Succession of coral associations during a Givetian transgressive-regressive cycle in Queensland

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The small solitary coral dominated, *Grypophyllum–Chostophyllum* association, a pioneer coral community, is widely distributed at the base of the Givetian Burdekin Formation of north Queensland in the mixed arkose-carbonate sediments. It is succeeded by fasciculate coral dominated, *Dendrostella trigemme* association, which is mainly associated with wackestone or bioclastic calcirudite of inner shelf, lagoonal or protected environments. The *Australophyllum–Sanidophyllum* association, *Blysmatophyllum–Iowaphyllum schlueteri* association, and *Spongophyllum* association, all dominated by *in situ*, large massive coral colonies, formed biostromal deposits on the margins of the basin. They developed in nearshore environments during the maximum flooding in the region. The *Aphyllum salmoni–Stringophyllum (Neospongophyllum) bipartitum* association indicates relatively deeper, mid-outer shelf environments connected with maximum flooding in the depocentre and least terrigenous influx. The massive coral dominated *Endophyllum columna–Stringophyllum (Stringophyllum) isactis* association, developed in the initial regressive phase, forms a distinctive biostromal unit at the top of the Burdekin Formation. The *Lekanophyllum* association developed at the base of the Cultivation Gully Formation in a very shallow nearshore environment with a large terrigenous influx as a result of the basin wide, relatively rapid regression. It is characterised by the abundant occurrence of solitary corals and large sized, cerioid *Endophyllum columna*, which often formed micro-atolls. Rugose corals were better adapted than stromatoporoids to survive of mud influx.

Key words: Givetian, corals, associations, palaeoecology, growth form.

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Introduction

Fanning River Group is one of the best exposed, fossiliferous, Middle Devonian coralline limestone and sandstone sequences of eastern Australia. Its three formations of the lower Big Bend Arkose of conglomerate and sandstone, the middle Burdekin Formation of predominantly carbonates and the upper Cultivation Gully Formation of shale, siltstone and sandstone represent a major transgressive-regressive cycle of late Middle Devonian age in the Burdekin Basin, north Queensland. Rugose corals from the Fanning River Group were first recorded by Clarke (*in* Leichhardt 1847), and were studied systematically by various authors (Jack & Etheridge 1892; Hill 1942; Zhen 1991, 1994; Zhen & Jell in press). However, the palaeoecological aspects of these well preserved coral faunas have not been focused on previously. This paper aims to demonstrate that different coral communities of the Fanning River Group were restricted within separate habitats by physical, chemical and biological factors. Therefore, growth form and distributional pattern of corals within the group are important environmental indicators. In the Fanning River Group, corals, along with algae and stromatoporoids, are the dominant fossil groups and were important stabilizing, colonizing and framework building organisms during the development of the carbonate factory (Jones & Desrochers 1992). The high diversity of the Fanning River Group coral faunas indicates a strong ecological and environmental control over the distribution of genera or even species in the basin. Coral occurrence was closely related to carbonate deposition in the group. Corals, as well as algae and stromatoporoid skeletons, and their skeletal debris provided the major sources for the construction of this carbonate dominated succession. In this paper coral associations representing either pioneer, colonizing, climax or conclusive stages of the carbonate deposition will be presented. Their distribution (Figs 3, 4) and the relationships between coral external growth form and environments will be used to depict the facies mosaic within the basin.

UQL refers to University of Queensland localities and registered under the Geological Museum locality catalogue system (for details also see Zhen 1991, 1994; Zhen & Jell in press). All the studied thin sections and specimens carrying a UQF number are housed in the Geological Museum, University of Queensland.

Geological setting

The Burdekin Basin (Fig. 1), as an intracratonic extensional basin, covers about 7500 square kilometres of the Townsville hinterland, north Queensland. The late Middle Devonian Fanning River Group forms the basal part of the Burdekin Basin sequences, except for the Mount Podge area situated at the northwest corner of the Basin, where a late Emsian transgression occurred (Zhen *et al.* 1993; Zhen 1995). The southern boundary of the basin with the Lolworth Ravenswood Province is very sharp, and the Fanning River Group is rarely exposed south of Hann and Fletcher creeks. Lang *et al.* (1990) regarded this lineament as the southwestern margin of the basin. The Burdekin Basin is fault-bounded with the Broken River Province to the northwest. Presenting a striking contrast to the Burdekin Basin, the Graveyard Creek Subprovince, about 100 km

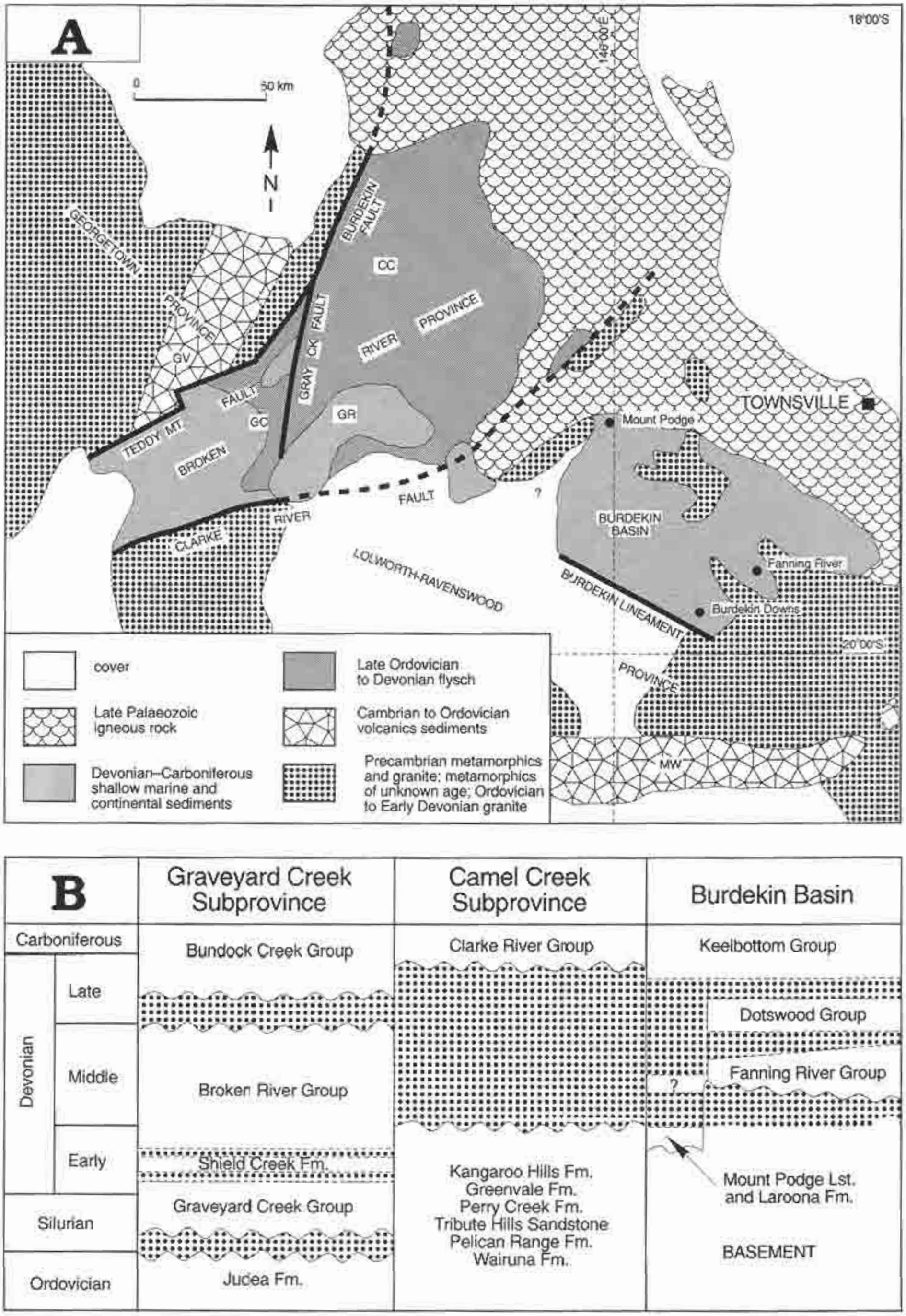


Fig. 1. Locality (A) and structural framework (B) of the Townsville hinterland (modified from Withnall *et al.* 1988). Abbreviations: CR — Clarke River Basin, CC — Camel Creek Subprovince, GC — Graveyard Creek Subprovince, GV — Greenvale Subprovince, MW — Mount Windsor Subprovince.

northwest (Fig. 1), consists of thick Ordovician–Silurian turbidite and shelf deposits, and Late Silurian–Middle Devonian shelf carbonate and siliciclastic deposits (Withnall & Lang 1990).

The thickness of the group varies from a few metres to about a hundred metres towards the north and northwest margins of the basin, and is much thicker in the southeast part of the basin (Fanning River and Calcium areas; Fig. 2) with a maximum thickness of just under 800 m. The Big Bend Arkose consisting of the marine or partly non-marine conglomerates and very coarse to fine grained arkosic sandstones with a thickness varying from less than one metre to 500 m is overlain unconformably or nonconformably on Proterozoic metamorphics or Ordovician–Early Devonian volcanic and plutonic rocks of the basement. The deposition and thickness of this conglomerate and sandstone unit were largely controlled by the topography induced by active block faulting or reactivation of basement syn-depositional faulting (Lang *et al.* 1990). Terrigenous clasts were mainly derived from local sources. In the northwestern part of the basin (Kirkland Downs and Boundary Creek areas; Fig. 2) they were mainly from the local metamorphic sources, while in the eastern part of the basin, from granodiorite sources of the Ravenswood Complex to form typical arkose. Corals first occur in the calcareous sandstone at the top of the Big Bend Arkose. The Burdekin Formation developed in shelf marine environments is much more widely exposed with a measured, maximum thickness of nearly 500 m in the Fanning River area (Fig. 2). It thins towards the Dotswood High and pinches out into sandstones of tidal or nearshore facies (Figs 2, 4). In places, it interfingers with the arkose. Corals and stromatoporoids are the major megafossil groups in this limestone unit. The overlying Cultivation Gully Formation consisting of calcareous siltstone, shale, and fine grained sandstone is poorly preserved in most areas. It was deposited in a relatively rapid regressive phase. The group is overlain disconformably by the Late Devonian Dotswood Group of mainly non-marine conglomerate and sandstone (redbeds and associated facies).

Preservation and alteration

Preservational states of coral faunas from the Fanning River Group vary considerably over the region studied. Many specimens have well preserved external and internal structure and microstructure as well. Some slightly silicified specimens normally have poorly preserved microstructure, such as the specimens from the base of the Cultivation Gully Formation at Horse Shoe Bend. Specimens from Calcium and Reid Gap area are poorly preserved because of post-Devonian metamorphism in the area. The most important diagenetic effect on coral preservation is slight recrystallization resulting in obliteration of some fine skeletal structures and, on occasion, even of megastructures, e.g. reduction of the length of septa and modifying

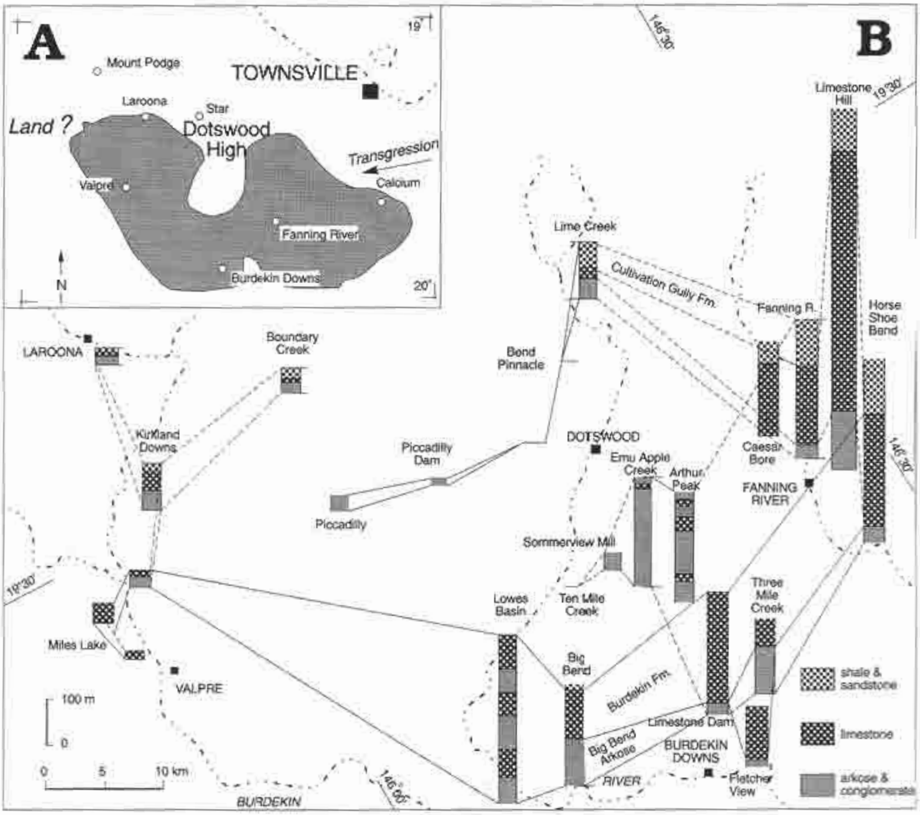


Fig. 2. □A. Outline of the depositional area in the Middle Devonian Burdekin Basin. □B. Major stratigraphic sections and correlation of the the Fanning River Group, showing that the group is thickest in the eastern part of the basin and thins towards northwest (Dotswood High) and west. The three lithologies correspond to three formations, but in places like Lowes Basin and Arthur Peak, they are interfingering. Therefore the group can not easily be subdivided into formations (modified from Wyatt & Jell 1980).

the tabulae and dissepiments. Some specimens show that structures, such as the tabularium, might be greatly simplified by recrystallization. This is clearly shown in a few longitudinal sections referred to *Charactophyllum (Spinophyllum) trochoides* (Hill 1942). In one specimen, small, incomplete, closely spaced, horizontally floored tabellae (unrecrystallized) occur in the lower parts of the thin section, whereas in the upper part of the section, the large, widely spaced, horizontal structures (pseudotabulae, formed by recrystallization) replaced the original tabellae (Fig. 5A). In other examples, septa may appear strongly withdrawn from the axis due to the recrystallization in the axial area of the corallite. This suggests that the recrystallization may generally initiate from the axial area of the corallites, probably because sea water was more easily trapped in the inter-tabular space, when these coral skeletons were buried in the sediments. Deformation also selectively changed morphological characters of corals preserved. Destruction of the fossils was often caused by compressional and dilational systems (Logan 1984) of the carbonate deformation. For example, many colonies of *Sanidophyllum kirklandense* were found with corallites closely gathered and with their wide calical expansions lost by solution along well developed stylolites between neighbouring corallites.

The susceptibility of corals and stromatoporoids to crushing and fragmentation is likely to be selective and depends, in part, upon external shape of an individual. In the Fanning River Group corals are preserved in three basic modes: (1) in transported rubble (Fig. 6A), (2) in the growth position in which they lived (Fig. 6B–C, E–F), or (3) overturned to moderately abraded but not transported far from where they grew (Fig. 6D). Sediment binding and encrusting corals and stromatoporoids are more likely to have been preserved in growth position than other forms. Many massive corals, such as *Endophyllum*, *Xystriphyllum*, *Australophyllum*, *Spongophyllum*, *Taimyrophyllum*, and encrusting corals, such as *Heliolites* and *Alveolites*, were constructors of the biostromes and bioherms. Branching corals, such as *Centristela* sp., *Aphyllum salmoni*, *Nadotia*? *lophophylloides*, *Planetophyllum* sp., *Cladopora* sp., and *Thamnopora* sp. are rarely preserved in their growth position. Their destruction was mainly attributed to seasonal storms. Most solitary corals of the Fanning River Group lived on soft, unstable substrata, and when they died, their skeletons could be easily turned over, with most of them remaining in their original habitats or nearby.

Distribution and palaeoecology of coral associations

The Fanning River Group succession is incompletely preserved and crops out as isolated, partly fault-bounded areas within the basin. This has made it difficult to reconstruct the depositional setting and the basin geography. The formation of the basin was controlled by regional tectonic movement, mainly downwarping of the basement, and the palaeoecological and sedimentological data indicate that the Fanning River Group strata were mainly deposited in shallow water, shelf marine environments ranging from coast plan to mid-outer shelf (Lang *et al.* 1990). Corals and stromatoporoids are very abundant in the Fanning River Group often forming distinctive bio-sedimentological structures like biostromes and bioherms. The spatial and temporal distributional pattern of the eight coral associations in the group, as demonstrated in Figs 3, 4 and Tab. 1, shows that various habitats reflected by their lithology and sedimentological features in the regional, depositional context contained remarkably different communities. This was the result of interplay of various parameters of the environment and the organisms. The basin floor topography, depositional rate, energy level and depth of sea water were probably the most important environmental constraints on the distribution of the Givetian coral associations. Therefore, coral palaeoecology, especially

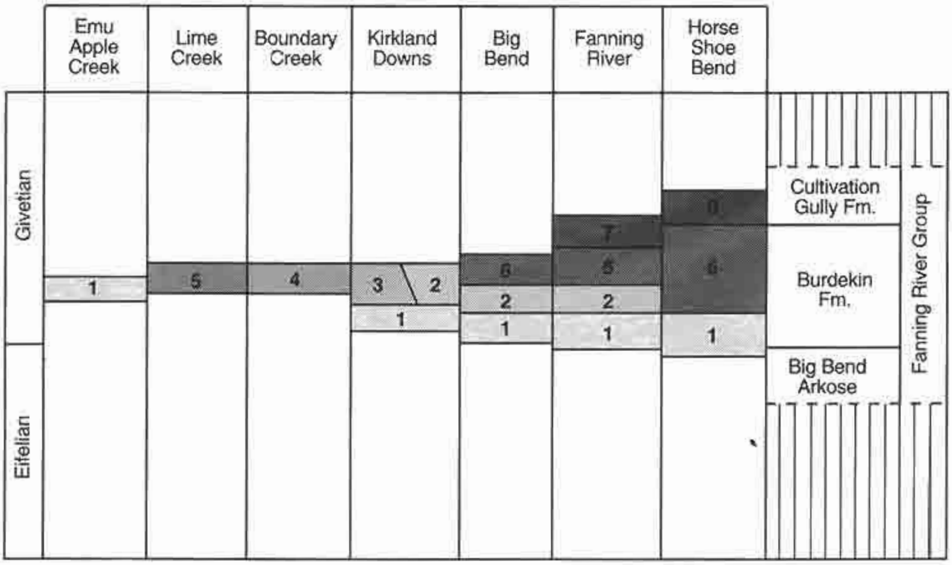


Fig. 3. Correlation of eight coral associations from the Fanning River Group. Abbreviations: 1 — *Grypophyllum–Chostophyllum* association, 2 — *Dendrostella trigemme* association, 3 — *Australophyllum–Sanidophyllum* association, 4 — *Blysmatophyllum isisense-Iowaphyllum schlueteri* association, 5 — *Spongophyllum* association, 6 — *Aphyllum salmoni–Stringophyllum (Neospongophyllum) bipartitum* association, 7 — *Endophyllum columna–Stringophyllum (Stringophyllum) isactis* association, 8 — *Lekanophllum* association.

coral growth form (Fig. 7), distribution of coral associations and their relationships with sediments are useful for the regional biostratigraphic studies and reconstruction of the facies architecture across the basin.

Fanning River Group coral faunas exhibit great diversity. The *Grypophyllum–Chostophyllum* association, marking the beginning of carbonate deposition, is most widely distributed at the basal part of the Burdekin Formation associated with calcareous sandstone and sandy limestone which represent mobile, unstable substrata. It is overwhelmingly dominated by small horn-shaped solitary corals (Fig. 7), including some 26 rugose coral taxa (Tab. 1). Most of them had a similar life strategy. Although many of these species extended into the succeeding associations (Fig. 8), their populations were greatly reduced and became subordinate elements. Distribution of the *Grypophyllum–Chostophyllum* association indicates that transgression was spread from southeast to northwest towards Dotswood High (Fig. 4). Both *Dendrostella trigemme* and *Aphyllum salmoni–Stringophyllum (Neospongophyllum) bipartitum* associations are dominated by fasciculate corals (Fig. 7). The former developed in the protected inner shelf area, while the latter in deeper, mid-outer shelf environments. The *D. trigemme* association occurring in the lower-middle part of the Burdekin Formation represents the colonizing stage in the development of the carbonate factory. It exhibits much lower diversity (Tab. 1), but was rather densely populated and widely distributed. *D.*

trigemme is the dominant species and is more often preserved as segments in the bioclastic calcirudite (up to 75% of the volume of fossils). In the southeastern part of the Basin (from Big Bend to Fanning River) *Dendrostella trigemme* association was often succeeded by a stromatoporoid dominated association forming widely distributed stromatoporoid biostromes and bioherms (Figs 4, 6C, F). Associations 3–5 and 7 are dominated by massive rugose corals typically forming biostromes (Figs 4, 7). The *Australophyllum–Sanidophyllum* association, *Blysmatophyllum isisense–Iowaphyllum schlueteri* association and *Spongophyllum* association were contemporaneous and developed during the most widespread stage of carbonate deposition. They represent three isolated or partially isolated communities distributed near the north and northwestern margin of the basin (Fig. 4). The *A. salmoni–S. (N.) bipartitum* association developed only in the southeastern part of the basin (depocentre). Biostratigraphic correlation and sedimentological evidence suggest that this association was developed during the maximum flooding of the basin (Fig. 4). The associated lithology in the type section (Fig. 8) is represented by a unit of dark coloured, flaggy wackestone containing least terrigenous material. Stromatoporoids are very rare in this unit, and corals are also sparse, mainly *Cladopora*. The *Endophyllum columna–Stringophyllum (Stringophyllum) isactis* association and the *Lekanophyllum* association dominated by massive and solitary corals are the youngest communities developed in the regressive phase in the Fanning River and Horse Shoe Bend areas (Fig. 4).

***Grypophyllum–Chostophyllum* association (1)**. – This association, developed in the pioneer phase of the carbonate sedimentation over the siliciclastic sea floor, is widely distributed at the top of the Big Bend Arkose and the basal part of the Burdekin Formation in the Reid Gap–Calcium, Fanning River–Horse Shoe Bend, Fletcher View–Burdekin Downs, Arthur Peak–Emu Apple Creek, Three Mile Creek, Miles Lake, and Kirkland Downs areas, but best known from the Fanning River area, 3.3 km northeast of the Fanning River Homestead (Fig. 8). The associated lithology is dominantly sandy limestone and calcareous arkose. Following the transgression, this association replaced the older gastropod and bivalve associations which are distributed in the arkose of the upper Big Bend Arkose.

These solitary corals were able to establish themselves as thickets or clusters on the fine to medium grained siliciclastic deposits. Many of them can be regarded as opportunistic species defined by Levinton (1970) as physiological generalists which may allow quick colonization of areas being previously sparse with organisms, when environments become favourable. They were initially attached to sedimentary grains or hard skeletal fragments of dead corals or other organism and subsequently became detached from them and rested free on the sea floor as soft substrate dwellers. Neuman (1988) referred to this life strategy as the 'liberosessile forms'. He suggested that 'corallites of liberosessile forms often have strongly dilated septa'. This was particularly so in species of

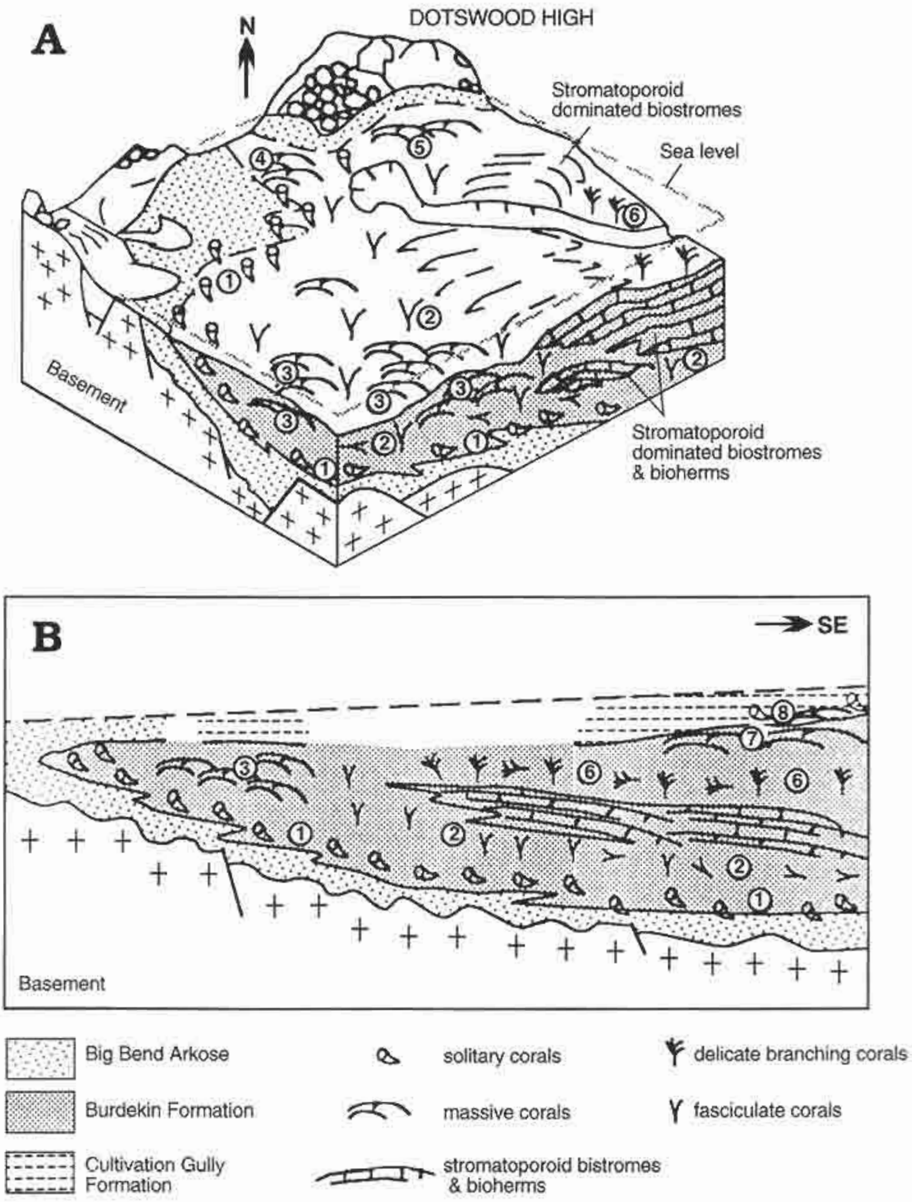


Fig. 4. Cartoon diagrams showing the spatial (A) and temporal (B) distribution of the coral associations (1–8 within the circles referring to the eight coral associations, see Fig. 3).

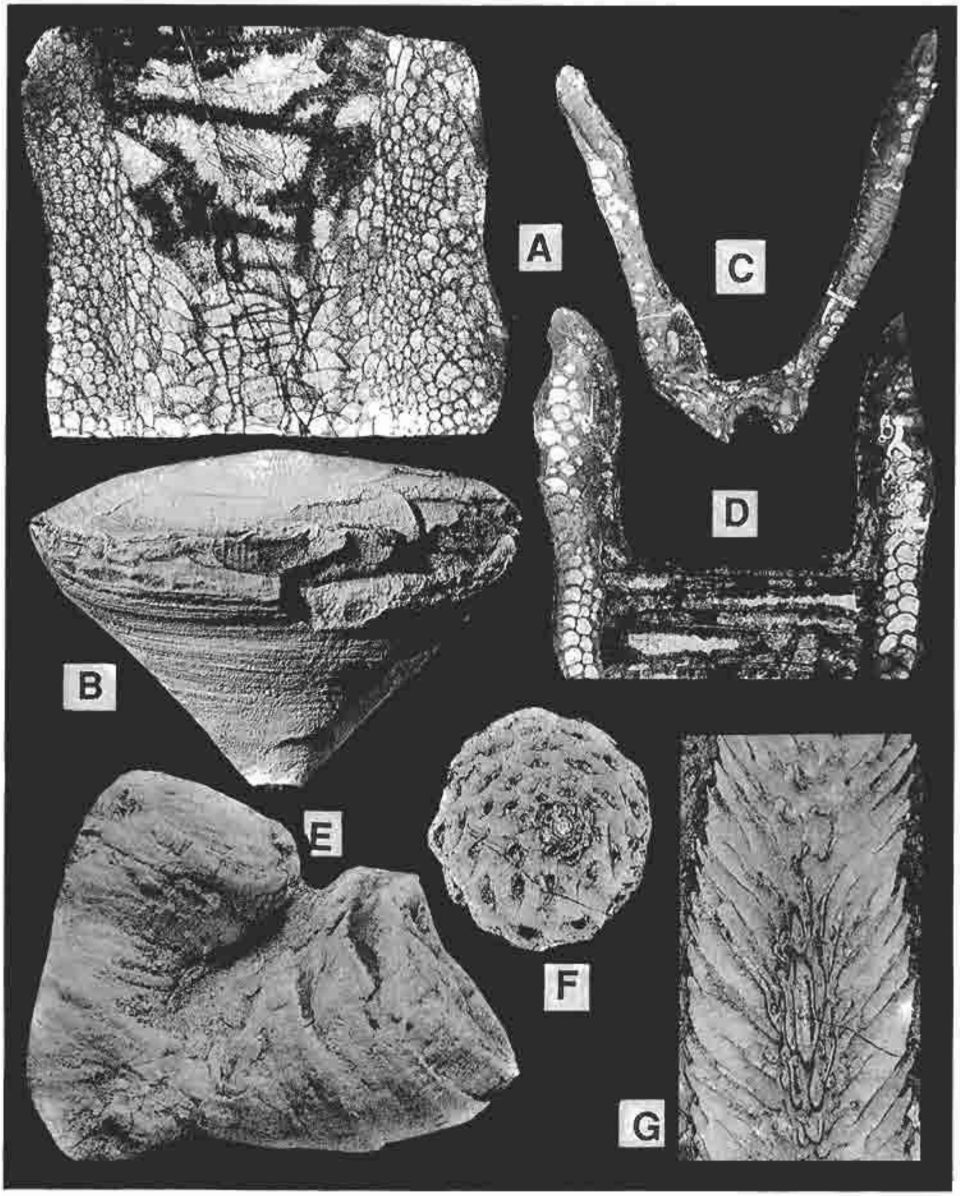
Charactophyllum, *Temnophyllum*, and *Chostophyllum* in the Fanning River Group. They are generally small in size, ceratoid or trochoid, subcylindrical in late stage, and straight or curved. Many developed calicular offsets to cope with the unfavourable soft, mobile substrate.

Moving sand on unstable substrata is physically destructive to corals, especially colonial forms (Jackson 1977). Since colonial forms were superior space competitors in hard-substratum environments, conversely more adaptable pioneer solitary forms with high recruitment rate were suggested to have a preferential advantage on soft, mobile sand substrata (Copper 1988). Abundant solitary forms on the siliciclastic sea floor might greatly increase the carbonate productivity in the form of their skeletons, which may shift, overturn, break or be buried in sediments, in turn providing the necessary stabilization for survival of the forthcoming colonial forms (Jackson 1977).

***Dendrostella trigemme* association (2).** – This is an association characterised by the acme of *Dendrostella trigemme* in the Burdekin Formation, forming easily recognized marker beds. The pioneer solitary rugose coral association was typically succeeded by the flourishing of this fasciculate coral-dominated association (Figs 3–4, 7), including *Dendrostella trigemme*, *Fasciphyllum immersum*, *Sociophyllum irregulare*, *Disphyllum* sp., *Centristela* sp., *Nadotia*? *lophophylloides*, *Thamnopora* sp., *Syringopora* sp., ramose forms of *Alveolites*, ramose stromatoporoids *Stachyodes* sp., thin cylindrical solitary rugose corals, such as *Acanthophyllum (Neostringophyllum)*? *sweeti*, *Pseudomicroplasma australe*, and large solitary corals, such as *Dohmophyllum clarkei*. Large loosely coiled and brevicone nautiloids have been found in the same strata. In the middle part of the Fanning River section (Fig. 8), *Dendrostella trigemme* reached its maximum development forming a distinctive unit dominated by dismantled *Dendrostella trigemme* branches along with *Stringophyllum (S.) quasinormale*, *Sociophyllum irregulare*, *Fasciphyllum immersum*, *Dohmophyllum clarkei*, *Pseudomicroplasma australe*, *Stringocephalus* sp., *Thamnopora* sp., branching *Alveolites*, and stromatoporoids. The same unit is well exposed about 1 km to the northwest of the Fanning River, with numerous *in situ* colonies of *Dendrostella trigemme* and *Disphyllum* sp. forming biostromes. The *Dendrostella trigemme* association is also recognized near the Limestone Hill, as well as in the Fletcher View, Calcium, Miles Lake, and Kirkland Downs areas (Fig. 2). However its distribution tends to be patchy. The lithology associated with the association is dominated by wackestone and bioclastic calcirudite.

These branching corals with relatively fast growth rate formed patches of groves in the wave protected areas, such as channels, grooves, pools and the lee side of topographic highs indicating a relative deeper or protected, low energy environment, and might be periodically damaged by storms. Delicate branching forms, such as *Fasciphyllum immersum*, *Centristela* sp. and ramose stromatoporoids are rarely found in their growth position. Both *Dendrostella trigemme* and *Sociophyllum irregulare* exhibit two slightly different growth forms. Dendroid colonies with long, widely spaced

Fig. 5. ❑A. *Charactophyllum (Spinophyllum) trochoides* (Hill): longitudinal section UQF79111, from UQL5486-2, showing the original tabellae in the lower part and the pseudotabulae (result of recrystallization) in the upper part; *Grypophyllum–Chostophyllum* association, Fanning River, at the base of the Burdekin Formation, Givetian; × 4. ❑B. *Calceola sandalina*



(Linnaeus), lateral external view from convex side of UQF78568 from UQL5442-3, Horse Shoe Bend, Cultivation Gully Formation, Givetian, *Lekanophyllum* association; × 1. ❑C. *Chostophyllum* sp., UQF78311 from UQL5435-3, Fanning River, at the base of the Burdekin Formation, Givetian, *Grypophyllum–Chostophyllum* association; × 4. ❑D. *Planetophyllum* sp., longitudinal section of UQF77927 from UQL5425-3, Big Bend, Burdekin Formation, Givetian, *Aphyllum salmoni–Stringophyllum (Neospongophyllum) bipartitum* association; × 4. ❑E. *Charactophyllum (Spinophyllum) trochoides* (Hill), external lateral view of UQF79109 from UQL5429-1, Fletcher View, at the base of the Burdekin Formation, Givetian, *Grypophyllum–Chostophyllum* association; × 2. ❑F–G. *Cladopora* sp. transverse and longitudinal section of UQF78783 from UQL5462-2, Three Mile Creek, Burdekin Formation, Givetian; × 8.

corallites indicate relatively low energy and would be adapted to a fast depositional rate, while the relatively robust, low branching forms with short, straight and closely spaced corallites (Fig. 6E) suggest a less protected, more turbulent, depositional setting. *Pseudomicroplasma australe* found in this facies is mostly long cylindrical forms with a height up to 50 cm (Fig. 6D). This association is rather widely distributed except in the areas around Boundary Creek and Lime Creek (Fig. 2), where the Fanning River Group is much thinner than in the southern areas around the Fanning River (Fig. 8). In the areas near Kirkland Downs and Miles Lake *Grypophyllum–Chostophyllum* association occurs only briefly at the base of the limestone unit and the succeeding *Dendrostella trigemme* association developed as small patches.

***Australophyllum–Sanidophyllum* association (3).** – This is a coral association developed in the Kirkland Downs area during the maximum flooding of the transgression (Figs 3, 4 and Tab. 1). Areas around Kirkland Downs, Miles Lake and Valpre were near the west and northwest margins of the basin (Fig. 2). In this region, the Burdekin Formation with abundant rugose corals is much thinner (2 m) than to the southeast. The *Grypophyllum–Chostophyllum* association developed at the base of the Burdekin Formation is replaced by the *Dendrostella trigemme* association or by the *Australophyllum–Sanidophyllum* association (Figs 3, 4). In the latter, *Australophyllum cyathophylloides yohi* is the most abundant species (Tab. 1), massive to hemispherical in form. Colonies are up to 50 cm in diameter, many in their growth position, and form major framework of the biostromes. The matrix of the biostromes is dominated by wackestone and minor packstone.

***Blysmatophyllum isisense–Iowaphyllum schlueteri* association (4).** – This is a small association found in the Burdekin Formation in a few small outcrops exposed along Boundary Creek and its tributaries near the Paynes Lagoon Homestead (Zhen 1994). The Burdekin Formation in the Boundary Creek area is thin with a maximum thickness of 2 m (Fig. 2). Many coral colonies are in growth position, others are overturned or broken. *Blysmatophyllum* and *Iowaphyllum* are the most common elements, most of which are *in situ*, domal or tabular with a maximum diameter of 50 cm, and associated with oncolites and debris of large crinoid stems. Differing from the Kirkland Downs area to the southwest, this area may have been closer to a source of siliciclastics, but the rate of subsidence may have been much less. The associated lithology is characterised by the sandy wackestones with a relatively higher content of terrigenous mud or sand, mainly metamorphic derived quartz sand clasts.

Fig. 6. ❑A. Thick bedded sandy bioclastic calcirudite: UQL5472, Kirkland Downs, lower part of the Burdekin Formation, Givetian. ❑B. A micro-atoll formed by an *Endophyllum columna* colony within the calcareous sandstone and shale at the base of the Cultivation Gully Formation, Givetian, UQL5486-11, Fanning River; the geological hammer is sitting along the rim of the micro-atoll. ❑C. Massive stromatoporoid framestone, UQL5429-2, Fletcher View,

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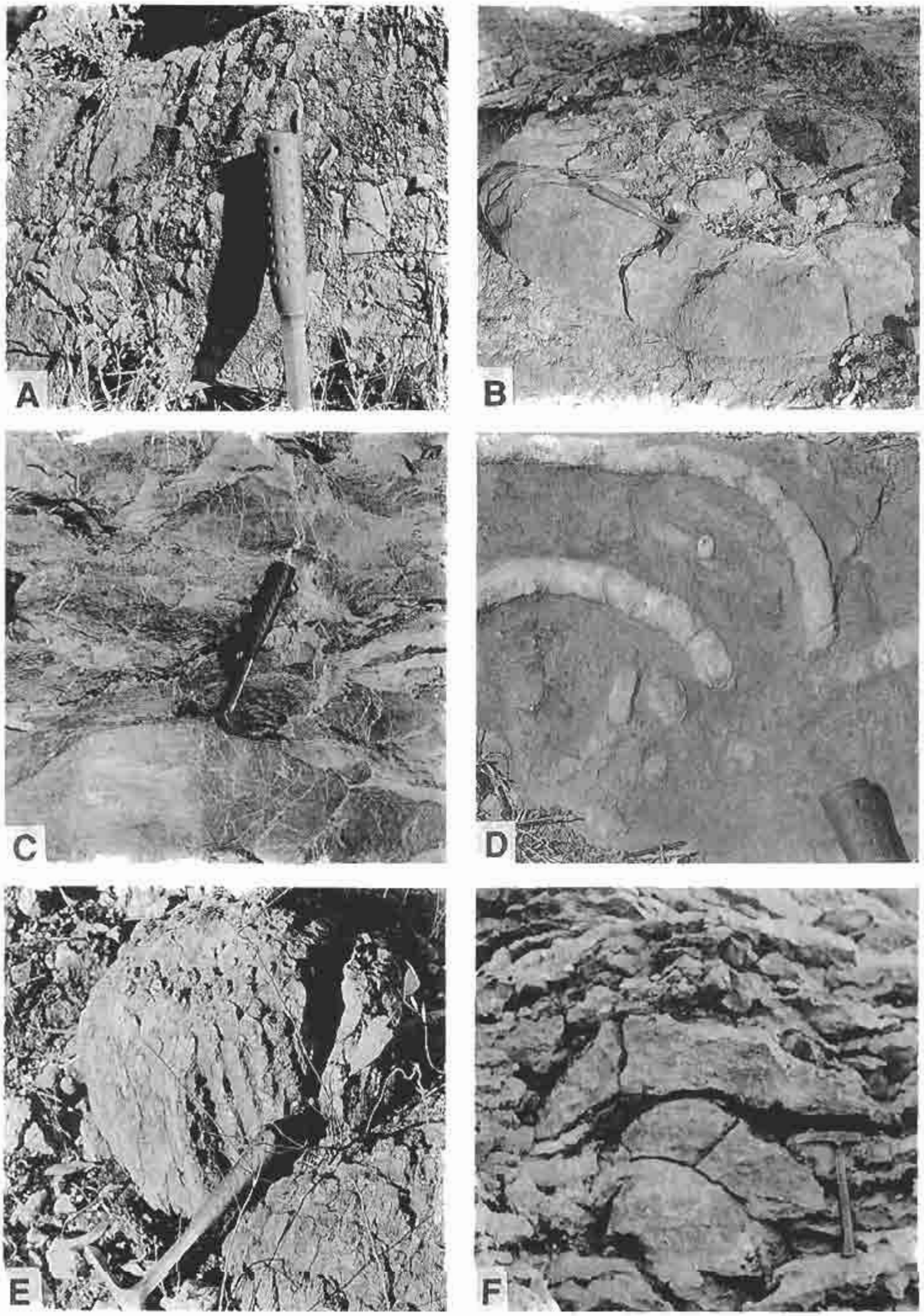

Burdekin Formation, Givetian. ❑D. Large cylindrical *Pseudomicroplasma australe* from thin to medium bedded wackestone, UQL5428-2, Big Bend, Burdekin Formation, Givetian. ❑E. *In situ Sociophyllum irregulare* colonies showing closely spaced, sturdy corallites, UQL5486-9, Fanning River, Burdekin Formation, Givetian. ❑F. *In situ* stromatoporoids forming bioherms, UQL5429, Fletcher View, Burdekin Formation, Givetian.

Tab. 1. Distribution of rugosan species in the eight coral associations. A – abundant; C – common; and R – rare (1–8 refer to the eight coral associations, see caption of Fig. 3 for the full names).

	Coral associations							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Lythophyllum proliferum	C			R				
Microplasma caespitosum							C	
Pseudomicroplasma australe	A	C	C		R	C	C	C
Zonophyllum kwangsiense	R						R	
Lekanophyllum fultum								A
Lekanophyllum sp.								A
Calceola sandalina	C	C				R		A
Loyolophyllum sp.				C	C			
Dendrostella trigemme	R	A				R		
Aphyllum salmoni		R				C		
Centristela sp.		C	R					
Endophyllum columna columna							A	C
Endophyllum columna subsp. nov.								C
Endophyllum jelli					A			
Iowaphyllum schlueteri				C				
Blysmatophyllum isisense				C				
Blysmatophyllum multigemme				C				
B.? sp.				C				
Sanidophyllum kirklandense			C					
Sanidophyllum sp.	C							
Spongophyllum (B.) variabilis					A			
Nadotia? lophophylloides	C	C						
Australophyllum cyathophylloides yohi			A					
Xystriphyllum dotswoodense					A			
Xystriphyllum sp.			C	C				
Taimyrophyllum crassiseptatum			C					
Taimyrophyllum sp.			C					
Acanthophyllum (Acanthophyllum) sp. A	C							
Acanthophyllum (Acanthophyllum) sp. B		C	C	C		R		
Acanthophyllum (N.)? sweeti	C	C						
Dohmophyllum clarkei	A	R				C	R	
Grypophyllum curvatum	A							
Grypophyllum sp.	A							
Fasciphyllum immersum	R	A	C			R		
Stringophyllum (S.) quasinormale	C	C				C		
Stringophyllum (S.) isactis	R						C	
Stringophyllum (N.) bipartitum						C	R	
Sunophyllum sp. A	C							
Sunophyllum sp. B	C							
Sociophyllum irregulare	C	A				R	R	
Sociophyllum sp.		R						
Disphyllum (Disphyllum) sp.		A						
Amaraphyllum amoenum					A			
Argutastrea sp.			R					
Charactophyllum (C.)? excavatum	C							
Charactophyllum (C.) sp.	C							
Charactophyllum (Spinophyllum) trochoides	A	C	C					
Temnophyllum sp.	C	C				R	R	
Chostophyllum sp.	C							
Chostophyllum ?gregorii	C					R		
Aristophyllum planotabulatum	C							
Planetophyllum sp.	R	R				C		

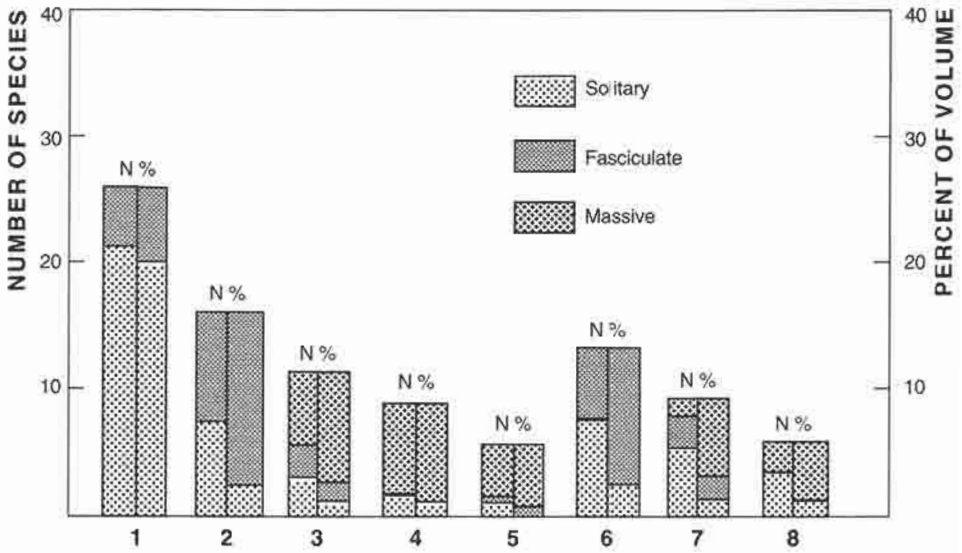

Fig. 7. Diversity of the eight coral associations and their composition of three major growth forms from the Fanning River Group. Abbreviations: N — number of species, the right column indicating the volume quantity by percentage (%). 1 — *Grypophyllum–Chostophyllum* association. 2 — *Dendrostella trigemme* association. 3 — *Australophyllum–Sanidophyllum* association. 4 — *Blysmatophyllum isisense–Iowaphyllum schlueteri* association. 5 — *Spongophyllum* association. 6 — *Aphyllum salmoni–Stringophyllum (Neospongophyllum) bipartitum* association. 7 — *Endophyllum columna–Stringophyllum (Stringophyllum) isactis* association. 8 — *Lekanophllum* association.

The calicular expansions developed in *Blysmatophyllum* helped it to survive in this sandy environment with the influx of large quantity of siliciclastic particles.

***Spongophyllum* association (5)**. — This association characterises the Burdekin Formation exposed in the Lime Creek. It had a relatively low diversity of only some six rugose coral species (Tab. 1), but was rather densely populated. Most of the coral colonies are preserved as *in situ* colonies, domal, hemispherical, or massive in growth form with a diameter up to 60 cm. The Lime Creek area situated to the northeast of the Dotswood High has a thin sequence of the Fanning River Group of less than 100 m thickness (Fig. 2). The thin limestone unit, less than 30 m thick, of mainly wackestone is similar to that in the Boundary Creek area on the other side of the Dotswood High. It contains abundant massive corals forming biostromes in the similar nearshore environments. The mainly domal and hemispherical growth form of corals and the lithology characterised by containing relatively less terrigenous material suggest that the association was perhaps developed on a relatively steeper sea floor with a more open marine context, farther away from sources of siliciclastics during the maximum flooding (Fig. 4).

***Aphyllum salmoni–Stringophyllum (Neospongophyllum) bipartitum* association (6)**. — This association is defined in the upper part of the

Burdekin Formation in the Fanning River–Horse Shoe Bend, Fletcher View–Burdekin Downs, and Big Bend areas (Fig. 2). In the Fanning River area (Fig. 8) this association occurs at the upper part of the Burdekin Formation. The loosely branching forms, such as *Aphyllum salmoni* and *Planetophyllum* sp., are the dominant rugosan species of the association. They are preserved as long cylindrical segments and are associated with delicate branching tabulate coral *Cladopora*. The very long segments of these species preserved in the unit suggest that they grew to a substantial height, and their very loosely branching growth form with long, slender corallites indicates a low water turbulence. The associated lithology in the Fanning River area is mainly flaggy, dark grey coloured floatstone or wackestone with comparatively least terrigenous influx. The fossil volume in this unit is also remarkably reduced in the Fanning River and Horse Shoe Bend area. All these palaeontological and sedimentological data indicate that this association was developed in a relatively deeper, mid-outer shelf environment (Fig. 4). However at Big Bend, Fletcher View and Burdekin Downs, this association is characterised by abundant *Cladopora* and occurs in the upper part of the Burdekin Formation overlying the *Amphipora* beds and the crinoid grainstone and packstone. These *Cladopora* rich beds are often silicified, enabling very good specimens to be extracted by dissolving the rock in acid.

***Endophyllum columna–Stringophyllum (Stringophyllum) isactis* association (7).** — This association is well developed at the top of the Burdekin Formation in the Fanning River area (Fig. 8) where an almost continuous belt consisting of *in situ* coralla extends along the southern and southwestern foot of hills situated to the east of the Fanning River. *Endophyllum columna* colonies are dominant (Tab. 1), mostly *in situ*, domal to hemispherical in shape of up to 100 cm in diameter forming the framework of a large biostrome in the Fanning River area. The associated lithology is mainly wackestone with a relatively high content of terrigenous mud or silt. It represents a shallow water, nearshore, medium energy environment. The temporal succeeding of this association over the older, relatively deeper water, *Aphyllum salmoni–Stringophyllum (Neospongophyllum) bipartitum* association indicates a significant shallow-ward event in the basin.

***Lekanophyllum* association (8).** — A well-preserved brachiopod-coral community was recovered in the fine calcareous sandstone of the lower Cultivation Gully Formation at Horse Shoe Bend. Many large tabular-shaped colonies of a new chronosubspecies of *Endophyllum columna* are found *in situ* in the calcareous sandstone. It mainly differs from its probable ancestor occurring at the top of the Burdekin Formation at the Fanning River area (Zhen & Jell in press) by having a flat growth surface and a larger corallite diameter. Solitary rugose corals, such as *Lekanophyllum fultum*, *L.* sp., *Pseudomicroplasma australe* and *Calceola sandalina* are common (Tab. 1), as well as tabulate corals, such as plate-like *Alveolites*, encrusting *Aulopora*, and bottle-like sponges and brachiopods.

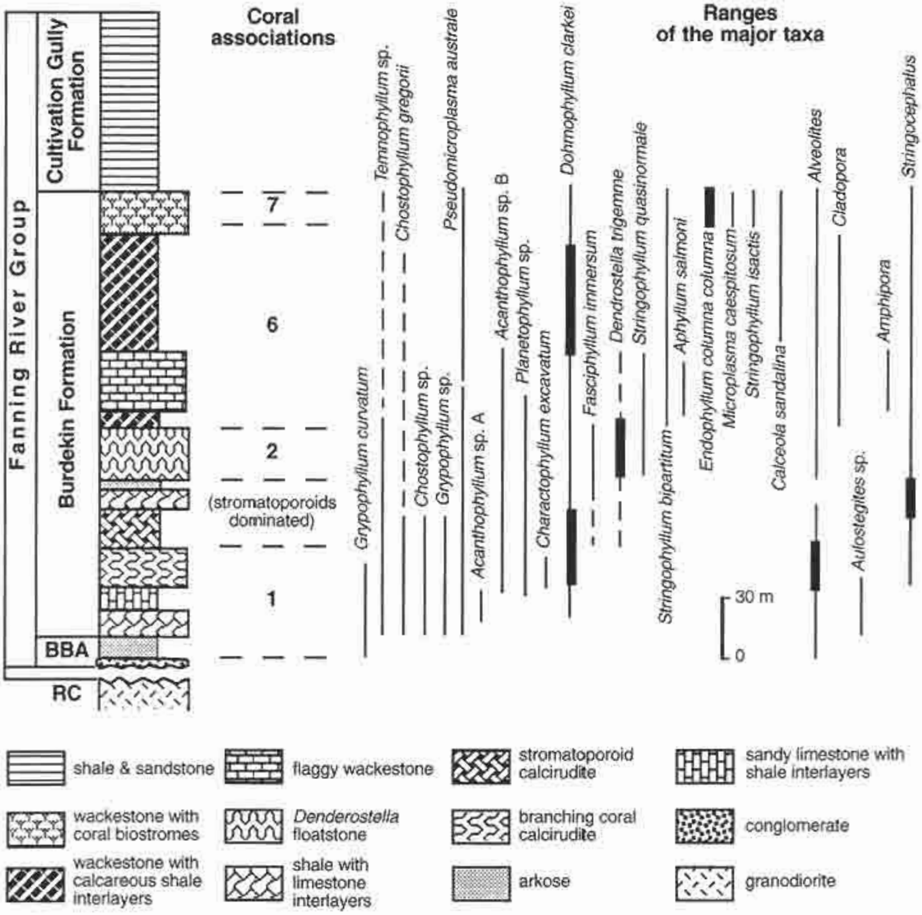

Fig. 8. Stratigraphic ranges of the coral associations in the type section of the Fanning River Group, along the eastern bank of the Fanning River and in the Cultivation Gully, Fanning River. Abbreviations: BBA — Big Bend Arkose, RC — Ravenswood Complex.

The growth surface of *Endophyllum* colonies are flat as a result of predominantly lateral growth. Composition of the association might have been connected with muddy, unstable, siliciclastic environments. Owing to falling sea-level and rapid influx of siliciclastic material, this community was soon suppressed. Hallock & Schlager (1986) suggested that input of large quantity nutrients, especially nitrates and phosphates, in terrestrial runoff might be one of the important causes for suppressing of the growth of coral communities.

Micro-atolls (Fig. 6B) formed by the type subspecies of *Endophyllum columna*, up to 2 m in diameter and 70 cm in height, are in growth position in yellow calcareous shale and fine-grained sandstone at the base of the Cultivation Gully Formation in the Fanning River area. They experienced briefly the similar unfavourable environment, as the *Lekanophyllum* association from Horse Shoe Bend area. These coral micro-atoll structures showing strong lateral growth indicate a uppermost subtidal to lowermost peritidal depositional setting. They are comparable with the *Chaetetes* micro-atolls in the Middle Carboniferous of southeastern Arizona (Connolly *et al.* 1989). Similar micro-atoll structure formed by *Tetradium cribriforme* is also reported from the Late Ordovician Cliefden Caves Limestone Group, central New South Wales (Webby *et al.* in press).

Symbiosis

In the Burdekin Formation, stromatoporoids often have numerous caunopores, which have been referred to *Syringopora* (Mori 1970; Kershaw 1987). Mistiaen (1984) compared the microstructure of these tiny tubes and *Syringopora* from the Silurian of Gotland, and concluded that the caunopore microstructure is different from the free-living *Syringopora* skeleton. In specimens of *Stromatopora* from the framestone at Fletcher View, these caunopores are 0.3–0.6 mm in diameter, straight, perpendicular to the growing surfaces of the stromatoporoids, and occasionally connected with each other by connecting tubuli, which are much thinner than the caunopores themselves. In some specimens, they are more closely spaced than in others, commonly 0.6–1.5 mm apart from axis to axis, but with some having the walls in contact. The caunopore walls in transverse sections are about 0.1 to 0.2 mm thick and typically with a thinner outer layer and a thicker inner layer; they are composed of very fine fibrous sclerenchyme tissue perpendicular to the outer surface (Mistiaen 1984: pl. 1: 2). The two free-living species of *Syringopora* occurring in the Burdekin Formation have a much larger corallite diameter and are not conspecific with the intergrowing species. Typically smaller diameters, and thinner walls and other structural elements were probably the result of the intergrowing relationship, since they were well protected by the stromatoporoid skeleton. Mori (1970) noticed that this intergrowth relationship in the Silurian of Gotland was restricted to massive reef limestones. However, Young & Noble (1989) indicated that it was common in open shelf facies and absent from high-energy shallow water facies in the Silurian of eastern Canada. In the Burdekin Basin, intergrowths between stromatoporoids and *Syringopora* caunopores occur mainly in the stromatoporoid biohermal facies at Fletcher View area.

Hemispherical colonies formed by stromatoporoid/tabulate coral (*Aulostegites*) intergrowth (Fig. 9A–C) are also common. Differing from the commensal relationship between stromatoporoids and *Syringopora*, stromatoporoids and *Aulostegites*, in this case, are encrusting each other repeatedly. The domed mounds up to 15 cm in diameter are the result of competing for space between these two organisms. Regularity of the alteration of layers dominated by stromatoporoids and *Aulostegites* respectively indicates the periodical change of environmental factors, which

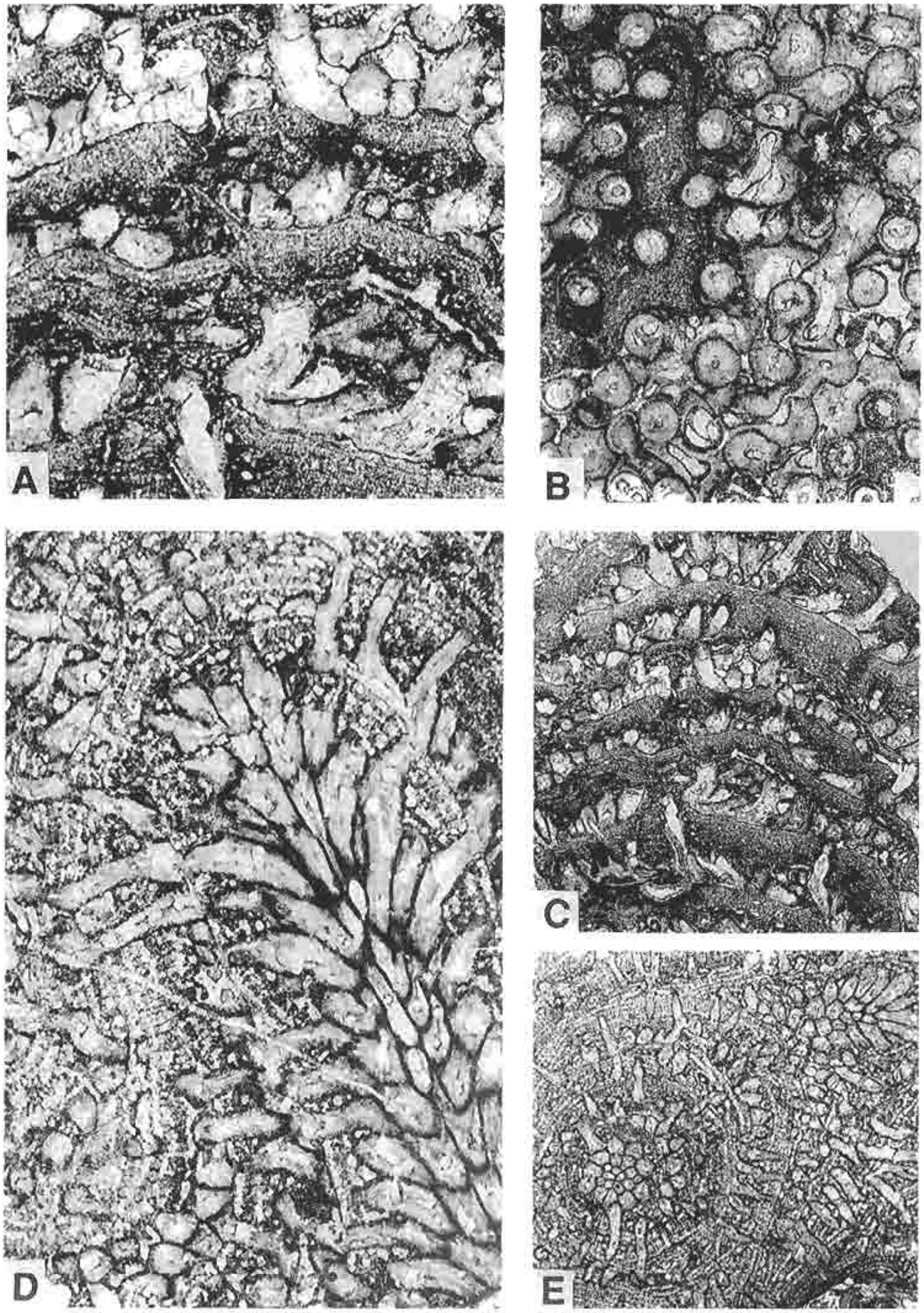

Fig. 9. □A–C. Encrusting relationship between *Aulostegites* and a stromatoporoid; longitudinal (A, × 5; C, × 2) and transverse (B, × 5) section of UQF78175 from UQL5429-3, Fletcher View, Burdekin Formation, Givetian. □D–E. Intergrowth relationship between branching *Cladopora* and stromatoporoid; longitudinal (D, × 6) and transverse (E, × 2.5) UQF78831 from UQL5473-3 Fletcher View, Burdekin Formation, Givetian.

might be favourable for the stromatoporoids at one time and *Aulostegites* at the other. Similar stromatoporoidr–ugosan and stromatoporoid–tabulate intergrowths also occur in the biohermal–biostromal environments, but their relationships are unclear. Slender corallites of *Cladopora* extend a long way through the encrusting stromatoporoids which form thick ramose, finger-like skeleton around the axial branches of *Cladopora* (Fig. 9D, E). The delicate branches of *Cladopora* consist of slender corallites which were initiated by budding at the axial area of the branches and diverged towards the lateral surface at their adult stage. Formation of this kind of branching growth form was controlled by two factors. Firstly, budding always occurred in the axial area and the young corallites were vertically growing along the axis. Secondly, the growth of adult corallites became suspended soon after they diverged away from the axis of the branches. However in the case of *Cladopora* intergrowing with stromatoporoids as shown in Fig. 9D–E, adult corallites continued growing into the stromatoporoid skeleton as caunopores. This indicates that branching growth form in *Cladopora*, and other genera with a similar growth form, might be largely the result of hydrodynamic control.

In a few specimens of *Alveolites*, *Torquaysalpinx* sp. (Fig. 10A) occurs, with tubes of 0.5–1.2 mm in diameter. They extend irregularly in the corallites and often cut through the coral skeleton; the growth pattern is not predictable. These tubes have very thin walls and irregular tabulae. Fine spiral tubes, *Helicosalpinx* sp. (Fig. 10B), of diameter 0.2–0.3 mm have their spiral axes parallel to the growth direction (corallite axis) of the corallites. They probably had openings among the living polyps. Walls of these spiral tubes are about 0.02 mm thick, and are often thickened by fine fibrous coral sclerenchyme. These tubes were likely formed when corals were alive; a commensal or mutulistic relationship between their producers (possibly microconchid lophophorates; Weedon 1991) and tabulate corals or stromatoporoids is therefore postulated. They could have benefited from such a relationship by protection from predators, stabilization in agitated environments, and elevation above the sediment-water interface (Elias 1984).

Discussion on the coral growth form

The growth of modern corals is mainly influenced by nutrient availability, sea water oxygen level, carbonate content, temperature and salinity. Distribution of hermatypic corals is also limited by the water depth (Hallock 1988). Growth form is controlled by the interaction of environmental variables and phylogenetic constrains. The external shapes of corals and stromatoporoids are often considered as indicators of the environments in which they lived (Noble 1970; Różkowska 1980; Zhang 1981; Bjerstedt & Feldmann 1985). On the cliff or steep sea floors, surface light and water clarity seem to play important roles in the distribution and zonation of zooxanthellate corals (Hallock & Schlager 1986), while on the ramp form or gentle slope sea floors, energy level and water depth seem to be more important. On the other hand, Stearn (1982) basically opposed the view to regard the shapes of reef builders as specific guides to environments of modern or ancient reefs. He pointed out that the shapes of reef-builders were controlled by the interaction of a great many environmental variables with phylogenetic and developmental constrains in the organism.

Graus *et al.* (1977) suggested that colony shape, orientation and distribution might be developed by a combination of hydrodynamic 'pruning' and genetic control of growth in relation to water movement. Chamberlain (1978) analysed skeletal mechanics in living corals and strengthened the conclusions of Graus *et al.* (1977). He pointed out that massive growth forms would be more resistant to fracturing than branching structures. On the modern Great Barrier Reefs (Maxwell 1968), branching corals are the most abundant species, reaching their maximum development in the living coral zone of more or less sheltered environments behind the algal rim and on the reef front of relatively deeper water environments. Thin fragile corals mainly occur in the relatively deeper water, reef slope and in the grooves below the level of severe wave action or on the side walls of the spurs and depressions in the reef front, where they are sheltered from strong wave action. The thin platy, foliose corals also favour the side walls or depressions, mainly distributed on the lower reef front. Solitary forms mainly occur in pools or moats of the outer reef flat and on the terraces of the reef slope. Massive corals are mainly distributed in the middle and inner reef flat forming clusters or micro-atolls. Encrusting corals occur on the outer reef flat and the reef front of high energy environments. In the Fanning River Group, fasciculate corals are also the most abundant species, but preserved in most cases as fragments, while massive or tabular corals, which are common in the medium to relatively high energy environments, are largely in their growth position. Laminar or tabular shaped corals could occur in relatively high energy, shallow water environment, and their low profile was mainly the result of high water turbulence. However, laminar or tabular forms were also common in relatively deeper, moderately low energy environment, and foliose forms were especially common on the side walls.

In respect of growth form, rugose corals in the Fanning River Group are within three major categories, massive (cerioid, subcerioid, thamnasterioid, and aphroid), fasciculate (dendroid, phaceloid, and loosely fasciculate), and solitary. Tabulate corals are dominated by massive, ramose or fasciculate forms. Laminar or foliose forms are also common. Both tabulate and rugose corals had similar ecological requirements. However some tabulate corals like *Aulopora* and *Alveolites*, were more tolerant to terrestrial mud or sand influx. They could survive in the siliciclastic dominated deposits by means of encrusting on the dead skeletons of corals or other organisms.

Stratigraphically, there were two major stages of massive coral development in the Fanning River Group. Massive forms, including cerioid *Endophyllum, Spongophyllum, Xystriphyllum* and *Australophyllum*, thamnasterioid *Taimyrophyllum*, and aphroid *Iowaphyllum*, developed in shallow, medium-high energy, nearshore environments, and were wave-resistant framework builders. They are mainly distributed along the north and western margins of the basin, often forming patchy biostromes. *Endophyllum columna*, representing a stratigraphically higher level, forms biostromes at the top of the Burdekin Formation and micro-atolls at the basal part of the Cultivation Gully Formation in the Fanning River and Horse Shoe Bend areas. These micro-atolls formed by coral polyps continuously growing around the margin of the tabular shaped colonies, as the invading algae and siliciclastic sediment suppressed the polyps in the central region of the colony. Studies of modern coral micro-atolls growing on the Great Barrier Reef (Scoffin & Stoddart 1978) indicated that the dead, flat central surface of micro-atolls reflects approximately the water/air interface. Fossil records of these micro-atolls formed by corals (Webby *et al.* in press) and *Chaetetes* (Connolly *et al.* 1989) are useful indicators of very shallow water deposition developed near the boundary between subtidal and peritidal (intertidal) zones.

Fasciculate corals were mainly developed in depressions and grooves on the sea floor or on the lee side of biostromes or bioherms reflecting more or less protected, low energy environments (Tab. 2). They were most important forms during the colonizing stage of the establishment of the carbonate factory in the basin, such as *Dendrostella trigemme, Fasciphyllum immersum*, and *Centristela* sp. in the inner shelf setting. More delicate branching forms like *Cladopora, Aphyllum salmoni*, and *Planetophyllum* sp. were typically more offshore, very abundant in the mid-outer shelf setting (Fig. 4). Fasciculate forms had a faster growth rate and a higher reproduction rate of both budding and planulae to cope with frequent, mainly storm-generated destruction. However, *F. immersum* colonies intergrowing with large domal skeletons of stromatoporoids were also common in relatively high energy environments of bioherms and biostromes. Forms like *Dendrostella trigemme, Disphyllum (D.)* sp., and *Sociophyllum irregulare* can also form wave resistant, domal or hemispherical colonies in the environments with moderate water turbulence by means of developing shorter, closely spaced corallites, evidenced by the *D. trigemme–Disphyllum (D.)* sp./stromatoporoid biostromes developed at the lower part of the Burdekin Formation in the Fanning River area. Branching forms characterised by lack of dissepiments and by having widely spaced tabulae and a wide, flat-bottom calice, as typical *Dendrostella trigemme* and *Aphyllum salmoni*, might have much faster growth rate than those with a wide dissepimentarium consisting of small dissepiments and a tabularium of the incomplete, closely spaced tabellae, as typical *Acanthophyllum* and *Dohmophyllum* of solitary forms. This assumption is further supported by the very abundant occurrences of segments of these

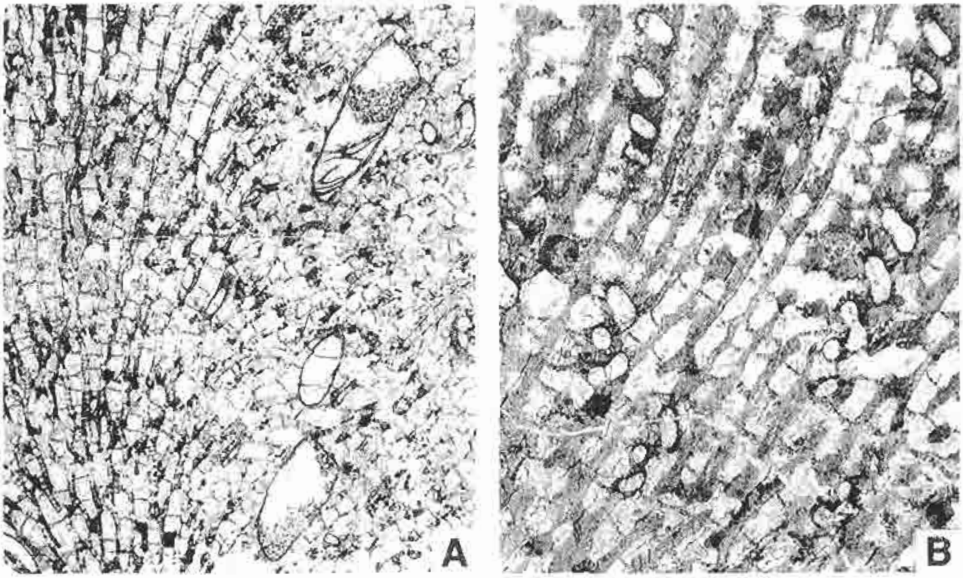

Fig. 10. ❑A. *Torquaysalpinx* sp. in *Alveolites* sp. 1: UQF78757 from UQL5462-1, Three Mile Creek, Burdekin Formation, Givetian, × 6. ❑B. *Helicosalpinx* sp. in *Alveolites* sp. 2: UQF77943 from UQL5425-4, Big Bend, Burdekin Formation, Givetian, × 10.

fasciculate corals in the Burdekin Formation. They often form distinctive marker beds as spaghetti rock, but preservation in their life position is much less common. The spacing between horizontal elements (tabulae and dissepiments) in corals corresponds to periods of active skeletal secretion and growth, and the horizontal elements themselves represent periods of pauses in their growth (Wells 1969). The alternation between active and inactive periods of the skeletal secretion might be due to the results of polyp response to some environmental periodicity, such as season, tide or surface light.

Many genera of the family Pachyporidae of Tabulata, represented by *Cladopora* and *Thamnopora* in the Fanning River Group, are characterised by their slender branching growth form and by budding consistently, coming out from the axial area of each individual branch (Fig. 5F, G). The young polyps grew straight upwards along the growing axis and then diverged laterally in various angles, which are important characteristics in defining the genera or species of this group. Compared with massive forms, the polyps of these branching forms had a much shorter life span. Their growth or secretion of skeleton was suspended soon after they were completely overlain vertically by other younger corallites. This accelerated and speedy reproduction and growth scenario made them possible to keep up with fast depositional rate. Therefore these branching forms had a much faster net vertical growth rate (Tab. 2) than other growth forms.

Some coral species of the Fanning River Group show wider morphological variability than others in respect of growth form and corallite size. In

Tab. 2. Relationships between coral growth form, growth rate, and some environmental parameters to which the corals could be adapted.

Growth form		**Taxonomic form**	**Vertical growth**	**horizontal growth**	**V : H**	**Water turbulence**	**Depositional rate**
Solitary	discoid	Rugosa	slow	fast	<0.2	moderatly high-medium	moderatly low
	patellate	Rugosa	slow	fast	0.2–0.4	moderatly high-medium	moderatly low
	turbinate	Rugosa	moderate	moderate	0.4–1.0	medium	medium
	trochoid	Rugosa	moderate	moderate	1.0–1.5	medium	medium
	ceratoid	Rugosa	fast	slow	>1.5	moderatly low	moderatly high
	cylindrical	Rugosa	fast	slow	>3.0	moderatly low	high
Compound	encrusting	Tabulata	slowest	fastest	<0.1	high	low
	laminar & tabular	Rugosa & Tabulata	slow	fast	0.1–0.3	high-moderatly low	low
	domal & hemispheric	Rugosa & Tabulata	medium	medium	0.3–0.6	medium	medium
	irregular & massive	Rugosa & Tabulata	medium	medium	0.5–1.5	medium	medium
	spherical	Rugosa & Tabulata	medium	medium	0.6–2.0	medium	medium
	robust branching	Rugosa & Tabulata	fast	slow	>2.0	medium-low	medium-high
	delicate branching	Rugosa & Tabulata	fast	slow	>5.0	low	high

the pioneer stage of the establishment of the carbonate factory, for instance, *Pseudomicroplasma australe* is straight or slightly curved, normally small with turbinate to trochoid forms characterised by rapid, lateral growth. In low energy environments, they are subcylindrical or cylindrical. These cylindrical forms were oriented vertically, with their proximal part slowly sinking into the sediment, concurrent with weight increase during growth (Elias 1984; Neuman 1988). Scolecoid forms indicate frequent overturning or rolling in the life time due to current or wave action. Geniculate specimens show that they survived by being able to grow upwards after overturning. *Alveolites* coralla are thin, and plate-like when associated with solitary coral dominated associations. These thin plates with large surface area just above the soft substrate could effectively prevent colonies from sinking into the sediments (Laboute 1988). Ramose forms of *Alveolites* are most commonly associated with fasciculate corals, whereas massive and encrusting forms of *Alveolites* played an important role in the construction of biostromes and bioherms. Phaceloid–subcerioid endophylloids with calical expansions, such as *Sanidophyllum* and *Blysmatophyllum*, were common in muddy, nearshore environments forming coral biostromes. Calical expansions were particular to this group and counteractive to the turbidity of the muddy or sandy sediments, and were also a rather effective way to provide a substrate for their new offsets in the unfavourable muddy environments.

Most solitary forms had a wider range of adaptability in the development of the carbonate factory of the Fanning River Group, and could tolerate soft or mobile substrata. Solitary corals, especially those small horn-shaped forms (Fig. 5B–C, E), were most important elements in the pioneer rugose coral communities and in the conclusive phase of regression. In the lower part of the Burdekin Formation and the basal part of the Cultivation Gully Formation, they are very abundant with high diversity. These solitary corals with a liberosessile life strategy (Neuman 1988) were rather competitive forming clusters on the soft or mobile substrata. For example, *Calceola sandalina* (Fig. 6B) is a typical free-living species that needed no hard support (Stolarski 1993).

Rejuvenescence constrictions are very common in many solitary rugose corals of the pioneer community of the Fanning River Group, such as *Pseudomicroplasma australe*, *Charactophyllum*, *C. (Spinophyllum)*, and *Temnophyllum*, and are typically more prominent in the proximal part of corallites (Fig. 5E). They might represent the dormant stages of normal calcification of the polyps, and periods of siltation. Pandolfi (1984) suggested that rejuvenescence was directly correlated with the physical environment and was in response to rapid sedimentation. In some specimens rejuvenescence constrictions were mainly induced by changing of growth direction when corals fell over and continued upwards growth (Neuman 1988). Most solitary rugose corals of the *Grypophyllum–Chostophyllum* association have deep V-shaped calicular floor, such as *Chostophyllum* sp. (Fig. 5C). Based on the study of recent scleractinian corals, Hubbard & Pocock (1972) suggested that a deep V-shaped calicular floor may help the polyp to reject sediments better than a flat floored calice (Fig. 5D), since V-shaped calicular floor has two sets of highly efficient muscle tissues. In contrast, a planar floor form has muscle tissue perpendicularly attached to it. Therefore it is inefficient in sediment rejection. Flat floored calices are common in the *Dendrostella trigemme* and *Aphyllum salmoni* associations.

The coral growth rate and its logical relationships with water turbulence and depositional rate are summarized in Tab. 2 based on the studies of recent and fossil corals (Chappell 1980; Różkowska 1980; Hallock 1988; James & Bourque 1992). Generally speaking, the growth of corals can be subdivided into net vertical growth and horizontal growth. The growth form is theoretically the expression of different ratios or combinations of the growth rates in the vertical and horizontal directions, varying from cylindrical or slender branching forms at one end to the encrusting or laminar forms at the other (Chappell 1980). In case of solitary rugose corals, cylindrical or subcylindrical forms show predominantly vertical growth, while discoid or patellate forms were the results of predominantly horizontal growth. The compound forms of rugose and all tabulate corals are more complicated in respect of their growth form, but they have a similar scenario with fasciculate or slender branching forms showing predominantly vertical growth and with laminar or encrusting forms showing predominantly horizontal growth.

Obviously the vertical growth rate could be accelerated or promoted by means of reducing the total covering area if polyps try to catch up with rising sea level or with relatively faster depositional rate, to avoid being drowned or buried. When the vertical growth is stagnated especially in the shallow, high energy environments, coral polyps intend to grow laterally by means of an increase of the covered area. In the other words, slender branching corals with high profile typically inhabited the areas of relatively deeper or protected, low energy environments, where the depositional rate was normally faster. Laminar or encrusting forms were more competitive in the shallow, high energy environments, with robust branching, spherical, hemispherical, massive and domal forms typical for various transitional environments in between. Micro-atolls were formed, when polyps grew only around the lateral margin of the colonies to form a rimmed edge and concave central area.

Conclusions

Growth forms of rugose corals in the Fanning River Group are important environmental indicators, since coral distribution was ecologically controlled. Solitary forms could tolerate soft, previously barren substrata and most of them have broad geographical distribution. Fasciculate forms flourished in the low energy, relatively deeper water or protected environments, and sustained the hydrodynamic destruction by their faster growth and higher reproduction rates. Massive corals formed biostromes in medium-high energy, shallow water environments and were major framework builders. Corals of dominantly massive forms including the *Australophyllum–Sanidophyllum* association in the Kirkland Downs area, *Blysmatophyllum–Iowaphyllum* association in the Boundary Creek area, and *Spongophyllum* association in the Lime Creek area formed biostromes fringing the north and northwestern margins of the basin. These communities, characterised by the abundant large massive forms and by the higher ratio of endemic elements, developed during the maximum flooding of the transgression in the basin.

The coral faunas demonstrate that the transgression reached the maximum development during the early Givetian (Zhen & Jell in press), with coral and stromatoporoid biostromes widely expanding towards previous nearshore areas. In the areas around north and northwestern margin of the basin (Kirkland Downs, Boundary Creek, and Lime Creek), biostromes developed in an inner shelf setting during the maximum flooding of the basin form the major part of the Burdekin Formation succession. In the depositional centre, two biostromal units developed in the similar inner shelf setting can be recognised in the Burdekin Formation succession. The lower biostromal unit mainly formed by the stromatoporoids in the Big Bend and Fletch View areas and by corals (mainly *Dendrostella trigemme* and *Disphyllum* sp.) and stromatoporoids in the

Fanning River area during the transgressive phase of the basin. The upper biostromal unit developed in the early regressive phase, with *Endophyllum columna* colonies forming the framework was only recognised in the Fanning River area. The succession stratigraphically between these two biostromal units in these areas was mainly deposited in relatively deeper water, mid-outer shelf environments (Fig. 4).

The influx of terrestrial clastics was the most destructive factor for the functioning of the carbonate factory. Rugose corals were more adaptable than stromatoporoids and generally better able to survive in unfavourable environments with sand or mud influx, and formed small biostromes in shallower, nearshore, sandy environments, e.g. in the Boundary Creek area and in the lower part of the Cultivation Gully Formation in the Fanning River-Horse Shoe Bend area, while stromatoporoids were mainly distributed in the more offshore areas away from influx of terrigenous material.

Corals, as well as algae and stromatoporoids, provided major sources for the carbonate sediment of the Fanning River Group. The carbonate deposition initiated from the wide spreading of *Grypophyllum–Chostophyllum* association, through colonizing phase characterised by widely distributed fasciculate corals in the topographic lows and massive coral-stromatoporoid biostromes and bioherms on the topographic highs, and finally reached its climax phase during the maximum flooding of the basin. Carbonate deposition was suspended when erosion of exposed shelf, resulting from the regression in the region, brought a large quantity of clastics into the depositional area.

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References

Bjerstedt, T.W. & Feldmann, R.M. 1985. Stromatoporoid paleosynecology in the Lucas Dolostone (Middle Devonian) on Kelleys Island, Ohio. *Journal of Paleontology* **59**, 1033–1061.

Chamberlain, S. 1978. Mechanical properties of coral skeleton: compressive strength and its adaptive significance. *Paleobiology* **4**, 419–435.

Chappell, J. 1980. Coral morphology, diversity and reef growth. *Nature* **286**, 249–252.

Connolly, W.M., Lambert, L.L., & Stanton, R.J. 1989. Palaeoecology of lower and middle Pennsylvanian (Middle Carboniferous) *Chaetetes* in North America. *Facies* **20**, 139–168.

Copper, P. 1988. Ecological succession in Phanerozoic reef ecosystems: Is it real? *Palaios* **3**, 136–152.

Elias, R.J. 1984. Paleobiology of solitary rugose corals, Late Ordovician of North America. *Palaeontographica Americana* **54**, 533–537.

Graus, R.R., Chamberlain, J.A., & Boker, A. 1977. Structural modification of corals in relation to waves and currents. In: S.H. Frost, M.P. Weiss, & J.B. Saunders (eds) Reefs and related carbonates-ecology and sedimentology. *Studies in Geology, American Association of Petroleum Geologists* **4**, 135–153.

Hallock, P. 1988. The role of nutrient availability in bioerosion: consequences to carbonate build-ups. *Palaeogeography, Palaeoclimatology, Palaeoecology* **63**, 275–291.

Hallock, P. & Schlager, W. 1986. Nutrient excess and the demise of coral reefs and carbonate platforms. *Palaios* **1**, 389–398.

Hill, D. 1942. The Middle Devonian rugose corals of Queensland (3): Burdekin Downs, Fanning River and Reid Gap, north Queensland. *Proceedings of the Royal Society of Queensland* **53**, 229–68.

Hubbard, J.A.E.B. & Pocock, Y.P. 1972. Sediment rejection by recent scleractinian corals: a key to palaeo-environmental reconstruction. *Geologische Rundschau* **61**, 598–626.

Jack, R.L. & Etheridge, R. Jr. 1892. Geology and palaeontology of Queensland and New Guinea. *Geological Survey of Queensland Publication* **92**, 1–768.

Jackson, J.B.C. 1977. Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. *American Naturalist* **111**, 743–767.

James, N.P. & Bourque, P.-A. 1992. Reefs and mounds. In: R.G. Walker & N.P. James (eds) *Facies Models: Response to Sea Level Change*, 323–347. Geological Association of Canada, Ontario.

Johes, B. & Desrochers, A. 1992. Shallow platform carbonates. In: R.G. Walker & N.P. James (eds) *Facies Models: Response to Sea Level Change*, 277–301. Geological Association of Canada, Ontario.

Johnson, D.P., Belperio, A.P., & Hopley, D. 1986. A field guide to mixed terrigenous-carbonate sedimentation in the central Great Barrier Reef Province, Australia. *Australasian Sedimentologists Group Field Guide Series No. 3*, 173 pp. Geological Society of Australia, Sydney.

Kershaw, S. 1987. Stromatoporoid-coral intergrowths in a Silurian biostrome. *Lethaia* **20**, 371–380.

Laboute, P. 1988. The presence of scleractinian corals and their means of adapting to a muddy environment. *Proceedings of the 6th International Coral Reef Symposium, Australia, 1988, vol. 3*, 107–111. Townsville.

Lang, S.C., Fleming, P.J.G., Jell, J.S., Zhen, Y.Y., & Cook, A. 1990. The Devonian–Carboniferous intracratonic Burdekin Basin, north Queensland: I. Carbonate-siliciclastic facies of the Fanning River Group. *Proceedings, Pacific Rim Congress 1990, Volume III*, 621–630. Australasian Institute of Mining and Metallurgy, Melbourne.

Leichhardt, L. 1847. *Journal of an Overland Expedition in Australia, from Moreton Bay to Port Essington, a Distance of Upward of 3000 miles, During the Years 1844–5*. 544 pp. Boone, London.

Levinton, J.S. 1970. The paleoecological significance of opportunistic species. *Lethaia* **3**, 69–78.

Logan, B.W. 1984. Pressure responses (deformation) in carbonate sediments and rocks analysis and application, Canning Basin. In: P.G. Purcell (ed.) *The Canning Basin, W.A.*, 235–251. Proceedings GSA/PESA Canning Basin Symposium, Perth, 1984.

Maxwell, W.G.H. 1968. *Atlas of the Great Barrier Reef*. 258 pp. Elsevier, Amsterdam.

Mistiaen, B. 1984. Comments on the caunopore tubes: stratigraphic distribution and microstructure. *Paleontographica Americana* **54**, 501–508.

Mori, K. 1970. Stromatoporoids from the Silurian of Gotland, part II. *Stockholm Contributions in Geology* **22**, 1–152.

Neuman, B.E.E. 1988. Some aspects of life strategies of Early Palaeozoic rugose corals. *Lethaia* **21**, 97–114.

Noble, J.P.A. 1970. Biofacies analysis, Cairn Formation of Miette Reef Complex (Upper Devonian) Jasper National Park, Alberta. *Bulletin of Canadian Petroleum Geology* **18**, 493–543.

Pandolfi, J.M. 1984. Environmental influence on growth form in some massive tabulate corals from Hamilton Group (Middle Devonian) of New York State. *Palaeontographica Americana* **54**, 538–542.

Różkowska, M. 1980. On Upper Devonian habitats of rugose corals. *Acta Palaeontologica Polonica* **25**, 597–611.

Scoffin, T.P. & Stoddart, D.R. 1978. The nature and significance of microatolls. *Philosophical Transactions of the Royal Society of London* **B284**, 99–122.

Stearn, C.W. 1982. The shapes of Paleozoic and modern reef-builders: a critical review. *Paleobiology* **8**, 228–241.

Stolarski, J. 1993. Ontogenetic development and functional morphology in the early growth stages of *Calceola sandolina* (Linnaeus, 1991). *Courier Forschungsinstitut Senckenberg* **164**, 169–177

Webby, B.D., Zhen, Y.Y., & Percival, I.G. (in press). Ordovician coral- and sponge-bearing associations: distribution and significance in valcanic island shelf to slope habitats, eastern Australia. *Proceedings of Seventh International Symposium on Fossil Cnidaria, 1995, Madrid.*

Weedon, M.J. 1991. Microstructure and affinity of the enigmatic Devonian tubular fossil *Trypanopora*. *Lethaia* **24**, 227–234.

Wells, J.W. 1969. The formation of dissepiments in Zoantharian corals. In: K.S.W. Campbell (ed.) *Stratigraphy and Palaeontology: Essays in honour of Dorothy Hill*, 17–26. Australian National University Press, Canberra.

Withnall, I.W., Lang, S.C., Jell, J.S., McLennan, T.P.T., Talent, J.A., Mawson, R., Fleming, P.J.G., Law, S.R., Macansh, J.D., Savory, P., Kay, J.R., & Draper, J.J. 1988. Stratigraphy, sedimentology, biostratigraphy and tectonics of the Ordovician to Carboniferous, Broken River Province, north Queensland. *Australasian Sedimentologists Group Field Guide Series No.5*. 200 pp. Geological Society of Australia, Sydney.

Withnall, I.W. & Lang, S.C. 1990. Tectonic history of the Palaeozoic Broken River Province, north Queensland. *Proceedings, Pacific Rim Congress 1990, Volume II*, 315–323. Australasian Institute of Mining and Metallurgy, Melbourne.

Wyatt, D.H. & Jell, J.S. 1980. Devonian and Carboniferous stratigraphy of the northern Tasman orogenic zone in the Townsville Hinterland, north Queensland. In: R.A. Henderson & P.J. Stephenson (eds) *The Geology and Geophysics of Northeastern Australia*, 201–228. Geological Society of Australia, Queensland Division, Brisbane.

Young, G.A. & Noble, J.P.A. 1989. Variation and growth of a syringoporid symbiont species in stromatoporoids from the Silurian of eastern Canada. *Memoir of the Association of Australasian Palaeontologists* **8**, 91–98.

Zhang, Z. 1981. *Early to Middle Devonian stratigraphy and tabulate coral faunas from western part of South Qinling Range*. 208 pp. Science Press (Beijing). [in Chinese]

Zhen, Y.Y. 1991. *Devonian rugose coral faunas and biostratigraphy of the Fanning River Group, north Queensland*. Ph.D. thesis, University of Queensland.

Zhen, Y.Y., Lang, S.C., & Jell, J.S. 1993. A new biostratigraphic framework and lithostratigraphic nomemclature for the Devonian Fanning River Group, Burdekin Basin, north Queensland. *Queensland Government Mining Journal* **94**, 7–14.

Zhen, Y.Y. 1994. Givetian rugose corals from the northern margin of the Burdekin Basin, north Queensland. *Alcheringa* **18**, 301–343.

Zhen, Y.Y. 1995. Late Emsian rugose corals of the Mount Podge area, Burdekin Basin, north Queensland. *Alcheringa* **19**, 193–234.

Zhen, Y.Y. & Jell, J.S. (in press) Middle Devonian rugose corals from the Fanning River Group, north Queensland, Australia. *Palaeontographica* **A**.

Streszczenie

Kopalny zapis środkowodewońskiejj transgresji morskiej (maximum we wczesnym żywecie) w północnej części stanu Queensland pozwala na prześledzenie sukcesji zespołów koralowców w miarę rozwoju i zaniku zbiornika morskiego. Pierwsze korale pojawiły się w tym regionie podczas sedymentacji wapnistych piaskowców w stropie Big Bend Arkose. Dominują w tym zespole pojedyncze korale *Grypophyllum* i *Chostophyllum*; występuje tam również swobodnie leżąca na dnie *Calceola*. Jest to epoka największego zróżnicowania gatunkowego korali, ale większość z nich to formy pojedyncze, z niewielkim udziałem gałązkowych. Pełnomorskim warunkom niewątpliwie odpowiada nadległa formacja Burdekin, sięgająca 500 m miąższości. Udział korali pojedynczych zmniejsza się stopniowo (wraz z tym i zróżnicowanie taksonomiczne zespołów), pojawiają się natomiast masywne kolonie. Biostromy z koralami i stromatoporami rozprzestrzeniały się w jej trakcie ku obszarom uprzednio przybrzeżnym. Stadium transgresywne reprezentuje dolna część formacji z koralami *Dendrostella trigemme* i *Disphyllum*; stadium regresywne część górna z koloniami *Endophyllum columna*; w obydwu spory udział mają korale o masywnych koloniach. Pośrodku występuje zespół maximum transgresji zdominowany przez korale pojedyncze i gałązkowe. Korale, glony i stromatopory były głównym źródłem osadu wapiennego. Zapis regresji kontynuuje nadległa formacja Cultivation Gully, złożona z wapiennych mułowców, łupków i drobnoziarnistych piaskowców, odpowiadająca stosunkowo szybkiej fazie regresywnej. Dopływ terrygenicznego materiału klastycznego był głównym czynnikiem, który doprowadził do zaniku sedymentacji węglanowej na szelfie. Korale czteropromienne stosunkowo lepiej od stromatopor znosiły dopływ piasku i mułu, tworząc małe biostromy nawet w płytkich przybrzeżnych środowiskach piaszczystych.