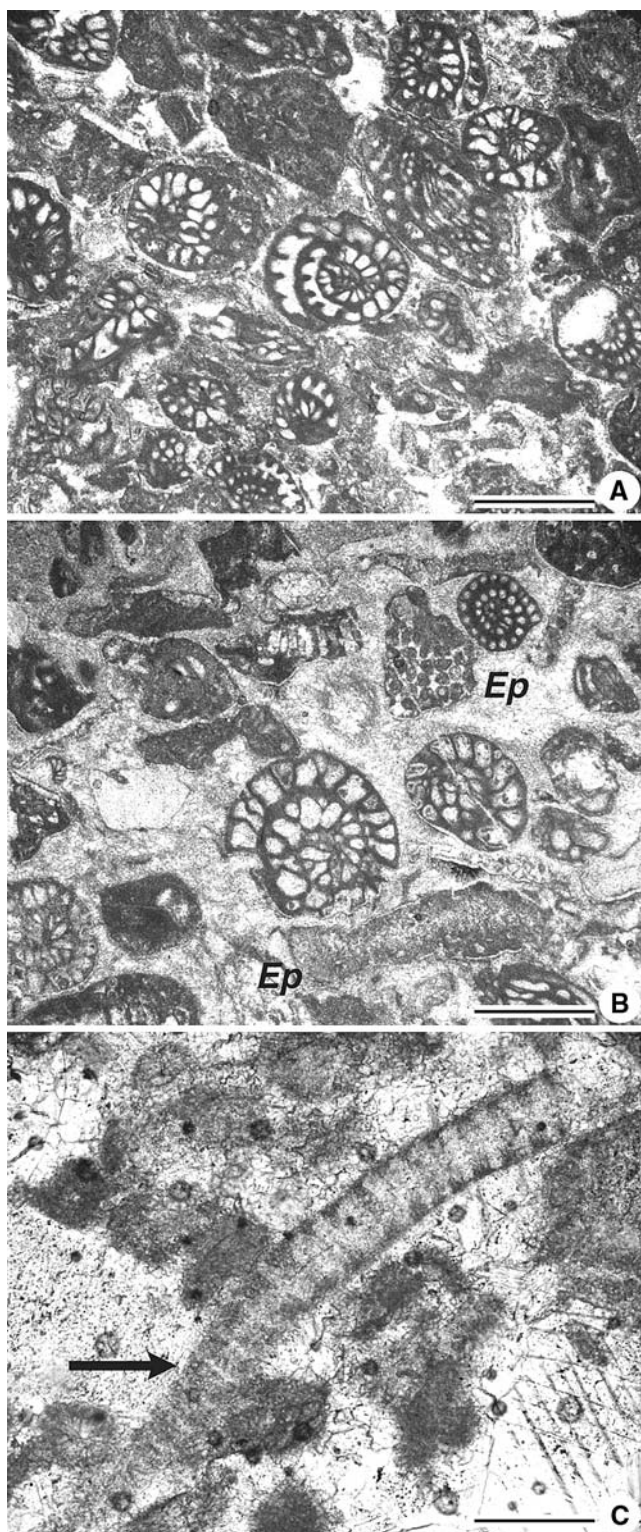oid algal boundstone, are larger than the co-occurring phylloid algal thalli (*PH*). **b** Boundstone composed of auloporid coral colonies (*arrows*) and phylloid algal thalli (*upper part*). Framework pores are filled by cements (*Ce*)

Fusulinids (*Fusulinella* sp., *Pseudostaffella* sp., *Fusulina* sp., and *Triticites* sp.), solitary and colonial corals (*Nephelophyllum* sp., *Pseudotimania* sp., *Streptophyllidium* sp., *Diversiphyllum* sp., and auloporid corals) (Fig. 4), and brachiopods (*Choristes* sp., *Neospirifer orientalis*, and *Orthotichia marmerea*) are commonly associated with the phylloid algal facies. The high-diversity assemblages are not confined to cavities as commonly seen in similar reefs elsewhere (Toomey 1976, 1980; Samankassou and West 2002; Forsythe 2003): e.g., the co-occurring auloporid corals locally form patches consisting of boundstone (Fig. 4b). Furthermore, the size of many organisms exceeds twice that of the phylloid algal thalli (Figs. 4a and 5). Some layers or pockets within the

Fig. 5 Photomicrographs of reef substrate and core. **a–b** Reef-substrate facies composed of bioclastic packstone. Bioclasts include fragments of phylloid algae (*PH*), fusulinids (*arrow*), crinoids (*Cr*) and brachiopods (*Br*). Peloids are common. Some grains show micritic envelopes. **c–d** Phylloid algal boundstone facies typically composed of large algal thalli (*PH*) enclosing framework voids variously filled with peloids (*Pe*), peloidal crusts (*arrow*), and cements (*Ce*). **e** Auloporid (*Au*) coral boundstone. Dense corallite enclose framework voids as in phylloid algal boundstone. **f** Bryozoans (*arrow*) are major components in the boundstone facies. As for phylloid algal-dominated facies, peloids and early marine cements are ubiquitous. **g** Well-preserved crinoid (*Cr*) stem along with phylloid algal thalli (*PH*) in boundstone facies. The evidence of framework is demonstrated by cement-filled voids (*arrow*) and the irregular surface of peloidal-clotted areas separated from bioclasts. **h** Enlargement of peloidal area from **c**, showing different-sized, early cemented peloids (*arrow*). *Scale bar* is 0.5 mm for all figures

rock volume. Overall, botryoidal cements predate radiaxial cements. The widespread marine cements and the importance of their occurrence are the focus of another publication currently in preparation by the authors and will not be further developed herein.

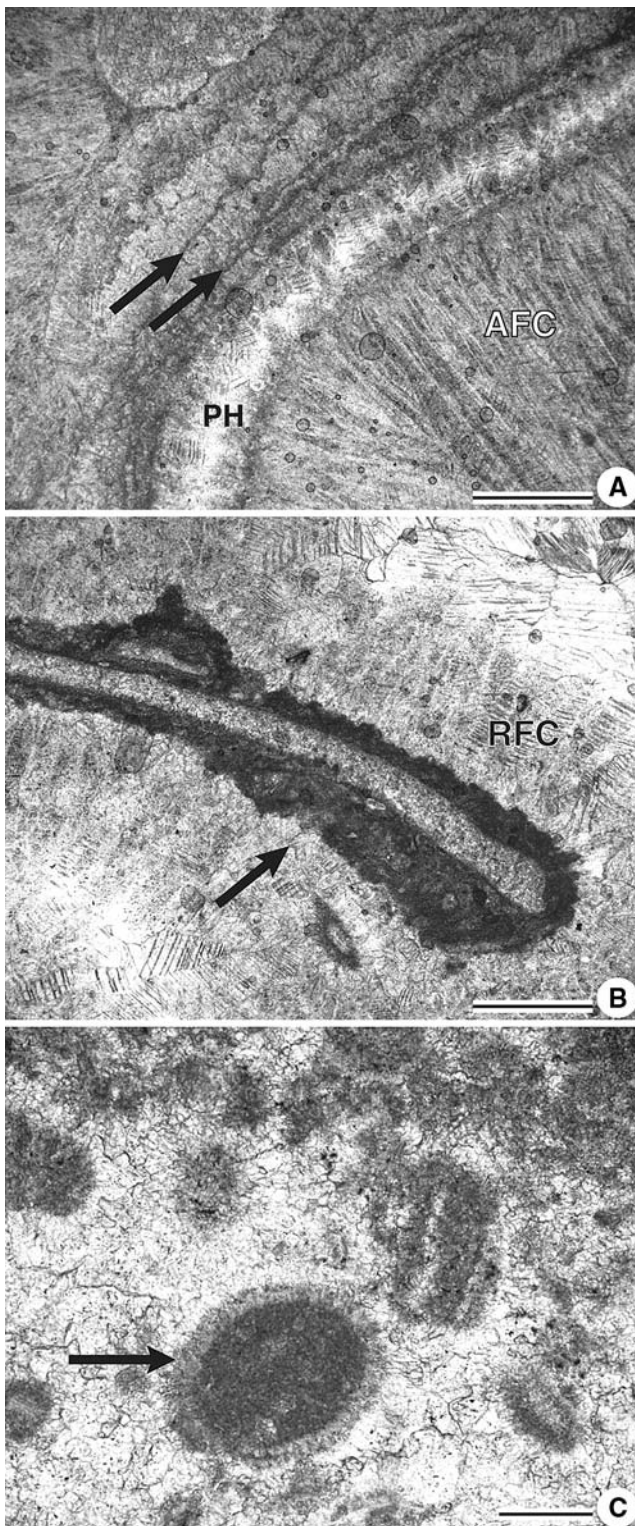## Paleoecology: interpretation and discussion

Phylloid algae lack modern representatives. Thus, most of ecological parameters drawn from any analysis may appear speculative. However, criteria deduced from fossil assemblages coupled with textural analysis of rocks may allow the pinpointing of some valuable information.

Biodiversity, ecological community

A low-diversity fossil assemblage characterizes time-equivalent phylloid algal mounds, as reported in many previous studies (Pray and Wray 1963; Gray 1967; Heckel and Cocke 1969; Crowley 1969; Toomey and Winland 1973; Wilson 1975, 1977; Toomey 1976; Flügel 1979; Toomey and Babcock 1983; Pol 1985). Toomey (1976) assumed that phylloid algae colonized the actual sea bottom and dominated the living space, excluding most other shallow-water organisms. Thus, biota within algal-dominated meadows were confined to those living in cavities and/or attached to algal leaves (e.g., brachiopods, fusulinids, and ostracodes) (Toomey 1976; Forsythe et al. 2002; Samankassou and West 2003).

One can speculate, that like modern algae, phylloid algae might have produced poisonous substances that kept other organisms away from the areas that they successfully and rapidly colonized. Low-diversity algal mounds occurring throughout Pennsylvanian and Permian deposits strongly support this assumption (Flügel 1979; Toomey 1991; Forsythe et al. 2002; Samankassou 2003; Samankassou and West 2003). Indeed, chemical defense used by algae is documented from studies of recent reefs (Hay 1997; Paul 1997) and other environments (G. Gerdes, personal communication, 1998). However, the overall high diversity of gregarious sessile organisms, e.g., the intergrowth of algae with corals (some of which twice the size of algal thalli) and numerous large brachiopods in the algal-dominated reefs studied contradicts the "poisoning hypothesis." Thus, in terms of biodiversity, the Ziyun example represents a unique and novel case to date.

reefs are particularly rich in foraminifers (predominantly fusulinids) (Fig. 6a). The top of the reef is rich in fusulinids and includes fragments of the algae *Epimastopora* and *Beresella* (Fig. 6b, c).

Botryoidal, acicular fibrous, and radiaxial fibrous cements (Fig. 7) represent 20–30, locally over 50% of the

Fig. 7 Early marine cementation is conspicuous throughout the mound core. Cements include multiple generations of botryoidal cements separated by thin micritic layers (**a**, *arrows*), acicular fibrous (**a**, *AFC*), and radiaxial fibrous (**b**, *RFC*) cements. Peloids show rims of marine cements (**c**, *arrow*). Locally, phylloid algal thalli are encrusted prior to marine cementation (**b**, *arrow*). *Scale bar* is 0.5 mm for **a** and **b**, and 0.1 mm for **c**

Temperature and water depth

Phylloid algae in south China, assumedly photosynthetic green algae, are associated with colonial corals and fusulinids: this may point to a shallow-water depositional environment within the photic zone. The growth of phylloid algal reefs is interpreted to have taken place between the lower limit of the photic zone (the deepest) and the zone close to the lower limit of the wave activity (the shallowest) (see Doherty et al. 2002; Samankassou 2003). Considering the wide depth ranges of modern green algae and algal mounds (e.g., 20–100 m for *Halimeda* mounds in the eastern Java Sea; Roberts and Phipps 1988), a precise water depth cannot realistically be deduced. The fact that the phylloid algal reefs studied were not subaerially exposed despite eustatic sea-level changes on the order of 100 m during Pennsylvanian (Heckel 1986, 1994; Soreghan and Giles 1999; Joachimski et al. 2006) points to important water depths of several tens of meters during reef growth. Furthermore, the paleogeographic position of south China in low-latitudes during Pennsylvanian (Scotese 1997) may allow for the assumption of light penetration into an important water depth.

Salinity

The high-diversity biotic association including brachiopods, foraminifers, bryozoans, and corals points to open, normal-marine conditions (Wilson 1975), in agreement with the overall depositional environment (see below). Furthermore, carbon and oxygen isotopic composition of brachiopod shells and marine cement indicate marine value (author's unpublished data).

Nutrients

Although non-conclusive, attempts were made to compare phylloid algae with *Halimeda* (see Martin et al. 1997; Davies et al. 2004). If phylloid algal reefs, to some extent, compare to modern *Halimeda* mounds, then some assumptions concerning nutrients can be made. Indeed, some occurrences of *Halimeda* mounds were related to upwelling of deep, nutrient-rich waters; e.g., in the Java Sea, Indonesia (Roberts et al. 1987, 1988) and the Great Barrier Reef Province, Australia (Drew and Abel 1988; Marshall and Davies 1988).

Settings of phylloid algal might be linked to zones of upwelling and, thus, to high levels of nutrients. Current paleogeographic reconstructions do not allow the precise identification of such zones. However, the high-diversity fossils described above (especially the presence of corals) do not point to eutrophic conditions during the growth of algal reefs in Guizhou. Subsequently, nutrients were obviously not

decisive for the occurrence and extensive growth of phylloid algae in Guizhou. Also, phylloid algal reefs studied are not ideal fossil analogs for the upwelling-driven modern *Halimeda* reefs.

Depositional environment

A depositional environment at the shelf margin was assumed for the area studied (GGMRB 1987). The ubiquitous synsedimentary marine cementation that requires intense seawater circulation in open, normal-marine conditions represents a solid argument in support of this interpretation, as does the widespread occurrence of botryoidal cements, in analogy to modern seaward platform margins (e.g., off Belize; James et al. 1976; James and Ginsburg 1979).

Furthermore, the depositional environment assumed agrees well with that inferred for phylloid algal mounds in the Canadian Arctic Archipelago, in which marine cements (including botryoidal cement) represent a major component in volume and importance in stabilizing the reef structure (Davies 1977; Beauchamp et al. 1989). Such resemblance led Davies et al. (2004) to draw some analogies between modern algal buildups occurring off Australia and Late Paleozoic phylloid algal mounds. Carbon and oxygen isotopic compositions of marine cements originating from the studied reefs point to "normal" marine values assumed for the Pennsylvanian seawater (author's unpublished data) and compare well with the values obtained from the Canadian examples (Davies 1977).

Conclusion

Phylloid algal reefs are parts of the sedimentary record of Pennsylvanian deposits in south China, like in contemporaneous deposits nearly worldwide. Along the same line, algal mounds occur in cyclic sequences that reflect the pervasive Late Paleozoic glacio-eustatic sea-level fluctuations (Heckel 1994). However, no horizon exhibiting subaerial exposure was identified, pointing to overall high rates of subsidence and/or important water depth for the depositional environment that kept the actual seafloor in a subtidal position despite of glacio-eustatic sea-level fluctuations.

Algal reefs grew on stabilized shoals, as observed in other examples (e.g., Samankassou 2001; see also Chisholm and Kelley 2001). As for most of their counterparts elsewhere, shallowing commonly interrupts reef growth (Wilson 1972, 1975), as evidenced by accumulation of foraminifers in distinct layers interpreted as result of high-energy levels.

Algal reefs in Guizhou differ from examples reported to date by the high biodiversity of organisms other than phylloids. This contrasts to previous views that phylloid algal

"meadows" dominated the actual seafloor, excluding other biota (Toomey 1976, 1980). Also, the pervasive marine cements (up to 50%) including botryoidal cement are noteworthy.

Algal reefs developed at platform margins, a depositional environment similar to that of modern *Halimeda* mounds in Java, off Bahamas, and Australia (Roberts et al. 1987, 1988; Freile et al. 1995; Marshall and Davies 1988; Davies et al. 2004). Whereas nutrients were decisive in the growth of *Halimeda* reefs (Marshall and Davies 1988), algal reefs reported herein seemingly grew in depositional environments of low nutrient levels.

Further detailed studies are needed to recognize and understand the spectrum of algal-dominated reefs widespread in the investigated area and to sort out the triggering factors. Furthermore, the extensive marine cementation and the high-diversity biota co-occurring with phylloid algae need to be put into a wider perspective.

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