



STROMATOPOROID PALAEOECOLOGY IN THE FRASNIAN (UPPER DEVONIAN) BELGIAN PLATFORM, AND ITS APPLICATIONS IN INTERPRETATION OF CARBONATE PLATFORM ENVIRONMENTS

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Abstract: Stromatoporoid faunas in the Frasnian of southern Belgium are abundant in the carbonate platform environments present in this area. Stromatoporoids dominate the large skeletal organisms and occur principally in biostromes. The stromatoporoid assemblage is represented by a small number of taxa. Stromatoporoid genera include *Actinostroma*, *Amphipora*, *Atelodictyon*, *Clathrocoilon*, *Salirella*, *Stachyodes*, *Stictostroma*, *Stromatopora* and *Trupetostroma* which are present in environments ranging from the outer, outer intermediate, inner intermediate and inner zones and associated biostromes. Most large skeletal stromatoporoids are low profile, which reinforces the conclusions of previous studies that low-profile growth forms were the most success-

ful stromatoporoid forms. These low-profile forms are likely to have been important sediment stabilisers that may have led to expansion of the carbonate factory. Growth forms vary between facies, indicating some degree of environmental control on form; for example, laminar in the intermediate zone, bulbous and domical in the inner and outer zones. Stromatoporoid taxa vary in occurrence across the environmental gradient from shallow to deep. There is some taxonomic control on growth forms, with some taxa showing more variability than others in different environments.

Key words: Stromatoporoid, Late Devonian, Frasnian, palaeoecology, platform, biostrome.

THE Devonian Period was a time of intense reef proliferation, and most reefs were characterized by relatively low diversity (Kiessling *et al.* 1999). The Givetian and Frasnian epochs are widely considered to be the most important time periods of stromatoporoid and reef growth worldwide, and the Frasnian is a crucial period for stromatoporoids as they were strongly affected by the Frasnian/Famennian mass extinction (e.g. Hubert *et al.* 2007).

The Belgian Frasnian is characterized by extensive carbonate platform development. Platform geometry was relatively complex and evolved during time, probably from a block-faulted ramp to a shelf carbonate system with well-developed lagoonal deposits. Evolution of the platform is still not fully understood and beyond the scope of this paper. Carbonate platform palaeoenvironments range from mud mounds in the deeper southern basin to shallow-water bedded carbonates in the northern basin. This study focuses mostly on the well-bedded carbonate

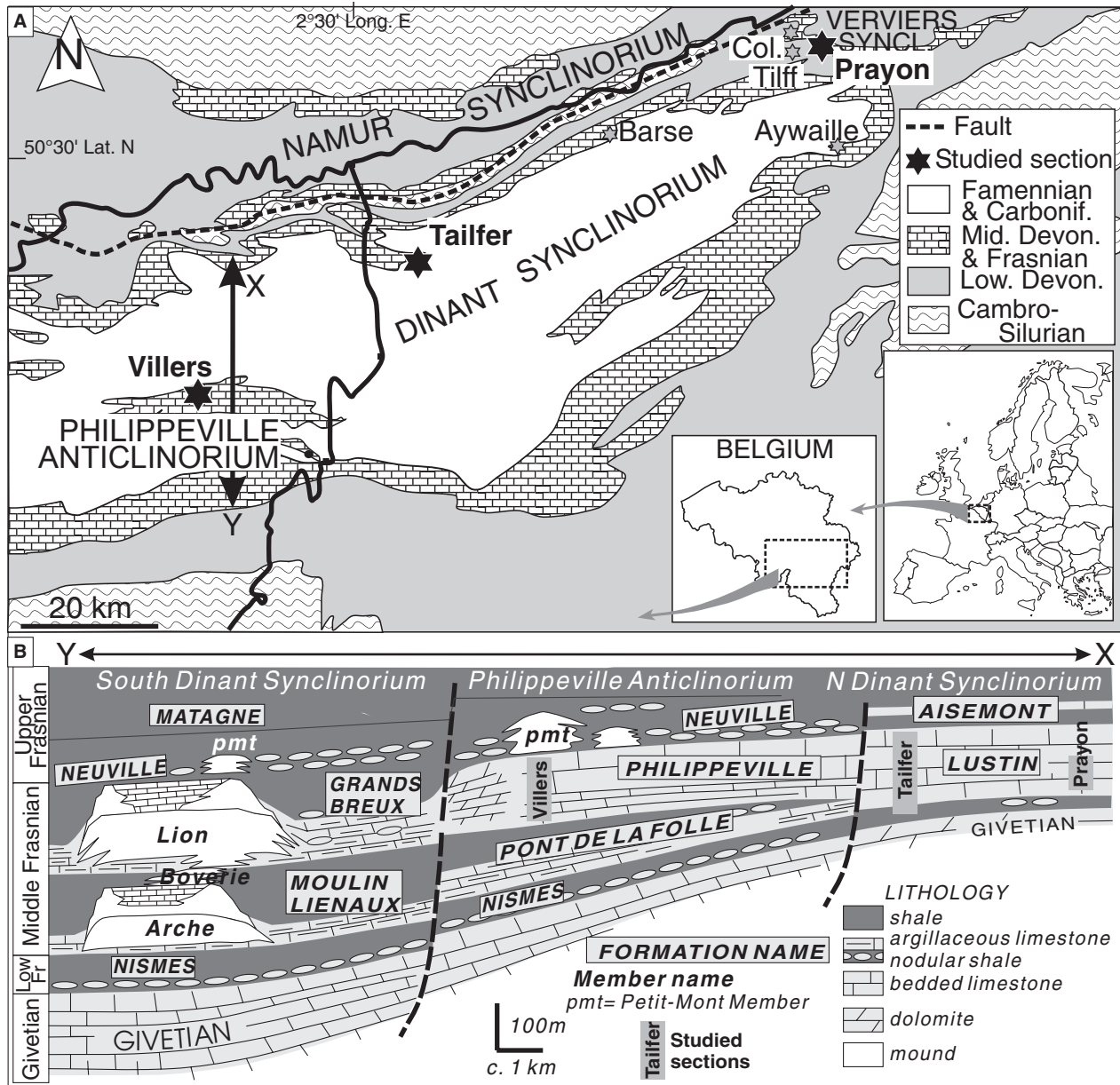
platform, from outer to inner zones (da Silva and Boulvain 2004). The carbonate platform succession is mainly built by fourth-order shallowing-upward sequences, but two main third-order sedimentary shifts are recorded: (1) a transition from mostly argillaceous sediments to the carbonate platform, during the lower Middle Frasnian; (2) the Middle Frasnian is divided by an important sequence boundary leading to the transition from more distal sediment (mostly outer and intermediate) to proximal sediments (with some palaeo-exposure evidences) (da Silva and Boulvain 2004).

The first major study of Devonian stromatoporoids in Belgium was the pioneering taxonomic work of Lecompte (1951, 1952), later developed into an ecological framework by Cornet (1975) who surveyed the distribution of taxa across a range of facies. Stromatoporoids are arguably the most important reef-building fossil in the Frasnian of Belgium. The current paper is built on previous research on stromatoporoids and on a well-developed

sedimentary background, including facies analysis, magnetic susceptibility and isotope studies (da Silva and Boulvain 2002, 2004, 2006, 2008). This paper attempts a comprehensive survey of stromatoporoids in the Frasnian using a large collection of new material from a range of key sites. The aim is to interpret the palaeoecology of stromatoporoids in the study area and apply the interpretations to enhance understanding of the analysis of sedimentary environments of this important period of reef facies development.

GEOLOGICAL SETTING

Southern Belgium belongs to the northern part of the Rhenohercynian fold and thrust belt. Frasnian carbonates and shales are exposed along the borders of the Dinant, Verviers and Namur Synclinoria and in the Philippeville Anticlinorium (Text-fig. 1). The platform can be divided into three main depositional areas characterized by a different facies association, carbonate production rate and sedimentary evolution (da Silva and Boulvain 2006). A



TEXT-FIG. 1. Geological setting of the Frasnian of Belgium. A, geological map with studied outcrop locations. Those sites sampled in this study are shown by black stars; additional sites referred to in the text are shown by grey stars (Col. corresponds to the Colonster section). B, North–South section of the Frasnian basin before Variscan deformation, with the different Formations and Members (section X–Y from Text-Fig. 1A).

brief description of this features and geological history is given here, as background to the stromatoporoid analysis.

During the Middle Frasnian, the most distal part of the platform was located along the southern border of the Dinant Synclinorium, the intermediate zone corresponds mainly to the Philippeville Anticlinorium and the shallowest zone crops out in the northern part of the Dinant Synclinorium, the Namur Synclinorium and the Verviers Synclinorium.

The southern border of the Dinant Synclinorium is characterized by carbonate mound sedimentation with associated flank and off-mound facies. Carbonate mounds occurred at three levels during the Middle Frasnian, and are in ascending order the Arche, La Boverie and Lion Members belonging to the Moulin Liénaux (Arche and Boverie mounds) and Grands Breux (Lion mound) Formations (Text-fig. 1B; Boulvain 2007).

In the Philippeville Anticlinorium, the carbonate mound-bearing levels were replaced by shales and argillaceous limestones (Pont-de-la-Folle Formation) followed by bedded limestone consisting of open-marine facies and biostromes (Philippeville Formation) (Text-fig. 1B; Boulvain *et al.* 1999).

Along the northern border of the Dinant Synclinorium and the Verviers Synclinorium, the Middle Frasnian is represented by the Lustin Formation (Text-fig. 1B), which consists of bedded limestones, exhibiting a distinct proximal aspect with lagoonal facies and paleosols (da Silva and Boulvain 2002, 2004).

The outcrops studied here are, from the shallowest position to the deepest, as follows: Prayon (Lustin Formation, Verviers Synclinorium), Tailfer (Lustin Formation, northern border of the Dinant Synclinorium) and Villers (Philippeville Formation, Philippeville Anticlinorium) (Text-fig. 1B). Biostromes are numbered on the different sections, and these biostrome numbers will be used in the text (Text-fig. 2, Villers biostromes: V1 to V4; Tailfer biostromes: T1 to T15 and Prayon biostromes: P1 to P7).

MATERIAL AND METHODS

High-resolution field logging and observation, with detailed sample collection, was accompanied by comprehensive thin-section examination of stromatoporoids and associated sedimentary rock samples, to develop as complete a picture as possible of the distribution and ecology of stromatoporoids. The sampling mode is one sample at least every 50 cm but in the biostromes, a higher density of stromatoporoid samples was collected, to collect a representative number of taxa and growth forms and to collect several samples from each level studied. A total of 695 samples (324 for Tailfer, 88 for Prayon and 283 for Villers) were collected (but not all contained

stromatoporoids), and a total of 2149 stromatoporoids was counted. Two thin sections (longitudinal and tangential) for each specimen were made for identification of the stromatoporoids.

The relationship between growth forms and stromatoporoid species was not always possible to determine. In some cases, samples were collected and stromatoporoids were identified but the external growth form was not determinable because of poor outcrop quality, or because of orientations of stromatoporoids in the outcrop that prevented a clear view of the growth form. In other cases, data on stromatoporoid growth forms were collected, but samples could not be removed from the outcrop for identification.

Biostrome terminology is based on Kershaw (1994) and stromatoporoid growth form terminology on Kershaw (1998). Considering domical and bulbous growth forms, an oblique section of a domical form could be confused with a bulbous form, so these have been classified as domical and bulbous in unequivocal cases and as domical-bulbous (DB) for ambiguous growth shapes.

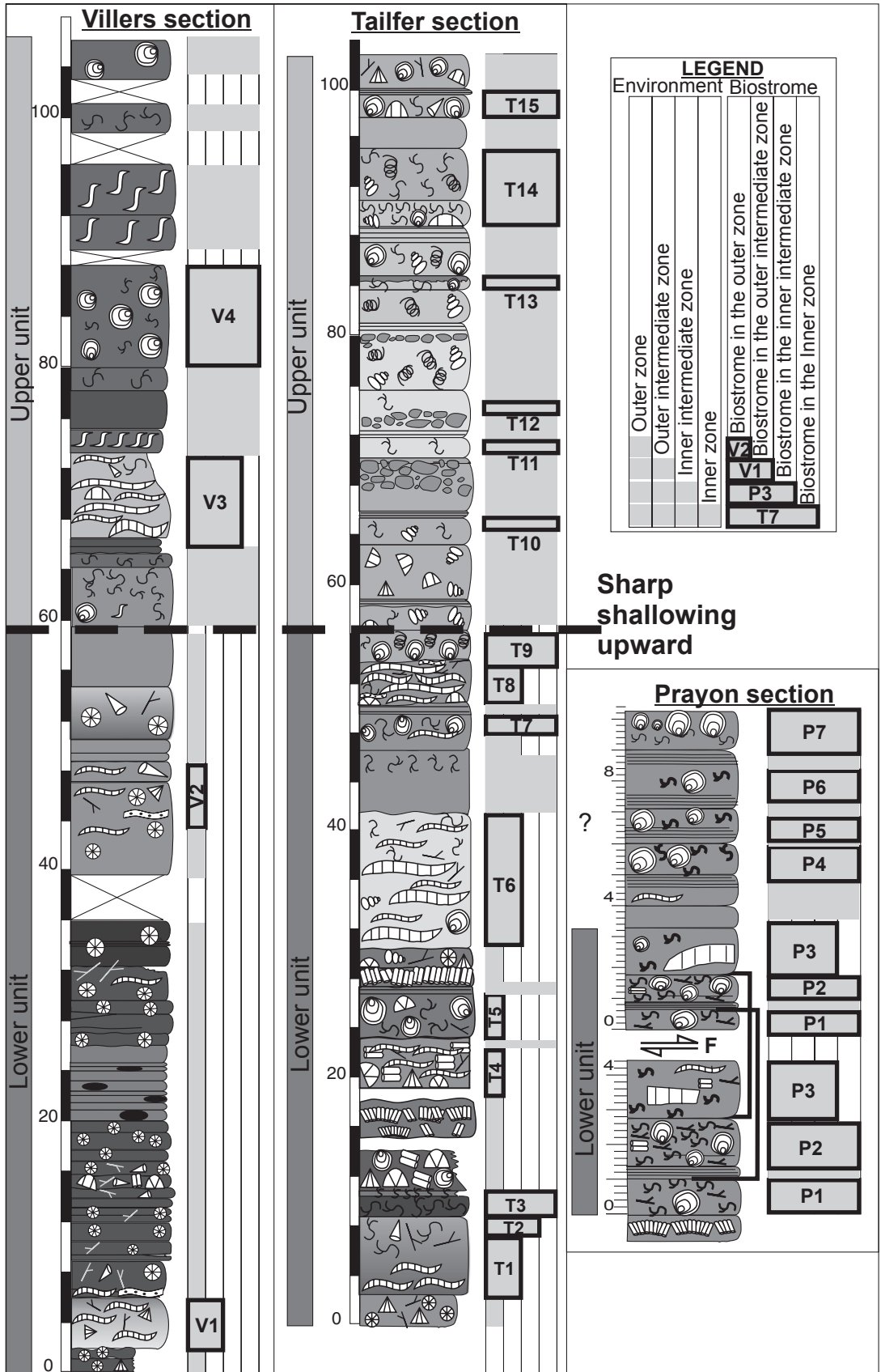
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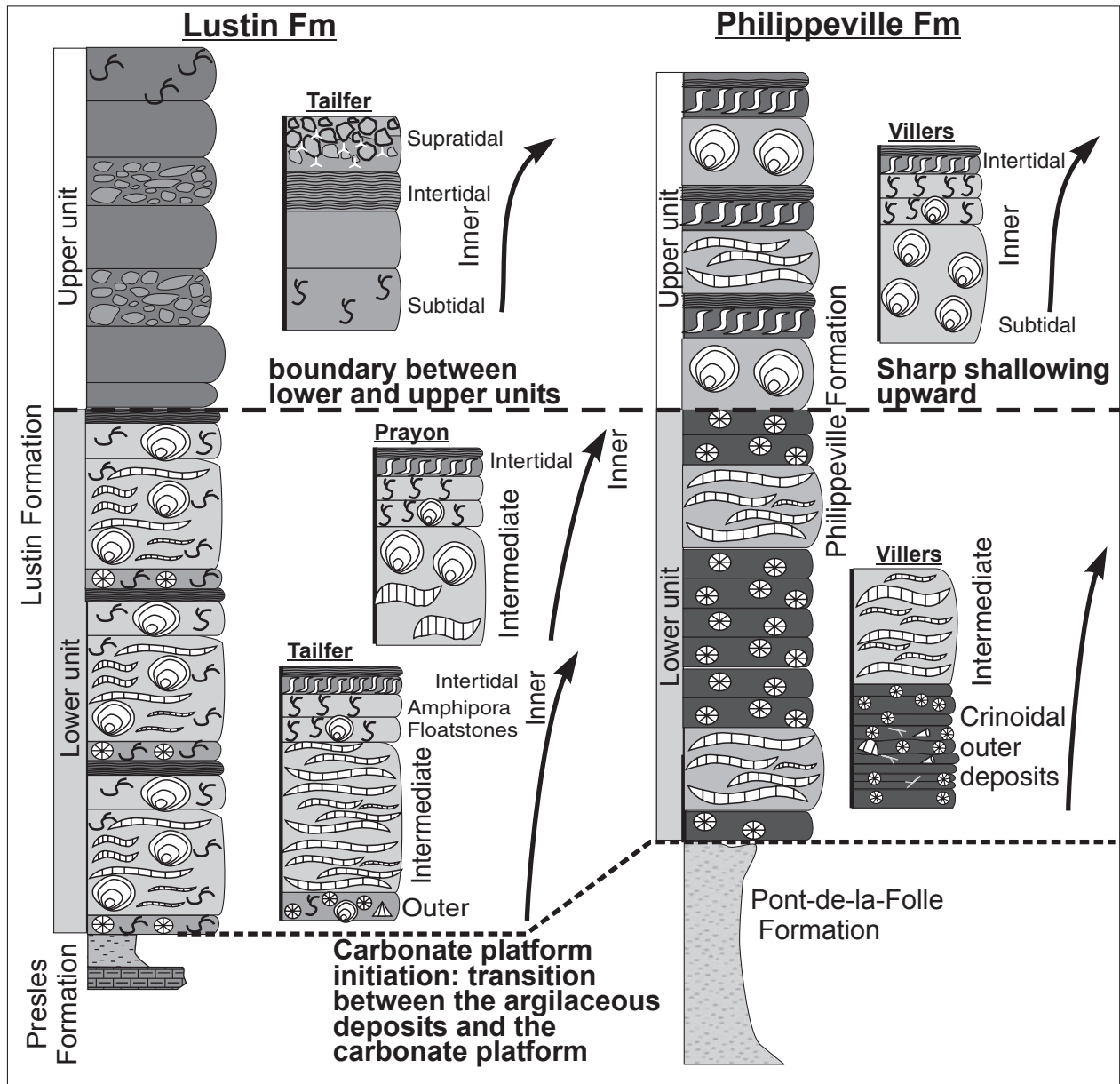
Depositional model and biostromes

In order to place the stromatoporoids in a general environmental setting for palaeoecological analysis, a sedimentological model (Text-fig. 3; da Silva and Boulvain 2004) is summarized below, with particular focus on biostromes. In this sedimentological model, different biostromes and corresponding sedimentary environments are identified and can be distinguished following three main criteria: (1) biostrome classification (Kershaw 1994), composition, geometry, scale and internal bedding; (2) growth morphology of the stromatoporoids and (3) associated fauna. Four zones may be identified as follows:

Inner zone. This zone is dominated by micritic sediment, rich in paleosiphonocladales and peloids; biostromes are developed mostly in the subtidal portions of this zone. Stromatoporoid growth forms are principally branching (abundant *Amphipora*), bulbous and domical. The intertidal facies consists of wackestone and packstone with codiacean algae (*Umbrella*), mudstone with ostracods and laminated grainstone with peloids. The supratidal zone is characterized by strongly brecciated decimetre- to metre-thick intervals cut by desiccation cracks related to paleosols.

Inner intermediate zone. This zone displays a mixing or alternation of characteristics from the inner and outer





TEXT-FIG. 4. Simplified sequence-stacking pattern of the Lustin and Philippeville Formations, with main sedimentological events. For the legend, see Text-Figure 3.

Baird 1996; Elrick 1996; George *et al.*, 1997; Whalen *et al.* 2000; Chen *et al.* 2001). The medium-scale sequences are identified by the stacking of small-scale sequences; they are metre-thick and show both transgressive and regressive trends. They are mainly asymmetric, where most of the thickness of a sequence is regressive, indicative of rapid transgressions, followed by slow regressions. Thus, the stromatoporoid biostromes are most appropriately interpreted as having formed in transgressive to highstand settings. These sequences were interpreted as related to eustatic movements (da Silva and Boulvain 2006). A consistent large-scale sedimentological pattern is recognized

all over the area, over distances of more than 200 km (da Silva and Boulvain 2006). This pattern comprises:

Carbonate platform initiation. This shows transition from argillaceous to carbonate sediments (Text-fig. 4), but not synchronous in the basin. In the northern border of the Dinant Synclinorium, the transition occurs at the boundary between the lower and Middle Frasnian (boundary between Presles and Lustin Formations) and in the Philippeville Anticlinorium, it occurs later, in the lower part of the Middle Frasnian (boundary between Pont-de-la-Folle and Philippeville Formations). Before this transition,

the platform is characterized by argillaceous sediments, with a few carbonate beds with some crinoids and brachiopods. The relatively sharp transition corresponds to the reef-colonization phase (packstone to rudstone with coarse crinoids and tabulate corals) and installation of main biostromal structures (and stromatoporoids).

Sharp shallowing upward. An important facies shift, with a sharp shallowing (Text-figs 2, 4) is observed during the Middle Frasnian, with a transition from the outer to intermediate zones (lower unit, called 'biostromal unit' in da Silva and Boulvain 2006) to mostly inner zones with subaerial exposures (upper unit, called 'lagoonal unit' in da Silva and Boulvain 2006) (Text-fig. 4). In detail, the three sections studied show the following features (see also Text-fig. 2): (1) in the Villers section, the lower unit corresponds to the first 60 m of the section which are built up by outer zone deposits dominated by crinoidal black argillaceous carbonates alternating with biostromes from the intermediate zone. The upper unit presents inner intermediate and inner zone sediments; (2) in Tailfer, the first 55 m of the section are built by fourth-order sequences starting with outer zone crinoidal packstone followed by outer intermediate zone biostromes or starting directly with biostromes. These sequences are capped by inner zone rocks (subtidal or intertidal). The upper unit presents an alternation of inner zone rocks and brecciated levels (paleosols); (3) in Prayon, because of exposure problems it is much more difficult to identify the two units, but comparison can be made with other outcrops in an attempt to locate this section in the Frasnian succession. The Prayon section starts with a *Disphyllum* biostrome and this kind of biostrome is only observed in the lower unit (observations in Tailfer, Tilff, Barse and Aywaille sections in da Silva 2004; location of these sections on Text-fig. 1). Biostrome P3 (Text-fig. 2) is an inner intermediate zone biostrome which belongs to the lower unit. The upper levels (biostromes P4 to P7 on Text-fig. 2) are all inner zone rocks and might belong to both units.

STROMATOPOROID AND PALAEOENVIRONMENTS

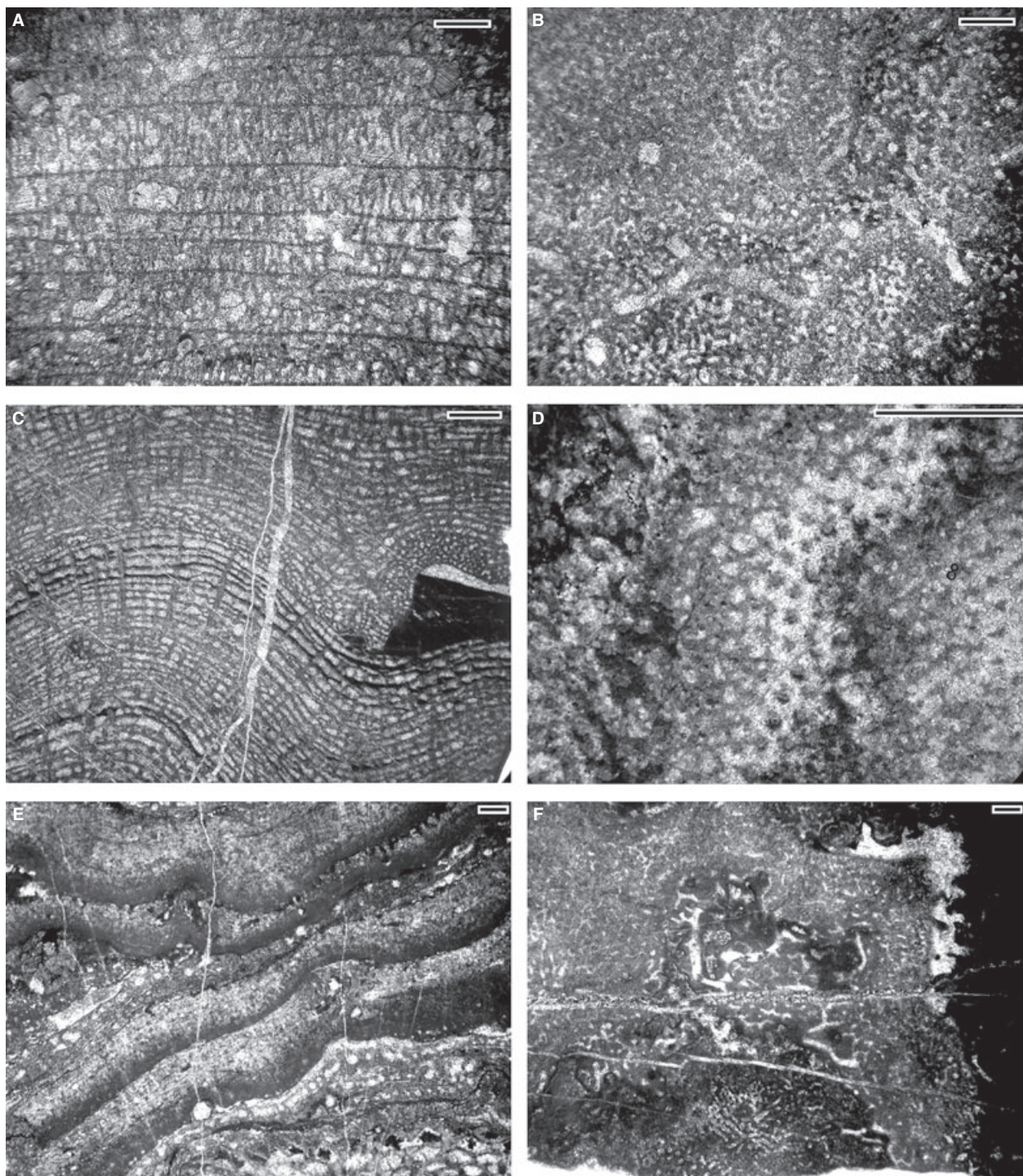
The following genera have been identified in this study: *Actinostroma* (Text-fig. 5C, D), *Amphipora*, *Atelodictyon* (Text-fig. 5A, B), *Clathrocoilona* (Text-fig. 5E, F), *Salairilla* (Text-fig. 7E, F), *Stachyodes* (*Stachyodes australe* (Text-fig. 8A, B) is identified as a separate taxon within this genus, owing to its consistent laminar growth form), *Stictostroma* (Text-fig. 6), *Stromatopora* (Text-fig. 7C, D) and *Trupetostroma* (Text-fig. 7A, B). Stromatoporoid systematics follows the scheme proposed by Stearn *et al.* (1999).

Inner zone

This environment (occurring in the lower and upper units, Text-fig. 2) presents autoparabiostrome to allobiostrome floatstones with matrix dominated by paleosiphonocladales and peloids. The biostromes are interbedded with rocks of intertidal (algal mats) and supratidal origin (paleosols). The most common stromatoporoid (Text-fig. 9), in terms of numbers of specimens is clearly the branching *Amphipora* (which can reach 100 per cent of the stromatoporoid fauna, but note that these are presumed delicate forms found only as fragments), followed by branching *Stachyodes*, *Clathrocoilona*, DB *Actinostroma* and *Stictostroma*. The stromatoporoids are commonly overturned and sometimes broken. DB forms do not exceed 20 cm. In Prayon, they are often strongly altered, overturned, slightly ragged (the raggedness can be asymmetrical) and can be expanded at their tops (examples on Text-fig. 9). Furthermore, overgrowths of the same species or another species in another direction are observed. Encrustations, mostly by *Clathrocoilona*, are very common and occur in almost all species as well as branching tabulate corals (but does not affect *Amphipora* for reasons which are not clear). In some cases, multiple layer encrustation of *Clathrocoilona* can reach more than 10 cm thick. Encrustations are always better developed on one side (i.e. either the upper or lower surface). Intergrown tubes and borings commonly occur in all species except *Amphipora*. *Stictostroma* contains a very large number of intergrown tubes (more than a hundred on an 8-cm sample, example on Text-fig. 8C, D), and there appears to be specific interrelation between these two organisms. The nature of this relationship is not clear from the current samples, so that discriminating between competitive intergrowth, mutualism, commensalism and parasitism cannot be made at present. Full details of the interrelationship between stromatoporoids and corals will be published elsewhere (da Silva *et al.* in press). Borings are present mostly in *Actinostroma* and to a lesser extent in *Stictostroma*, *Clathrocoilona*, *Trupetostroma* and *Stachyodes*.

Inner intermediate zone

The inner intermediate zone deposits formed during the lower unit of Prayon (P3) and Tailfer (T2), and in the upper unit of Villers (V3) (Text-fig. 2); they are characterized by metre-thick autoparabiostromes to allobiostromes presenting intermediate characters between the outer intermediate and inner zones. In Tailfer, this inner intermediate zone is dominated by branching stromatoporoids, in Villers by branching, tabular and laminar stromatoporoids and in Prayon by laminar and tabular



TEXT-FIG. 5. *Atelodictyon*, *Actinostroma* and *Clathrocoilona*. A, *Atelodictyon*, sample V-100'C from Villers locality; longitudinal section showing thin planar continuous laminae, bladelike pillars, which are locally irregularly branched. B, *Atelodictyon*; sample V-100'C from Villers locality; tangential section; showing local labyrinthine galleries. C, *Actinostroma*, sample T-53-13C from Tailfer locality; longitudinal section; thick continuous pillars dominating the structure. D, *Actinostroma*; sample T-53-13C from Tailfer locality; tangential section with colliculi laterally persistent. E, F, *Clathrocoilona*; Sample PrB-24A, from Prayon locality, longitudinal section (E), with thick extensive tissue and stacking of different layers and tangential section (F) showing thick pillars. Scale bar represents 1 mm.

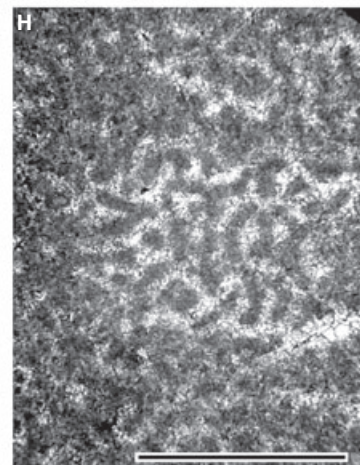
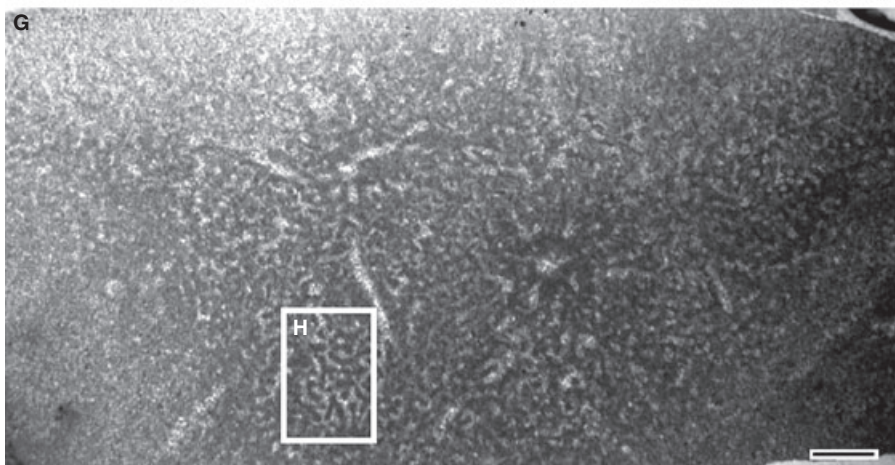
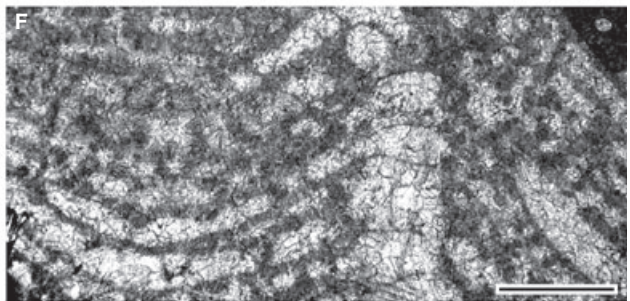
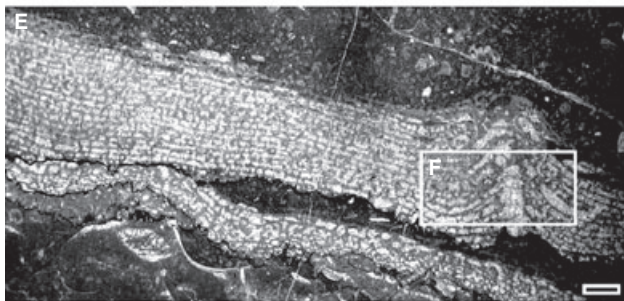
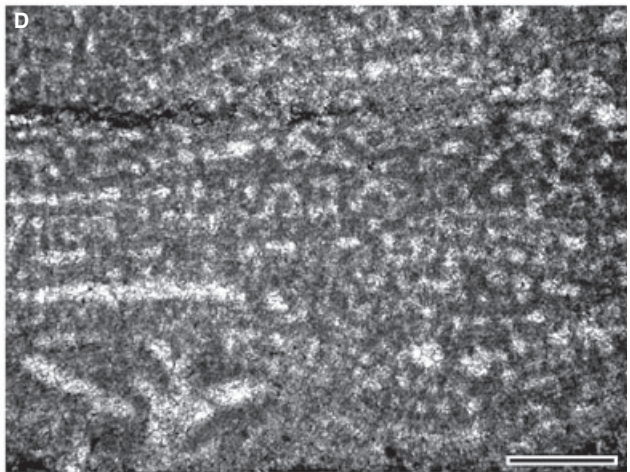
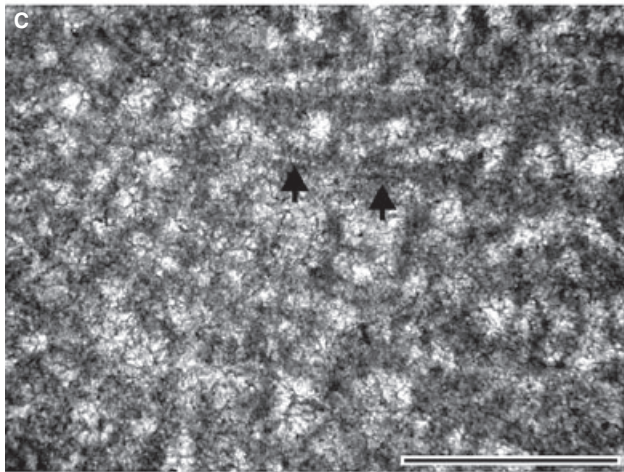
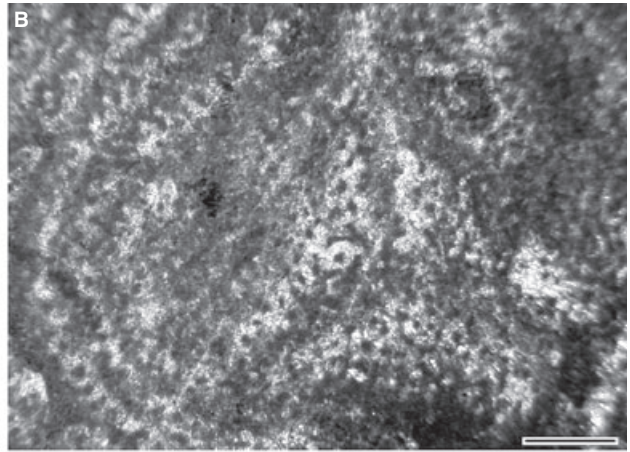
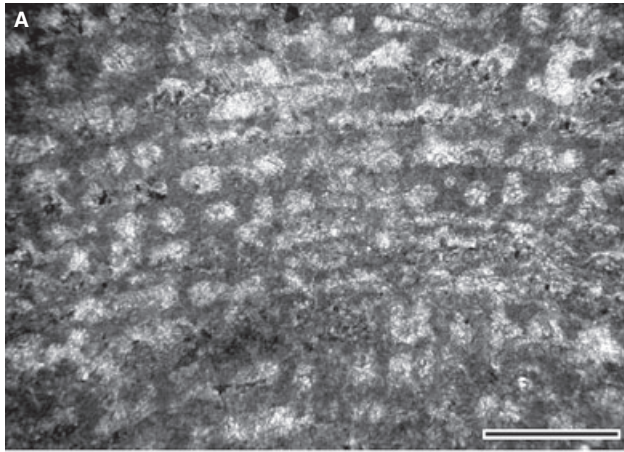
followed by DB growth forms. Branching growth forms are always found lying on their side. The laminar and tabular stromatoporoids are mostly not in place, are commonly overturned and exhibit some broken edges. Ragged margins are uncommon. In summary, in terms of the number of specimens, branching *Stachyodes* is the most abundant stromatoporoid genus in this intermediate zone (Text-fig. 10) and then, depending on the locality, tabular *Actinostroma* or tabular *Trupetostroma* are common, as well as branching *Amphipora*.

Outer intermediate zone

Outer intermediate zone facies are observed in the lower unit of Tailfer (T1, T6 and T8, Text-fig. 2) and Villers (V1, Text-fig. 2). In the Villers section, the laminar stromatoporoid biostromes are interbedded in outer argillaceous black crinoidal beds. In Tailfer, they are interbedded with both outer and inner facies. These auto- to autoparabiostromes are metre to 3-metre-thick beds, with a high content of mud and rare ostracods, and the stromatoporoids are low profile (Text-fig. 11), with some branching skeletons. Other reef builder organisms of this outer intermediate zone are some branching and massive tabulate corals (*Alveolites*), and fasciculate (*Disphyllum*), massive (*Hexagonaria*) or solitary rugose corals. Common other skeletal elements include brachiopods and ostracods (with commonly the two intact valves still in contact), crinoids, and bryozoans.

Three types of biostromes are recognizable:

1. *Biostrome type 1*. Automicrite in which stromatoporoids are uncommon, with very thin laminar *S. australe* and *Stictostroma* (2–5 mm thick, with a few *Stictostroma* reaching cm-thick size). All specimens of *S. australe* are in growth orientation, with no evidence that any have been overturned; therefore, they are considered to be in place. Some samples of *Stictostroma* are in growth position, while others are broken, indicating disturbance, presumably by turbulence. Specimens of both *S. australe* and *Stictostroma* are encrusted by other specimens of either the same or another genus. Both genera also contain growth interruptions, with sediment layers; in some cases, *S. australe* forms an anastomosing laminar fabric with sediment layers. Some primary cavities are observed under the *S. australe*, indicated by some encrusters on their lower surface or by a fibrous early marine cement fringe on the edge of the cavity. These cavities are also typically partly filled by geopetal, microbial, clotted peloids. The substrate on which *S. australe* and *Stictostroma* specimens are found consists of micrite, other stromatoporoids and skeletal debris, suggesting an ability to grow on surfaces of different types. A depositional succession occurs repeatedly in this facies (Text-fig. 12A–C): (1) Brachiopod shells packstone to grainstone; (2) stromatoporoids, *S. australe* and *Stictostroma* level; (3) mud dominated facies, characterized by a high proportion of automicrite, clotted structures, diffuse peloids, mud encrustations and fine micrite. In some case, clotted laminated peloids and micrites have built centimetre-thick mound shapes (Text-fig. 12C). These biostromes are occurring at the basis of Tailfer and Villers sections (biostromes T1 and V1 in Text fig. 2).
2. *Biostrome type 2*. Micrite and laminar and tabular stromatoporoid dominated biostromes: in these biostromes, the proportion of micrite and stromatoporoids is more or less equal. The matrix is generally light grey and rich in small bioclasts or shows a clotted, finely laminated and locally peloidal fabric (Text-fig. 12D–F). Some micritic encrustations are observed (0.2 mm-thick irregular encrustations, mostly around brachiopods, Text-fig. 12E). The stromatoporoids are mostly *Stictostroma* and branching *Stachyodes* with a few *Amphipora* and *Clathrocoelona*. Laminar and tabular *Stictostroma* commonly have well-developed astrorhizal mamelons and can present some more irregular wavy shape; they can also present a ragged outline, irregular shape and interruptions of growth with internal sediment and/or cement (examples on Text-fig. 11). The maximum thickness of these low-profile stromatoporoids is around 10 cm. Organisms are commonly well preserved, but some debris is also present. Biostrome type 2 occurs in Tailfer section (biostrome T6 in Text-fig. 2).
3. *Biostrome type 3*. Stromatoporoid (40–50% of the rock and mm- to cm- thick) floatstone associated with a few tabulate corals. Stromatoporoids are almost entirely laminar (98% of specimen numbers) with rare encrusting growth shapes. *Stictostroma* is the most abundant (82 per cent by number of specimens). Astrorhizal mamelons are frequent and face upwards as well as downward, corresponding to in life position and overturned stromatoporoids (Text-fig. 13A). Pressure solution is abundant on the edge of laminar stromatoporoids, so it is difficult to consider their preservation state, but they rarely seem broken. A decimetre-thick alternation is observed, of mostly in place structures (facing the right way up laminar stromatoporoids, with clotted mud) alternating with reworked structures (facing upward and downward stromatoporoids, with stromatoporoids and tabulate corals debris) (Text-fig. 13A). Some laminar stromatoporoids show interruptions of growth with sediment layers and ragged margins (examples on Text-fig. 11). Biostrome type 3 occurs in Tailfer section (biostrome T8 in Text-fig. 2).



The three types of biostromes started mostly on calcareous gravels (example of type 3 biostrome base is shown in Text-fig. 13B) and after the basal colonization phase, stromatoporoids mostly grew on muddy substrate. In this zone, bioerosion is not common, in keeping with the paucity of bioerosion in Palaeozoic reef systems generally. Encrustations are commonly observed, mainly by microbial films and rarely by *Clathrocoilon* or *S. australe*. Rare intergrown organisms (calcified tubes) or encrusters, serpulid worms and borings are also present in *S. australe*, *Stictostroma* and *Clathrocoilon*.

These three types of biostromes are characterized by the most important development of cavities compared to the other zones. Centimetric cavities are commonly present under the laminar stromatoporoids (mostly under *Stachyodes australe*) or as fenestrae or stromatactis in the clotted sediment. Early cementation is rare and occurs mostly as a millimetric fibrous cement border on the edge of cavities. Cavities are then filled by coarse dog tooth cement (interpreted as a meteoric cement, da Silva and Boulvain 2008) and by saddle dolomite (interpreted as late burial cement, da Silva and Boulvain 2008).

Outer zone

Outer zone deposits are observed in the lower unit of Tailfer (T4 and T8, Text-fig. 2) and Villers (V2, Text-fig. 2). Stromatoporoid-dominated autoparabiostromes to allobiostromes, several tens of cm-thick, are observed intercalated in the dark crinoidal beds. The most abundant (in terms of numbers of specimens) stromatoporoid growth forms (Text-fig. 14) are branching *Stachyodes* (cm-thick) followed by tabular and laminar (2–5 cm thick), DB (max. 30 cm in diameter), with some encrusters. Tabular/laminar growth forms and DB growth forms are commonly observed in different biostromes (low profile in V6 and lower part of T4 and DB profiles in upper part of T4 and T6, Text-fig. 2). Stromatoporoids are commonly broken (especially the thin fragile *S. australe*), and broken pieces of tabular *Stictostroma* and *Salairella* are commonly found lying together. The DB stromatoporoids appear well rounded on the outcrop, no ragged margins were observed. They seem to have been transported and are commonly encrusted by a millimetric-thick layer of *Clathrocoilon*. Serpulid worms, borings by unspecified

bioeroders, and encrustations by *Clathrocoilon* have also been observed.

The stromatoporoid fauna of this outer zone (Text-fig. 14) is in decreasing order of numerical abundance: branching *Stachyodes*, followed by low-profile *Stictostroma*, *Salairella* and *S. australe*, high-profile *Actinostroma*, branching *Amphipora* and encrusting *Clathrocoilon*. These stromatoporoids are mostly broken and/or overturned, and the branching profiles are always lying on their side and are commonly strongly damaged.

Overall, although branching *Stachyodes* is the most abundant taxon numerically in all facies and sedimentological zones, all *Stachyodes* are present as broken pieces, and therefore are numerically over-represented. In terms of bulk abundance and outcrop surface, low-profile forms and DB growth forms are under estimated.

DISCUSSION

The purpose of this study is to investigate the relationship between paleoenvironments and stromatoporoid growth forms and taxa, so that sedimentological evidence can assist understanding of the controls on stromatoporoid growth, and aspects of stromatoporoid ecology may enhance palaeoenvironmental analysis. Special attention is directed at the relationship between substrate and stromatoporoids, on the taphonomy of the skeletons and diversity.

Growth of benthic reef communities is affected by abiotic factors such as intensity of light, turbidity, hydraulic energy, topography and nature of the substrate (e.g. Dolphin and Klovan 1970; Stearn 1982; Vennin *et al.* 2004). Distribution of coral morphology in modern environments shows a general pattern governed by wave stress, light intensity, nutrients and substrate (Chappell 1980). However, stromatoporoids developed internal and external structures different from modern coral reef builders and they might occur in different paleoenvironments; there is also no evidence of photoreponse in stromatoporoids (see Kershaw 1998 for a review).

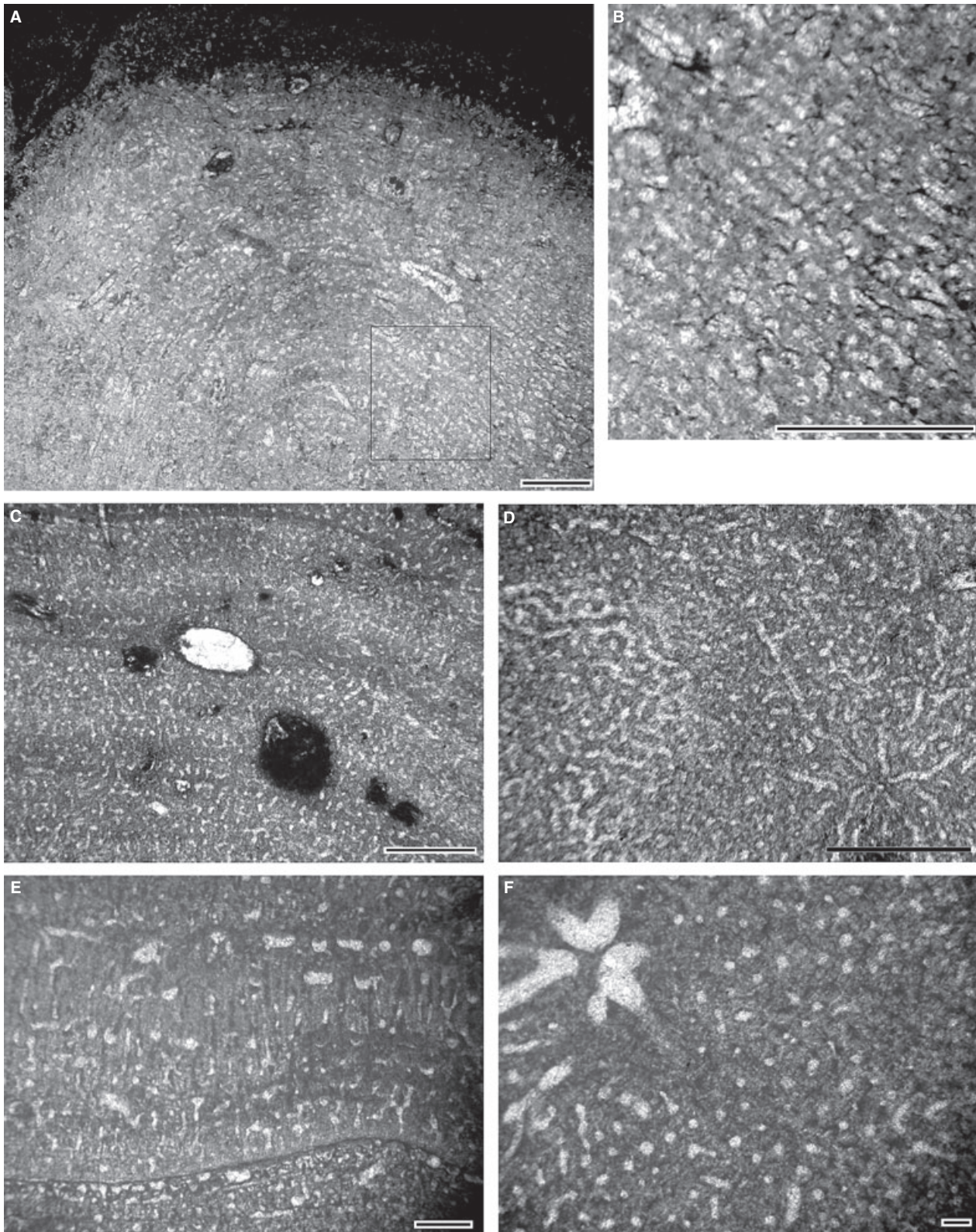
As described in the sedimentological section, two main sedimentary events are observed, corresponding to important changes in the stromatoporoid fauna and growth forms:

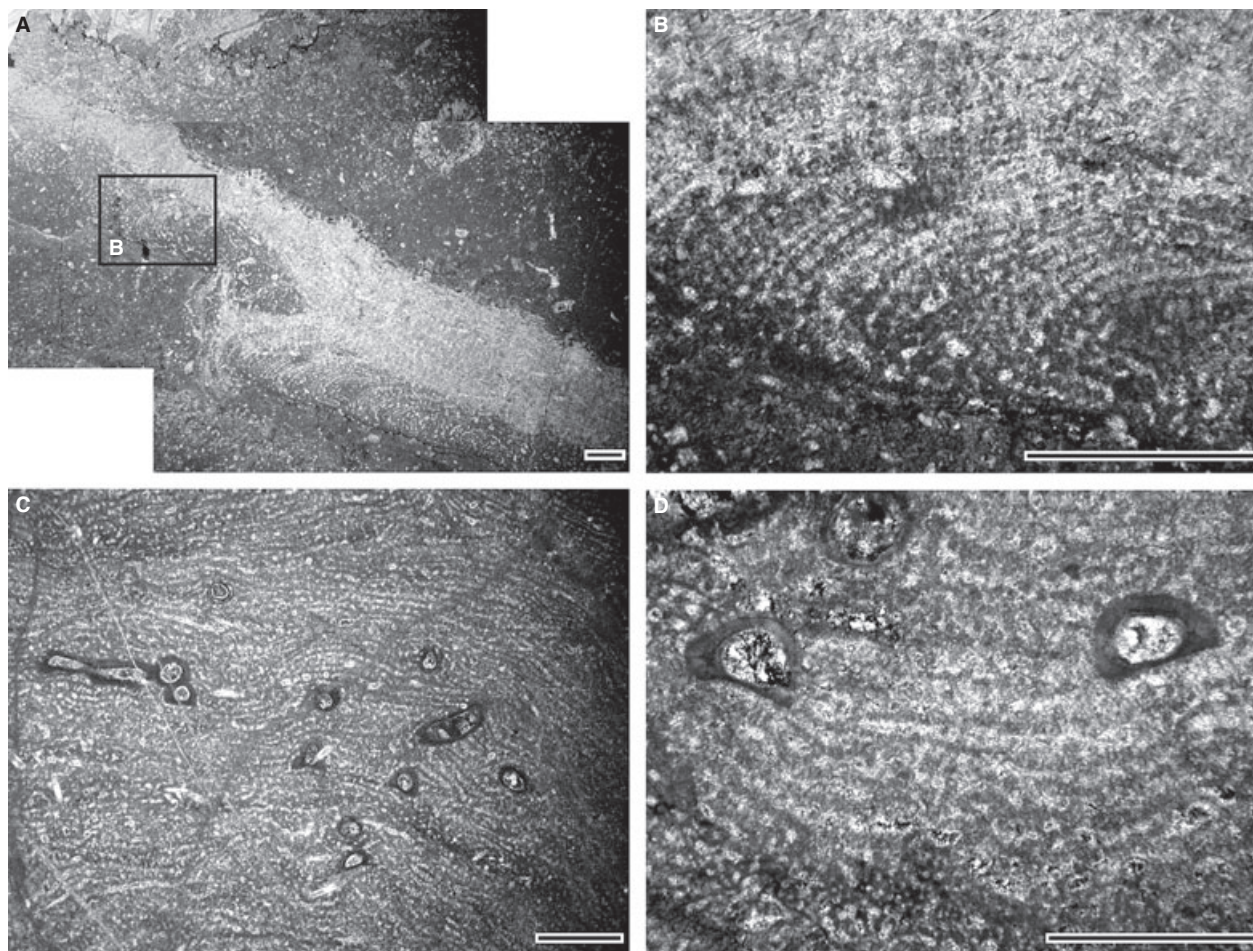
1. Transition from argillaceous deposits to a carbonate platform, initiating the carbonate platform, allowed

TEXT-FIG. 6. *Stictostroma*. A, *Stictostroma*; sample V62D' from Villers locality; longitudinal section showing continuous laminae and confined to an interlaminar space, not systematically superposed spool-shaped vertical elements. B, *Stictostroma*; sample V-62D' from Villers locality, tangential section. C, D, *Stictostroma*; sample T-42-6 from Tailfer locality, longitudinal section showing a grid aspect, and locally on Text-figure 6C, 'tripartite' laminae (arrows). E, F, *Stictostroma*; sample T-53-2 from Tailfer locality, longitudinal section – in F, zoom on an astrorhizae. G, H, *Stictostroma*; sample T-42-3B from Tailfer locality, tangential section, with astrorhizae (on picture G) and zoom on the vermiform vertical elements (picture H). Scale bar represents 1 mm.

the appearance of stromatoporoids with mostly low-profile growth forms that may have acted as sediment stabilizers. This is the case in Tailfer and Villers, but

also in many sections in the area, such as Aywaille, Barse and Colonster (da Silva 2004 and location of these sections on Text-fig. 1).





TEXT-FIG. 8. *Stachyodes (australe)* and intergrown organisms. A, B, *Stachyodes australe*; sample PrB-26E from Prayon locality, longitudinal section. C, D, *Stictostroma*; sample PrB-24A, from Prayon locality; longitudinal section showing intergrown organisms. Scale bar represents 1 mm.

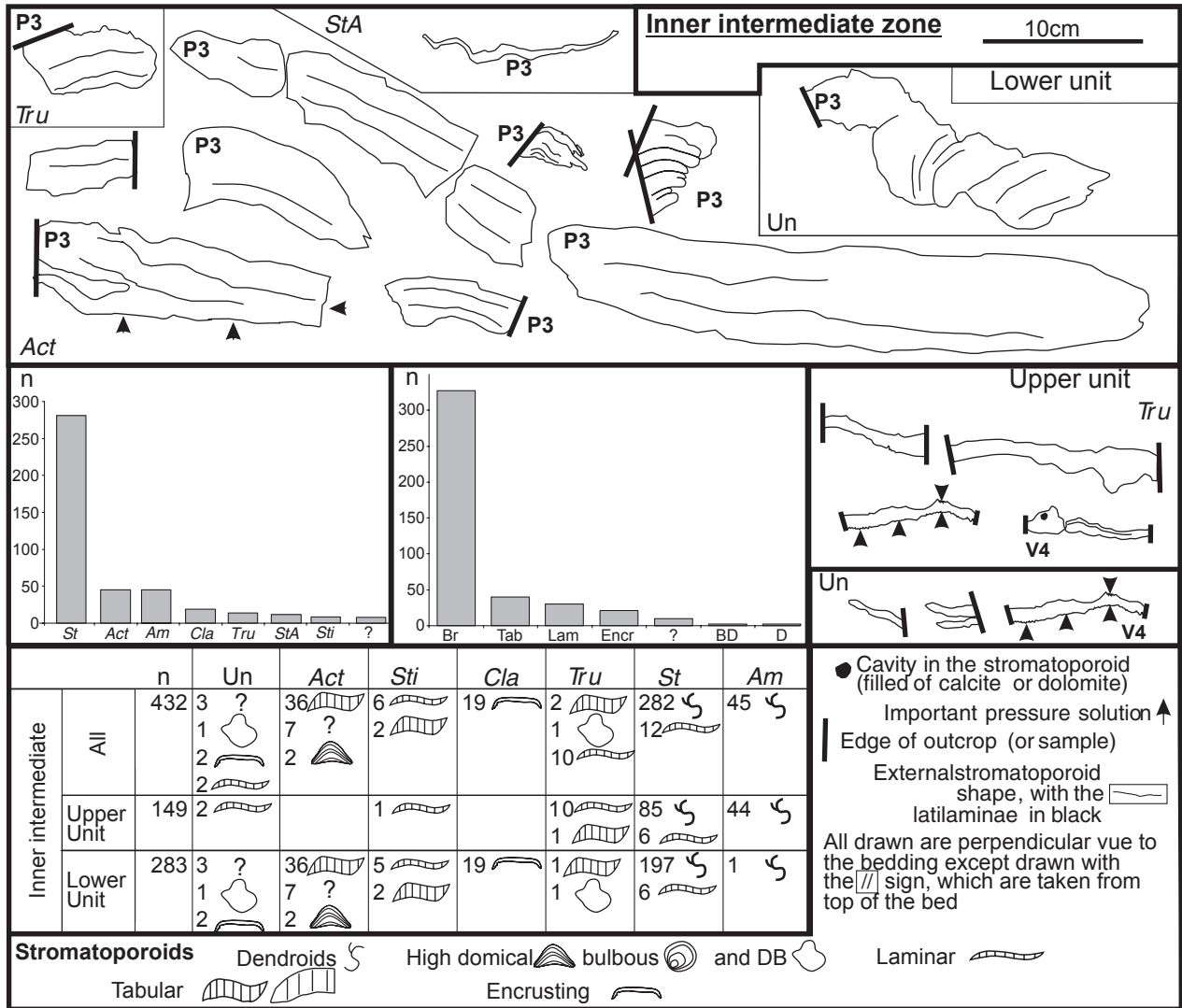
2. Transition, within the carbonate platform between its lower part (called the lower unit), dominated by low-profile stromatoporoids, to its upper part (called the upper unit), corresponds to a shift to rocks comprising largely the inner facies, with a strong decrease (disappearance in most places) of low-profile forms, replaced by high-profile forms and small branching (*Amphipora*) growth forms.

These general patterns are interpreted primarily as a response to variations in environmental energy, with some relationship between taxa and environment, discussed below.

Growth forms and environments

In this study, a strong relationship between palaeoenvironments and growth forms is observed (Text-figs 15, 16): tabular growth forms are mostly observed in outer, outer intermediate, and inner intermediate zone environments, laminar growth forms are dominant in the outer intermediate zone but are also observed in the inner intermediate zone; DB are mostly observed in the inner zone as well as the branching, encrusting and irregular growth forms. DB high-profile forms are almost never observed associated with low-profile tabular/laminar

TEXT-FIG. 7. *Trupetostroma*, *Stromatopora* and *Salairella*. A, B, *Trupetostroma*; sample PrB-24L from Prayon locality; longitudinal section, showing a grid with short pillars and relatively important dissepiments. C, *Stromatopora*; sample T-36-11 from Tailfer locality, longitudinal section showing cassiculate, oblique structure. D, *Stromatopora*; sample T-36-11 from Tailfer locality, tangential section showing labyrinthic network and astrorrhizae. E, *Salairella*; sample V-63A from Villers locality, longitudinal section showing long coenosteles, locally divided. F, *Salairella*; sample V63A from Villers locality, tangential section showing a close network with autotubes and astrorrhizae. Scale bar represents 1 mm.

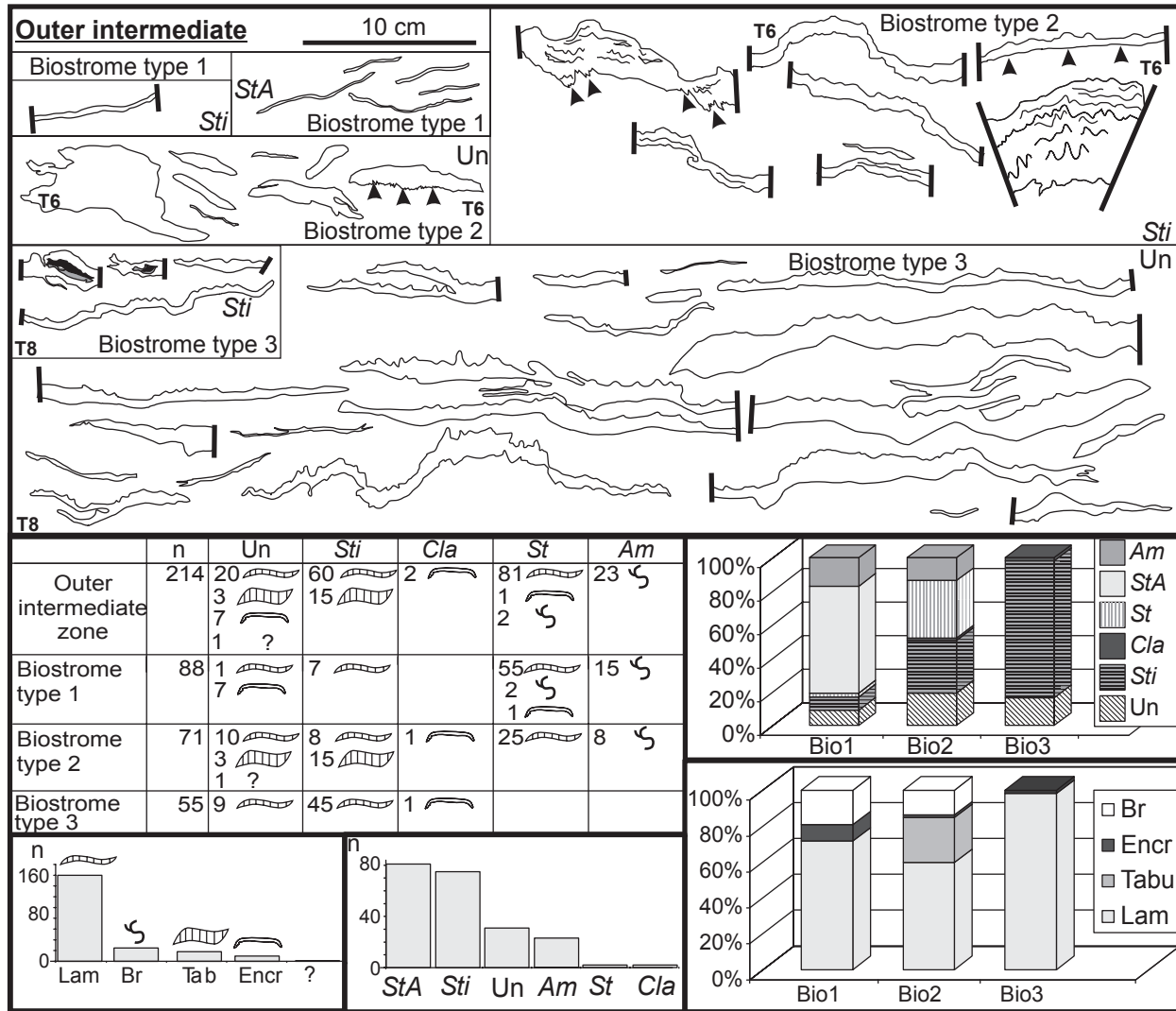


TEXT-FIG. 10. Growth forms of stromatoporoids, numbers of specimens and distribution of growth forms within taxa, from the Inner intermediate zone, in the lower and upper units. Annotation on or on the side of the stromatoporoids (P3, V4) correspond to the main biostromes defined in Text-figure 2. For the list of abbreviations and legend, see Text-figure 9.

growth forms. However, taxonomic control is also obviously important and some genera are only observed in one or two growth forms. *Amphipora* is observed as only branching skeletons and *Clathrocoilon* as only an encrus-

ter and *Stachyodes* is always branching except in the case of the laminar *Stachyodes australe* (these are well-established relationships between growth form and taxa; Stearn *et al.* 1999). *Stictostroma* is mostly low profile but can

TEXT-FIG. 9. Growth forms of stromatoporoid and numbers of specimens from the Inner zone, in the lower and upper units. For the legend, see Text-figure 10. Annotations on, or on the side of, the stromatoporoids (P1, P2, T5, V4, P7) correspond to the main biostromes defined in Text-figure 2. The distribution of growth forms across taxa are not given in this figure, because most samples are abraded or affected by pressure solution, and are nearly all of domical to bulbous form. Abbreviations for Text-figures 9–11 and 14: Undetermined (Un), *Actinostroma* (Ac), *Amphipora* (Am), *Atelodictyon* (Ate), *Clathrocoilon* (Cla), *Salirella* (Sal), *Stictostroma* (Sti), *Stachyodes* (St), *Stachyodes australe* (StA), *Stromatopora* (Str) and *Trupetostroma* (Tru) and Bulbous (Bu), Bulbous domical (BD), Domical (D), Branching (Br), Encrusting (Encr), Irregular (Irr), Laminar (Lam) and Tabular (Tab). n = number of stromatoporoids observed.



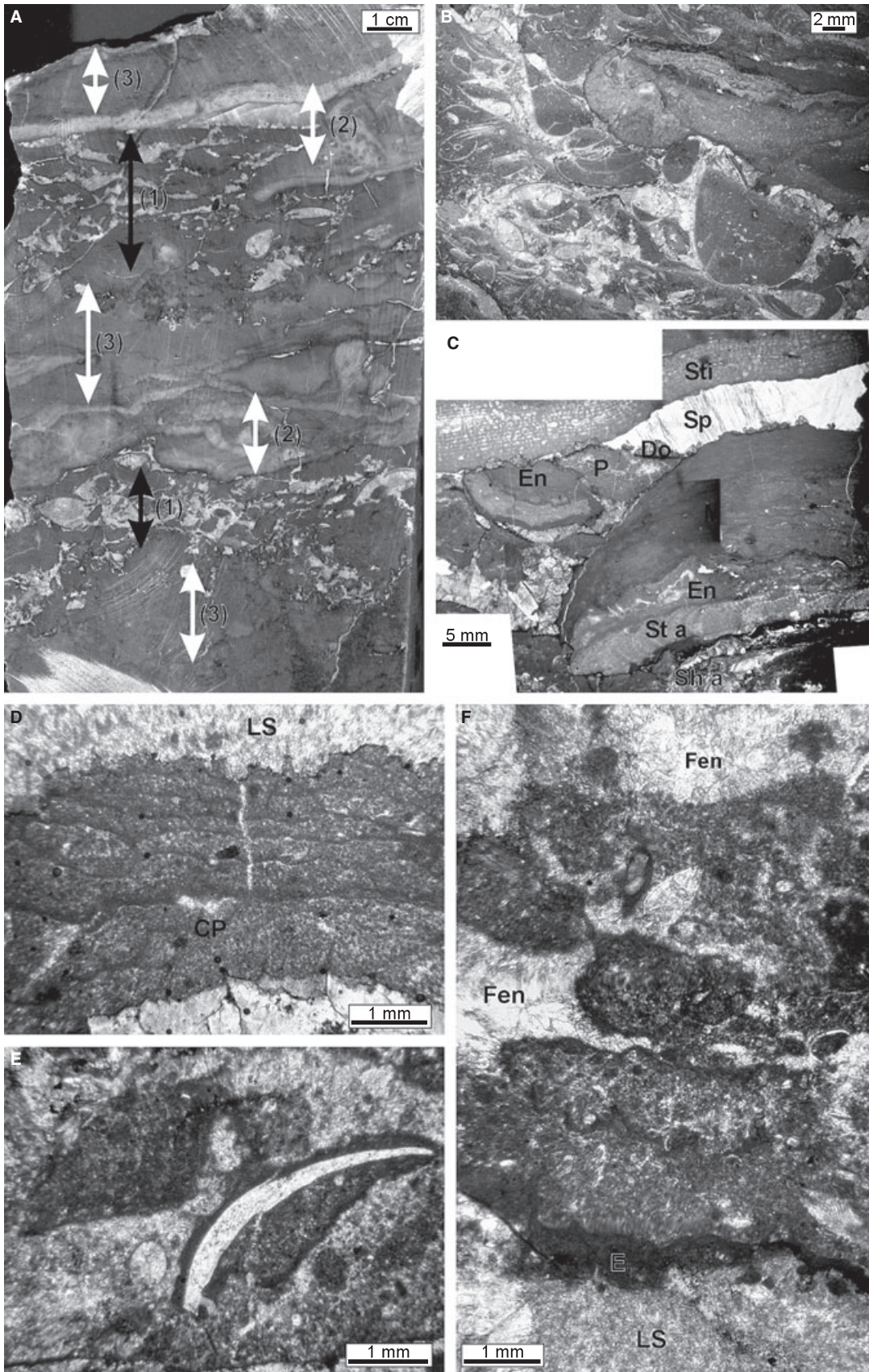
TEXT-FIG. 11. Growth forms of stromatoporoids, numbers of specimens and distribution of growth forms within taxa, from the outer intermediate zone (biostrome types 1 (Bio1), 2 (Bio2) and 3 (Bio3)). Annotations on or on the side of the stromatoporoids (T1, T4, T6, V3) correspond to the main biostromes defined in Text-figure 2. For the list of abbreviations and legend, see Text-figure 9.

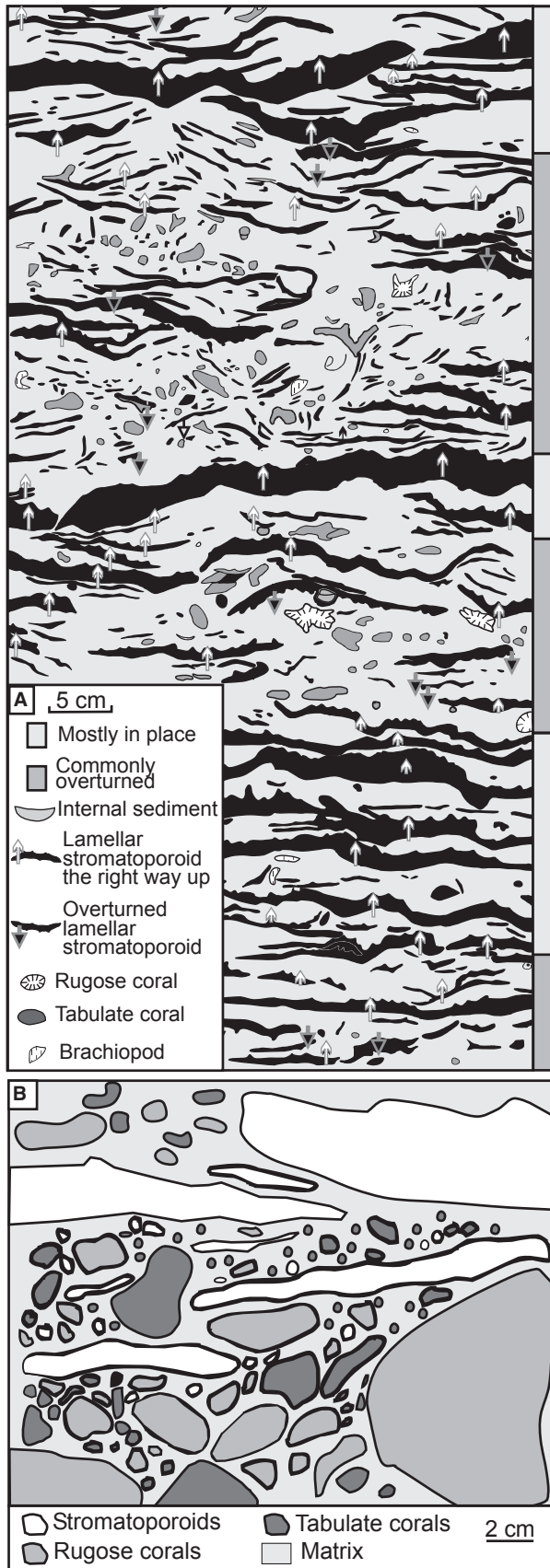
also occur as DB growth forms; and *Actinostroma* developed thick tabular growth forms or high profile mostly domal shapes.

The inner zone contains stromatoporoids of maximum 30 cm diameter. This is in contrast to the much larger specimens (up to 500 cm) found in a similar setting in the Frasnian of the Canning Basin, Australia (Wood

2000), and the difference in size may be because of variations in long-term stability of a substrate surface for growth and development of individual stromatoporoids. Thus in the Belgian Frasnian biostromes, reworking was an important interruption in stromatoporoid growth, with overturned and broken stromatoporoids in all sections and grainstone texture in Villers. Ragged margins (where

TEXT-FIG. 12. Photographs of specimens from the outer intermediate zone, Pictures A to C are from biostrome type 1 and pictures D to F from biostrome type 2 (all pictures from Tailfer section). A, (1) alternation of shell accumulations, (2) stromatoporoid-dominated levels and (3) mud-dominated levels. B, shell accumulation with a grainstone texture and a stromatoporoid growing on the top. C, alternation of shell accumulation (sh a), stromatoporoids and mud (St a is *Stachyodes australe*, En are encrusters, M is a microbial mound accumulation, P is a clotted peloidal accumulation, Do is dolomite, Sp is sparite and Sti is *Stictostroma*). D, laminar accumulation of clotted peloids (PG), under a laminar *Stictostroma* (LS). E, brachiopod encrusted by micrite. F, clotted micrite (CP), fenestrae (Fen) and encrustation (E) following an undetermined strongly altered laminar stromatoporoid (LS).





they can be proved as caused by sediment processes) and growth recovery following turnover are indicative of growth interruption events (mostly in Prayon, some examples on Text-fig. 9). In Prayon biostrome P2 (Text-fig. 2), most of the stromatoporoids have important and abundant encrustations, intergrown organisms, as well as borings, which could be explained by a relatively slow sediment deposition rate, allowing encrustation and bioerosion of the stromatoporoids during their residence on the sea floor. Encrustations are always more developed on only one side of any individual stromatoporoid (which may be either the upper or lower surface); overturning of stromatoporoids was not so common. So, this zone was probably affected by short-term high-energy events, leading to reworking of stromatoporoids. However, substrate was probably relatively stable allowing important bioerosion of stromatoporoids, but not stable enough to allow stromatoporoids to develop large sizes.

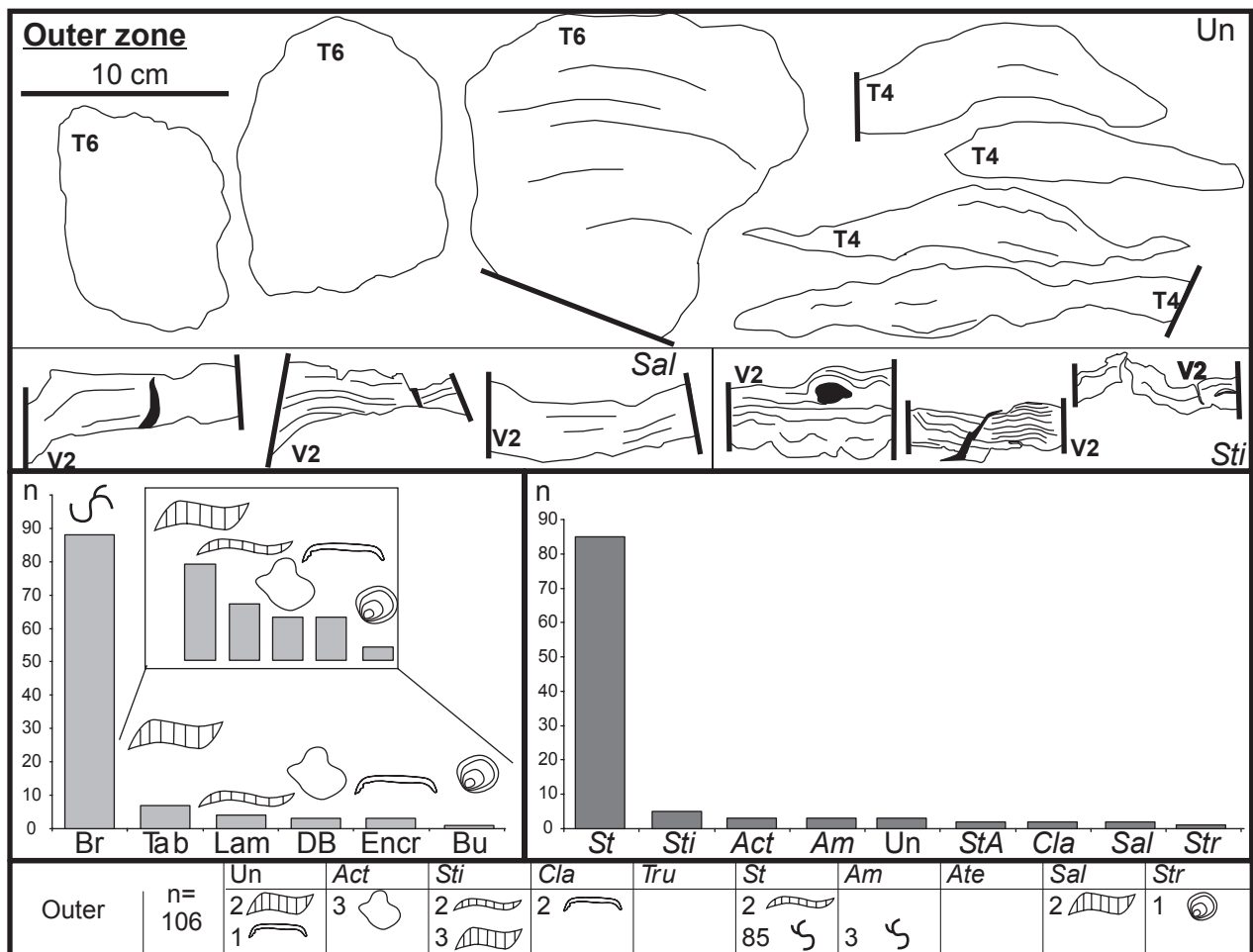
In the inner intermediate zone (Text-fig. 10), biostromes are dominated by branching stromatoporoids in Tailfer, by tabular and laminar stromatoporoids in Villers and by laminar and tabular followed by DB growth forms in Prayon. Branching *Stachyodes*, commonly adapted to low-energy environments are observed associated with mostly in place structures, even fragile structures (clotted structures and microbial laminations). As reported by Machel and Hunter (1994) and Wood (2000), the association of *Stachyodes* and *Amphipora* is mostly observed in back-reef areas. So, these biostromes probably developed in protected areas, just inboard of the biostromal zone. The tabular stromatoporoids (in biostromes V3 and P3, Text-fig. 2) are mostly overturned, and sometimes broken, indicating reworking, probably by storm events. However, in some areas, mud and clotted sediments are preserved indicating that this environment probably developed mostly in low energy. Deposition of debris in layers indicates episodic higher-energy events.

In the outer intermediate zone, the low-profile growth forms are the most abundant growth forms. Low-profile stromatoporoids would have presented advantages in deeper zones or more turbid zone in case of soft sediment to avoid sinking (Kershaw 1998), for substrate stabilization, stability during time of higher energy and low sedimentation rate (Kershaw 1990). In type 1 biostromes, the fact that stromatoporoids remain very thin (millimetre-thick) indicates a quiet water environment interrupted by rare events of sedimentation. The relationship between stromatoporoids and microbial organisms




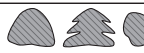

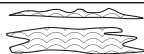





TEXT-FIG. 13. Sketch from the Tailfer section, biostrome type 3 (T9). A, middle part of the biostrome, showing the alternation of mostly in place structures and overturned stromatoporoids. B, lower part of the biostrome, colonizing phase.

(which formed automicrite sediments on the sea floor) is difficult to determine. Certainly, there is no evidence that the stromatoporoids reacted to the presence of microbial organisms in the samples studied. More generally, direct competition between benthic skeletal organisms such as stromatoporoids and corals seems to be uncommon in Palaeozoic reefs (Fagerstrom *et al.* 2000). Furthermore, evidence of growth interruptions like anastomosed growth forms and raggedness are observed, which may be explained by a mixture of sedimentation events interrupting growth, and formation of primary cavities (Kershaw *et al.* 2006) as well as (presumably) frequent higher energy events revealed by alternation of tempestite and mud-*Stachyodes australe* levels, which could explain the cessation of stromatoporoid growth. Type 2 biostrome presents mostly thicker flat shapes with more ragged boundaries, with also wavy shapes and very well developed mamelons. These could indicate a higher sedimentary rate and also a quieter environment,

with less storm events (because grainstones and reworked levels are not common in comparison with the two other biostrome types), allowing stromatoporoids to reach greater thicknesses. Type 3 biostrome presents an alternation of upright and overturned stromatoporoids (Text-fig. 13A). Upright stromatoporoids are surrounded by micritic matrix and overturned stromatoporoids are surrounded by micritic matrix, together with tabulate corals and stromatoporoid debris. This biostrome developed in a quiet environment that was subject to episodic storms which disrupted the biota and overturned the stromatoporoids. For the three biostromes it seems that the averaged sedimentary rate was relatively high, with mostly local automicrite production. The presence of automicrite in some layers may have created a more lithified sea floor. Stromatoporoids were probably quickly buried as they are very often in place (or at least overturned but not broken) and are not commonly affected by bioerosion.



TEXT-FIG. 14. Growth forms of stromatoporoids, numbers of specimens and distribution of growth forms within taxa, from the outer zone. Annotations on or on the side of the stromatoporoids (T2, T3, V2) are corresponding to the main biostromes defined in Text-figure 2. For the list of abbreviations and legend, see Text-figure 9.

Stromatoporoid	Morphology	Size	Substrate	'Reefal structure'	Environmental zone
<i>Amphipora</i>	Thinly branched 	mm to cm	Never observed in place associated with peloids and algae	Patches, always broken	Inner
<i>Stachyodes</i>	Thick branches 	cm	Never observed in place associated with almost all sediments	Patches, always broken	Inner intermediate Outer
	Thinly laminated to anastomosed 	mm thick dm large	On mud, shells or encrusting other strom (Sti. or StA.)	"Microbial biostromes" Colonization phase	Outer intermediate
<i>Actinostroma</i>	Domical - Bulbous or DM ragged or smooth 	few cm to 50 cm	Growing mostly on mud Sometimes on <i>Actinostroma</i>	Biostromes - patches	Inner Outer
	Tabular 	few cm to 5 m	Growing mostly on mud Sometimes on <i>Actinostroma</i>	Biostromes - patches	Inner intermediate
<i>Stictostroma</i>	Laminar - Tabular Ragged margins mamelons 	cm to dm thick/dm to m large	Growing mostly on mud	"Microbial biostromes"	Outer intermediate
	Domical - Bulbous ragged or smooth 	cm to dm large	Never observed in place. Associated with peloids and algae	Biostromes - patches	Inner
<i>Clathrocoilonia</i>	Encrusting 	mm to dm thick	Growing always on hard debris stromatoporoids, tabulate, ...	Biostromes - patches	Inner interm. Inner
<i>Trupetostroma</i>	Bulbous - DM ragged or smooth 	cm - dm	Mostly not in place, associated with peloids and algae	Biostromes - patches	Inner
	Tabular - laminar 	cm thick, dm large often broken	Mostly not in place, associated with mud	Biostromes - patches	Inner intermediate
<i>Salirella</i>	Tabular 	cm thick, dm large often broken	Crinoidal substrate	Biostromes - patches	Outer

TEXT-FIG. 15. Description of the main stromatoporoid morphologies and their distribution on the platform in relation to the substrate, biostrome and environment. *Sti.* = *Stictostroma* and *StA.* = *Stachyodes australe*.

The biostromes in the outer zones are dominated by tabular or DB growth forms (Text-fig. 14), associated with mostly argillaceous mud and very small sized debris with only some coarser levels indicating a sedimentary dynamic mainly based on low-energy sedimentation, with temporary higher energy events like storms. Low-profile stromatoporoids would have presented the same advantages described below (to avoid sinking on soft sediment, substrate stabilization, stability during time of higher energy and competition for space). All these factors could be invoked in this case. The fact that they reach a relatively thick size without important growth interruption seems to confirm the low sedimentation rate. The biostromes dominated by DB stromatoporoids were strongly dolomitized, and the DB stromatoporoids are lying in all directions, and were probably transported. So the reasons why this biostrome present mostly DB growth forms instead of tabular are difficult to assess.

Substrate

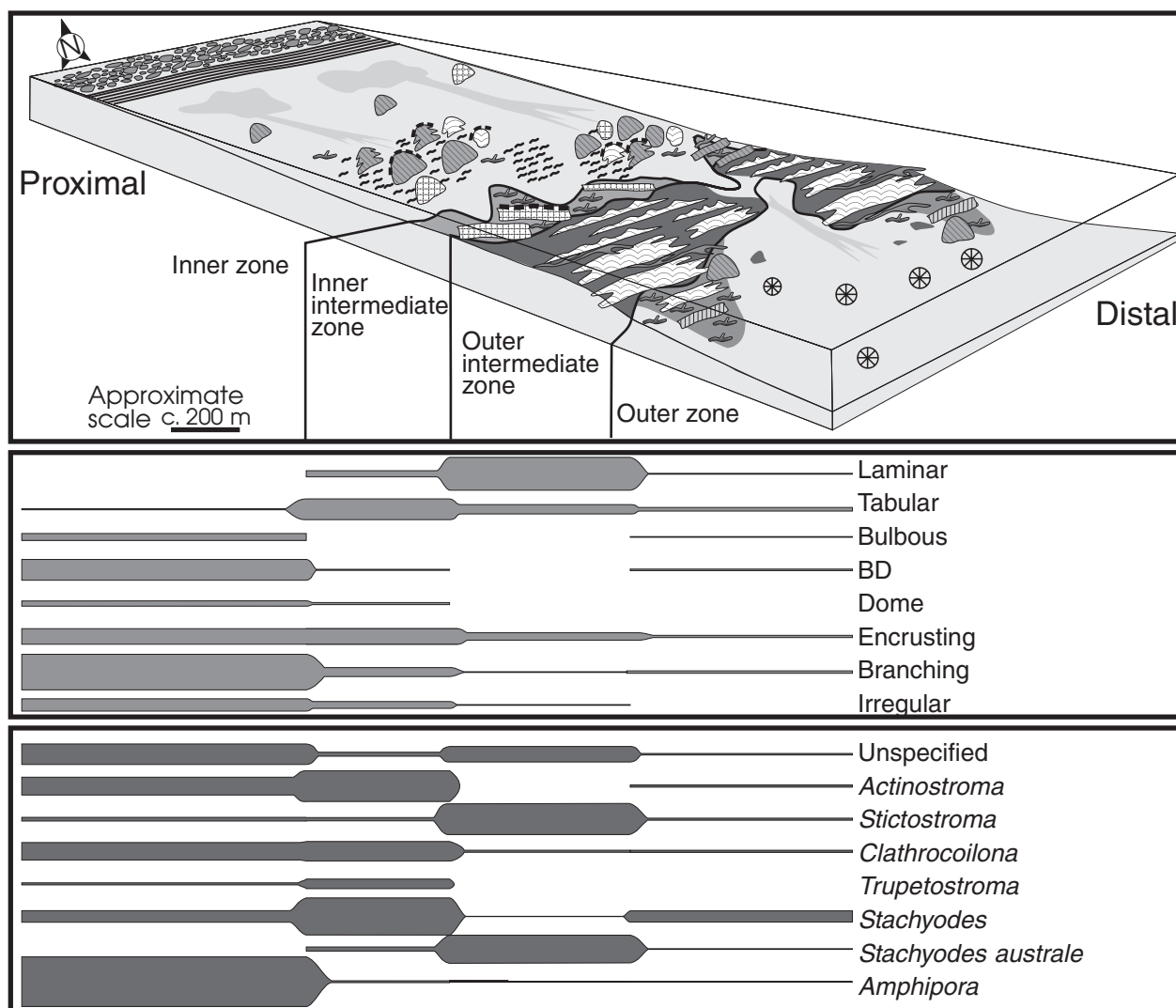
Substrate preference of stromatoporoids is not often observed in the study area because of pressure solution and reworking. However, growth on both hard surfaces (dead skeleton of other organisms) and soft sediment were observed for all kinds of stromatoporoid, except *Clathrocoilonia*, which is observed as only an encruster. Primary cavities were observed under *Stachyodes australe*

showing their ability to actively form cavities, by growing above the substrate. This ability of *S. australe* to form primary growth framework cavities was emphasized by Wood (1998), but the recognition of primary cavities has difficulties, as discussed by Kershaw *et al.* (2006). The fact that stromatoporoids are found upside down in the outer and inner intermediate zone facies, and the interfingering of the skeleton with muddy sediment, provides evidence that stromatoporoids were lying on the sea floor with no attachment and presumably were therefore able to establish themselves on a muddy substrate.

Kershaw (1990) suggested that lateral growth to form low profiles gave stromatoporoids a selective advantage; in this study, the abundance of low-profile forms on muddy substrates is obvious. Biostromes in the outer intermediate zone all initiated on a gravel substrate suggesting flat morphologies were suitable as sediment stabilisers. Furthermore, the transition between the argillaceous formations Pont-de-la-Folle and Presles to the carbonate formations Philippeville and Lustin is characterized by low-profile forms.

Diversity and ecological zones

In most of the zones, the stromatoporoid assemblage is strongly dominated by branching specimens (except the outer intermediate zone, dominated by laminar forms). The diversity could be characterized as intermediate in



TEXT-FIG. 16. Synthesis of the distribution of Stromatoporoids and stromatoporoid growth form along the platform model. The key to stromatoporoids is shown on Text-figure 11.

most of the zones, with between eight and nine genera observed, except in the outer intermediate zone (six genera). In the outer intermediate zone, of the three types of biostromes, type 1 is rich in automicrite with few stromatoporoids, while types 2 and 3 are stromatoporoid-rich. The biostromes in this zone contain the greatest concentration of stromatoporoids, but have the lowest diversity, with strong dominance of *Stictostroma* in biostrome type 3, and *Stachyodes australe* and *Stictostroma* in biostrome types 1 and 2. Analyses of diversity in modern reefs showed that intense competition under favourable conditions between reef builders leads to low diversity (references in Kershaw 1981, p. 1293). Thus, while the Belgian biostromes are clearly not equivalents of modern coral reefs, they are the environments where reef-building fossils (stromatoporoids and corals) are most abundant in these

Devonian sediments. Nevertheless, the distinctiveness of three different biostrome types shows that this zone shows important facies complexity.

However, in the other zones (outer, inner intermediate and inner), even if the total assemblage is commonly between eight and nine genera, in individual beds, the assemblage is often dominated by one or two genera. In the inner zone, some patches are characterized by accumulations of only *Amphipora* (very low diversity).

Taphonomy

The degree of damage sustained by stromatoporoids varied depending on their depositional environment and taxonomy. The best preserved skeletons are from the outer

intermediate zone biostromes probably because of the high carbonate production rate and lower energy which allowed a rapid burial without strong skeletal degradation. *S. australe* can be observed as debris, even in the outer intermediate zone, probably because of this very fragile thin structure, and the laminar *Stictostroma* is commonly complete in the outer intermediate zone but in the outer and inner intermediate zones, it commonly has broken edges. *Amphipora* and branching *Stachyodes* are always found lying on their side, whatever the depositional facies. *Actinostroma*, mostly observed in the inner intermediate and inner zones, is often broken, affected by borings and recrystallization.

So, taphonomy of stromatoporoids in this case appears to be partly related to the depositional environment (wave agitation during deposition, sedimentary rate) and to the taxonomy and growth forms (branching growth forms more fragile, as well as probably *S. australe* and *Actinostroma*).

CONCLUSIONS

This work on Frasnian stromatoporoids from southern Belgium has attempted to provide a comprehensive view of the stromatoporoid assemblages and their application in facies analysis. The following major points emerge from this study:

1. The depositional area can be divided into four main zones where different kinds of biostromes, containing distinctive stromatoporoid assemblages, are observed: (1) the inner zone presents isolated biostromes with algae, abundant *Amphipora* and DB growth forms; (2) the inner intermediate zone is characterized by a mixture of characters from the outer intermediate and inner zones (abundant mud and algae), with mostly branching, laminar and tabular growth forms; (3) the outer intermediate zone presents biostromes dominated by laminar stromatoporoids and mud; (4) the outer zone is dominated by finely crinoidal argillaceous carbonates with biostromes dominated by branching, tabular and DB growth forms.
2. Stromatoporoids are the most abundant large skeletal organisms in the facies studied, with principal occurrence in biostromes. Stromatoporoid assemblages tend to have one species that is more abundant than the other, which is consistent with other detailed studies of stromatoporoid faunas. Diversity is minimal in the outer intermediate biostrome, but the faunas there are the most abundant, indicating that this is the most favourable environment for stromatoporoids in the Frasnian of Belgium.
3. There is some evidence of taxonomic control on growth forms (e.g. *Actinostroma* mostly DB or tabular and *Stictostroma* mostly laminar). However, variability of form within taxa indicates some degree of environmental control on growth form (low profile in the outer intermediate and higher profile in the inner zone).
4. There is a strong environmental control on stromatoporoid occurrence, and the stromatoporoid faunas are governed by externally driven environmental changes. The first stromatoporoids to form in the sequence (at the transition between argillaceous and carbonated environments) are characterized by low-profile growth forms, which may have played an important role in stabilizing and colonizing the substrate, and therefore promoting the carbonate factory development.

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