

Astogeny of amural colonial Rugosa from the Famennian of the Sudetes - a palaeoenvironmental study

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ABSTRACT:

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The astogeny of three species of the amural rugosan genus *Scruttonia* coming from the Famennian so-called main limestone cropping out in Dzikowiec (the Middle Sudetes) is described. The colonies studied reveal cyclomorphic variation usually regarded as seasonal in nature. The character and shape of the colony as well as the character of the internal skeletal elements has been investigated to determine the colony-sediment interactions. The character of those interactions and the taphonomy of the colonies helped to make a determination of the colony growth rate and the sedimentation rate of the beds where colonial corals occur.

Key words: Colonial Rugosa, Astogeny, Taphonomy, Palaeoecology, Devonian (Famennian).

INTRODUCTION

The Upper Famennian strata of Dzikowiec (Sudetes, southern Poland) contain a unique assemblage of massive colonial rugose corals. Following the late Frasnian/early Famennian crisis colonial corals became very rare, so the unique fauna of Dzikowiec is probably the richest assemblage of colonial corals known throughout the world for this time interval. The fauna is represented by three species of the amural genus *Scruttonia*, dominated by the colonies of *S. kunthi* (FRECH, 1885).

Amural colonies (*sensu* SCRUTTON 1998) are generally not very common among colonial rugosans, but their highly-integrated skeletons, as well as internal and external variability caused by environmental changes, may give some important information about the palaeoecological conditions. Internal and external cyclomorphic variation (so called growth bands) of the

skeletal structures within Palaeozoic rugose colonial corals have been already used to estimate the growth rates of coralla (FAUL 1943; SCRUTTON 1983, 1989, 1998; EZAKI & KATO 1989; GAO & COPPER 1997). The seasonal nature of these alternating high- and low-density bands in corals is generally accepted and recently documented by stable isotope changes in scleractinian corals (see e.g. DULLO & *al.* 1996 a, b; WATANABE & *al.* 1999). Similar isotopic analyses have also been made for Palaeozoic rugosans (BERKOWSKI & BELKA 1999), the data obtained from *Scruttonia kunthi*, described here appear very promising but still need to be confirmed by wider investigations in other sites of the world.

The aim here is to investigate the colony development (astogeny) of these corals and to estimate their growth rate and the rate of sedimentation taking into account the internal cyclomorphic changes of the skeleton, the shape of the colony and the character of surrounding sediment.

GEOLOGICAL SETTING

The Famennian corals studied occur within the strata which are exposed in the abandoned Wapnica Quarry

in Dzikowiec (Ebersdorf in German literature). The quarry is situated within the Bardo Mountains in the Middle Sudetes (Text-fig. 1A). The section of Wapnica has been known as a classic geological site in Europe

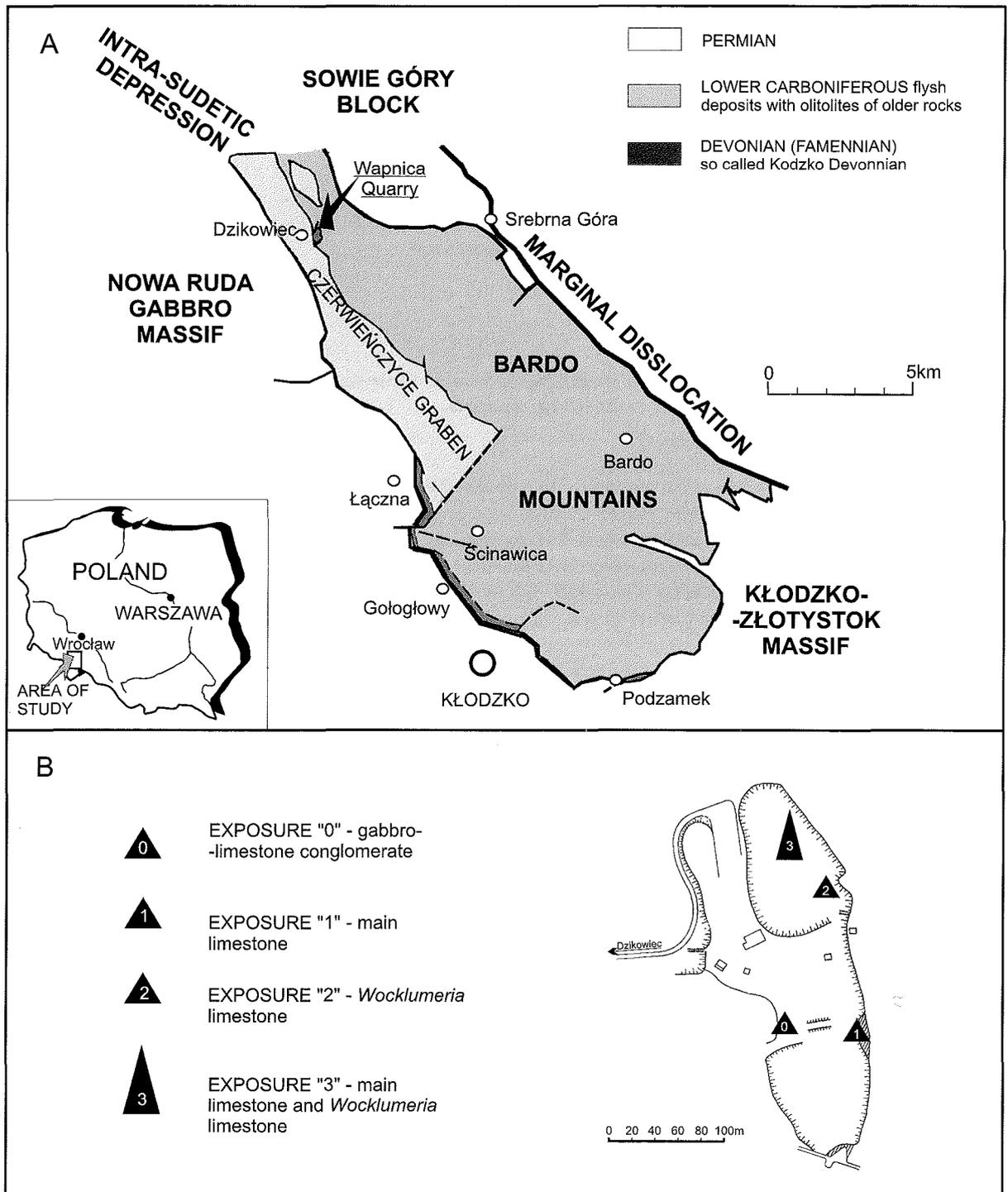


Fig. 1. Locality of the exposures investigated; A – Simplified geological map of the Bardo Mountains after OBERC 1972 – Dzikowiec Village underlined; B – Sketch of the Wapnica Quarry at Dzikowiec; exposures indicated as triangles

since the eighteenth century and now is regarded as a part of an autochthonous complex called Wapnica Fm (see ŻAKOWA 1963, WAJSZYCH 1986).

The first description of the section was made by TIETZE (1970), but the most complete sub-division of the whole section was described by GÜRICH (1902). He carefully studied the geological sections from the south to the north of the quarry and distinguished a complete succession. The section starts from the gabbroic crystalline basement through (α) crustal limestone with gabbro debris, (β) dark-mottled limestone, (γ) crinoidal limestone, (δ) red limestone with gabbro gravel, (ϵ) dark-grey nodular limestone (Hauptkalkmain limestone), (ζ) *Clymenia* beds, and (η) lower gneissic sandstone of the „Kulm”. BEDERKE (1924) presented a similar lithological sub-division regarding, however the first four units α , β , γ , δ of GÜRICH (1902) as basal limestone. Only part of the section is accessible now i.e. lower part of basal limestone containing gabbroic-limestone conglomerate is cropping out on the western wall of the quarry (exposure 0 on Text-fig. 1B), upper part of the main limestone (eastern wall - e.g. exposures 1 and 3 on Text-fig. 1B) and *Clymenia* beds (eastern wall - e.g. exposures 2 and 3 on Text-fig. 1B). The lower carboniferous Kulm beds disconformably cover all exposures on the eastern wall of the quarry.

The majority of the research done at Dzikowiec concerns the biostratigraphy of the cephalopod limestone (*Clymenia* beds *sensu* GÜRICH 1902 and BEDERKE 1924). These beds belong in fact, to the uppermost Famennian and the lowermost Tournaisian. Additionally, the section reveals a stratigraphic gap including Devonian-Carboniferous boundary and thus it has been divided into *Wocklumeria* and *Gattendorfia* limestone (SCHINDEWOLF 1937, OBERC 1957, LEWOWICKI 1959, WEYER 1965, FREYER 1968 and recently KORN 1993 and DZIK 1997).

The dating of the base of the Wapnica Formation remains unclear. Initially according to German researches (TIETZE 1870; GÜRICH 1900, 1902, 1914; DATHE 1901; BEDERKE 1924, SCHINDEWOLF 1937), only the *Clymenia* beds (*Wocklumeria* limestone) was attributed to the Famennian, whereas the gabbroic-limestone conglomerate, and main limestone were considered to be of Frasnian age. In fact, the age of the lower part of the basal limestone is difficult to determine because of the lack of well-preserved index fossils. Only the forams *Quasiendothyra communis* and *Q. cf. kobeitusana* have been determined to species level (STANISZEWSKA 1991). The upper part of main limestone was dated with conodonts by FREYER (1968) and CHOROWSKA and RADLICZ (1987) as the *P.*

quadrantinodosa to *P. styriacus* Zones, which corresponds to the *P. marginifera* and *P. postera* Zones of ZIEGLER and SANDBERG (1990). However, data on forams (CHOROWSKA and EMERLE-TUBIELEWICZ 1990) suggest that the deposition of the main limestone took place even later, within the *Quasiendothyra radiata* Zone, which corresponds to the upper *P. expansa* or lower *S. praesulcata* Zone. As only the lower part of the *S. praesulcata* Zone may be represented at Dzikowiec in the topmost part of the overlying *Wocklumeria* limestone, the Main Limestone cannot be younger than the *P. expansa* Zone (a detailed discussion is presented in BERKOWSKI, in press).

Lithology of investigated exposures

Rugose corals were investigated in three exposures of the Wapnica Quarry (Text-fig. 1B), but the occurrence of the studied colonial assemblages is restricted to the main limestone in exposures 1 and 3.

Exposure 1 is located in the middle part of the eastern wall of the quarry (Text-fig. 1B), where the upper 12 m. of the main limestone is cropping out (Text-fig. 2). The top of the main limestone is covered disconformably by the “gneissic” sandstone and conglomerate of the „Kulm”. The boundary between the foraminiferal zones Df3 γ and Df3 δ was identified between 1 and 2 m from the base of the section (Text-fig. 2; L. HANCE, personal communication). The main limestone is dark-grey and distinctly bedded (bed thickness 5-26 cm). Beds are wavy to nodular and alternate with thin (2-4 cm) beds of black marly shale. Microfacies are not diverse. Most commonly they represent a packstone with forams *Quasiendothyra communis communis*, *Q. communis regularis*, *Q. radiata*, *Rectoavesnella*, and *Rectoglomospiranella* (L. HANCE, personal communication). Apart from the forams, the cyanobacterium *Girvanella*, kameneids, solenoporaceans, calcisphaeres, crinoids, and the problematic fossil *Menselina magna* are common. Less numerous are ostracodes and small articulate brachiopods. Corals occur within the whole section of the main limestone. Fifteen coral-bearing beds have been distinguished (Text-fig. 2). Colonial corals are embedded in a life position. Thamnasterioid *Scruttonia kunthi* (FRECH), aphroid *Scruttonia* sp. A (BERKOWSKI, in press), and fragments of a presumably phaceloid colony of *Heterostrotion* sp. are restricted to the lower and middle parts of the section. Thamnasterioid-aphroid colonies of *Scruttonia*

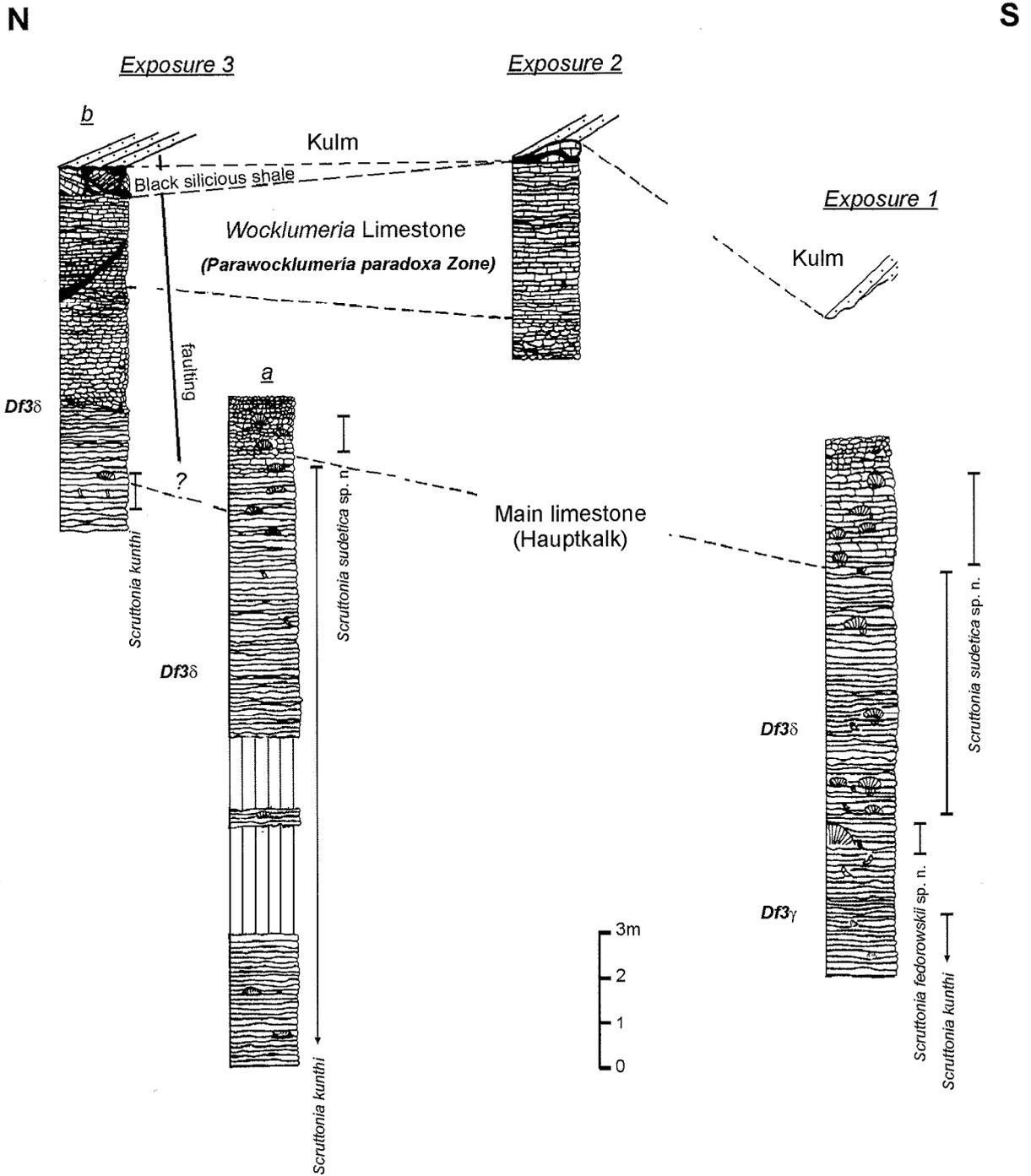


Fig. 2. Correlated lithologic logs of the exposures situated on the eastern wall of the Wapnica Quarry; ranges of the coral taxa studied are indicated; stratigraphy of the main limestone based on forams

sp. B (BERKOWSKI, in press) occur in the uppermost part. Solitary corals are less common and badly preserved. They represent columellate taxa like *Clisiophyllum* sp., *Dibunophyllum* aff. *praecursor*, one

undetermined genus and tabulophyllomorphs *Tabulophyllum* sp.

Scruttonia colonies were often found on the tabulate coral *Syringopora*. Apart from corals, here and

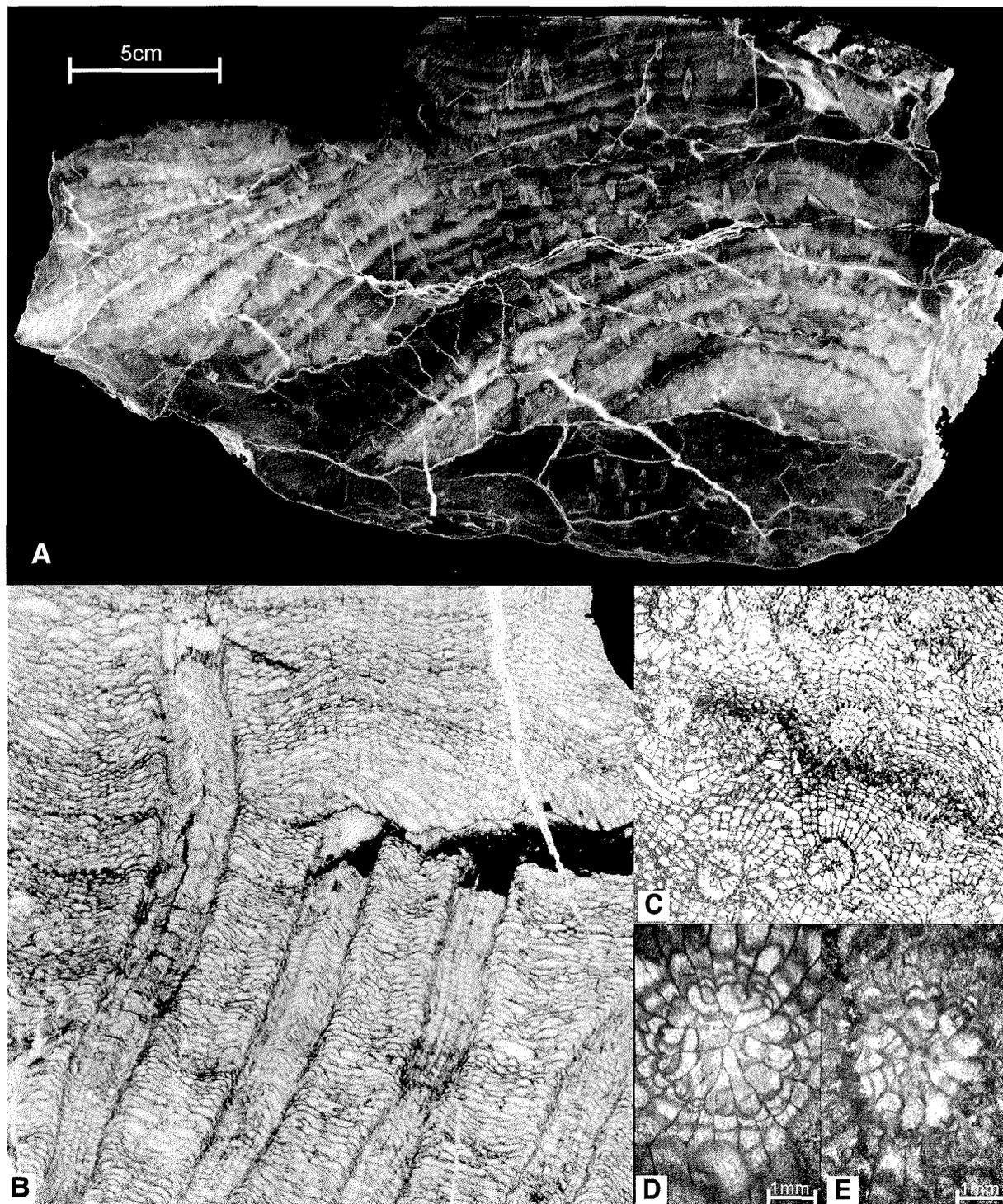


Fig. 3. Internal characters of *Scruttonia kunthi* (FRECH); A – polished transverse-oblique section of the colony UAM Tc – B\02\DI\07a; alternating high- and low-density growth bands are clearly visible within the colony; below the colony a phaceloid colony of *Syringopora* sp. is visible; Dzikowiec, exposure 1, the Main Limestone Df γ or δ , which correspond to the *P. expansa* Zone; B – longitudinal thin section $\times 4$ revealing high- and low-density banding; on the right side a lateral notching corresponding to the high-density band is visible; C- transverse-oblique thin section ($\times 4$) revealing different type of skeletal structures in high (darker) – and low (lighter)–density bands; D – transverse thin section of the corallite from a low density band (thin skeletal elements); E – transverse thin section of the corallite from a high density band (thickened skeletal elements)

there massive stromatoporoids occur in their life position. Large gastropods *Serpulospira crassitesta* (TRETZE 1870; DZIK 1994, p. 35), bivalves, and articulate brachiopods occur sporadically.

Exposure 3 is located in the northern part of the Wapnica Quarry, on the eastern and north eastern wall (Text-fig. 1B). The main limestone and *Wocklumeria* limestone cropping out there are of the greatest thickness in the quarry, although not complete (Text-fig. 2). The exposure consists of two parts cut by a fault. The lower one (exposure 3a) consists of the main limestone of similar lithology as in exposure 1, the upper (exposure 3b) includes the upper part of the main limestone and the overlying *Wocklumeria* limestone covered by black siliceous shale, the "gneissic" sandstone and conglomerate of the „Kulm”. Coral assemblages of the main limestone in exposures 3a and b are very similar to those of exposure 1, but generally poorer and less diversified. Some solitary taxa and aphroid *Scruttonia* sp. A are absent, whereas both thamnasterioid taxa of *Scruttonia* occur in this same sequence as in exposure 1 (i.e. *S. kunthi* in the lower part and *S. sp. B* in the upper part).

ASTOGENY AND TAPHONOMY

The succession of colonial *Rugosa* within the main limestone

Three species of *Scruttonia* were examined within the section of the main limestone: thamnasterioid *S. kunthi* (Frech), *S. sp. B* (BERKOWSKI, in press) and aphroid *S. sp. A* (BERKOWSKI, in press). The aphroid species *S. sp. A* is restricted to only one bed. It is suggested here that this species represent a temporal immigrant from an other site. Thamnasterioid colonies occur within almost the entire section of the main limestone exposed nowadays in the Quarry. They reveal a significant variation of tabularial size (dimensions of tabularia and the number of septa) and a gradual transition from a thamnasterioid into a thamnasterioid-aphroid structure. These size variations seem to represent a gradual phylogenetic trend, which differentiates two separate species: *Scruttonia kunthi* with generally smaller corallites is restricted to the lower and middle part of the section and *Scruttonia sp. B* possessing larger corallites is known only in the uppermost part of the main limestone section. All colonies investigated were found in life position. Each colony begins and ends its existence within

a single carbonate bed, which is alternated by black shale.

Thamnasterioid colonies

The shape and growth strategy

Small colonies representing only the younger stages of astogeny are plate-like and centrally slightly elevated (tabular), their W/H (width vs. high) ratio often exceeds 3. Larger and older ones reveal less regular shape caused by sediment influx and partial burial especially in their lateral parts (Text-fig. 3A), but still their character remains tabular or slightly domal with a W/H ratio between 2 and 3. Within

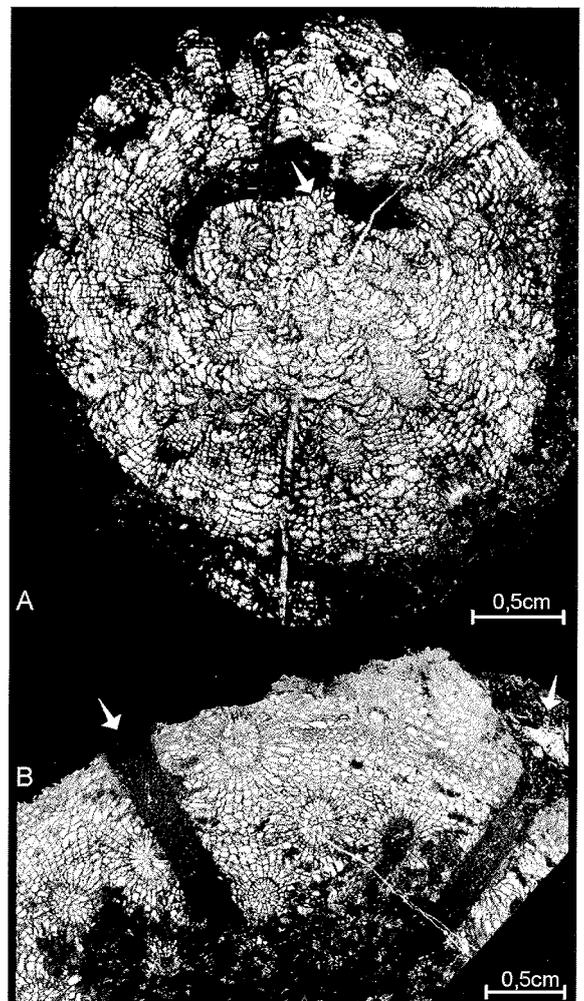


Fig. 4. A – transverse section of the juvenile colony; proto-coralite marked by an arrow; B – transverse thin section of the upper surface of the colony; two planar boring channels are marked by arrows

thamnasterioid *S. kunthi* (FRECH), clear density banding is visible on polished surfaces (Text-fig. 3A) and in thin sections (Text-fig. 3B, C). The growth strategy is strictly peripheral (*sensu*: Scrutton 1998).

Early astogeny

A protocorallite was identified within only one colony of *S. kunthi* (FRECH) (Text-fig. 4A). Its arrangement suggests, that before the process of offsetting started it bent downward within soft muddy sediment. Successive offsetting in most colonies was restricted to the peripheral parts of the colony i.e. near the common holotheca. The direction of growth of young offsets was centrifugal (offsets are almost parallel to the bedding plane) and then when they were sufficiently distanced from the other colony members they become more perpendicular to the colony surface. Offsets appear within a pocket that developed on the marginal dissepiments just near the colony external wall – the holotheca (details of increase described by BERKOWSKI 2001 in press). This lateral increase is extracalicular, but even with careful examination of increase it is impossible to determine the bud's parent corallite. Thus, it cannot be excluded that it is a kind of coenenchymal increase attributed rather to Tabulates and absent within rugosans according to Scrutton (1998). Internal marginarial skeletal elements consist mostly of dissepiments, which are widely spaced at the young stages of astogeny. More densely packed dissepiments developed later in astogeny and are accompanied by common septa in thamnasterioid colonies. It seems that structures become more densely packed when the colony had stabilised itself within the soft sediment against sinking.

Astogeny of the mature colony

After colony stabilisation, band-like structures within the internal skeletal elements are observable mainly in *S. kunthi* (FRECH). The clear banding seems to be annual in nature. High and low density bands differ not only in structure but also in stable isotope content (BERKOWSKI & BELKA 1999) and are the most characteristic features concerning intracolony variability. The skeletal elements of corallites differ strikingly in high- and low-density bands: in high-density bands they reveal strong thickenings, and the septa possess strong carinae (Text-fig. 3D,E). The high-density bands are correlated with notches caused by partly burial of the colony margins, whereas low-density bands represent periods of intensive rejuvenescence of the buried parts of the colony (Text-fig. 3B).

Although, the young stages of offsets are often visible within the upper surface of high-density bands, their development was continued within low-density bands. The notched shape of mature colonies may reflect the peripheral strategy of colony growth in a generally quiet sedimentary regime, interrupted occasionally by minor, rapid influxes of fouling sediment.

Taphonomy

Colonies initiated their growth within the soft muddy sediment. The sediment was, however, often baffled by the phaceloid tabulate coral *Syringopora* (Text-fig. 3A-base), which made the sediment more stable for colony settlement. The duration of colony growth was estimated from the alternating high and low-density bands as between 1,5-26 years. The upper surfaces of the colonies are often very well preserved and are covered by thin layers of pyrite, which is now often oxidised. This suggests rather rapid burial of the colony.

Planar boring-channels filled with the sediment were noted within the uppermost portion of some colonies (Text-fig. 4B). They cross calices and common skeletal tissue, and there is no sign of the later rejuvenescence of the destroyed parts of the colony. Hence, the borings seem to have taken place after colony burial.

Aphroid colonies

The shape, growth strategy and intracolony variability

The early astogeny of these colonies is unknown due to the absence of small colonies within the bed where they occur. The proximal and marginal parts of the colonies are mostly destroyed. The mature colonies are extraordinary large, exceeding 50 cm in diameter and about 35 cm in height (Text-fig. 5A). Colonies are tabular with almost flat surfaces and seem to reveal a peripheral growth strategy. The cenosteum is strictly aphroid and composed of rather flat and large dissepimental vesicles (Text-fig. 5). Corallites possess the largest diameters of tabularia (Text-fig. 5C, D) among the species studied and are very long, up to 21 cm. They grew perpendicular to the colony surface. Their septa are mostly disconnected in the axis (Text-fig. 5C, D). Intercolony variability within aphroid colonies is less distinct than within the studied thamnasterioid taxa. The mainly cyclo-morphic variation is not regular. Banding is marked by sediment influx, which often covered much of the colony surface, not only in the lateral parts (Text-fig. 5A, B). Sediment covered mostly the marginarium,

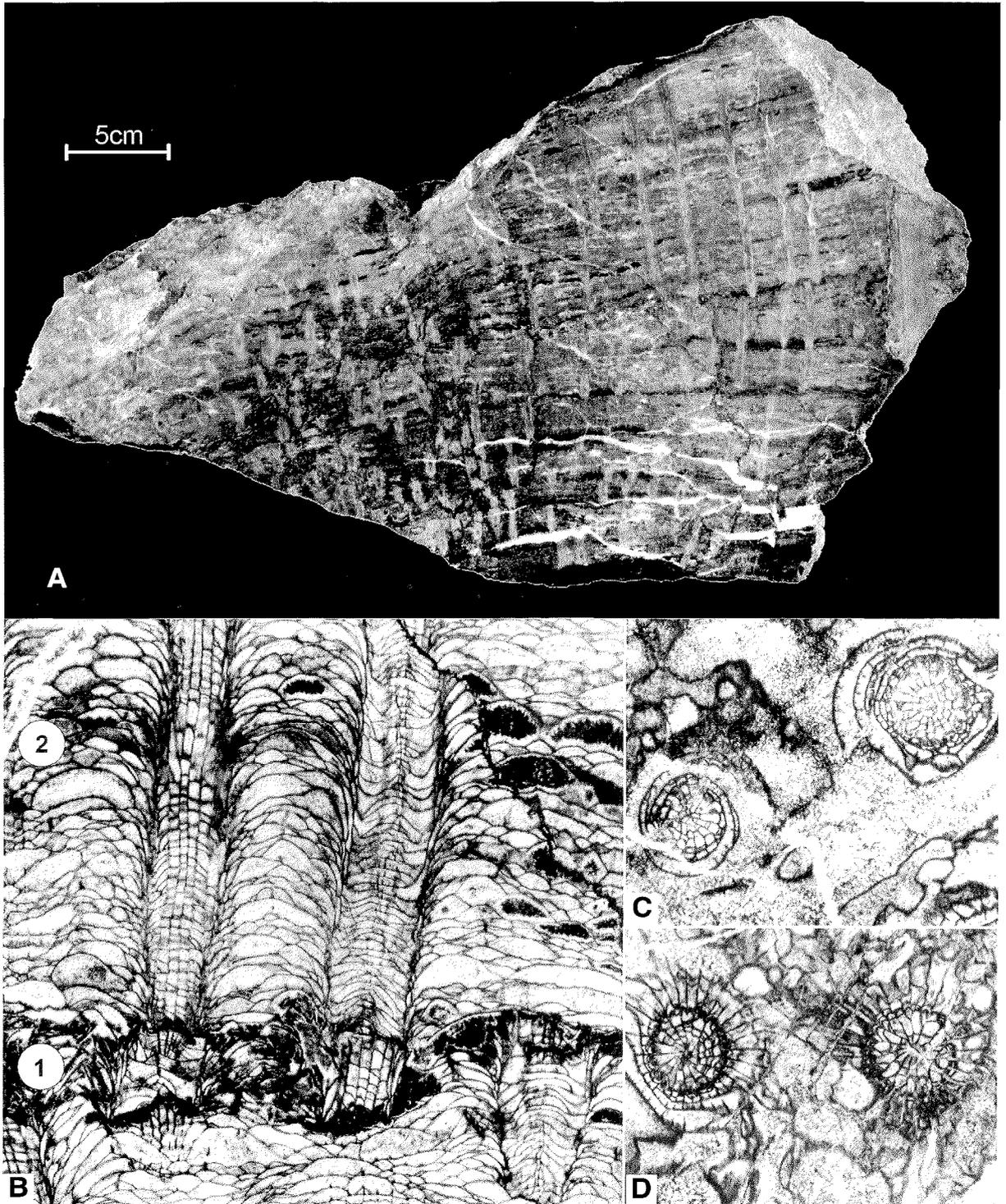


Fig. 5. Internal characters of aphroid *Scruttonia* sp. A (BERKOWSKI, in press); A – polished transverse section of the colony UAM Te – B\02\DI\05; banding marked by sediment cover within the colony; B- longitudinal thin section $\times 4$. Sediment cover: (1) strong sediment influx covering most of the entire colony – corallites killed; (2) minor sediment influx covering only a part of cenosteum – corallites survive, dissepiments around corallites more steeply arranged. C- transverse section of the colony ($\times 4$) with the section just above the band enriched with sediment; D- transverse section of the colony ($\times 4$) with the section below the band enriched with sediment

whereas protruding corallites to a large extent prolonged their growth; some of them reveal the phenomenon of rejuvenescence. Some of them, however, stopped growth and are covered partly or wholly by sediment and later by rejuvenated common tissue. Dissepiments within the bands affected by fouling sediment are markedly larger and much more steeply arranged around the corallites, which seem to possess deeper calices in this case.

Taphonomy

The colonies studied are fragmentally preserved, so it is impossible to determine their exact dimensions. However, the size of the fragments exemplifies probably the largest massive colonies known in the Famennian. Dissepimental vesicles are often tiered due to later diagenesis and compaction. Hence, they were much more delicate than those occurring within the unaffected bands. Free spaces occurring within the buried bands are often filled with thick layers of palisade-type cements. The latter cements occur also within the large vesicles.

Estimating sedimentation rate

The cyclomorphic variations described above allows the calculation of the growth rate in colonies of *S. kunthi* and *S. sp. A* (Text-fig. 6A,B). The statistics

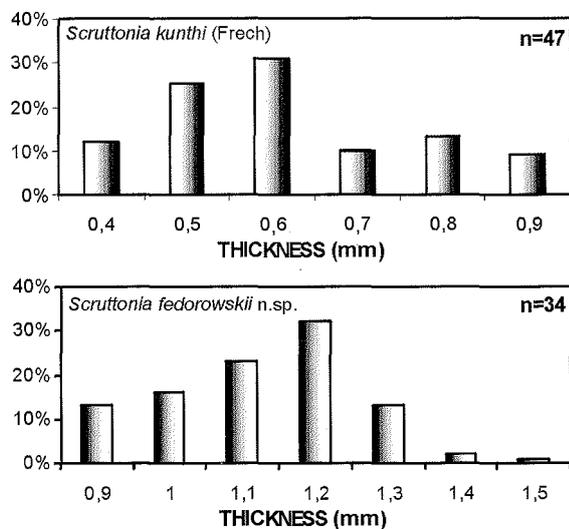


Fig. 6. Measured thickness of the alternating growth bands in the colonies studied: (high + low density bands) in *Scruttonia kunthi* (FRECH) and (enriched with sediment + "normal" bands) in *Scruttonia sp. A* (BERKOWSKI, in press)

show that colonies of *S. sp. A* grew about twice as fast as colonies of *S. kunthi*.

By assuming that the growth rate of the colony and the general rate of sedimentation seemed to be more or less equal it is possible to evaluate the sedimentary regime reflected within the beds where the colonies occur. For thamnasterioid colonies of *S. kunthi* and *S. sp. B* possessing tabular or slightly domal shape and densely developed skeletal structures, where clear density banding is easy recognisable, the model illustrated in Text-fig. 7A, reflecting minor fluctuation of sedimentation rate, is proposed.

The aphroid *S. sp. A*, developed as flat tabular body, and possessing loose and large skeletal elements, displays a different type of colony-sediment interactions (Text-fig. 7B). The cyclic appearance of bands enriched with sediment covering almost all the colony surface and alternating surfaces of recovery, show that the aphroid colonies could survive even during stronger sediment influx.

CONCLUSIONS

1. The sedimentation rate during the deposition of the upper part of the main limestone (beds with colonies) was rather quiet and stable, interrupted by minor fluctuations caused by seasonal increase of sediment influx, reflected in thamnasterioid colonies as lateral notching correlated with high density bands of the internal skeleton.
2. One bed containing aphroid colonies probably represents higher sedimentation rates, where thamnasterioid colonies with densely packed internal skeletal elements are absent, because of "too fast" sedimentation.
3. The presence of seasonal cyclomorphic variations within the internal skeleton in thamnasterioid colonies allows the calculation of approximate growth rate of the colonies. It varies within thamnasterioid *S. kunthi* between 0,4-0,9mm per year.
4. The cyclomorphic variations within aphroid *S. sp. A* are less distinctly marked only by relatively larger and more vertically arranged dissepiments in bands enriched in sediment. The distance between the tops of the one-type bands varies between 0,9-1,5mm. It is suggested here, that those variations caused by sediment influx could be also regarded as seasonal because of their regular pattern.
5. High-density banding in thamnasterioid colonies, frequently associated with marginal notching and bands enriched with sediment often covering most of the colony surface in aphroid colonies, might reflect a seasonal increase in water turbidity.

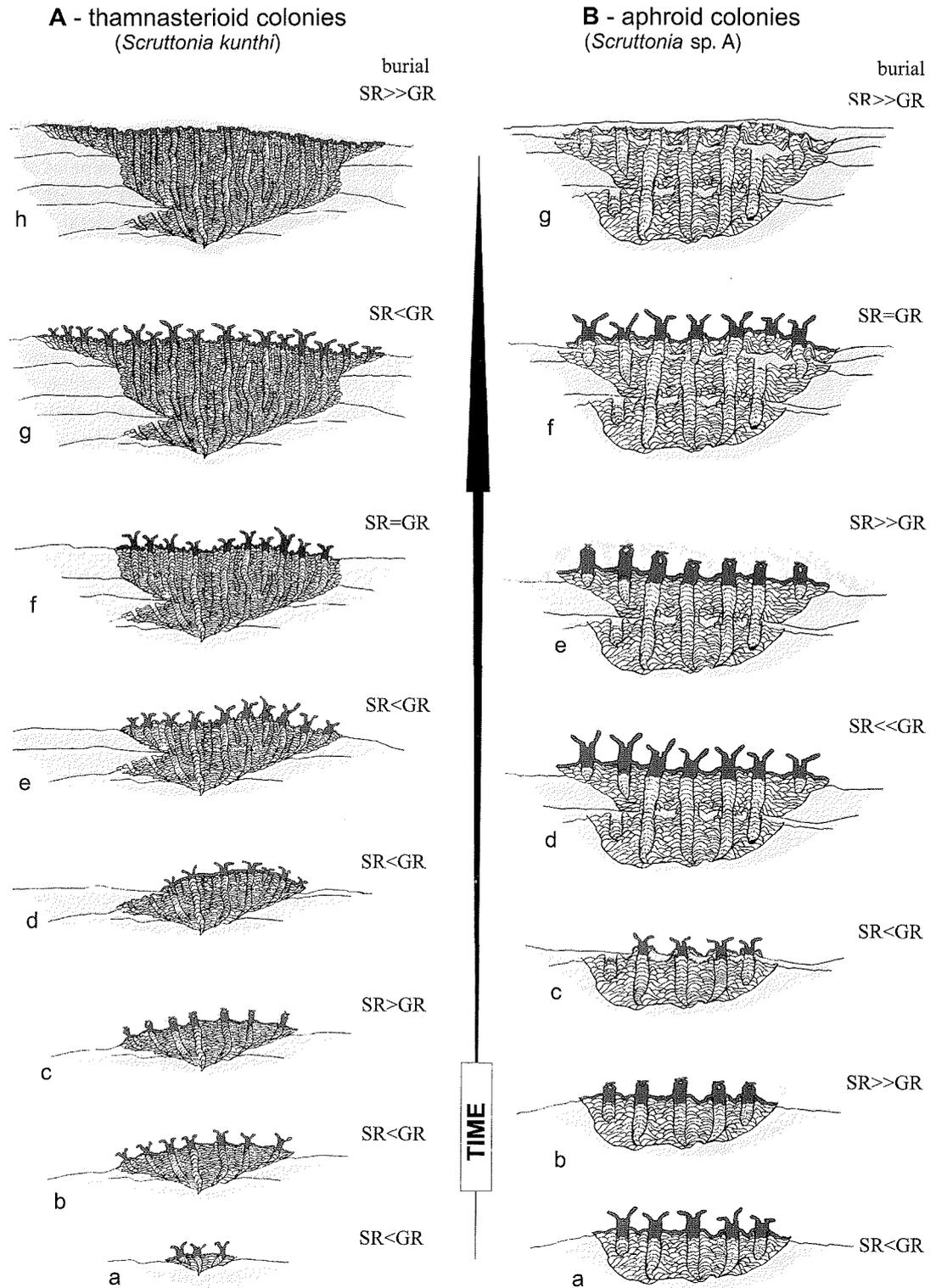


Fig. 7. Idealized reconstruction of successive astogenetic stages in: A-thamnasterioid *Scruttonia kunthi* (FRECH) and B - aphroid *Scruttonia* sp. A (BERKOWSKI, in press) - based on field and laboratory observations; SR - sedimentation rate, GR - growth rate

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