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 microprolum. Algae: Halysis, ‘solenoporaceans’, Vermiporella. Cyanobacteria: Bevocastria, Girvanella, Hedstroemia, Subtifloria. Microprolum: ?Chabakovia, Garwoodia, ?Issinella, Ishella, Paraepiphyton, Rothpletzella, Shuguria, ?Stenophycus, Tharama, Wetheredella. As a whole, the abundance of algae, cyanobacteria and microprolum 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 mass extinction events, 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 they 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, microprolum) show changes in their relative proportions through the transition. From Givetian to Famennian the proportions of algae and cyanobacteria decrease and the proportion of microprolum 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 northern

J. Paleont., 84(4), 2010, pp. 569–587
Copyright © 2010, The Paleontological Society
0022-3360/10/0084-0569$03.00
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, Hejiuzhai, 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. 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 Gelaohé 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 conformity 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 Gelaohé 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 Formation 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 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
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 Formation (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
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 (Halysts, “solenoporaceans,” Vermiporella), and microproblematica (?Chabakovia, Garwoodia, ?Issinella, Izhella, Parampephyton, Rothpletzella, Shuguria, ?Stenophycus, Tharama, Wetherdella).

**Stage distribution.**—These major groups—algae, cyanobacteria, 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 3](image3) Raw occurrence data. The total number of horizons in each stage in which each taxon was recorded, showing both definite and uncertain identifications.

![Figure 4](image4) 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.

![Figure 5](image5) 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).
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 Subtilloria, 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 PALAEOBIOLOGY**

**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 Middle 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
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 spongiodes* 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 CALCIFIED THALLUS, BROAD CENTRAL CAVITY, THIN WALL PIERCED BY SIMPLE NUMEROUS CLOSERLY 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 Schieferrgebirge. 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 micromorphological 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 Ulotruchales (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, THIN WALL, MICRICRIC.

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 oncoidal 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 Gasperiella, in ‘nodular codiaceans’ (Bourque et al., 1981, fig. 5; Mamet et al., 1992, p. 218). Nonetheless, Hedstroemia and Ortonella are better compared with rivulariaceous 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, SINUOUS TO IRREGULARLY TANGLED, WALL THIN, MICRICRIC.

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).
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,
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 epipelagic, 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). *Subtifloria 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*.

**MICROPOROBLEMATICA**

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 *Ludlowia* Kordé, 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.

**Figure 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 oncocid 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 *Gaspeissiella* could be regarded as “nodular
ciodaeans.” 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 Lujaizhai 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 sinusoidal calcareous tubes, 1–2 mm 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 reeval 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...
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

Type species.

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

SECCAL 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 microp problematica) (Fig. 6). Cyanobacteria and algae declined in diversity from Frasnian to Famennian, whereas microp problematica 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 Izella 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, Izella, 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. Intrat-
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 Kiesling (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 oncocids 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 Halyysis 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. Paraeoepiphyton, 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, Paraeoepiphyton, Shuguria) deposits that are major components of oncocids, 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 reeval 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 oncocids (e.g., Rothpletzella) and reefs (e.g., Izhella). Specifically, taxa more common in reefs and oncocids include Bevocastra, Girvanella, Izhella, Paraeoepiphyton, Rothpletzella, and Wetheredella; those more common in non-reef facies include Halyysis, "solenoporaceans", Vermiporella, Girvanella, Hedstroemia, Subtifloria, and ?Issinella. Subtifloria is recognized here for the first time from the Late Devonian. Halyysis 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.

ACKNOWLEDGMENTS

We thank Journal of Paleontology reviewers Bernard Mamet and Michael Whalen, and editor Brian Pratt, for thoughtful and very helpful suggestions that improved this
REFERENCES


BOGUSH, O. I., R. M. I VANOVA, AND V. A. L UCHININA. 1990. Izvestkovye material. Fan Wei and Yibu Wu were stalwart field assistants.

BOGUSH, O. I., R. M. I VANOVA, AND V. A. L UCHININA. 1990. Izvestkovye material. Fan Wei and Yibu Wu were stalwart field assistants.

BOGUSH, O. I., R. M. I VANOVA, AND V. A. L UCHININA. 1990. Izvestkovye material. Fan Wei and Yibu Wu were stalwart field assistants.

VOGUS, O. I., R. M. I VANOVA, AND V. A. L UCHININA. 1990. Izvestkovye material. Fan Wei and Yibu Wu were stalwart field assistants.


ACCEPTED 20 MARCH 2010