MID-LATE DEVONIAN CALCIFIED MARINE ALGAE AND CYANOBACTERIA, SOUTH CHINA

QI FENG,[1] YI-MING GONG,[1,2] AND ROBERT RIDING[3]

[1]Key Laboratory of Biogeology and Environmental Geology of Ministry of Education of China, and State Key Laboratory of Geological Processes and Mineral Resources, China University of Geosciences, Wuhan, 430074, China, <qifeng.cug@gmail.com>; [2]Key Laboratory of Biogenic Traces and Sedimentary Minerals of Henan Province, Henan Polytechnic University, Jiaozuo, Henan, 454003, China, <ymgong@cug.edu.cn>; and [3]Department of Earth and Planetary Sciences, University of Tennessee, Knoxville, Tennessee 37996-1410, USA, <riding@cardiff.ac.uk>

ABSTRACT—Givetian, Frasnian and Famennian limestones from southern China contain microfossils generally regarded as calcified algae and cyanobacteria. These are present in 61 out of 253 sampled horizons in four sections from three widely spaced localities in Guangxi and southern Guizhou. Three of the sections sampled are Givetian-Frasnian-Famennian; one section is Frasnian-Famennian. They include reef and non-reef carbonates of shallow marine platform facies. The following taxa are identified with differing degrees of confidence, and placed in algae, cyanobacteria or microproblematica. Algae: *Halysis*, 'solenoporaceans', *Vermiporella*. Cyanobacteria: *Bevocastria*, *Girvanella*, *Hedstroemia*, *Subtifloria*. Microproblematica: ?*Chabakovia*, *Garwoodia*, ?*Issinella*, *Izhella*, *Paraepiphyton*, *Rothpletzella*, *Shuguria*, ?*Stenophycus*, *Tharama*, *Wetheredella*. As a whole, the abundance of algae, cyanobacteria and microproblematica increases by 34% from Givetian to Frasnian, and declines by 63% in the Famennian. This secular pattern of marked Famennian decrease does not support recognition of them as "disaster forms" in the immediate aftermath of late Frasnian extinction. Nonetheless, their survival into the Famennian could indicate tolerance of environmental stress, independence of changes in food supply, morphologic plasticity, and ability to occupy a range of habitats and depths. Uncertainties concerning the affinities of the problematic taxa hinder assessment of their significance.

INTRODUCTION

THE PROMINENCE of microbial carbonates in the immediate aftermaths of some Phanerozoic mass extinctions suggests that they flourished when metazoans were temporarily reduced (Schubert and Bottjer, 1992). This view has found support in studies of end-Permian (Kershaw et al., 1999), end-Ordovician (Sheehan and Harris, 2004), and end-Devonian (Whalen et al., 2002; Stephens and Sumner, 2003, p. 1300; Riding, 2006, p. 335) extinctions. A complicating factor is that, although microbial carbonates may be common just after extinction events, they are often not scarce immediately prior to them. This raises the question whether calcified microbes actually increased in absolute abundance following metazoan extinctions, or were only made more conspicuous by their survival as other groups declined. Evaluation of these possibilities requires detailed study of microbial carbonate abundance both before and after mass extinction. This in turn presents the non-trivial problem of distinguishing various types of microbial carbonate and associated calcified microbial fossils and confidently evaluating their origins and affinities.

We examined Late Devonian carbonate sequences across the Frasnian-Famennian transition at four locations in three widely spaced areas of southern China (Fig. 1). The associated fossils and other indicators suggest that these are generally normal salinity shallow marine facies. They locally include reefs but are dominantly non-reefal. We sampled the Givetian-Frasnian-Famennian sequence in three of the sections, and just the Frasnian-Famennian sequence in one section, and identified calcified microfossils commonly referred to algae or cyanobacteria. The three main groups (algae, cyanobacteria, microproblematica) show changes in their relative proportions through the succession. From Givetian to Famennian the proportions of algae and cyanobacteria decrease and the proportion of microproblematica increases. But these changes in proportion are overshadowed by a marked decline in abundance of all three groups at the Frasnian-Famennian transition.

REGIONAL SETTING

Devonian siliciclastic and then carbonate sediments were deposited over large areas in South China during northerly-directed marine transgression, while a landmass persisted to the north and northwest (Tsien et al., 1988; Bai et al., 1994). The spatial distribution of sediment accumulation was strongly affected by basement structure (Zhao et al., 1996 and references therein). Carbonate platforms up to 1,500 m thick and 100s of kilometres in extent developed during the Mid-Late Devonian (Givetian-Famennian) (Chen and Tucker, 2003, fig. 2), separated by linear basins. This pattern has primarily been attributed to coeval extensional tectonics (Zhao et al., 1996, fig. 8). The carbonates and their associated sediments, mainly shales and mudstones with cherts, are now extensively exposed in tower karst landscapes of Guangxi and southern Guizhou. Details of these sequences, and the interplay of sea-level change and tectonism that shaped their development, have been intensively studied (Ding, 1947; Kuang et al., 1989; Wu et al., 1994; Shen and Yu, 1996). In the Guilin area of Guangxi, for example, Frasnian-Famennian reefal margins separate platform interiors from slope facies (Shen and Zhang, 1994; Shen et al., 1997; Chen et al., 2002; Shen and Webb, 2004a). In the Famennian, these reefs contain abundant calcimicrobes (Shen et al., 1997). Similar Frasnian-Famennian facies have been examined at many other locations in the region (Gong et al., 2002; Ma et al., 2008). These include the localities described here at Yangdi (Xu et al., 2006) and Shenwan (Li and Wang, 1991), both near Guilin, at Liujing farther to the south near Nanning (Liao, 2002; Chen and Tucker, 2003), and at Dushan to the northwest in Guizhou (Wang et al., 2006).

METHODS

Locations.—The four successions examined and sampled (Dushan, Liujing, Yangdi, and Shenwan) occur in three areas more than 300 km apart in south central China: southern Guizhou (Dushan), southern Guangxi (Liujing), and north-
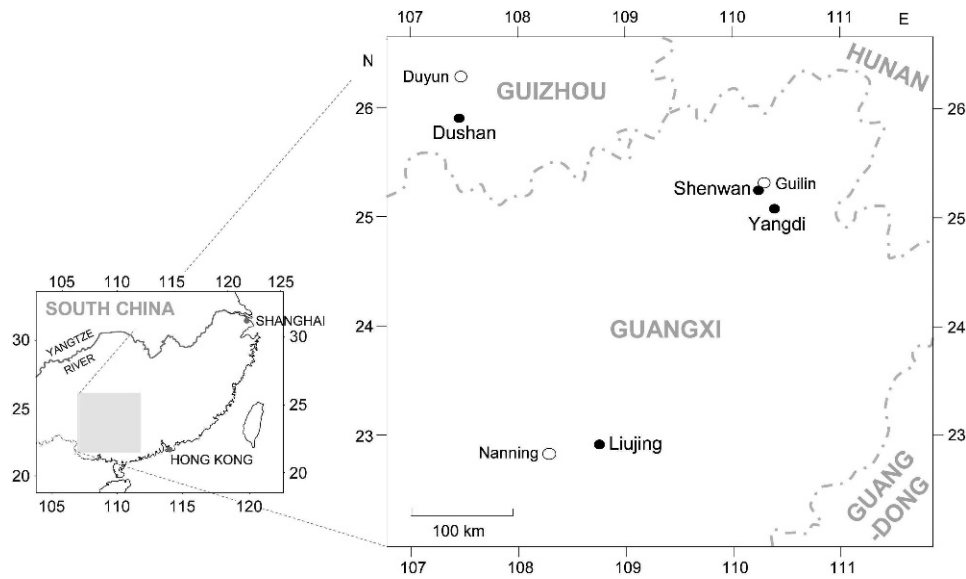
FIGURE 1—Locations of the sections studied in southern China.

eastern Guangxi (Yangdi and Shenwan, near Guilin) (Fig. 1). All four sections are predominantly shallow water carbonates and mudrocks. Their age is Givetian-Famennian, except at Shenwan where only the Frasnian-Famennian was sampled. The thickest succession is at Dushan (~950 m). At Liujing it is ~310 m and at Yangdi ~250 m; the Shenwan succession is much thinner, ~50 m (Fig. 2).

Samples.—At the four sections, 253 carbonate horizons were sampled: 54 from the Givetian; 89 from the Frasnian; 110 from the Famennian. The basis for the stage subdivisions is described below; there is some uncertainty regarding them in most of the sections. Six hundred, seventy-nine thin-sections were prepared from the samples. Of these, 200 thin-sections are from the Givetian, 360 from the Frasnian, and 119 from the Famennian. Sixty-one horizons, represented by 189 thin-sections, contained calcified microfossils commonly referred to algae or cyanobacteria that we were able to recognize, although in six of these horizons our identifications remain uncertain. Of these 189 thin-sections, 42 are from the Givetian, 122 from the Frasnian, and 25 from the Famennian. The samples and thin-sections are deposited in the collections of the Faculty of Earth Sciences, China University of Geosciences, Wuhan. The raw data showing the number of horizons in which each genus occurs in each stage (including uncertain identifications) are shown in Figure 3.

STRATIGRAPHIC SECTIONS

Dushan.—Dushan town is 50 km south of Duyun. The section sampled is a composite of three sections that begin at Dahekou, 4 km NNE of Dushan, and extend west and southwest to Baihupo, 2 km west of Dushan, via Jiwozhai, Hejiazhai, Lujiazhai and Wuliqiao (see Wang, 2004, fig. 1; Wang et al., 2006, fig. 1). The Lower Devonian and the Eifelian consist largely of clastic sediments. The Givetian and Upper Devonian is dominantly carbonate, but locally represented by sandstone (Songjiaqiao Formation) (Fig. 2). Biostratigraphic subdivision has been based on brachiopod, coral, miospore and foraminifer fossils. A Givetian age is indicated for the Jipao and Jiwozhai formations by the brachiopod *Stringocephalus*, and a Frasnian age for the Lujiazhai Member by *Cyrtospirifer* (Liao, 2003). Miospores (Gao, 1981) and foraminifers (Wang, 1987) indicate that the

Gelaohe and Zhewang formations are latest Devonian (Liao, 2003). Location of the Frasnian-Famennian boundary near the base of the dolomitic Sifangpo Member remains uncertain.

Sequence stratigraphy has been used to augment this biostratigraphic subdivision of the sequence. The disconformity at the top of the Tunshang Formation is widely recognized throughout Guizhou and Guangxi provinces and has been regarded as the Eifelian-Givetian boundary (Wu et al., 1994; Wang et al., 1997; Wang, 2001). The thin (~1 m) transgressive black shale horizon near the base of the Wangchengpo Formation has been taken to mark the Givetian-Frasnian boundary (Wang, 2001). Gao (1981) placed the Devonian-Carboniferous boundary within the Gelaohe Formation on the basis of miospore assemblages. However, Wang and Wang (1996) suggested placing this boundary at a maximum flooding surface in the lower part of Tangbagou Formation. The Frasnian-Famennian boundary at Dushan has traditionally been regarded as the contact of the Wangchengpo and Yaosuo formations (Guizhou Bureau of Geology and Mineral Resources, 1987). It has also tentatively been placed in the lower part of the dolomitic Sifangpo Member (Wang and Chen, 1999; Wang et al., 2006, fig. 3), but this remains uncertain.

Liujing.—The Liujing area, 60 km east of Nanning, Guangxi (Fig. 1), displays a fossiliferous Devonian succession that appears complete except for the upper part of the Famennian (above the *Palmatolepis crepida* zone) (Tao et al., 1986; Chen et al., 1995), and is regarded as a standard section for the marine Devonian in South China (Kuang et al., 1989). We sampled the Mid-Late Devonian part of this succession between Liujing train station and Nazu village about 2 km to the south-east (see Li and Liu, 2002, fig. 1). The Eifelian Najiao Formation and the upper part of the Rongxian Fomation are dolomite. The overlying Mintang and Gubi formations, and the lower part of Rongxian, are limestone. Givetian and Frasnian ages for the Mintang and Gubi respectively (Wu, 1997) are supported by conodont faunas (Kuang et al., 1989; Bai et al., 1994; Jiang et al., 2000). However, the precise location of the Frasnian-Famennian boundary in this section is uncertain. The basal part of the Rongxian contains *P. gigas* (Frasnian), and the middle part of the formation contains *P. triangularis* (Famennian) (Zhang et
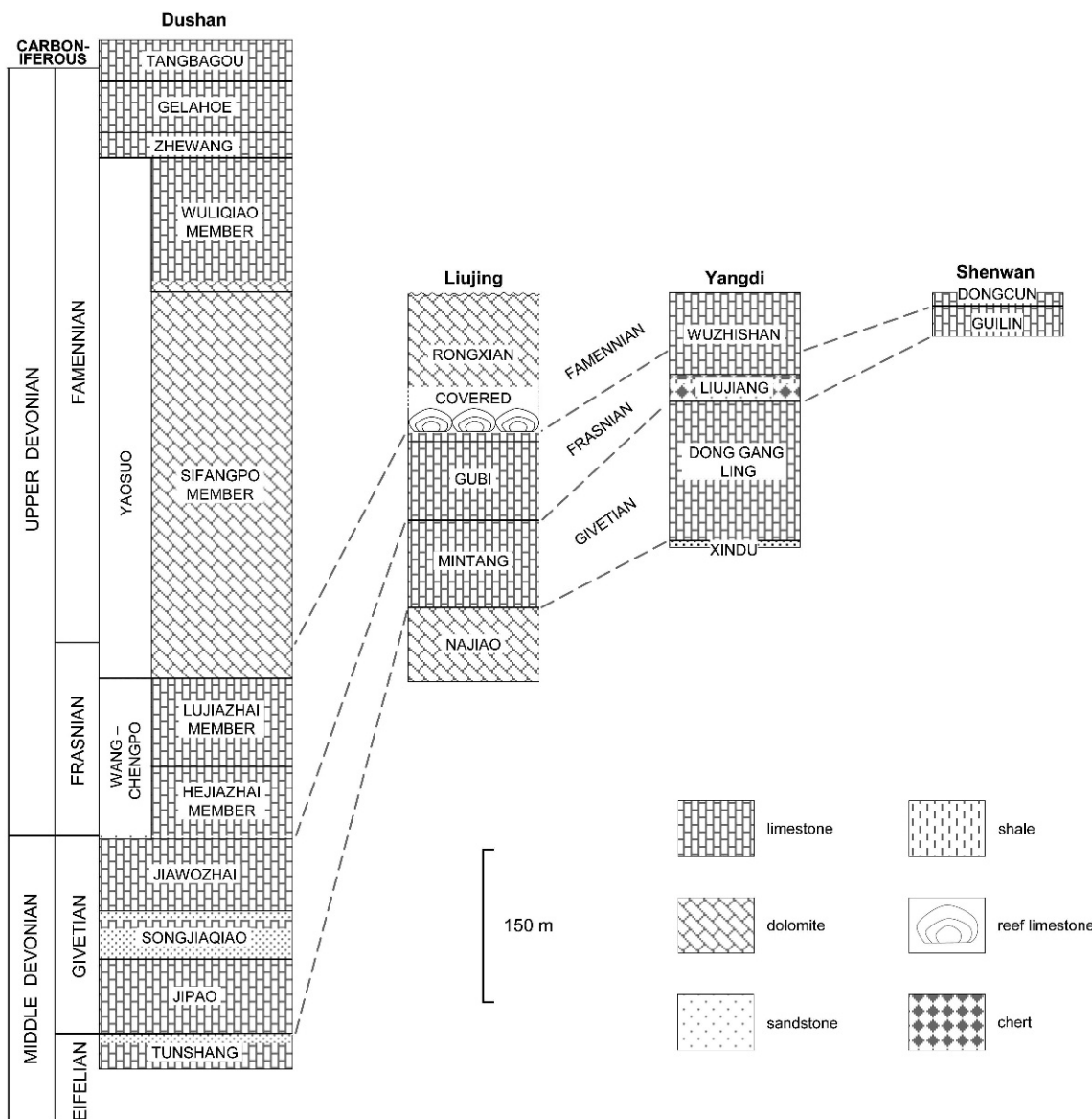
FIGURE 2—Stratigraphic sections sampled. Stage boundaries are approximate. Alternative transliterations of lithostratigraphic names: Donggangling/Tongkanling, Gelaohe/Kolaohe, Guilin/Kuelin, Liujiang/Liukiang, Wuzhishan/Wuchishan.

al., 2007). The intervening sequence is a 20 m thick reefal unit followed by an unexposed interval. Zhang et al. (2007) suggested that Frasnian-Famennian boundary could be located at the base of the reef. However, it remains possible that this reef in the lower part of the Rongxian Formation is latest Frasnian in age.

Yangdi.—Yangdi village is on the Li River, 35 km SSE of Guilin, Guangxi (Fig. 1). We sampled the roadside section ~4 km west of Yangdi, about halfway between the Li River and the main north-south road from Guilin to Yangshuo. It has been suggested that the Xindu Formation (sandstone) at the base of the section is Eifelian, and that the overlying bioclastic and laminated limestones and dolostones of the Donggangling Formation are Givetian (Zhong et al., 1992). However, this has been questioned by Shen and Yu (1996), who suggested that the Eifelian-Givetian boundary could be placed within the upper part of the Xindu Formation. The Frasnian is represented by the Liujiang Formation (interbedded shale and chert with limestone lenses) and the lower part of the Wuzhishan Fomation (bioclastic limestone and

marl). Conodonts (Ji, 1994; Gong et al., 2005) indicate that the upper part of the Wuzhishan Formation, dominated by lenticular occasionally oolitic limestones, is Famennian (Xu et al., 2004; Xu et al., 2006) (Fig. 2).

Shenwan.—The Guilin and Dongcun formations, both of which have been described as back reef deposit (Li and Wang, 1991), occur at Shenwan, ~8 km south-west of Guilin city (Fig. 1). The Guilin Formation, mainly grainstone interbedded with dolostone, contains abundant *Amphipora* and local deposits of bulbous stromatoporoids. The Dongcun Formation is dominated by laminated fenestral limestones (Li and Wang, 1991; Shen and Yu, 1996) that are locally oolitic (Fig. 2). Conodonts (Ji, 1989a, 1989b) indicate a Frasnian age for the Guilin Formation (Li and Wang, 1991). The facies change between the Guilin and Dongcun formations has been suggested to reflect onset of Famennian regression and the Frasnian-Famennian mass extinction (Shen and Yu, 1996).

Thus, recognition of the Frasnian-Famennian boundary is only firmly constrained by conodont faunas in the Yangdi section. The boundary section is dolomitized in the Dushan
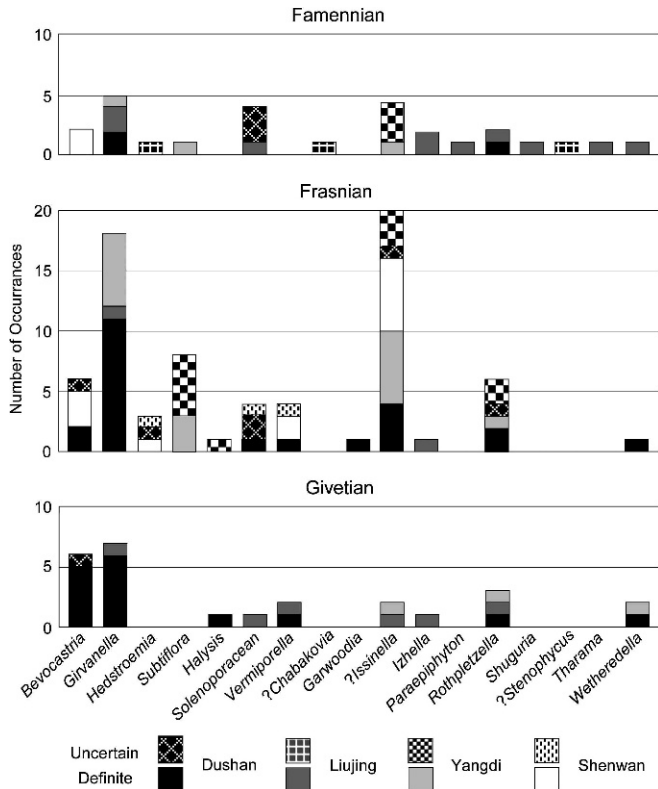
FIGURE 3—Raw occurrence data. The total number of horizons in each stage in which each taxon was recorded, showing both definite and uncertain identifications.

[Figure 3 — bar charts: Famennian, Frasnian, Givetian. Y-axis: Number of Occurrances. Legend: Uncertain / Definite; Dushan, Liujing, Yangdi, Shenwan. X-axis taxa: Bevocastria, Girvanella, Hedstroemia, Subtiflora, Halysis, Solenoporacean, Vermiporella, ?Chabakovia, Garwoodia, ?Issinella, Izhella, Paraepiphyton, Rothpletzella, Shuguria, ?Stenophycus, Tharama, Wetheredella.]

		Cyanobacteria				Algae — Red	Algae — Green		Microproblematica							
Stage	Section	*Bevocastria*	*Girvanella*	*Hedstroemia*	*Subtiflora*	*Halysis*	*Solenoporacean*	*Vermiporella*	*Garwoodia*	*?Issinella*	*Izhella*	*Paraepiphyton*	*Rothpletzella*	*Shuguria*	*Tharama*	*Wetheredella*
Famennian 110	Dushan		2										1			
	Liujing		2			1				2	1		1	1	1	1
	Yangdi		1		1				1							
	Shenwan	2														
	Subtotal	2	5		1	1			1	2	1		2	1	1	1
Frasnian 89	Dushan	2	11			1		1	1	4			2			1
	Liujing		1								1					
	Yangdi		6		3					6			1			
	Shenwan	3		1				2		6						
	Subtotal	5	18	1	3	1		3	1	16	1		3			1
Givetian 54	Dushan	5	6			1		1					1			1
	Liujing		1				1	1	1	1			1			
	Yangdi								1				1			1
	Subtotal	5	7			1	1	2	2	1			3			2

FIGURE 4—Summary of definite taxonomic occurrence data from Fig. 3, together with the total number of horizons sampled in each stage. "Definite" indicates that the fossil observed conforms to its description; this has not been possible in the cases of ?*Chabakovia* and ?*Stenophycus*.

section and its precise location is uncertain at Liujing and Shenwan.

STRATIGRAPHIC DISTRIBUTION

Data.—The raw and definite occurrences of the calcified microfossils in each stage are shown in Figures 3 and 4 respectively. "Definite" is used to indicate that the fossil observed conforms to its description, even though its name may be uncertain due to taxonomic questions, as with ?*Issinella*. Using just the definite identifications, we added together the number of horizons in each stage in which each genus occurred. For example, in the Famennian of all four sections, *Girvanella* was definitely identified in 5 horizons. This abundance value was then divided by the total number of horizons *in the same stage*, to obtain the relative abundance value. For example, from all four sections, 110 horizons were sampled in the Famennian. Thus, the relative abundance of *Girvanella* in the Famennian is 5/110=0.045. These relative abundance data for each genus are shown in Figure 5. The same data are expressed in pie diagrams to show the relative abundance and proportions of major groups for each stage (Fig. 6).

Major groups.—Based on assessment of likely affinity (see Systematics) we recognize three major groups among these taxa: sheath calcified cyanobacteria (*Bevocastria*, *Girvanella*, *Hedstroemia*, and *Subtifloria*), algae (*Halysis*, "solenopora-ceans," *Vermiporella*), and microproblematica (?*Chabakovia*, *Garwoodia*, ?*Issinella*, *Izhella*, *Paraepiphyton*, *Rothpletzella*, *Shuguria*, ?*Stenophycus*, *Tharama*, *Wetheredella*).

Stage distribution.—These major groups–algae, cyanobac-teria, microproblematica–are present in all four sections (Dushan, Liujing, Yangdi, Shenwan) and in all three stages (Givetian, Frasnian, Famennian). The relative proportions of these groups do not change very significantly from stage to stage, but the abundance of all three is substantially lower in the Famennian. Thus, from Givetian to Frasnian the total abundance of the three combined groups increases by 34%; and from Frasnian to Famennian this value decreases by 63% (Fig. 6). The most noticeable changes in proportions are (i) increase in microproblematica through the sequence: 33% Givetian, 42% Frasnian, 50% Famennian; (ii) reduction in algae: 17% Givetian, 8% Frasnian, 6% Famennian, and (iii)

[Figure 5 — bar charts: Famennian, Frasnian, Givetian. Y-axis: Occurred times / Sampled beds. X-axis taxa: Bevocastria, Girvanella, Hedstroemia, Subtiflora, Halysis, Solenoporacean, Vermiporella, ?Chabakovia, Garwoodia, ?Issinella, Izhella, Rothpletzella, Paraepiphyton, Shuguria, ?Stenophycus, Tharama, Wetheredella.]
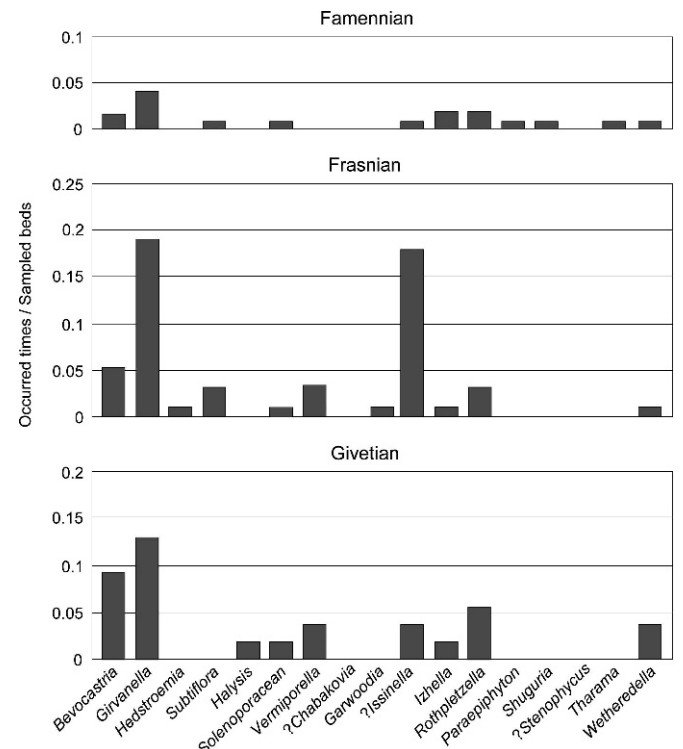
FIGURE 5—Relative abundance values for each taxon per stage, derived by dividing number of definite taxon occurrences per stage by the total number of horizons sampled in each stage (from data in Fig. 4).
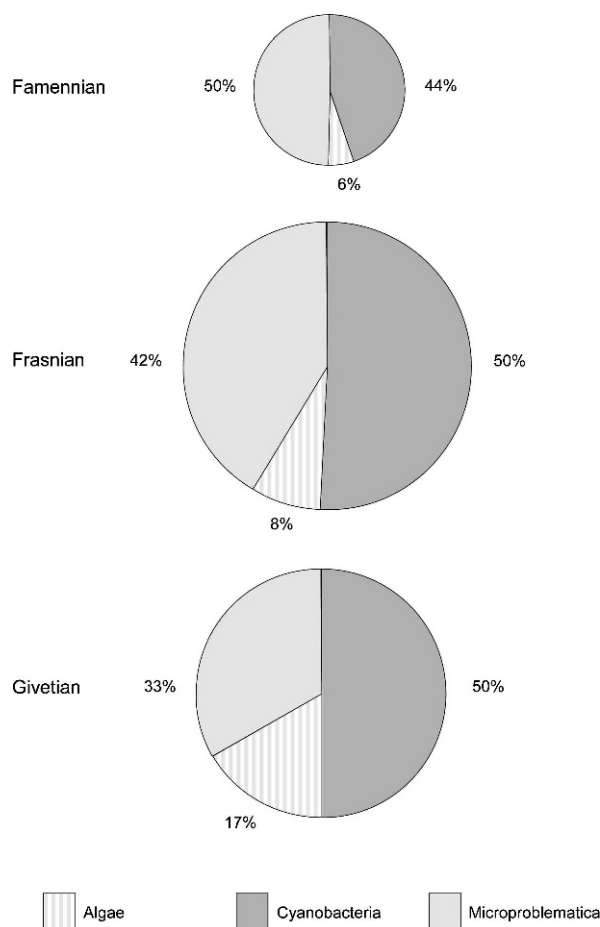
FIGURE 6—Abundance, represented by pie diagram areas, and relative proportions of the major groups (algae, cyanobacteria, microproblematica) per stage, based on definite recognition data (Fig. 5). Note the marked reduction in abundance of all groups in the Famennian.

decline in the proportion of cyanobacteria: 50% Givetian, 50% Frasnian, 44% Famennian.

Cyanobacteria are much more common than algae in all three stages, and *Girvanella* is the most abundant taxon in each stage. Sheath-calcified cyanobacteria diversity and abundance increase from Givetian to Frasnian, and are reduced in the Famennian. Calcified algae are only relatively conspicuous in the Givetian and their abundance progressively decreases through the Frasnian and Famennian. The overall abundance of cyanobacteria is similar to the combined abundance of algae and microproblematica in the Givetian and Frasnian; but in the Famennian, microproblematica became slightly more abundant than cyanobacteria. ?*Issinella* especially is locally abundant in the Frasnian, and *Rothpletzella* is relatively conspicuous in all stages. Typically reefal genera such as *Izhella* and *Wetheredella* are present in all three stages. Other reefal taxa include *Paraepiphyton*, *Tharama*, and *Shuguria*, together with possible *Chabakovia* and *Stenophycus*. These "other reefal taxa" are all quite uncommon in the sections studied here, and have only been encountered in the Rongxian reef horizon at Liujing, which is either latest Frasnian or earliest Famennian in age.

Facies diversity.—In addition to the Rongxian reef, which is counted here as two horizons, we sampled a number of other reef-related, mainly stromatoporoidal, horizons in the Givetian and Frasnian of the Dushan and Liujing sections, and in the Frasnian of Shenwan. We also encountered oncoid beds

with encrusting forms such as *Rothpletzella*, in the Givetian of Yangdi, and *Girvanella* in the Frasnian of Dushan. Nonetheless, many of the sampled horizons are non-reefal bedded limestones, among which bioclastic packstones are common. *Girvanella* occurs as crusts on other skeletons but, together with *Subtifloria*, also occurs as loosely tangled flocs that may have been epiplanktic and occurs in wackestones. In addition, we sampled bioclastic, oolitic and peloidal grainstones, and also fenestral micrites. Our samples therefore appear to be broadly representative of a wide range of relatively unrestricted shallow marine carbonate platform top, margin and upper slope facies.

SYSTEMATIC PALAEONTOLOGY

Repository.—Specimens illustrated here are housed in the collection of the Faculty of Earth Sciences, China University of Geosciences, Wuhan. They are identified by the thin-section numbers cited in the figure captions.

The systematic attributions, descriptions and discussion are by RR.

ALGAE

Division? RHODOPHYTA Wettstein, 1901
Class? RHODOPHYCEAE Rabenhorst, 1863
Order? CORALLINALES Silva and Johansen, 1986
Family uncertain
Genus HALYSIS Høeg, 1932

Type species.—*Halysis moniliformis* Høeg, 1932.

Discussion.—Riding and Braga (2005) interpreted *Halysis* as a unistratose sheet of cells, and compared it with thin laminar coralline red algae such as Neogene *Lithoporella* (Foslie) Foslie and *Lithophyllum* Philippi. *Lithoporella* has cells commonly 50–75 µm in size (Riding and Braga, 2005, p. 838), and this range is comparable with those in our *Halysis* specimen. Our suprageneric classification follows Riding and Braga (2005).

HALYSIS ?YUI (Bian and Liu, 1999)
Figure 7.1

Oedogonium yui BIAN AND LIU, 1999, p.49, pl. 1, figs 1–6.

Description.—Thallus thin, flexuous; a single layer of laterally linked, calcified, large square to rounded rectangular, cells; wall thin, micritic.

Dimensions.—Cell width (large dimension) 48–88 µm (mean 66 µm); cell height (small dimension) 25–59 µm (mean 38 µm) ($N = 29$) (Fig. 8).

Occurrence.—Extremely scarce. Present in only 1 of 253 sampled horizons: 2% of Givetian sampled horizons. In stromatoporoid-bearing bioclastic packstone-grainstone.

Discussion.—*Halysis yui* was first described as the green alga *Oedogonium* from the Ashgill (Late Ordovician) of Jiangxi Province, China, by Bian and Liu (1999), and placed in *Halysis* by Riding and Braga (2005, p. 837). The cells in *H. yui* are <70 µm in largest dimension. Our specimen is small. The type-species, *H. moniliformis* Høeg, has cells with largest dimension in the range 80–210 µm (Riding and Braga, 2005, p. 836), compared with 48–88 µm in our specimen. In this relatively small cell size, and in having more flattened external surfaces, our specimen more closely resembles *Halysis yui* than *Halysis moniliformis*. The first described and oldest *Halysis* specimens are from the early Upper Ordovician of Norway (Høeg, 1932) and the genus has been reported up to the Mid-Devonian (Miretskaya, 1988 pl. 33, fig. 2). In the Givetian *Halysis* is therefore at, or near the top, of its known range. We are not aware of younger occurrences of *Halysis* elsewhere. It
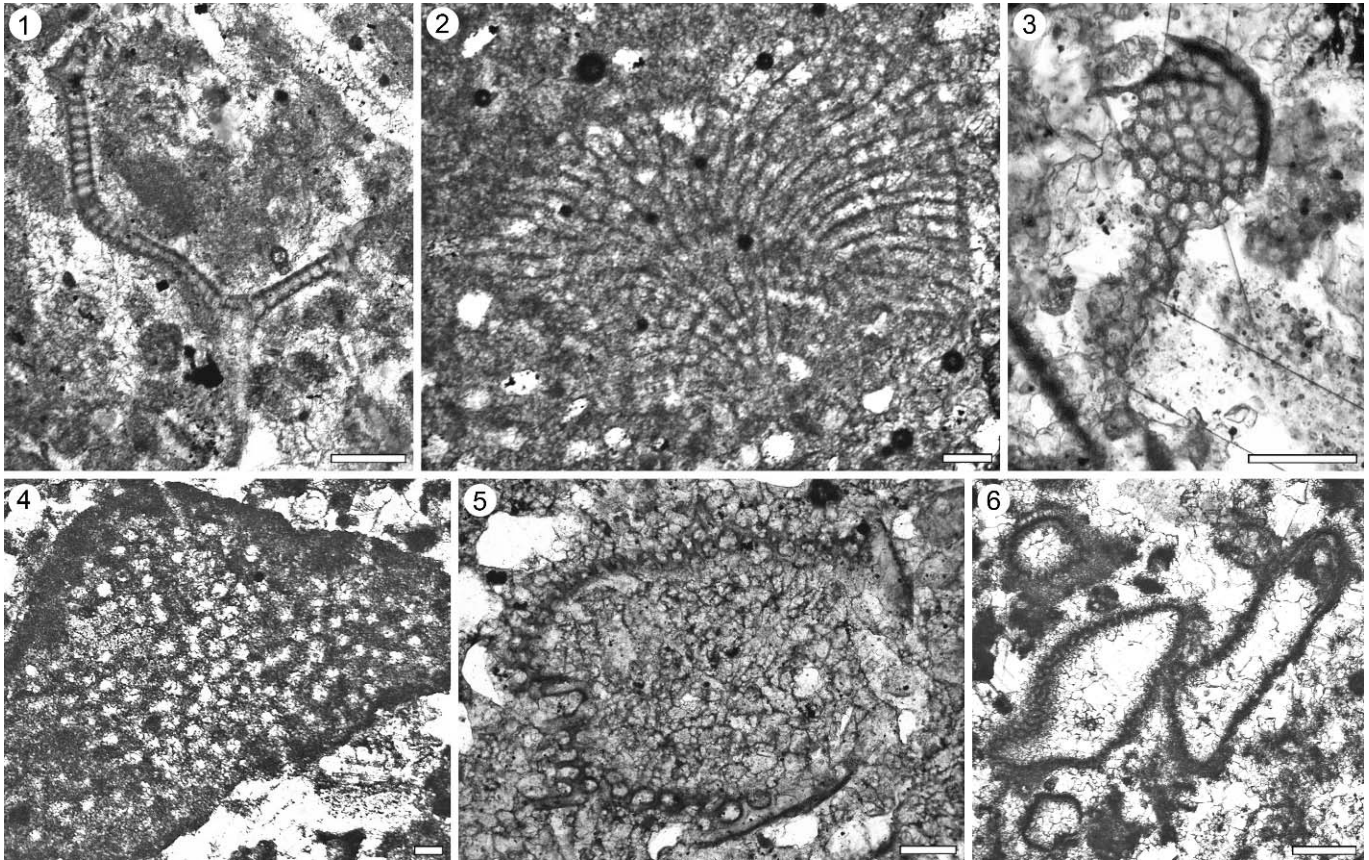
FIGURE 7—Calcified algae. All scale bars = 100 μm. *1, Halysis* (thin-section D₂jw32-3-1), Givetian, Dushan section; *2,* "Solenoporacean" (thin-section D₃l33-1-2), Frasnian, Dushan section; *3,* "Solenoporacean" (thin-section D₃l44-8-2), Frasnian, Dushan section; *4,* "Solenoporacean" (thin-section D₂mt4-1), Givetian, Liujing section; *5, Vermiporella* (thin-section D₂jp), Givetian, Dushan section; *6, Vermiporella* (thin-section D₃gl-1-a), Frasnian, Shenwan section.
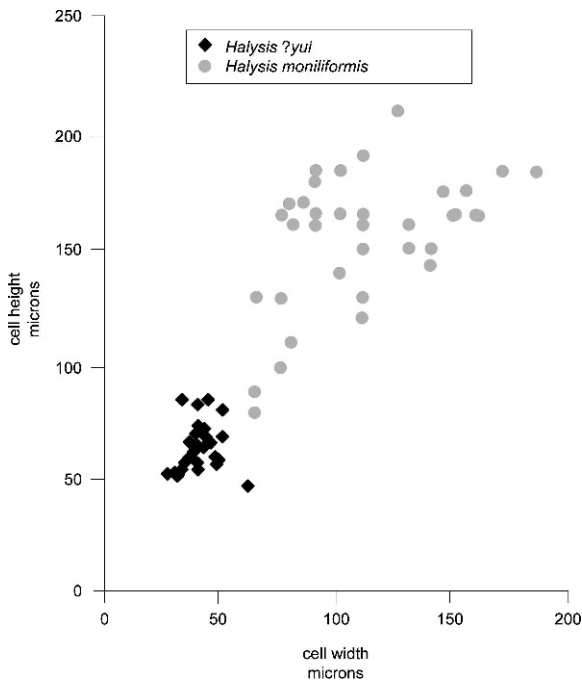

FIGURE 8—*Halysis ?yui* size measurements (filled diamonds) compared with *Halysis moniliformis* type-specimens (grey circles). *H. moniliformis* data from Riding and Braga (2005, fig. 2). In cell size, *H. ?yui* is comparable with extant unistratose coralline algae such as some *Lithoporella* species (see Riding and Braga, 2005, p. 838).

is therefore possible that *Halysis* went extinct at the Frasnian-Famennian boundary; but this requires further study.

"Solenoporaceae gen. et sp. indet."
Figure 7.2–7.4

Description.—Calcareous nodular skeleton, composed of radiating curved or slightly sinuous juxtaposed fan-like filaments, filaments rounded to polygonal in cross-section, wall thin, micritic.

Dimensions.—Small radial and rounded millimetric nodules, up to 2 mm in size. Internal filament diameter 27–95 μm; wall thickness 6–16 μm.

Occurrence.—Undifferentiated "solenoporaceans" are present in 3 of 253 sampled horizons: 2% of Givetian sampled horizons; 1% of Frasnian sampled horizons; 1% of the Famennian sampled horizons. They occur as fragments in skeletal packstone-grainstone and in reef framestone.

Discussion.—Fossils conventionally regarded as members of the Solenoporaceae Pia are in need of comprehensive revision. The chaetetid *Solenopora* Dybowski, based on *Solenopora spongioides* Dybowski, 1877 (p. 124, pl. 2, fig. 11a, b), is not congeneric with most species attributed to *Solenopora*, and solenoporaceans currently appear to represent a mixture of mainly algae, cyanobacteria and sponges/metazoans (Brooke and Riding, 1998). We encountered very few specimens of this heterogeneous group in our samples. Those that we record as "solenoporaceans" have cellular morphologies consistent with red algae. However, we do not attempt to establish their taxonomy or affinity more precisely.

Class ULVOPHYCEAE Mattox and Stewart, 1984
Genus VERMIPORELLA Stolley, 1893

Type species.—*Vermiporella fragilis* Stolley, 1893.

VERMIPORELLA MYNA Wray, 1967
Figure 7.5, 7.6

Description.—Lobate inflated irregular hollow calcifed thallus, broad central cavity, thin wall pierced by regular simple numerous closely spaced pores.

Dimensions.—Overall external thallus size ~1 mm, wall thickness 30 μm, pore diameter 33 μm.

Occurrence.—Present in 5 of 253 sampled horizons: 4% of Givetian sampled horizons, 3% of Frasnian, and none of the Famennian sampled horizons. These specimens occur in bioclastic peloid packstone-grainstone.

Discussion.—*Vermiporella* ranges Ordovician to Permian and was first reported from the Devonian by Wray (1967, p. 31). Our few specimens have inflated lobate thalli with thin porous walls, and closely resemble both *V. myna* described by Wray (1967) from the Frasnian of the Canning Basin and *V.* cf. *myna* described by May (1992, p. 18) from the upper Eifelian of Rheinisches Schiefergebirge. Wray (1967, p. 31) noted that *V. myna* may not be congeneric with *V. fragilis* Stolley. *Vermiporella fragilis* is locally common in the Ordovician and typically has somewhat larger thalli (e.g., Riding and Fan, 2001, p. 796).

Vermiporella generally resembles the extant genus *Dasycladus* and has therefore widely been regarded as a dasycladalean (e.g., Tappan, 1980, p. 892; Berger and Kaever, 1992, table 2.9). Internal micromorphic details, such as septa and oospore-like bodies, in silicified Ordovician *V. fragilis*, suggest comparisons with ulotrichalean green algae Kozlowski and Kazmierczak (1968). To reflect these various green algal affinities we place *Vermiporella* in the Ulvophyceae, which can encompass both Dasycladales and Ulotrichales (Lewis and McCourt, 2004, table 2).

CYANOBACTERIA
Genus BEVOCASTRIA Garwood, 1931

Type species.—*Bevocastria conglobata* Garwood, 1931.

BEVOCASTRIA sp.
Figure 9.1

Description.—Calcareous tubular filaments, varied diameter, sinuous and closely packed, forming compact tangled masses, wall thin, micritic.

Filament dimensions.—External diameter 47–98 μm (mean 63 μm); wall thickness 7–23 μm (mean 16 μm) ($N = 14$) (Fig. 10).

Occurrence.—Present in 12 of 253 sampled horizons: 9% of Givetian sampled horizons, 6% of Frasnian sampled horizons, 2% of the Famennian sampled horizons. *Bevocastria* typically occurs as thin, sub-millimetric, crustose masses on skeletons in reefal and oncoid facies.

Discussion.—In establishing *Bevocastria* from the Lower Carboniferous of northern England, Garwood (1931, p. 140) described the tubes as constricted at regular intervals. *Girvanella* generally consists of less tightly tangled tubes than *Bevocastria*, but the constrictions are the principal morphological distinguishing feature, and there is considerable overlap between these filamentous fossils if constrictions are not clearly developed. Relatively large *Girvanella*, including some recognized here, have tubes similar in size (~60–80 μm). *Bevocastria*, cannot be confidently distinguished from these unless constrictions are clearly present.

The small size and simple organization of *Bevocastria* invite comparisons with *Girvanella*, which can confidently be regarded as a cyanobacterium. However, no present-day analogues have been suggested for *Bevocastria*, and it has been included, along with *Garwoodia*, *Hedstroemia*, *Ortonella*, and *Gaspesiella*, in 'nodular codiaceans' (Bourque et al., 1981, fig. 5; Mamet et al., 1992, p. 218). Nonetheless, *Hedstroemia* and *Ortonella* are better compared with rivulariacean cyanobacteria and the concept of nodular codiaceans requires reconsideration (Riding and Fan, 2001, p. 802). Chuvashov et al. (1987, p. 30) considered *Bevocastria* to be a calcified cyanobacterium; this assignment is followed here.

Genus GIRVANELLA Nicholson and Etheridge, 1878

Type species.—*Girvanella problematica* Nicholson and Etheridge, 1878.

GIRVANELLA PROBLEMATICA Nicholson and Etheridge, 1878
Figures 9.2–9.5

Description.—Calcareous tubular filaments, uniform diameter, elongate, sinuous to irregularly tangled, wall thin, micritic.

Filament dimensions.—Two size populations can be distinguished, smaller with external tube diameter 8–40 μm (mean 21 μm); wall thickness 2–13 μm (mean 6 μm) ($N = 87$); larger with external tube diameter 47–76 μm (mean 59 μm); wall thickness 8–26 μm (mean 14 μm) ($N = 21$) (Fig. 11).

Occurrence.—*Girvanella* occurs as large and small filaments forming prostrate crusts on skeletons and as small tangled, probably semi-planktonic, masses in packstone-grainstones (Fig. 9.3). The larger forms are common in the Dushan section. Both large and small forms in combination are present in 30 of 253 sampled horizons: 13% of Givetian sampled horizons, 20% of Frasnian sampled horizons, 5% of Famennian sampled horizons.

Discussion.—*Girvanella* is a very long-ranging microfossil that is common in the Palaeozoic. Despite its morphological simplicity, it shows wide differences in tube arrangement (aligned versus irregularly coiled), packing (looser, closer), and size that have been used to establish species (e.g., Johnson, 1966). Of these, tube diameter is the single most widely used descriptor and is the basis for a large number of species (see Fournie, 1967). These size ranges often show considerable overlap, and stable circumscription of these taxa has yet to be established. The larger filaments in our samples overlap in tube diameter with those of *Bevocastria*; they differ in lacking the constrictions typical of *Bevocastria* tubes.

Girvanella has modern analogues in *in vivo* calcified sheaths of filamentous cyanobacteria (Riding, 1977).

Genus HEDSTROEMIA Rothpletz, 1913

Type species.—*Hedstroemia halimedoidea* Rothpletz, 1913.

HEDSTROEMIA sp.
Figure 9.6

Description.—Small nodules up to a few millimetres in size composed of juxtaposed radial calcareous tubes; tubes circular to irregular in cross section, may be dichotomously branched; wall thin, probably shared, micritic.

Filament dimensions.—Internal tube diameter ~85 μm; wall thickness ~36 μm.

Occurrence.—Extremely scarce. Confidently recognized in 1 of 253 sampled horizons: 1% of Frasnian sampled horizons. *Hedstroemia* occurs as a millimetric nodule (1.4 mm diameter) in bioclastic peloid packstone-grainstone (Fig. 9.6).
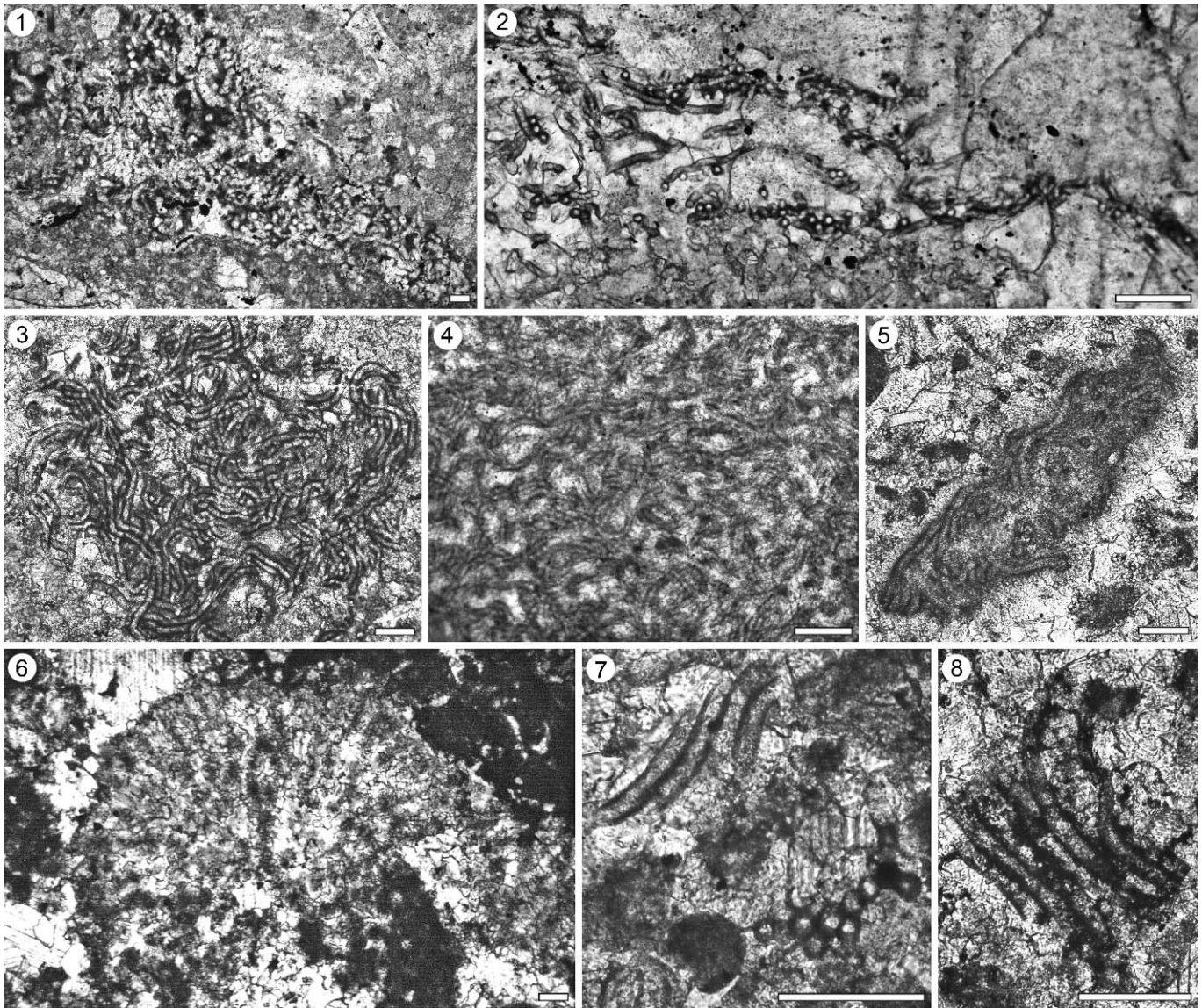
FIGURE *9*—Calcified Cyanobacteria. All scale bars = 100 μm. *1*, *Bevocastria* (thin-section D₂jp-12-1), Givetian, Dushan section; *2*, *Girvanella* (thin-section D₃l24), Frasnian, Dushan section; *3*, *Girvanella* (thin-section D₃w114-3), Famennian, Dushan section; *4*, *Girvanella* (thin-section D₂m-44-3), Givetian, Liujing section; *5*, *Girvanella* (thin-section D₃w40a), Famennian, Yangdi section; *6*, *Hedstroemia* (thin-section D₃gl-1-a), Frasnian, Shenwan section; *7*, *Subtifloria* (thin-section D₃w39-5), Frasnian, Yangdi section; *8*, *Subtifloria* (thin-section D₃lj5), Frasnian, Yangdi section.
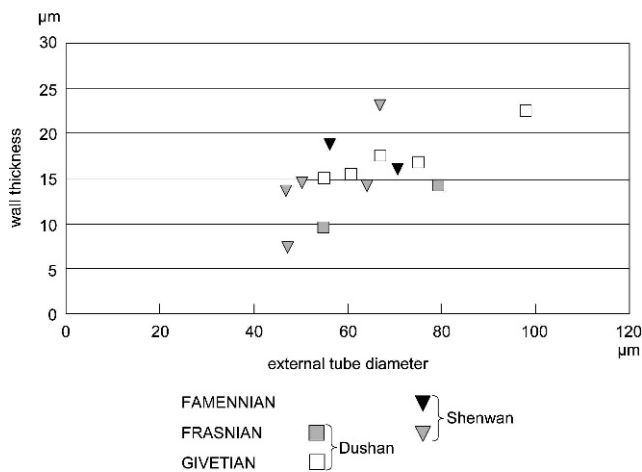
FIGURE *10*—*Bevocastria* sp. size measurements. Compare Figure 11.

Discussion.—*Hedstroemia* has been reported throughout the Palaeozoic and is locally common, e.g., in the Silurian (Riding and Watts, 1981; Riding and Soja, 1993). It is comparable with similar small nodular masses of radial tubes, such as *Botomaella* and *Cayeuxia*, as well as extant *Rivularia*.

Rothpletz (1913) regarded *Hedstroemia* as a calcareous alga and compared it with *Halimeda*; accordingly Johnson and Konishi (1959) regarded *Hedstroemia* as a codiacean. Riding and Watts (1981) compared *Hedstroemia* with the extant cyanobacterium *Rivularia*; this attribution is followed here.

Genus SUBTIFLORIA Maslov, 1956

Type species.—*Subtifloria delicata* Maslov, 1956.

SUBTIFLORIA sp.
Figure 9.7, 9.8

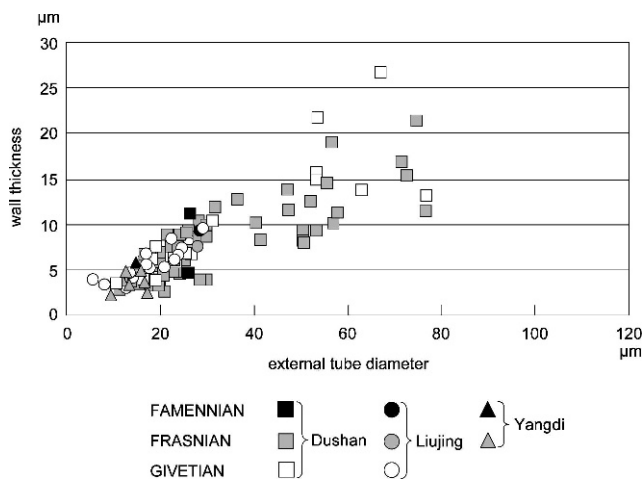*Description.*—Calcareous tubular filaments of uniform diameter, sub-parallel, closely packed, sinuous to straight,

FIGURE 11—*Girvanella* sp. size measurements. The specimens roughly fall into larger (>40 μm diameter) and smaller (<40 μm diameter) groups, the larger group overlapping in size with *Bevocastria* sp. (Fig. 10). Note that the larger specimens are from the Givetian-Frasnian of Dushan.

forming short discrete unattached bundles that are longer than wide, wall thin, micritic.

Filament dimensions.—External diameter 17–37 μm (mean 23 μm); wall thickness 4–12.5 μm (mean 6 μm) ($N = 11$) (Fig. 12).

Occurrence.—Present in 4 of 253 sampled horizons: 3% of Frasnian sampled horizons, 1% of Famennian sampled horizons. *Subtifloria* typically occurs in grainstones as small flake- or raft-like fragments that appear to have been epiplanktic, and/or detached from poorly attached masses.

Discussion.—*Subtifloria* resembles small *Girvanella* in tube diameter, and is distinguished by its generally aligned filaments. *Subtifloria* typically occurs as flake-like rafts. In Early Cambrian examples, these commonly exhibit cable-like intertwining (e.g., Riding, 1991a, fig. 4a) that we have not observed here.

This is the first confirmed report of *Subtifloria* younger than Lower Cambrian. ?*Subtifloria* was described from the Early and Mid-Ordovician of northern China (Riding and Fan, 2001, p. 790). *Subtiforia latissima* Luchinina from the Lower Carboniferous of the Kuzbass (Bogush et al., 1990, pl. 3, fig. 1) may be *Girvanella*. Several specimens encountered here show what appear to be aligned flake-like clusters of filaments in transverse section (Figs. 9.7–8). However, it remains difficult to confidently distinguish transverse sections that could represent of clusters of calcified spheres, from groups of tubes.

We infer that *Subtifloria* is a sheath-calcified filament cyanobacterium similar to *Girvanella*.

MICROPROBLEMATICA

Genus CHABAKOVIA Vologdin, 1939

Type species.—*Chabakovia ramosa* Vologdin, 1939.

?CHABAKOVIA sp.
Figure 13.1

Description.—Narrow dendritic chambered branches arising from sub-spherical hollow chambers; chambers in branches round to ovoid, indistinct; wall medium thickness, micritic.

Dimensions.—Branches 200–400 μm in length. Branch/chamber width ~50 μm.

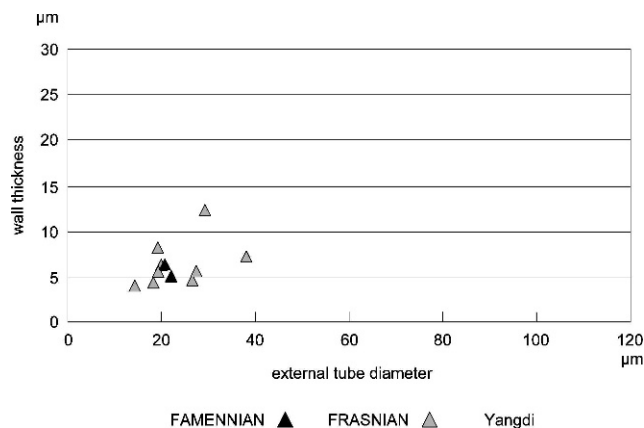*Occurrence.*—Extremely scarce. Present in 1 of 253 sampled horizons: 1% of Famennian sampled horizons. Together with

Paraepiphyton, *Shuguria*, ?*Stenophycus*, and *Tharama*, ?*Chabakovia* has only been observed in the basal Rongxian reef at Liujing.

Discussion.—*Chabakovia* was first described by Vologdin (1939) from the Early Cambrian of the southern Urals. It is characterized by dendritic series of small inflated bubble-like chambers (Pratt, 1984, p. 955; Riding and Voronova, 1985, pp. 61–62). Specimens in our single thin-section resemble *Chabakovia* in size and general form, and have elongate branches, but the thin-walled globular chambers typical of *Chabakovia* are not clearly seen here. The branches of our specimens somewhat resemble those of *Ludlovia* Korde, described from the Silurian of Alaska (Riding and Soja, 1993, p. 718). The branches in our specimens arise from hollow *Renalcis*-like chambers.

Vologdin (1939) regarded *Chabakovia* as an alga. Elias (1950) considered it to be a foraminifer.

Genus GARWOODIA Wood, 1941

Type species.—*Garwoodia gregaria* (Nicholson) Wood, 1941.

GARWOODIA sp.
Fig. 13.2

Description.—Calcareous tubular filaments, closely spaced within micritic matrix, probably radiating, wall thin, micritic.

Filament dimensions.—External diameter ~130 μm; wall thickness ~45 μm.

Occurrence.—Extremely scarce. Present in only 1 of 253 sampled horizons: 1% of Frasnian sampled horizons. *Garwoodia* occurs within a small oncoid in bioclastic wackestone.

Discussion.—*Garwoodia* was named by Wood (1941) for specimens in material collected by Wethered (1886, 1887) from the Lower Carboniferous of Gloucestershire, England. Wood (1941) illustrated subparallel-to-radial tubes of slightly variable thickness that, in longitudinal section, show distinctive right-angled branching. Our few specimens are transverse sections of tubes that in size, shape and arrangement closely resemble the transverse sections of *Garwoodia gregaria* shown by Wood (1941, pl. 14, fig. 1).

Wood (1941) considered *Garwoodia* to be an alga but did not specify its affinity more precisely. *Garwoodia* has features reminiscent of both calcified cyanobacteria and halimedacean green algae (see Riding, 1991b, p. 70). Johnson (1961) placed *Garwoodia* with *Halimeda*, and Bourque et al. (1981, fig. 5) suggested that *Bevocastria*, *Garwoodia*, *Hedstroemia*, *Ortonella*, and *Gaspesiella* could be regarded as "nodular
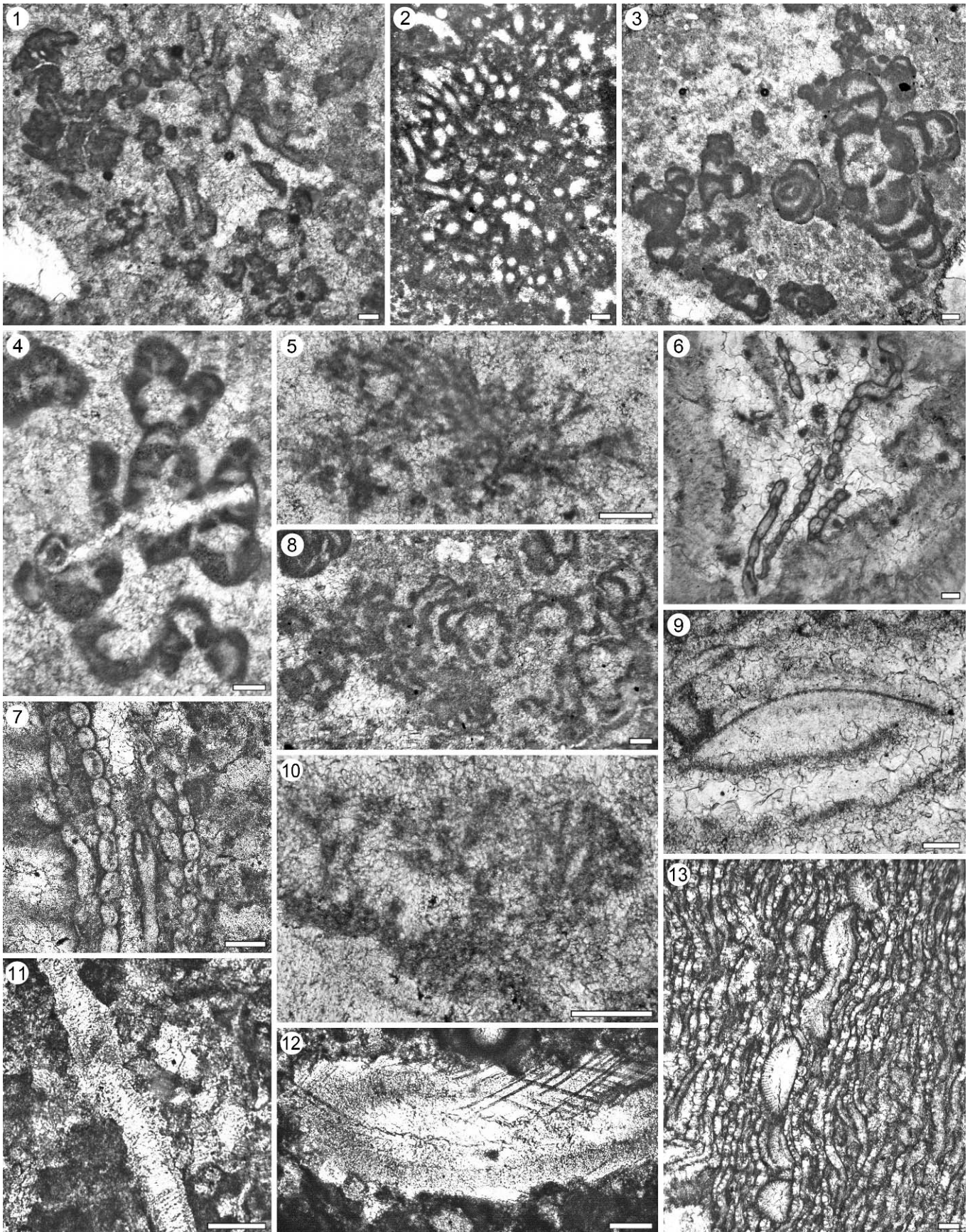

FIGURE 12—*Subtifloria* sp. size measurements.

FIGURE *13*—Microproblematica. All scale bars = 100 μm. *1*, ?*Chabakovia* (thin-section D₃r14-6-1), Famennian, Liujing section; *2*, *Garwoodia* (thin-section D₃h6-1), Frasnian, Dushan section; *3*, *Izhella* (thin-section D₃gb61-1-1), Frasnian Liujing section; *4*, *Izhella* (thin-section D₃r15-2-1), Famennian, Liujing section; *5*, *Paraepiphyton* (thin-section D₃r15-2-1), Famennian, Liujing section; *6*, *Rothpletzella* (thin-section D₂m-44-3), Givetian, Liujing
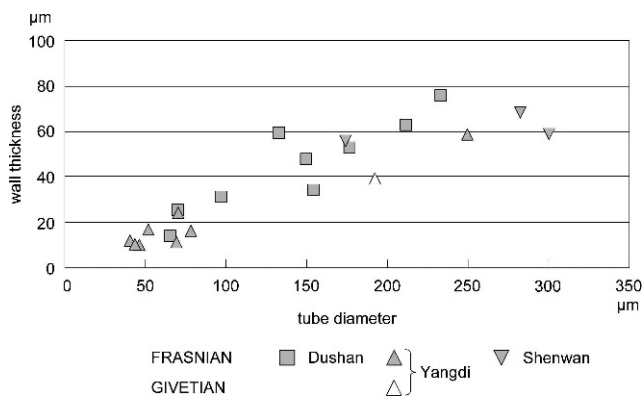
FIGURE 14—*?Issinella* sp. size measurements.

codiaceans." As noted for *Hedstroemia*, several of these taxa (*Hedstroemia*, *Ortonella*) much more closely resemble extant calcified cyanobacteria than green algae. The likely affinities of the others, and of *Garwoodia*, remain less clear.

Genus ISSINELLA Reitlinger 1954

Type species.—Issinella devonica Reitlinger, 1954

?ISSINELLA sp.
Figure 13.11, 13.12

Description.—Calcareous tube, straight to irregularly sinuous, septate; wall thick, light or dark in thin-section.

Dimensions.—Tubes typically up to 2 mm in length. External diameter 39–299 μm (mean 136 μm, $N = 21$); wall thickness 10–76 μm (mean 38 μm, $N = 21$) (Fig. 14).

Occurrence.—Present in 19 of 253 sampled horizons: 4% of Givetian sampled horizons, 18% of Frasnian sampled horizons, 1% of Famennian sampled horizons. *?Issinella* is locally very common, particularly in the Frasnian. It can be a major skeletal component of packstone-grainstone, as in the Frasnian at Dushan (uppermost Lujiazhai Formation) and Shenwan (Guilin Formation), and in the early Famennian (Wuzhishan Formation) at Yangdi. The tubes always appear to be fragmentary.

Discussion.—Reitlinger (1954) described *Issinella* from the late Frasnian Evlanovsk-Livensk layer in a borehole at Issa, near Penza, on the eastern Russian Platform, ~550 km southeast of Moscow. The identity of *Issinella* is linked to those of taxa such as *Jansaella* Mamet and Roux, 1975, *Uraloporella* Korde, 1950 and, to a lesser extent, *Nanopora* Wood, 1964. These fossils are straight to curved or sinuous calcareous tubes, 1mm in diameter, that occur in the Devonian-Carboniferous. Diameter is relatively constant in individuals, but ranges widely between individuals, from ~50–700 μm. The walls of *Issinella*, *Jansaella* and *Uraloporella* have less well-defined pores than *Nanopora* and can show variation between fibrous, often yellowish, and dark microgranular structure in thin-section. They have all often been compared with dasycladalean and udotealean green algae. Wall structure and pores, together with differences in septation and branching, are keys to recognition of these fossils. However, whether the wall structure is primary and pores are present,

can become conjectural. Occurrence of these fossils as fragments also often makes it difficult to judge whether the absence of features such as branching and septa is fortuitous.

Most of our specimens resemble Reitlinger's (1954) description of *Issinella* in having a thin, straight skeleton with light-colored wall, and locally being rock-forming. Reitlinger (1954, p. 80) noted that branching was not observed in the type material. The illustration of the type specimen shows the variable light and dark preservation of the wall. These features are also present in Givetian-Frasnian specimens from Alberta that Riding and Jansa (1974, pl. 1) attributed to *Uraloporella*, and that Mamet and Roux (1975a) used to create *Jansaella*, which differs from *Issinella* in showing branching and well-developed septa. However, as Mamet and Villa (1995) noted with regard to *Uraloporella*, it is often necessary to have numerous specimens to adequately characterize these fragmentary fossils and, so far as we know, this has yet to be achieved for *Issinella*. It is possible, therefore, that *Jansaella* is a junior synonym of *Issinella*. Assignment of our specimens to *?Issinella* sp. does not attempt to resolve these difficulties.

Reitlinger (1954) considered *Issinella* to possibly be a dasycladalean green alga. Occurrence of these fossils as fragments often makes it difficult to judge whether the absence of features such as branching and septa is fortuitous. This complicates not only taxonomic assignment, but also interpretation of affinity. Septa, and the style of branching that can be seen, for example, in *Jansaella ridingii*, preclude dasycladalean and udotealean affinities (Riding and Jansa, 1974, p. 1422; pl. 1, fig. 4). Riding and Jansa's (1974, p. 1421) recommendation that the systematic position of these fossils needs to be reviewed remains valid.

Genus IZHELLA Antropov, 1955

Type species.—Izhella nubiformis Antropov, 1955.

IZHELLA sp.
Figures 13.3, 13.4

Description.—Chambered microfossil in compact botryoidal clusters, wall lunate, thick, micritic, with deep clefts on inner surface.

Dimensions.—Maximum length 1–1.5 mm. Maximum chamber width 202–524 μm (mean 313 μm, $N = 10$); wall thickness 56–142 μm (mean 95 μm, $N = 10$) (Fig. 15).

Occurrence.—Present in 4 of 253 sampled horizons: 2% of Givetian sampled horizons, 1% of Frasnian sampled horizons, 2% of Famennian sampled horizons. Occurs in reefal facies.

Discussion.—Antropov (1955) described *Izhella* from the Frasnian of Russia. It has commonly been allied with *Renalcis*; Wray (1967, p. 46), for example, named specimens of *Izhella* in the Canning Basin *Renalcis turbitus*. *Izhella* can be distinguished from *Shuguria* by its thicker walls, fewer chambers and characteristic clefts that penetrate the inner surface of the wall (see Riding, 1991b, p. 69).

Antropov (1955, p. 47) regarded *Izhella* as a cyanobacterium. Hofmann (1975) suggested that *Renalcis* and similar fossils could be calcified gelatinous colonies of chroococcalean cyanobacteria. The clefts in the wall of *Izhella* have been attributed to cracking (Hofmann, 1975, p. 1131) and

section. *7*; *Rothpletzella* (thin-section D$_2$m-44-1), Givetian, Liujing section; *8*, *Shuguria* (thin-section D$_3$r15-3-1), Famennian, Liujing section; *9*, *?Stenophycus* (thin-section D$_3$r14-19), Famennian, Liujing section; *10*, *Tharama* (thin-section D$_3$r15-2-1), Famennian, Liujing section; *11*, *?Issinella* (thin-section D$_3$w1, Frasnian, Yangdi section; *12*, *?Issinella* (thin-section D$_3$g-19-2-a), Frasnian, Shenwan section; *13*, *Wetheredella* (thin-section D$_3$r14-5-1), Famennian, Liujing section.
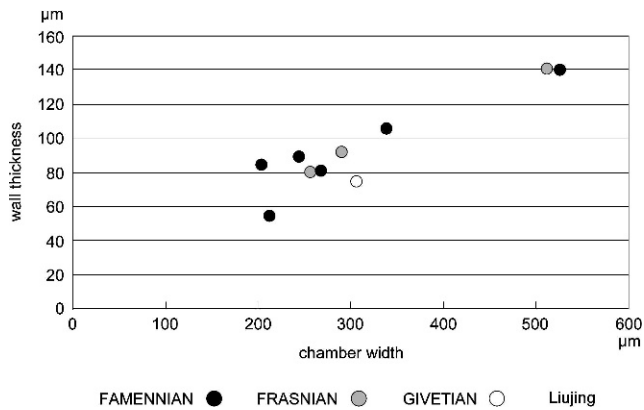
FIGURE 15—*Izhella* sp. size measurements.

FIGURE 16—*Rothpletzella* sp. size measurements.

shrinkage (Pratt, 1984, p. 966). Stephens and Sumner (2002, p. 232) considered that Canning Basin "renalcids" (*Izhella*, *Shuguria*) are neither cyanobacteria nor algae and may be calcified biofilm clusters.

Genus PARAEPIPHYTON Wray, 1967

Type species.—*Paraepiphyton caritus* Wray, 1967

PARAEPIPHYTON CARITUS Wray, 1967
Figure 13.5

Description.—Dendritic mass of narrow micritic branched filaments.

Dimensions.—Overall bush-like mass ~650 μm in length. Tube diameter ~12 μm.

Occurrence.—Extremely scarce. Present in 1 of 253 sampled horizons: 1% of Famennian sampled horizons. Together with *Izhella*, it has been recognized as a key reef-component of the Rongxian reef at Liujing (Zhang et al., 2007).

Discussion.—Wray (1967) described *Paraepiphyton* from the Frasnian and Famennian of the Canning Basin. *Paraepiphyton* was placed in synonymy with *Epiphyton* Bornemann by Riding and Wray (1972). Nonetheless, *Paraepiphyton* may be distinguished from *Epiphyton* by its small size and less regular branching. Until there is more clarity concerning circumscription of the numerous species of *Epiphyton*, and of similar taxa, it remains useful to recognize *Paraepiphyton*.

Genus ROTHPLETZELLA Wood, 1948

*Type species.*—*Sphaerocodium gotlandica* Rothpletz, 1908.

ROTHPLETZELLA sp.
Figure 13.6, 13.7

Description.—Calcareous tubular filaments, prostrate, forming sheet-like flat to undulose layers; wall thin, micritic.

Dimensions.—Filament internal short dimension (tube height) 31–105 μm (mean 62 μm, N = 12); wall thickness 5–32 μm (mean 13 μm, N = 12) (Fig. 16). We did not measure tube width, which depends upon the angle of section, but in sections that appear to be at right-angles to the tube axis, the width is typically ~1.5 × the tube height.

Occurrence.—Present in 8 of 253 sampled horizons: 6% of Givetian sampled horizons, 3% of Frasnian sampled horizons, 2% of Famennian sampled horizons. *Rothpletzella* forms thin reefal crusts up to at least 5 mm thick, and is the dominant component of oncoids up to 7 cm in diameter (e.g., in the middle part of the Donggangling Formation at Yangdi). Its skeletal preservation is variable over short distances in thin-section.
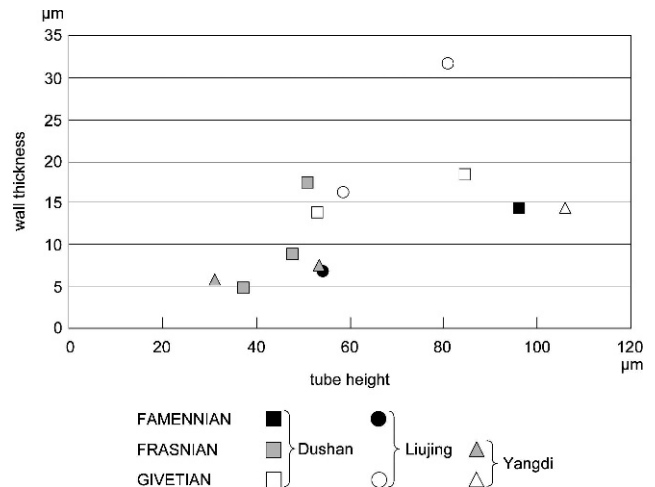
Although *Rothpletzella* is generally known to co-occur with *Wetheredella* (e.g., Adachi et al., 2007, p. 9), in our samples *Rothpletzella* is much more common than *Wetheredella*.

Wood (1948, pp. 17–18) suggested that *Rothpletzella* is a cyanobacterium or green alga. However, no extant analogues are known that shed light on these possibilities, and Riding (1991b, pp. 70–71) regarded *Rothpletzella* as a microproblematicum.

Genus SHUGURIA Antropov, 1950

Type species.—*Shuguria flabelliformis* Antropov, 1950.

SHUGURIA sp.
Figure 13.8

Description.—Chambered branched microfossil in compact clusters, wall thin, micritic.

Dimensions.—Maximum length 1.3 mm; chamber width ~285 μm; wall thickness ~70 μm.

Occurrence.—Extremely scarce. Present in 1 of 253 sampled horizons: 1% of Famennian sampled horizons. Only observed in one *Izhella*-dominated thin section from the basal Rongxian reef at Liujing.

Discussion.—Antropov (1950) described *Shuguria* from the Frasnian of Russia. Together with *Izhella*, it has commonly been allied with *Renalcis*. For example, Johnson (1964, p. 106) named *Shuguria* from south-east Australia *Renalcis devonicus*. *Shuguria* is characterized by numerous relatively thin walled chambers (see Riding, 1991b, p. 69). For comparisons, see *Izhella*.

Antropov (1950) regarded *Shuguria* as a foraminifer. Because of its broad similarities to *Renalcis* it has also commonly been regarded as a cyanobacterium (Johnson, 1964, p. 106; Wray, 1967, p. 45). In contrast, Stephens and Sumner (2002, p. 232) suggested that Canning Basin "renalcids" (*Izhella*, *Shuguria*) may be calcified biofilm clusters.

Genus STENOPHYCUS Fenton, 1943

Type species.—*Stenophycus teichertii* Fenton, 1943.

?STENOPHYCUS sp.
Figure 13.9

Description.—Arcuate convex-up to ovoid skeleton, thin-walled.

Dimensions.—Long dimension ~250–750 μm, height ~100–200 μm.

Occurrence.—Extremely scarce. ?*Stenophycus* is present in 1 of 253 samples: 1% of Famennian sampled horizons. ?*Stenophycus* has only been observed in the basal Rongxian reef at Liujing.

Discussion.—Fenton (1943) described *Stenophycus* from the Famennian of the Canning Basin and regarded it as 'an algal stromatolite'. Wray (1967, p. 22) re-described it and recognized "complex cellular tissue and probable reproductive organs." Our specimens somewhat resemble *Stenophycus* in overall shape but not in size, approaching an order of magnitude smaller. In addition, they do not show the typically stacked arrangement illustrated by Fenton (1943) and Wray (1967). Our identification of *Stenophycus* is therefore uncertain. It remains a very rarely reported fossil.

Fenton (1943) regarded *Stenophycus* as "an algal stromatolite." Wray (1967, pp. 21–24) described "probable" reproductive structures in the wall, and regarded it as a red alga.

Genus THARAMA Wray, 1967

Type species.—*Tharama glauca* Wray, 1967.

THARAMA GLAUCA Wray, 1967
Figure 13.10

Description.—Dense micritic filaments with short laterally expanding branches.

Dimensions.—Overall specimen 150 μm across. Branches up to ~40 μm long, ~10–25 μm in width.

Occurrence.—Extremely scarce. Present in 1 of 253 sampled horizons: 1% of Famennian sampled horizons. *Tharama* was only observed in the basal Rongxian reef at Liujing.

Discussion.—*Tharama* was described by Wray (1967) from the Frasnian and ?Famennian of the Canning Basin. It is very similar to *Amgaina* Korde (1973) from the Middle Cambrian of Siberia.

Wray (1967, p. 20, fig. 7, pl. 4, fig. 3, 4) described delicate cellular microfabric and regarded *Tharama* as a red alga. We have not observed cells in our single specimen. *Tharama* broadly resembles epiphytaceans and shares their problems of affinity.

Genus WETHEREDELLA Wood, 1948

Type species.—*Wetheredella silurica* Wood, 1948.

WETHEREDELLA sp.
Figure 13.13

Description.—Calcareous encrusting tubular filaments, with hemispherical to lunate cross-sections, forming undulose layers to small mutually encrusting masses; wall thin to thick, micritic to fibrous, possibly porous.

Dimensions.—Filament internal short dimension (tube height) 45–243 μm (mean 104 μm, $N = 8$); wall thickness 10–78 μm (mean 30 μm, $N = 8$) (Fig. 17).

Occurrence.—Present in 4 of 253 sampled horizons: 4% of Givetian sampled horizons, 1% of Frasnian sampled horizons, 1% of Famennian sampled horizons. *Wetheredella* occurs as thin layers in reef and oncoid crusts, commonly in associated with *Rothpletzella* (Fig. 13.13).

Discussion.—*Wetheredella*, like *Rothpletzella*, emerged from Wood's (1948) clarification of Silurian fossils previously mistakenly attributed to *Girvanella* (Wethered, 1893) and *Sphaerocodium* (Rothpletz, 1908). Wood (1948, pp. 18, 20) and May (1992, p. 21) suggested that *Wetheredella* is a foraminifer. Cyanobacterial (Copper, 1976) and green algal (Mamet and Roux, 1975b, pp. 156–170; Ischenko and
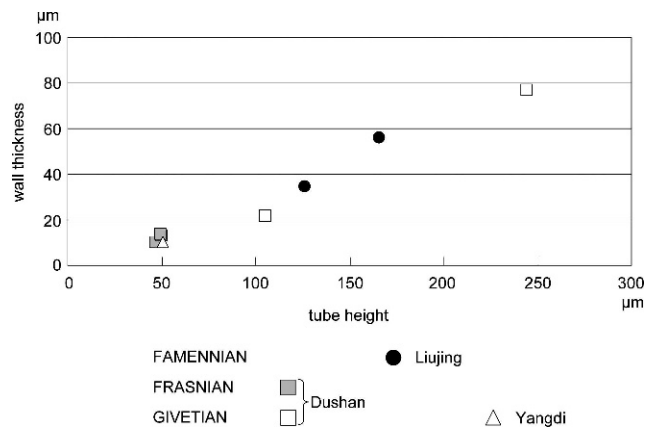

FIGURE 17—*Wetheredella* sp. size measurements.

Radionova, 1981) affinities have also been proposed. Riding (1991b, p. 72) considered *Wetheredella* to be a microproblematicum.

SECULAR ABUNDANCE

Abundance, diversity and facies distribution.—Our data from a broad spectrum of shallow normal marine Givetian-Frasnian-Famennian platform facies, including reefal and non-reefal, show that calcified microfossils commonly regarded as cyanobacteria and algae are present in all three stages but generally scarce as limestone-forming components. They declined significantly in abundance in the Famennian but retain their relative proportions with only minor changes (slight decrease in cyanobacteria and algae, slight increase in microproblematica) (Fig. 6). Cyanobacteria and algae declined in diversity from Frasnian to Famennian, whereas microproblematica increased. Individually, *Girvanella* is the most abundant taxon in each stage; but none of the three major groups recognized is generally abundant in any stage. Only a few genera locally approach rock-forming abundance, e.g., ?*Issinella* in bedded limestones, *Rothpletzella* in oncoids, and *Izhella* in reefs.

We found the three groups (algae, cyanobacteria, microproblematica) in 9 of the 110 Famennian horizons sampled; whereas they occurred in 39 of the 89 Frasnian and 13 of the 54 Givetian horizons. We observed no clear lithological and biotic differences between our Famennian samples and those of the Givetian and Frasnian that could account for this. We conclude that the observed decline in abundance of these groups in the Famennian is a real, rather than apparent, change.

Comparisons with previous studies.—Calcimicrobes, such as *Girvanella*, *Izhella*, *Rothpletzella*, and *Shuguria* (Copper, 2002, fig. 1, p. 37), are locally prominent components of oncoids, stromatolitic deposits and reefs in both the Frasnian and early Famennian (Chuvashov and Riding, 1984). They are generally well documented in the Frasnian from the Canning Basin (Wray, 1967; Playford et al., 1976; Webb, 1996, p. 953; George, 1999), Alberta (Mountjoy and Riding, 1981), and southern China (e.g., Shen et al., 2005, 2008), and from the early Famennian in the same areas (e.g., Playford, 1984; Wood, 2000; Stephens and Sumner, 2003; Whalen et al., 2002; Shen et al., 1997; Shen and Webb, 2004a, 2004b). However, it has proved difficult to establish whether they actually increased in absolute abundance from Frasnian to Famennian or simply were made more conspicuous by demise of metazoan reef-builders such as stromatoporoids and corals. Intra-

Frasnian extinctions are a complicating factor (Webb, 1996, p. 953; Playford et al., 2001). George and Chow (2002, p. 368) noted that in the Canning Basin, "major cyanobacterial reef-building had commenced in the latest Frasnian." In addition, it is likely that overall reef abundance changed. Webb (2002, p. 245) considered that "Famennian build-ups were not as numerous or widespread as their Frasnian precursors." These uncertainties may be reflected in differing assessments that have been made of algal-calcimicrobial abundance. For example, in the Urals Chuvashov et al. (1993, p. 115) reported decline in algae (sensu lato) from Frasnian to Famennian, followed by recovery as the Famennian progressed. In contrast, Copper (2002, p. 50) considered that calcimicrobes persisted and expanded from the Frasnian to Famennian. Similarly, compilation of global data by Flügel and Kiessling (2002, fig. 8) shows increase in the proportion of "microbes" in reefs from <20% in the Frasnian to 60% in the Famennian. The general pattern of decline in abundance of these taxa that we observe therefore differs from some previous reports, and tends to support the view of Chuvashov et al. (1993, p. 115). In addition, our trend in the overall abundance (rather than proportions) of calcified cyanobacteria (Fig. 6) is similar to that reported by Arp et al. (2001, fig. 3d) based on a broad literature review: increase from Givetian to Frasnian, followed by Famennian decline.

SIGNIFICANCE

These results suggest several questions. What factors may have reduced the overall abundance of these calcified microfossils in shallow marine carbonates from the Frasnian to the Famennian? At the same time, in the context of Frasnian-Famennian shallow marine diversity loss, what contributed to their continued survival, albeit at lower abundances? In addition, what is the significance of loss of diversity in algae and cyanobacteria, and increase in diversity among microproblematica?

Sampling.—It is possible that our samples represent reef facies in the Givetian and Frasnian more than in the Famennian. Reduction in reef abundance among our samples could account for reduction in abundance of reefal microproblematica. On the other hand, this would not seem to account for reduced abundance of calcified cyanobacteria since they occur in non-reefal as well as reefal facies.

Saturation state.—Frasnian increase and Famennian decline of calcified cyanobacteria (also observed in a global context by Arp et al., 2001, fig. 3d) could be related to carbonate saturation. This is thought to be a prime factor influencing cyanobacterial calcification (Riding, 1993; Kempe and Kazmierczak, 1994) and calculated estimates suggest high Frasnian values of seawater carbonate saturation followed by Famennian decline (Riding and Liang, 2005, fig. 5a). In contrast, Chen and Tucker (2003, p. 105) invoked "elevated alkalinity and nutrient levels" to account for "colonization and *in vivo* or *post mortem* calcification of these microbial organisms" in early Famennian reefs at Guilin and Liujing.

Frasnian-Famennian extinction.—There was general reduction in marine diversity during the Mid-Late Devonian, particularly near the end of the Frasnian (McGhee, 1988). Although the overall scale of late Frasnian changes can be regarded as modest (Bambach et al., 2004, p. 532) in comparison with other Phanerozoic mass extinctions (Raup and Sepkoski, 1982), their effect on reef organisms was profound (Droser et al., 2000, pp. 676–677). Major casualties included stromatoporoid sponges and tabulate corals, whose skeletons had dominated reef structures since the Ordovician

(Copper, 1994). The survival of reefal algae and cyanobacteria and associated microproblematica therefore needs to be considered in the context of this dramatic reduction in the metazoan reef community (Copper, 2002, p. 31).

Possible causes of Late Devonian extinctions continue to be debated. Among many possible factors (McGhee, 1988; Racki, 2005), widespread anoxia that at least locally affected the photic zone (Brown and Kenig, 2004), is commonly considered an important contributory factor (e.g., Murphy et al., 2000; Bond et al., 2004). Since late Frasnian extinctions were concentrated in shallow water organisms (McGhee, 1988), it has been suggested that "calcimicrobes may have persisted because many forms grew over large depth ranges … They were able to survive in deep water (i.e., more than about 50 m deep) during the crisis that extinguished most elements of the shallow-water communities. The surviving calcimicrobes could then recolonize shallow-water environments after the crisis had passed" (Playford et al., 2001). This is certainly true for cyanobacteria, which have a wide depth distribution due to their ability to photosynthesize over a considerable light range (Ting et al., 2002). In addition, they possess unusually broad ecological tolerance (Cohen and Gurevitz, 2006). Another difference of course is that algal and cyanobacterial physiology essentially relies on photosynthesis.

Thus, although algae and cyanobacteria declined in abundance, their relative ability to survive into the early Famennian could indicate that the conditions responsible for metazoan extinctions were concentrated in very shallow water that did not include the entire photic zone and/or to changes in food supply. In addition, "ability … to adopt different morphologies" "may have allowed microbial communities to colonize the shallow-water environments opportunistically" following Frasnian-Famennian mass extinction (Stephens and Sumner, 2003, p. 1300). It seems reasonable to conclude that the taxa that survived into the Famennian were more tolerant of environmental stress (Whalen et al., 2002, pp. 143–145), and more adaptable, than the organisms that were eliminated. However, further assessment of these possibilities is hindered by uncertainties concerning the affinities of many of the microproblematica, such as *Rothpletzella* and *Izhella*, which are prominent among the Famennian survivors.

DISASTER FORMS

Metazoan competition (Garrett, 1970) has been emphasized in late Proterozoic stromatolite decline (Awramik, 1971), but it remains likely that other factors, including seawater carbonate saturation (Fischer, 1965; Grotzinger, 1990), were also important. Nonetheless, competitive exclusion retains significance for stromatolite studies, for example in the concept of microbial carbonates as "disaster forms" in the Phanerozoic (Schubert and Bottjer, 1992). Simply expressed, this is the view that stromatolites and related microbial carbonates might be expected to undergo relatively short-lived, but nonetheless conspicuous, increase in mass extinction aftermaths; expanding as their metazoan competitors declined (Schubert and Bottjer, 1995).

Consideration of Famennian microbial carbonates disaster forms has centred on whether they increase in absolute abundance or simply appear more common in the absence of stromatoporoids and corals. At Canning Basin, George (1999, p. 493) emphasized the importance of stromatolites before as well as after the Frasnian-Famennian boundary. In addition, George and Chow (2002, p. 367) noted that "during the Frasnian stromatoporoids were not volumetrically dominant, and that microbial communities and early marine cementation

played significant roles in building the rigid reef margins (Playford, 1984; Kerans, 1985; Webb, 1996; Wood, 1998).'' Whalen et al. (2002, p. 146) suggested that early Famennian thrombolites, stromatolites and oncoids in Alberta could be ''disaster forms.'' Studying Famennian stromatolites at Shatang, Guilin, however, Shen and Webb (2004b, p. 80) noted (like George, 1999) that microbialites ''are common in a variety of settings throughout the Late Devonian'' and concluded that ''the degree to which the Shatang stromatolites represent disaster taxa is equivocal'' (Shen and Webb, 2004b, p. 82). At Guilin and Liujing, Chen and Tucker (2003, p. 107) recognized two stages of ''massive faunal decline'' near the Frasnian-Famennian transition, the first associated with sea-level fall and the second with sea-level fluctuations and anoxia. At the Frasnian-Famennian boundary, they noted ''the coincidence of onset and blooms of cyanobacterial colonies with the biotic crisis in normal-marine benthic habitats'' (Chen and Tucker, 2003, fig. 13). They concluded that ''initiation of cyanobacterial colonies on platform margin slopes and the onset of extensive fenestral limestones with abundant calcispheres on platforms'' suggested eutrophic conditions (Chen and Tucker, 2003, p. 107). Chow et al. (2004, p. 916) concluded from the Canning Basin that deep-water stromatolites in the latest Frasnian and earliest Famennian indicate ''elevated environmental stresses'' but are ''not disaster taxa.''

Quantitative data are required to resolve questions of relative abundance. Our South China data indicate Famennian decline in the abundance of calcified algae, cyanobacteria and calcimicrobes generally. This is in contrast to Flügel and Kiessling's (2002, fig. 8) data, although it is important to note that Flügel and Kiessling's (2002) data are for reef composition, whereas our samples are dominantly non-reefal. It would be useful to be able to compare our results with detailed studies of microbial taxa in non-reefal as well as reefal facies through the Frasnian-Famennian transition elsewhere.

AFFINITIES

Elucidating the affinities of Palaeozoic calcified algae and cyanobacteria has long been recognized as a challenging task (Riding, 1977; Babcock, 1986). It is greatly assisted by extant analogues. In this study, algae such as *Halysis* and *Vermiporella* and calcified cyanobacteria such as *Girvanella*, *Hedstroemia* and *Subtifloria*, can be compared with extant groups. But this cannot confidently be done for many of the remaining taxa encountered. We have preferred to regard these as microproblematica rather than to speculate about their likely systematic positions, even in cases where suggestions of affinity have commonly been made. *Garwoodia*, for example, has been considered as a green alga (e.g., Bourque et al., 1981), and *Izhella*, *Rothpletzella* and *Shuguria* have often been regarded as cyanobacteria (e.g., Copper, 2002, fig. 3, p. 43), but we consider these assignments to be sufficiently uncertain to warrant caution. These problematic taxa can technically be considered to be calcified microbes, in the sense that they are microscopic organisms. But this description can be misleading if microbes are regarded as synonymous with bacteria. Recognition of these taxa as microproblematica therefore reflects a need to refocus attention on their affinities. These taxa present differing problems. *Paraepiphyton*, for example, does closely resemble algae and/or cyanobacteria. On the other hand, the long-standing view that *Izhella*, like similar *Renalcis*, could be a cyanobacterium (Hofmann, 1975) remains unresolved (Stephens and Sumner, 2002). More intractable still, *Rothpletzella* and *Wetheredella* show no clear indication of either algal or cyanobacterial affinity. It serves

no useful purpose to ascribe affinity without confidence. A research priority is to resolve the nature of these organisms that can be important components of Frasnian and Famennian reefs, and whose survival of Late Frasnian events can help to understand the significant changes that took place then. Although individually small, several of these taxa created layered (e.g., *Rothpletzella*, *Wetheredella*) or dendritic (e.g., *Izhella*, *Paraepiphyton*, *Shuguria*) deposits that are major components of oncoids, stromatolites and reefs. Their significant continuation in these roles, despite reduction in overall abundance, in the Famennian, like that of bona fide algae and cyanobacteria, reflects their ability to withstand the conditions that strongly affected other reef organisms during the Frasnian-Famennian transition.

CONCLUSIONS

Calcified microfossils commonly regarded as algae and cyanobacteria are present throughout the Givetian-Famennian in samples of shallow normal marine non-reefal and reefal carbonates from four sections in three widely separated areas of Guangxi and southern Guizhou, although some age uncertainties remain. We recognize seventeen taxa: three algae, four cyanobacteria and ten microproblematica. Many of these fossils are widespread throughout the sections we studied. In general, they are not very common, although some taxa are occasionally locally abundant as bioclasts (e.g., ?*Issinella*), and in oncoids (e.g., *Rothpletzella*) and reefs (e.g., *Izhella*). Specifically, taxa more common in reefs and oncoids include *Bevocastria*, *Girvanella*, *Izhella*, *Paraepiphyton*, *Rothpletzella*, and *Wetheredella*; those more common in non-reef facies include *Halysis*, ''solenoporaceans'', *Vermiporella*, *Girvanella*, *Hedstroemia*, *Subtifloria*, and ?*Issinella*. *Subtifloria* is recognized here for the first time from the Late Devonian. *Halysis* too is at the top of its described range.

Taken as a whole, the three major groups (algae, cyanobacteria, microproblematica) increase by 34% from Givetian to Frasnian and decline by 63% in the Famennian, whereas the changes in their relative proportions are less marked (Figs. 3–6). The proportion of algae declines: 17% Givetian, 8% Frasnian, 6% Famennian; the proportion of microproblematica increases: 33% Givetian, 42% Frasnian, 50% Famennian; and the proportion of cyanobacteria declines: 50% Givetian, 50% Frasnian, 44% Famennian.

Substantial decline in overall abundance of all these calcified microbes in the Famennian does not support their recognition as disaster forms that increased in the immediate aftermath of Late Frasnian extinctions. Nonetheless, their survival into the Famennian does suggest that they were environmentally tolerant. Cyanobacteria may have occupied a greater depth range than metazoan reef-builders that suffered extinction, such as corals and stromatoporoid sponges, as suggested by Playford et al. (2001). An additional possibility is that algae and cyanobacteria were independent of changes in food supply that may have affected metazoans at this time. In addition, a number of the taxa recorded here may also have been able to adopt a variety of overall morphologies (Stephens and Sumner, 2003). However, the large proportion of problematic taxa present hinders assessment of the overall ecological significance of this change in abundance. Clarification of the affinities of these fossils is overdue.

REFERENCES

ADACHI, N., Y. EZAKI, AND J. W. PICKETT. 2007. Interrelations between framework-building and encrusting skeletal organisms and microbes: more refined growth history of Lower Devonian bindstones. Sedimentology, 54:89–105.

ANTROPOV, I. A. 1950. New species of foraminifers in the Upper Devonian of some regions of the eastern Russian Platform. Izvestiya Kazanskovo Filial, Akademii nauk SSSR, Geol. Inst. Izvestiya, Seriya Geologia, Kazan, 1:21–33, 3 pls. (In Russian)

ANTROPOV, I. A. 1955. Blue-green algae from the Devonian of the central region of the eastern Russian Platform. Uchenye zapiski Kazanskogo gosudarstvennogo universiteta imeni V.I. Ulyanova-Lenina, Trudy O-va Estestvoispytatelei, 115, 8:41–53, 2 pls.

ARP, G., A. REIMER, AND J. REITNER. 2001. Photosynthesis-induced biofilm calcification and calcium concentrations in Phanerozoic oceans. Science, 292:1701–1704.

AWRAMIK, S. M. 1971. Precambrian columnar stromatolite diversity: reflection of metazoan appearance. Science, 174:825–827.

BABCOCK, J. A. 1986. The puzzle of alga-like Problematica, or rummaging around in the algal wastebasket., p. 12–26. *In* A. Hoffman and M. H. Nitecki (eds.). Problematic fossil taxa. Oxford University Press, New York.

BAI, S. L., Z. Q. BAI, X. P. MA, D. R. WANG, AND Y. L. SUN. 1994. Devonian events and biostratigraphy of South China. Peking University Press, Beijing. 303 p. (In Chinese)

BAMBACH, R. K., A. H. KNOLL, AND S. C. WANG. 2004. Origination, extinction, and mass depletions of marine diversity. Paleobiology, 30:522–542.

BERGER, S. AND M. J. KAEVER. 1992. Dasycladales. An Illustrated Monograph of a Fascinating Algal Order. G. Thieme Verlag, Stuttgart, 247 p.

BIAN, L. AND Z. LIU. 1999. Discovery of Late Ordovician algal fossils of Oedogoniales in Jiangxi Province, China. Acta Palaeontologica Sinica, 38:46–49, 1 pl. (In Chinese, with English abstract)

BOGUSH, O. I., R. M. IVANOVA, AND V. A. LUCHININA. 1990. Izvestkovye vodorosli verkhnego famena i nizhnego karbona Urala i Sibiri. Trudy IGIG SO AN SSSR (Nauka, Novosibirsk), 745:1–160, 32 pls.

BOND, D., P. B. WIGNALL, AND G. RACKI. 2004. Extent and duration of marine anoxia during the Frasnian-Famennian (Late Devonian mass extinction in Poland, Germany, Austria and France. Geological Magazine, 141:173–193.

BORZI, A. 1895. Studi algologici. Saggio di recherché sulla biologia delle alghe. A. Reber, Palermo. Fasc., 2 pp. i–vii, 119–378, pls. 10–31.

BOURQUE, P. A., B. MAMET, AND A. ROUX. 1981. Algues calcaires siluriennes du Synclinorium de la Baie des Chaleurs, Québec, Canada. Revue de Micropaléontologie, 24: 83–126.

BROOKE, C. A. AND R. RIDING. 1998. Ordovician and Silurian coralline red algae. Lethaia, 31:185–195.

BROWN, T. C. AND F. KENIG. 2004. Water column structure during deposition of Middle Devonian-Lower Mississippian black and green/gray shales of the Illinois and Michigan basins: a biomarker approach. Palaeogeography, Palaeoclimatology, Palaeoecology, 215:59–85.

CHEN, D. AND M. E. TUCKER. 2003. The Frasnian-Famennian mass extinction: insights from high-resolution sequence stratigraphy and cyclostratigraphy in South China. Palaeogeography, Palaeoclimatology, Palaeoecology, 193:87–111.

CHEN, D.Z., Q. Y. CHEN, AND M. S. JIANG. 1995. Carbon isotopic compositions and evolution in the Devonian marine carbonate rocks. Lithofacies Paleogeography, Chengdu, 15:22–28. (In Chinese, with English abstract)

CHEN, D. Z., M. E. TUCKER, J. Q. ZHU, AND M. S. JIANG. 2002. Carbonate platform evolution: from a bioconstructed platform margin to a sand-shoal system (Devonian, Guilin, South China). Sedimentology, 49:737–764.

CHOW, N., A. D. GEORGE, AND K. M. TRINAJSTIC. 2004. Tectonic control on development of a Frasnian-Famennian (Late Devonian) palaeokarst surface, Canning Basin reef complexes, northwestern Australia. Australian Journal of Earth Sciences, 51:911–917.

CHUVASHOV, B. AND R. RIDING. 1984. Principal floras of Palaeozoic marine calcareous algae. Palaeontology, 27:487–500.

CHUVASHOV, B. I., V. A. LUCHININA, V. P. SHUYSKY, I. M. SHAYKIN, O. I. BERCHENKO, A. A. ISHCHENKO, V. D. SALTOVSKAYA, AND D. I. SHIRSHOVA. 1987. Iskopaemye izvestkovye vodorosli (morfologiya, sistematika, metody izucheniya). Trudy Institutom Geologii i Geofizikii, Sibirskoy Otdeleniya, Akademii Nauk SSSR, Novosibirsk, 674:1–225.

CHUVASHOV, B. J., V. P. SHUYSKY, AND R. M. IVANOVA. 1993. Stratigraphical and facies complexes of the Paleozoic calcareous algae of the Urals. *In* F. Barattolo, P. De Castro, and M. Parente (eds.). Studies on fossil benthic algae. Boll. Soc. Paleont. Ital., Special Volume, 1:93–119.

COHEN, Y. AND M. GUREVITZ. 2006. The Cyanobacteria–ecology, physiology and molecular genetics, p. 1074–1098. *In* M. Dworkin, et al. (eds.). The Prokaryotes, volume 4: bacteria: firmicutes, cyanobacteria. Springer, New York.

COPPER, P. 1976. The cyanophyte *Wetheredella* in Ordovician reefs and off-reef sediments. Lethaia, 9:273–281.

COPPER, P. 1994. Ancient reef ecosystem expansion and collapse. Coral Reefs, 13:3–11.

COPPER, P. 2002. Reef development at the Frasnian/Famennian mass extinction. Palaeogeography, Palaeoclimatology, Palaeoecology, 181:27–65.

DING, W. J. 1947. Geological Research Report 191321930. Central Geological Research Bureau, Beijing. (In Chinese)

DROSER, M. L., D. J. BOTTJER, P. M. SHEEHAN, AND G. R. MCGHEE. 2000. Decoupling of taxonomic and ecologic severity of Phanerozoic marine mass extinctions. Geology, 28:675–678.

DYBOWSKI, W. 1877. Die Chaetetiden der ostbaltischen Silur-Formation. Russisch-Kaiserliche Mineralogische Gesellschaft zu St. Petersburg Verhandlungen, Series 2, 14(1878):1–134, pls 1–4.

ELIAS, M. K. 1950. Paleozoic *Ptychocladia* and related Foraminifera. Journal of Paleontology, 24:287–306.

FENTON, C. L. 1943. A new Devonian alga from Western Australia. American Midland Naturalist, 30:112.

FISCHER, A. G. 1965. Fossils, early life, and atmospheric history. Proceedings of the National Academy of Sciences, USA, 53:1205–1215.

FLÜGEL, E. AND W. KIESSLING. 2002. Patterns of Phanerozoic reef crises, p. 691–733. *In* W. Kiessling, E. Flügel, and J. Golonka (eds.). Phanerozoic reef patterns. SEPM Special Publication 72.

FOSLIE, M. 1909. Algologisker notiser, VI. Det Kongelige Norske Videnskabers Selskabs Skrifter, 1909, (2):1–63.

FOURNIE, D. 1967. Les Porostromata du Paleozoïque. Etude bibliographique. Bulletin du Centre de Recherches, Pau-SNPA, 1(1):21–41.

GAO, L. D. 1981. Late Devonian and early Carboniferous miospore zones from southeastern Guizhou and the boundary of the Devonian. Geology of Guizhou, Guiyang, 8:59–69. (In Chinese, with English abstract)

GARRETT, P. 1970. Phanerozoic stromatolites: noncompetetive ecologic restriction by grazing and burrowing animals. Science, 169:171–173.

GARWOOD, E. J. 1931. The Tuedian beds of northern Cumberland and Roxburghshire east of the Liddel Water. Quarterly Journal of the Geological Society of London, 87(1):97–157, pls 7–16.

GEORGE, A. D. 1999. Deep-water stromatolites, Canning Basin, northwestern Australia. Palaios, 14:493–505.

GEORGE, A. D. AND N. CHOW. 2002. The depositional record of the Frasnian/Famennian boundary interval in a fore-reef succession, Canning Basin, Western Australia. Palaeogeography, Palaeoclimatology, Palaeoecology, 181:347–374.

GONG, Y., B. LI, Y. SI, AND Y. WU. 2002. Late Devonian red tides and mass extinction. Chinese Science Bulletin, 47:1138–1144.

GONG, Y. M., R. XU, Z. D. TANG, Y. L. SI, AND B. H. LI. 2005. The Upper Devonian orbital cyclostratigraphy and numerical dating conodont zones from Guangxi, South China. Science in China, Series D Earth Sciences, 48:32–41.

GROTZINGER, J. P. 1990. Geochemical model for Proterozoic stromatolite decline. American Journal of Science, 290-A:80–103.

GUIZHOU BUREAU OF GEOLOGY AND MINERAL RESOURCES. 1987. Regional geology of Guizhou Province. Beijing Geological Publishing House, Beijing. (In Chinese, with English abstract)

HØEG, O. E. 1932. Ordovician algae from the Trondheim area. Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo I Matematisk-naturvidenskapelig Klasse, 4:63–96, pls 1–11.

HOFMANN, H. J. 1975. Stratiform Precambrian stromatolites, Belcher Islands, Canada: relations between silicified microfossils and microstructure. American Journal of Science, 275:1121–1132.

ISCHENKO, A. A. AND E. P. RADIONOVA. 1981. On the morphological characteristics and systematic position of Wetheredella Wood, 1948.

Questions of Micropalaeontology, 24:140–151. Academy of Science of the USSR. (In Russian)

JI, Q., 1989a. On the Frasnian-Famennian mass extinction event in South China. Courier Forschungsinstitut Senckenberg, 117:275–301.

JI, Q., 1989b. On the Frasnian conodont biostratigraphy in the Guilin area of Guangxi, South China. Courier Forschungsinstitut Senckenberg, 117:303–319.

JI, Q., 1994. On the Frasnian-Famennian extinction event in South China as viewed in the light of conodont study. Professional papers of stratigraphy and palaeontology, 24:79–107, Geological Publishing House, Beijing. (In Chinese)

JIANG, D. Y., G. DING, AND S. L. BAI. 2000. Conodont Biostratigraphy across the Givetian-Frasnian Boundary (Devonian) of Liujing, Change this to: Guangxi. Journal of Stratigraphy, Nanjing, 24:195–200. (In Chinese, with English abstract)

JOHNSON, H. M. 1966. Silurian Girvanella from the Welsh Borderland. Palaeontology, 9:48–63, pls. 6–12.

JOHNSON, J. H. 1961. Review of Ordovician algae. Colorado School of Mines Quarterly, 56(2):v–vii, 1–101.

JOHNSON, J. H. 1964. Lower Devonian algae and encrusting Foraminifera from New South Wales. Journal of Paleontology, 38:98–108.

JOHNSON, J. H. AND K. KONISHI. 1959. A review of Silurian (Gotlandian) algae. Colorado School of Mines Quarterly, 54(1):1–114.

KAH, L. C. AND R. RIDING. 2007. Mesoproterozoic carbon dioxide levels inferred from calcified cyanobacteria. Geology, 35:799–802.

KEMPE, S. AND J. KAZMIERCZAK. 1994. The role of alkalinity in the evolution of ocean chemistry, organization of living systems, and biocalcification processes. Bulletin de la Institut Océanographique (Monaco), 13:61–117.

KERANS, C. 1985. Petrology of Devonian and Carboniferous carbonates of the Canning and Bonaparte basins. Western Australian Mining and Petroleum Research Institute Report, 12, 302 pp. Unpublished.

KERSHAW, S., T. ZHANG, AND G. LAN. 1999. A microbialite crust at the Permian-Triassic boundary in south China, and its palaeoenvironmental significance. Palaeogeography, Palaeoclimatology, Palaeoecology, 146:1–18.

KORDE, K. B. 1950. On the morphology of the Dasycladaceae of the northern Urals. Doklady Akademii nauk SSSR, 73(3):569–571. (In Russian)

KORDE, K. B. 1973. Vodorosli kembriya (Cambrian algae). Academy of Sciences of the U.S.S.R., Transactions of the Palaeontological Institute, 139:1–350, Nauka, Moscow.

KOZLOWSKI, R. AND J. KAZMIERCZAK. 1968. On two Ordovician calcareous algae. Acta Palaeontologica Polonica, 13:325–346, 11 pls.

KUANG, G. D., M. T. ZHAO, Y. B. TAO, Y. B. SU, S. T. WANG, AND Y. Q. HUANG. 1989. The Standard Devonian Section of China: Liujing Section of Guangxi. China University of Geosciences Press, Wuhan, p. 1–145. (In Chinese with an English summary)

LEWIS, L. A. AND R. M. MCCOURT. 2004. Green algae and the origin of land plants. American Journal of Botany, 91:1535–1556.

LI, X. AND G. X. LIU. 2002. Structural characteristics of Devonian cover in Liujing, Guangxi. Guangxi Geology, 15:7–10. Nanning. (In Chinese, with English abstract)

LI, Z. L. AND C. Y. WANG. 1991. New geological time evidence of Guilin Formation. Journal of Stratigraphy, Nanjing, 15:153–154. (In Chinese)

LIAO, W. H. 2002. Biotic recovery from the Late Devonian F-F mass extinction event in China. Science in China Series D, Earth Sciences, 45:380–384.

LIAO, W. H. 2003. Devonian biostratigraphy of Dushan, Southern Guizhou and its coral extinction events. Acta Palaeontologica Sinica, Nanjing, 42(3):417–427. (In Chinese, with English abstract)

MA, X. P., C. Y. WANG, G. RACKI, AND M. RACKA. 2008. Facies and geochemistry across the Early-Middle Frasnian transition (Late Devonian) on South China carbonate shelf: comparison with the Polish reference succession. Palaeogeography, Palaeoclimatology, Palaeoecology, 269: 130–151.

MAMET, B. AND A. ROUX. 1975a. Jansaella ridingii, nouveau genre d'Algue? dans le Devonien de l'Alberta. Canadian Journal of Earth Sciences, 12:1480–1484.

MAMET, B. AND A. ROUX. 1975b. Algues dévoniennes et carbonifères de la Téthys occidentale (troisième partie). Revue de micropaléontologie, 18:134–187.

MAMET, B., A. ROUX, M. LAPOINTE, AND L. GAUTHIER. 1992. Algues ordoviciennes et siluriennes de l'Ile d'Anticosti (Québec, Canada). Revue de Micropaléontologie, 35:211–248.

MAMET, B. AND E. VILLA. 1995. A revision of the dasycladale alga Uraloporella (Chlorophycophyta, Upper Paleozoic, Asturias, Spain). Revista Española de Paleontología, No. homenaje a Guillermo Colom: 48–54.

MASLOV, V. P. 1956. Iskopaemye izvestkovye vodorosli SSSR. Trudy Instituta geologicheskikh nauk, 160:1–302. Akademii nauk SSSR, Moscow.

MATTOX, K. R. AND K. D. STEWART. 1984. Classification of the green algae: a concept based on comparative cytology, p. 29–72. In D. E. G. Irvine and D. M. John (eds.). The systematics of green algae. Academic Press, London.

MAY, A. 1992. Die Kalkalgen-Flora des Ober-Eifeliums und Unter-Givetiums (Devon) des nordwestlichen Sauerlandes (Rhieisches Schiefergebirge). Palaeontographica B, 228:1–28, 5 pls.

MCGHEE, G. R., JR. 1988. The Late Devonian extinction event: evidence for abrupt ecosystem collapse. Paleobiology, 14:250–257.

MIRETSKAYA, N. M. 1988. Calcareous algae and palaeobiocoenoses of the Mamontov Stage of the Middle Devonian in Salair, p. 93–97, pl. 33. In V. N. Dubatolov and T. A. Moskalenko (eds.). Calcareous algae and stromatolites; systematics, biostratigraphy, facies analysis. USSR Academy of Sciences, Siberian Branch, Institute of Geology and Geophysics, Novosibirsk, "Nauka." (In Russian)

MOUNTJOY, E. W. AND R. RIDING. 1981. Foreslope stromatoporoid-renalcid bioherm with evidence of early cementation, Devonian Ancient Wall reef complex, Rocky Mountains. Sedimentology, 28:299–319.

MURPHY, A. E., B. B. SAGEMAN, AND D. J. HOLLANDER. 2000. Eutrophication by decoupling of the marine biogeochemical cycles of C, N, and P: a mechanism for the Late Devonian mass extinction. Geology, 28:427–430.

NICHOLSON, H. A. AND R. ETHERIDGE, JR. 1878. A monograph of the Silurian fossils of the Girvan District in Ayrshire with special reference to those contained in the "Gray Collection." Vol. I, Fasciculus 1 (Rhizopoda, Actinozoa, Trilobita). W. Blackwood and Sons, Edinburgh, 135 pp.

PHILIPPI, R. 1837. Beweis dass die Nulliporen Pflanzen sind. Archiven der Naturgesellschaft, 3:387–393, pl. 9, figs. 2–6.

PLAYFORD, P. E. 1984. Platform-margin and marginal-slope relationships in Devonian reef complexes of the Canning Basin, p. 189–214. In P. G. Purcell (ed.). The Canning Basin, WA. Proceedings of the Geological Society of Australia/Petroleum Exploration Society of Australia Symposium, Perth.

PLAYFORD, P. E., A. E. COCKBAIN, E. C. DRUCE, AND J. L. WRAY. 1976. Devonian stromatolites from the Canning Basin, Western Australia, p. 543–563. In M. R. Walter (ed.). Stromatolites. Developments in Sedimentology 20, Elsevier, Amsterdam.

PLAYFORD, P. E., A. E. COCKBAIN, R. M. HOCKING, AND M. W. WALLACE. 2001. Novel paleoecology of a postextinction reef: Famennian (Late Devonian) of the Canning Basin, northwestern Australia: comment. Geology, 29:1155–1116.

PRATT, B. R. 1984. Epiphyton and Renalcis - diagenetic microfossils from calcification of coccoid blue-green algae. Journal of Sedimentary Petrology, 54:948–971.

RABENHORST, L. 1863. Kryptogamen-Flora von Sachsen, der Ober-Lausitz, Thuringen und Nordbohmen. Abteilung I. E. Krummer, Leipzig, 653 p.

RACKI, G. 2005. Towards understanding Late Devonian global events: few answers, many questions, p. 199–224. In J. Over, J. Morrow, and P. B. Wignall (eds.). Understanding Late Devonian and Permian-Triassic biotic and climatic events: towards an integrated approach. Developments in Paleontology and stratigraphy 20. Elsevier, Amsterdam.

RAUP, D. M. AND J. J. SEPKOSKI, JR. 1982. Mass extinctions in the marine fossil record. Science, 215:1501–1503.

REITLINGER, E. A. 1954. Devonian foraminifers from some sections of the eastern part of the Russian Platform. Trudy Vsesoyuznogo Neftyanogo Nauchno-Issledovatel'skogo Geologo-Razvedochnogo Instituta (VNIGRI), Paleontol., sbornik, 1:52–81, pls. 17–22. (In Russian)

RIDING, R. 1977. Calcified Plectonema (blue-green algae), a recent example of Girvanella from Aldabra Atoll. Palaeontology, 20:33–46.

RIDING, R. 1991a. Cambrian calcareous cyanobacteria and algae, p. 305–334. In R. Riding (ed.). Calcareous algae and stromatolites. Springer-Verlag, Berlin.

RIDING, R. 1991b. Calcified cyanobacteria, p. 55–87. In R. Riding (ed.). Calcareous algae and stromatolites. Springer-Verlag, Berlin.

RIDING, R. 1993. Phanerozoic patterns of marine CaCO3 precipitation. Naturwissenschaften, 80:513–516.

RIDING, R. 2006. Microbial carbonate abundance compared with fluctuations in metazoan diversity over geological time. Sedimentary Geology, 185:229–238.

RIDING, R. AND J. C. BRAGA. 2005. Halysis Høeg, 1932—an Ordovician coralline red alga? Journal of Paleontology, 79:835–841.

RIDING, R. AND J. FAN. 2001. Ordovician calcified algae and cyanobacteria, northern Tarim Basin subsurface, China. Palaeontology, 44:783–810.

RIDING, R. AND L. F. JANSA. 1974. *Uraloporella* Korde in the Devonian of Alberta. Canadian Journal of Earth Sciences, 11:1414–1426.

RIDING, R. AND L. LIANG. 2005. Geobiology of microbial carbonates: metazoan and seawater saturation state influences on secular trends during the Phanerozoic. Palaeogeography, Palaeoclimatology, Palaeoecology, 219: 01–115.

RIDING, R. AND C. M. SOJA. 1993. Silurian calcareous algae, Cyanobacteria, and Microproblematica from the Alexander terrane, Alaska. Journal of Paleontology, 67:710–728.

RIDING, R. AND L. VORONOVA. 1985. Morphological groups and series in Cambrian calcareous algae, p. 56–78. *In* D. F. Toomey and M. H. Nitecki (eds.). Paleoalgology: contemporary research and applications. Springer, Berlin.

RIDING, R. AND N. WATTS. 1981. Silurian algal reef crest in Gotland. Naturwissenschaften, 68:91–92.

RIDING, R. AND J. L. WRAY. 1972. Note on the ?algal genera *Epiphyton*, *Paraepiphyton*, *Tharama*, and *Chabakovia*. Journal of Paleontology, 46:918–919.

ROTHPLETZ, A. 1908. Ueber Algen und Hydrozoen im Silur von Gotland und Oesel. Kungl. Svenska Vetenskapsakademiens Handlingar, 43(5), 25 p., 6 pls.

ROTHPLETZ, A. 1913. Die Kalkalgen, Spongiostromen und einige andere Fossilien aus dem Obersilur Gottlands. Sveriges Geologiska Undersökning Ca, 10, 57 p., 10 pls, map.

SCHUBERT, J. K. AND D. J. BOTTJER. 1992. Early Triassic stromatolites as post-mass extinction disaster forms. Geology, 20:883–886.

SCHUBERT, J. K. AND D. J. BOTTJER. 1995. Aftermath of the Permian–Triassic mass extinction event; paleoecology of Lower Triassic carbonates in the western USA. Palaeogeography, Palaeoclimatology, Palaeoecology, 116:1–39.

SHEEHAN, P. M. AND M. T. HARRIS. 2004. Microbialite resurgence after the Late Ordovician extinction. Nature, 430:75–78.

SHEN, J. W. AND G. E. WEBB. 2004a. Famennian (Upper Devonian) calcimicrobial (*Renalcis*) reef at Miaomen, Guilin, Guangxi, South China. Palaeogeography, Palaeoclimatology, Palaeoecology, 204:373–394.

SHEN, J. W. AND G. E. WEBB. 2004b. Famennian (Upper Devonian) stromatolite reefs at Shatang, Guilin, Guangxi, South China. Sedimentary Geology, 170:63–84.

SHEN, J. W. AND C. M. YU. 1996. Stratigraphic boundaries on Devonian carbonate platform and reef complexes in Guilin, Guangxi. Journal of Stratigraphy, Nanjing, 20:1–8. (In Chinese, with English abstract)

SHEN, J. W., C. M. YU, AND H. M. BAO. 1997. A Late Devonian (Famennian) *Renalcis-Epiphyton* reef at Zhaijiang, Guilin, South China. Facies, 37:195–210.

SHEN, J. W. AND S. L. ZHANG. 1994. Evolution of the Devonian carbonate platform in Guilin, China. Sedimentary Facies and Palaeogeography, Chengdu, 14:1–10. (In Chinese, with English abstract)

SHEN, J. W., J. B. TENG, AND K. PEDOJA. 2005. Middle and Late Devonian microbial carbonates, reefs and mounds in Guilin, South China and their sequence stratigraphic, paleoenvironmental and paleoclimatic significance. Science in China, Series D, Earth Sciences, 48:1900–1912.

SHEN, J. W., G. E. WEBB, AND J. S. JELL. 2008. Platform margins, reef facies, and microbial carbonates; a comparison of Devonian reef complexes in the Canning Basin, Western Australia, and the Guilin region, South China. Earth Science Reviews, 88:33–59.

SILVA, P. C. AND H. W. JOHANSEN. 1986. A reappraisal of the order Corallinales (Rhodophyta). British Phycological Journal, 21:245–254.

STEPHENS, N. P. AND D. Y. SUMNER. 2002. Renalcids as fossilized biofilm clusters. Palaios, 17:225–236.

STEPHENS, N. P. AND D. Y. SUMNER. 2003. Famennian microbial reef facies, Napier and Oscar ranges, Canning Basin, Western Australia. Sedimentology, 50:1283–1302.

STOLLEY, E. 1893. Ueber silurische Siphoneen. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, 1893(2):135–146, pls 7, 8.

TAO, Y. B., G. D. KUANG, AND M. T. ZHAO, 1986. A comprehensive paleoecologic study on paleobiocoenosis of Devonian in Liujing, Guangxi. Geology of Guangxi, Nanning, 1:45–52. (In Chinese, with English abstract)

TAPPAN, H. 1980. The paleobiology of plant protists. Freeman, San Francisco, USA, 1028 p.

TING, C. S., G. ROCAP, J. KING, AND S. W. CHISHOLM. 2002. Cyanobacterial photosynthesis in the oceans: the origins and significance of divergent light-harvesting strategies. Trends in Microbiology, 10:134–142.

TSIEN, H. H., H. F. HOU, W. L. ZHOU, Y. WU, D. W. YIN, Q. Y. DAI, AND W. J. LIU. 1988. Devonian reef development and paleogeographic evolution in South China, p. 619–633. *In* N. J. McMillan, A. F. Embry,

and D. J. Glass (eds.). Devonian of the world. Canadian Society of Petroleum Geologists Memoir 14, volume 1.

VOLOGDIN, A. G. 1939. Arkheotsiaty i vodorosli srednego kembriya Yuzhnogo Urala. Problemy paleontologii, 5:210–245, Moscow University Publishing House, Moscow.

WANG, K. L. 1987. On the Devonian-Carboniferous boundary based on foraminiferal fauna from South China. Acta Palaeontologica Sinica, Nanjing, 4:161–173. (In Chinese, with English abstract)

WANG, Y. 2001. On outcrop sequence stratigraphy and sea level changes of Devonian in Dushan, South Guizhou. Guizhou Geology, Guiyang, 18:154–162. (In Chinese, with English abstract)

WANG, Y. 2004. Some trace fossils after the Frasnian-Famennian extinction in the Dushan area, southern Guizhou Province, China. Acta Palaeontologica Sinica, 43:132–141 (In Chinese, English abstract).

WANG, Y. AND H. D. CHEN. 1999. New data on the Frasnian-Famennian event boundary in the Dushan area, South Guizhou. Journal of Stratigraphy, Nanjing, 23:26–30. (In Chinese, with English abstract)

WANG, Y. AND X. L. WANG. 1996. Trace fossils near Devonian-Carboniferous boundary section in Dushan, Guizhou. Journal of Stratigraphy, Nanjing, 20:285–290. (In Chinese with English abstract)

WANG, Y., J. W. SHEN, AND Z. C. ZHOU. 1997. Ichnofacies and sequence stratigraphy of the lower-middle Devonian in Dushan county, southern Guizhou. Acta Micropalaeontologica Sinica, Nanjing, 13:203–213. (In Chinese, with English abstract)

WANG, Y., X. L. WANG, AND X. Y. SHI. 2006. Pioneer organisms after F-F mass extinction in Dushan region, Guizhou Province, and their significance in establishing new ecosystem. Science in China, Series D, Earth Sciences, 49:449–460.

WEBB, G. E. 1996. Was Phanerozoic reef history controlled by the distribution of non-enzymatically secreted reef carbonates (microbial carbonate and biologically induced cement)? Sedimentology, 43:947–971.

WEBB, G. E. 2002. Latest Devonian and Earl Carboniferous reefs: depressed reef building after the middle Paleozoic collapse, p. 239–269. *In* W. Kiessling, E. Flügel, and J. Golonka (eds.). Phanerozoic reef patterns, SEPM Special Publication 72.

WETHERED, E. 1886. On the structure and organisms of the Lower Limestone Shales, Carboniferous Limestone and Upper Limestones of the Forest of Dean. Geological Magazine New Series, Decade 3, Volume 3:529–540, 2 pls.

WETHERED, E. 1887. *Mitcheldeania* Nicholsoni. A new genus, from the Lower Carboniferous Shales of the Forest of Dean. Proceedings of the Cotteswold Naturalists Club, 9:77.

WETHERED, E. 1893. On the microscopic structure of the Wenlock Limestone, with remarks on the formation generally. Quarterly Journal of the Geological Society, London, 49:236–248.

WETTSTEIN, R. R. 1901. Handbuch der systematischen Botanik, Vol. 1. Deuticke, Leipzig, 201 p.

WHALEN, M. T., J. DAY, G. P. EBERLI, AND P. W. HOMEWOOD. 2002. Microbial carbonates as indicators of environmental change and biotic crises in carbonate systems: examples from the Late Devonian, Alberta basin, Canada. Palaeogeography, Palaeoclimatology, Palaeoecology, 181:127–151.

WOOD, A. 1941. The Lower Carboniferous calcareous algae *Mitcheldeania* Wethered and *Garwoodia*, gen. nov. Proceedings of the Geologists' Association, 52:216–226.

WOOD, A. 1948. "Sphaerocodium," a misinterpreted fossil from the Wenlock Limestone. Proceedings of the Geologists' Association, 59:9–22, pls. 2–5.

WOOD, A. 1964. A new dasycladacean alga, *Nanopora*, from the Lower Carboniferous of England and Kazakhstan. Palaeontology, 7:181–185.

WOOD, R. 1998. Novel reef fabrics of the Devonian Canning Basin, Western Australia. Sedimentary Geology, 121:149–156.

WOOD, R. 2000. Novel paleoecology of a postextinction reef: Famennian (Late Devonian) of the Canning Basin, northwestern Australia. Geology, 28:987–990.

WRAY, J. L. 1967. Upper Devonian calcareous algae from the Canning Basin, Western Australia. Professional Contributions of the Colorado School of Mines 3, 76 p.

WU, Y. 1997. The establishment of the system, series and stage boundaries and correlation of biostratigraphic and chronostratigraphic boundaries in the Devonian strata in South China. Lithofacies Palaeogeography, Beijing, 17:29–39. (In Chinese, with English abstract)

WU, Y., Y. M. GONG, AND D. Q. LI. 1994. Correlation of sequence stratigraphy to lithostratigraphy and chronostratigraphy of Devonian in South China. Earth Science Journal of China Universiity of Geoscienoes, Wuhan, 19:565–574. (In Chinese, with English abstract)

XU, B., Z. Y. GU, B. HU, AND Z. L. LI. 2004. The pattern of variations in carbon isotope of the Frasnian-Famennian limestone sequences in

Guangxi, Southern China. Acta Sedimentologica Sinica, Lanzhou, 22: 603–608. (In Chinese, with English abstract)

XU, R., Y. M. GONG, AND Z. D. TANG. 2006. Blooming of bacteria and algae: possible killer of Devonian Frasnian-Famennian Mass Extinction? Earth Science Journal of China University of Geosciences, Wuhan, 31:787–797. (In Chinese, with English abstract)

ZHANG, Z., Y. S. DU, Y. M. GONG, H. W. HUANG, X. W. ZENG, S. S. LI, AND Y. K. OU. 2007. Transformation from Devonian Givetian carbonate platform to Famennian bacteria-algae ecosystem in Litang isolated platform, Guangxi, and its significance. Earth Science Journal of China University of Geosciences, Wuhan, 32:811–818. (In Chinese, with English abstract)

ZHAO, X., M. B. ALLEN, A. G. WHITHAM, AND S. P. PRICE. 1996. Rift-related Devonian sedimentation and basin development in South China. Journal of Southeast Asian Earth Sciences, 14:37–52.

ZHONG, K., Y. WU, AND B. A. YIN. 1992. Devonian of Guangxi. China University of Geosciences Press, Wuhan, 384 p. (In Chinese)