Late Famennian Stromatoporoids from Dębnik Anticline, Southern Poland

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Famennian Stromatoporoidea from the *Quasiendothyra communis* Foraminiferal Zone and slightly younger strata from the Dębnik anticline, southern Poland, form a succession of three consecutive assemblages. Assemblages 1 and 3 consist of representatives of the order Clathrodictyida, while assemblage 2 is dominated by the order Labechiida. The clathrodictyids are represented by the genus *Gerronostroma*, and labechiids are represented by the genus *Stylostroma*. Species assigned here to the genus *Gerronostroma* show a network of amalgamated pillars in the central part of the columns, a feature regarded by previous authors as typical of the genus *Clavidictyon*. Two new species, *Stylostroma multiformis* sp. nov. and *Gerronostroma raclaviense* sp. nov., are described. Stromatoporoids from southern Poland differ from the Famennian fauna of western Europe, showing affinity to eastern European and Siberian Stromatoporoidea.

Key words: Porifera, Stromatoporoidea, Labechiida, Clathrodictyida, *Gerronostroma*, *Stylostroma*, ontogeny, phases, statistics, Famennian, Poland.

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Introduction

During Frasnian stromatoporoids were common in shallow marine environments. However, this reef-building group has been severely affected by the Frasnian/Famennian crisis. 17 genera became extinct during that time, or shortly after, although at least 20 persisted into Famennian (Stearn 1987).

Famennian stromatoporoid faunas are characterised by massive resurgence of the primitive order Labechiida. This group occurs in all post-Frasnian assemblages except for Western Europe and Kazakhstan. Some labechiids are also known from the Famennian of Germany, however they are rare (Weber 1999; Weber and Mistiaen 2001). The latest Devonian faunas are divided into three assemblages (Stearn 1987; Stearn and Halim-Diharja 1987). The first consists solely of the labechiids, the second comprises Labechiida mixed with Clathrodictyida. The third assemblage, with no representatives of labechiids, consists of clathrodictyids. The presence of the branching stromatoporoid *Clavidictyon,* commonly recognized in the Famennian, is another important feature of the second and third assemblages. However, taxonomic position of genus *Clavidictyon* remains unclear (Stearn et al. 1999).

The aim of the present study is to investigate the stromatoporoids from the Dębnik Anticline, and to compare them with other Famennian faunas described by the previous authors. The intraspecific and intraskeletal variations of the studied stromatoporoids are also evaluated.

Institutional abbreviation.—UAM, Institute of Geology, Adam Mickiewicz University, Poznań, Poland.

Geological setting

Famennian deposits outcrop in the Dębnik Anticline, located about 20 km north-west from Kraków (Fig. 1B). The structure is build up of the Givetian to Visean strata. The Famennian exposures are located in the eastern limb of the anticline (Racławka Valley) and on its southern margin near Żbik Village, however the latter are now strongly overgrown and hardly available (Mariusz Paszkowski, personal communication 2003).

Paszkowski (1995) divided the Middle and Upper Famennian deposits from Dębnik Anticline into two formations (Table 1). The stromatoporoid bearing strata belong to the Góra Żarska Member of the Dubie Formation and to the Racławka Formation.

Upper Famennian limestones of the Dębnik Anticline were deposited in a high energy environment, presumably on a storm-dominated carbonate ramp. Upper part of the profile is composed of a sequence of shallowing upward cyclothems, with uppermost members representing intertidal environments, with episodes of emersion (Paszkowski 1995).

Famennian stromatoporoids of the Dębnik Anticline were identified by a number of authors (Łaptaś 1982; Paszkowski 1996; Berkowski 2002; Flügel 2004), but only Gürich (1904) described one species, *Stromatoporella cracoviensis*, which is revised in this paper. Łaptaś (1982) was the first to notice the presence of labechiids within Upper Famennian strata. He mentioned single specimen of *Labechia* aff. *devonica*, but neither described nor illustrated this species. At the east-

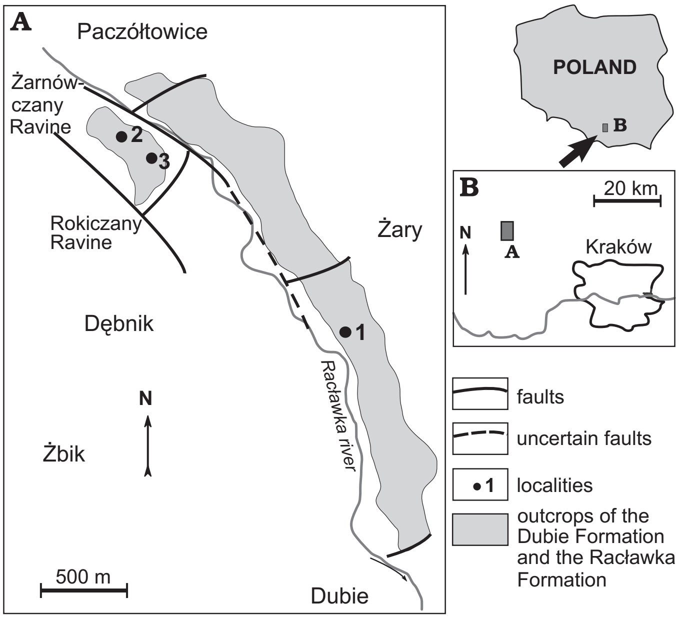

Fig. 1. Upper Famennian in the Racławka Valley, Dębnik Anticline, southern Poland. **A**. Simplified geological map of the Dębnik area. **B**. Simplied map of Kraków region, southern Poland.

ern slope of the Racławka Valley Paszkowski (1996) documented exposures of detritic limestones containing numerous *Stylostroma* skeletons. Berkowski (2002) noticed the presence of assemblage dominated by clathrodictyids. Labechiid stromatoporoids from Dębnik Anticline were illustrated by Flügel (2004: 501).

Nine outcrops, all situated in the eastern limb of the Dębnik Anticline, were investigated for the present study. Stromatoporoids were collected from three exposures, located on both slopes of the Racławka Valley between Dubie and Paczółtowice villages (Fig. 1A). The most complete profile (locality 1, Fig. 2A) displays strata belonging to both Dubie and Racławka Formations. The two other outcrops are resticted to the Góra Żarska Member (locality 3) and upper parts of the Racławka Formation (locality 2).

Locality 1 (Fig. 2A).—Eastern slope of the Racławka Valley, 0.9 km north of Dubie village. Lower part of the profile displays 9 m thick grainstone unit described by Paszkowski (1995) as Góra Żarska Member of the Dubie Formation. Numerous stromatoporoids are scattered within the sediments. Colonial rugose coral *Pseudoendophyllum raclaviense* Berkowski, 2002, tabulate corals (often penetrating stromatoporoid skeletons), solenoporacean *Parachaetetes*, crinoids, and brachiopods accompany the stromatoporoids. Described sediments were deposited in the shallow marine environment (Paszkowski 1995).

The lowest part of the Racławka Formation also occurs within the exposure 1, and is separated from underlying Dubie Formation by a 100 mm thick layer of silicified grainstones. The section is considered continuous in that part since no evidence of erosional surfaces was found. Stromatoporoids are present within nearly 20 m of the profile. Large (up to 10 cm thick) skeletons of stromatoporoids (labechiids) co-occur with gastropods in brownish-grey, marly biopelsparites. Foraminifers and conodonts are unknown from assemblage 2, thus its exact stratigraphic position remains undetermined.

The uppermost part of the exposure 1 is separated from the underlying strata by a 40 m gap. Stratigraphic position of this unit is unclear since no stratigraphically significant foraminifers were found. Dark grey and black, coarsely layered, poorly sorted grainstones belong to the Racławka Formation. A presence of numerous skeletons of stromatoporoid *Gerronostroma raclaviense* sp. nov., accompanied by *Syringopora* corals, solenoporacean *Parachaetetes*, and *Ortonella*, is the most important feature the uppermost part of exposure 1.

Locality 2 (Fig. 2B).—0.6 km south of Paczółtowice village, 30 meters south of Żarnówczany Dół ravine, and within the upper part of the Racławka Formation (Paszkowski, 1995). All samples were collected from the scree on the western slope of the Racławka Valley since no bedrock exposures were available. Dark grainstones contain skeletons of stromatoporoid *Gerronostroma raclaviense* sp. nov., accompanied by *Syringopora* corals and solenoporacean *Parachaetetes*.

Locality 3 (Fig. 2B).—So called "Gürich's Stromatoporoid Rock" (Gürich 1904) is located on the western slope of the Racławka Valley, 0.9 km south of Paczółtowice village and 70 m north of Rokiczany Dół ravine (Paszkowski 1996; Berkowski 2002). About 40 m of the Góra Żarska Member of the Dubie Formation is exposed at this location. Due to the presence of numerous faults the exact thickness of this unit is uncertain. The limestones contain abundant stromatoporoids, tabulate corals, colonial rugosans *Pseudoendophyllum raclaviense* Berkowski, 2002, solenoporacean *Parachaetetes* and brachiopods.

Table 1. Simplified lithostratigraphic scheme of the Famennian succession in the Dębnik area. After Łaptaś (1982), Narkiewicz and Racki (1984), and Paszkowski (1995).

	Łaptaś 1982	Narkiewicz and Racki 1984	Paszkowski 1995	
Famennian	Units G and H	Grained and Micritic Limestones	Rudawa Group	Racławka Formation
				Góra Żarska Member Dubie Formation
	Unit F	Platy Limestones		

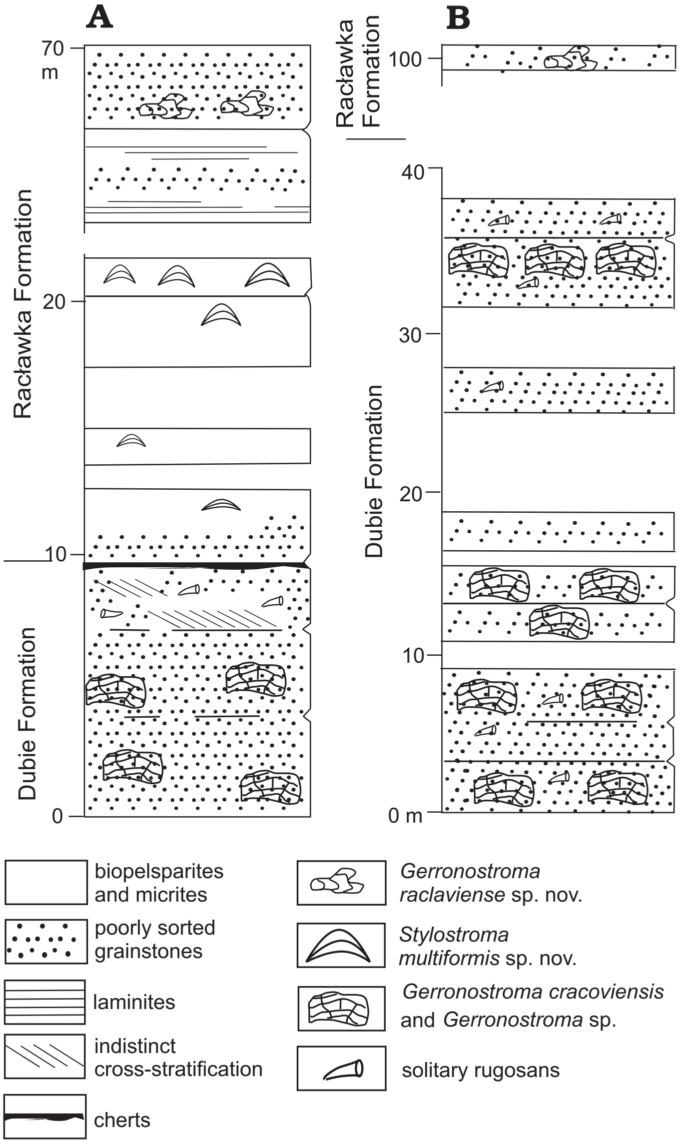

Fig. 2. Detailed profiles of the studied localities. **A**. Detailed profile of exposure 1, displaying succession of three stromatoporoid assemblages. **B**. Geological logs of locality 2 (uppermost part of the profile, Racławka Formation, all samples collected from the scree, no bedrock available) and exposure 3 (the so-called "Gürich's Stromatoporoid Rock").

Material and methods

140 samples of limestones from the Dubie and Racławka Formations were collected. Three additional rock fragments, found in the scree in the vicinity of the exposure 3, came from the collection of Błażej Berkowski (UAM). A total number of 160 longitudinal and vertical (transverse) thin sections from 75 specimens of stromatoporoids were prepared. All specimens were carefully studied and assigned to four species based on their internal structure. The statistical procedures were also applied as a supplemental tool. The nomenclature used in this paper follows that of Stearn et al. (1999). The terms introduced by Kershaw and Riding (1978) for describing stromatoporoid shapes were also used.

Species described in this paper reveal a wide range of variation within individual specimens. Thus, separate phases of each stromatoporoid species were described. The term "phases" was introduced by Stearn (1986). In his paper he suggested that variation in skeletal elements within individual specimens should be described in terms of phases, i.e., parts of skeleton showing similar inner structure. Those phases replace one another both laterally and perpendicular to the growth surface. This phenomenon is clearly visible in studied specimens.

The statistical procedures were applied as a supplemental tool, in order to verify species identifications. Numerical methods were not crucial for making taxonomic decisions, although they proved their utility for discrimination of species *Gerronostroma cracoviensis* (Gürich, 1904) and *Gerronostroma* sp. In other cases statistical procedures were used mainly to assign controversial and highly variable specimens to species.

Single factor analysis of variance (ANOVA), and its nonparametric equivalent, Kruskal-Wallis test, were applied to distinguish significant differences between the individual specimens assigned to the same genus. In those cases in which significant differences were detected by ANOVA or Kruskal-Wallis test, post hoc testing was performed using Tukey's method (Yandell 1997) and multiple comparison test after Kruskal-Wallis test (Siegel and Castellan 1988). Multiple t-tests and Kolmogorov-Smirnov tests were used as a supplemental tool, as far as the repetitions increase the risk of occuring the type I error. The 0.05 level of significance was attained.

For the purpose of statistical analysis measurements of several features were taken (Fig. 3). Order Labechiida were measured for height and span of cysts, number of cyst plates intersected by pillars, pillar length, and spacing of dissepiments. Analysis of *Gerronostroma* involved measurements of thickness of laminae and pillars, laminar and pillar spacings, pillar diameter, and pillar length. All data except the pillar diameter were gathered from longitudinal sections. Morphometric measurements were performed on scanned images of thin sections, using image analysis software developed by the author. This technique allowed to measure all skeletal elements visible in both longitudinal and vertical sections. A total number of 227,287 measurements were taken. Statistical analyses were accomplished using R software (http://www.r-project.org) and the Pgirmess package.

Systematic palaeontology

Phylum Porifera Grant, 1836

Class Stromatoporoidea Nicholson and Murie, 1878

Order Labechiida Kühn, 1927

Family Labechiidae Nicholson, 1879

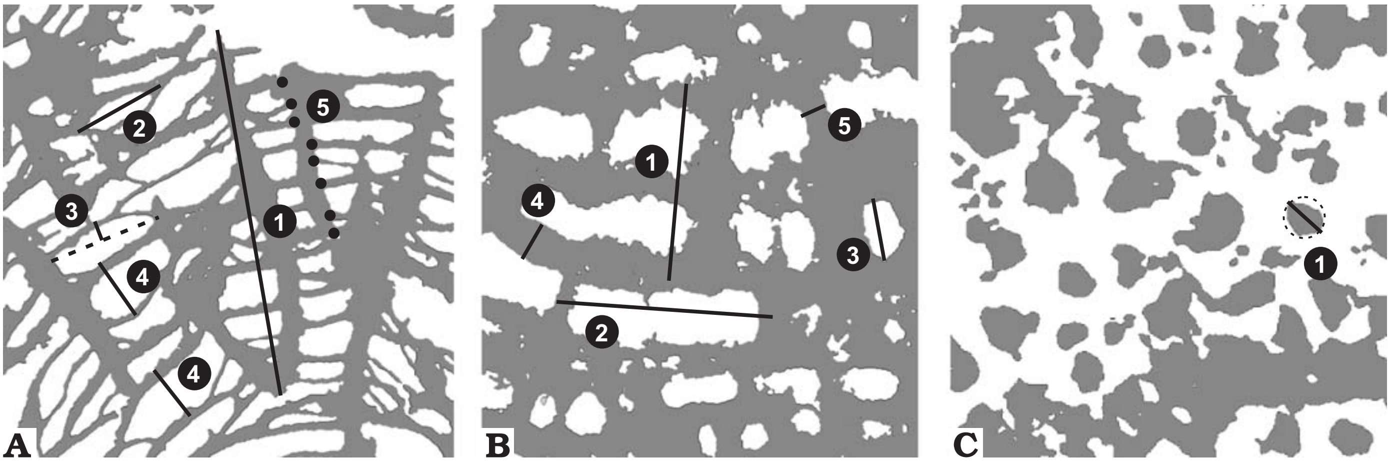

Fig. 3. Measurements taken for the purpose of statistical analysis. **A**. Measurements taken from longitudinal sections of Labechiida. 1, pillar length; 2, span of cysts; 3, height of cysts; 4, spacing of dissepiments; 5, number of cyst plates intersected by pillars. **B**. Measurements on *Gerronostroma* specimens (longitudinal sections). 1, pillar length; 2, pillar spacings; 3, laminae spacings; 4, thickness of laminae; 5, thickness of pillars. **C**. Measurements taken from transverse sections of *Gerronostroma*. 1, pillar diameter.

Genus *Stylostroma* Gorsky, 1938

Type species: *Stylostroma crassum* Gorsky, 1938; Famennian, Novaya Zemlya, Russia.

Stylostroma multiformis sp. nov.

Fig. 4A–D.

Etymology: From Latin adjective *multiformis*, having many forms and appearances.

Type material: Holotype, UAM RAC-LAB130 (two longitudinal thin sections and a single transverse section) and paratypes UAM RAC-LAB138, UAM RAC-LAB133, UAM RAC-LAB155.

Type locality: Eastern slope of the Racławka Valley, 0.9 km north of Dubie village, 150 m east from a small bridge over the Racławka stream, 25 meters above the valley floor (Fig. 1A, locality 1).

Type horizon: Lowest part of the Racławka Formation, 13 meters above the underlying Dubie Formation. Famennian.

Material.—29 specimens from locality 1, most of them complete.

Diagnosis.—*Stylostroma* with distinct mamelons, dichotomically branching pillars, dissepiments variable in size, and numerous denticles. Phases 2 and 3 with flattened cyst plates and simple pillars revealing cone-in-cone structure, and without mamelons. *Stylostroma multiformis* sp. nov. differs from *S. sinense* (Dong, 1964) by the absence of pillars branching in dendroid form, presence of phases lacking distinct mamelons, and by the relative abundance of pillars made up of invaginating cones. It differs from *S. crassum* Gorsky, 1938 by lacking mamelons in extensive parts of the skeleton.

Description.—Skeleton laminar or domical. Laminar specimens up to 5 mm thick. Their basal length not exceeding 100 mm. Heights of domical forms up to 100 mm. Mamelons distinct in most specimens, intersecting the skeletons at the distance up to 50 mm, on the surface showing a relief of up to 10 mm. Axial canals absent. Cysts of variable sizes, with spans up to 5 mm, and heights of up to 1.1 mm. Smaller cysts usually more convex, while larger flat, and thickened (up to 150 μm), simulating laminae in places. Cysts spaced 5–7 in 2 mm, in areas of thickened skeletal element 2–4 in 2 mm. Pillars 0.5–3.5 mm long, simple or upwardly branching, intersecting at least 3–4 cysts. In tangential sections cut as dots, locally form short walls in central parts of mamelon columns. Pillars commonly restricted to mamelons, but in laminar specimens spaced more regularly. Denticles numerous on tops of thickened cysts, in mamelon columns absent. The basal thickness of denticles not exceeding 250 μm. Some denticles transformed into small pillars, intersecting 1–2 cyst plates.

Intraskeletal variation within *Stylostroma multiformis* sp. nov. wide, allowing to distinguish three separate phases sensu Stearn (1989). In many specimens two phases mixed together, passing vertically or laterally into each other.

Phase 1 (Fig. 4A, D): Strongly mammilate skeleton, usually domical. Small specimens laminar, with basal length reaching up to several, but less than 100 mm. On the surface mamelons with distinct relief, up to 10 mm. Cysts moderately convex, with heights ranging 150–3000 μm, mostly thin, less than 80 μm thick, but in areas lacking pillars strongly thickened, up to 150 μm, and more convex with heights up to 1000 μm. In the vicinity of mamelons cysts closely spaced (5–7 in 2 mm), in other parts of skeleton larger, hemispherical, thickened, and widely spaced, 2–5 per 2 mm. Pillars simple, postlike, usually restricted to mamelon columns. Their inner structure compact, with the microstructure indistinguishable, probably due to dolomitisation. Relics of primary cone-in-cone structures absent. Pillars dichotomously branching, feather-like structures absent. In tangential sections pillars rounded, but in central zone of mamelons forming short walls, up to 1 mm (Fig. $4A_3$, lower right corner). Denticles short (not exceeding 400 μm), triangular, with basal diameter about 200 μm. On cysts between mamelon columns denticles numerous, rarely transformed into small pillars intersecting one or two cyst plates.

Phase 2 (Fig. 4B, D): Mamelons small with relief not exceeding 1.0 mm. Skeleton domical. Cysts convex, with heights up to 1.0 mm, and thickness up to 50 µm, strongly flattened, thickened up to 150 µm, occasionally simulating laminae. Cysts serve as a base for long pillars, intersecting 6–12 cysts, reaching lengths of up to 5 mm, commonly branching in upper parts. Long, branching pillars commonly adjacent to one another. In their vicinity cysts convex, forming indistinct mamelons. Short and unbranched pillars also common, passing 2–5 cyst plates, their length not exceeding 2.5 mm. Denticles common, usually rising from thickened cysts. In parts of the skeleton consisting of small cyst plates denticles rare.

Phase 3 (Fig. 4C, D): Skeleton laminar, up to 40 mm in diameter. Inclusions of sediment incorporated into the skeleton common. Upper surface smooth and flattened. Mamelons rare, rounded in tangential section, composed of limited number, up to 4, cyst plates. Cysts of variable size, with spans ranging 0.7–2.4 mm. Large cysts more common. Convex cyst plates rare, their top surfaces serving as bases for denticles, usually transformed into small pillars. Some cysts strongly flattened and thickened up 1to 150 µm, in places resembling laminae, with numerous denticles on their upper surfaces. Other cysts thinner, not exceeding 80 µm in thickness. Pillars common, usually resting on flattened cysts, not branching. Two types of pillars present: up to 3 mm long, more than 200 µm thick, intersecting at least 6 cysts; and short rods, usually superposed denticles attached to flattened cysts. The latter common in parts of the skeleton with the predominance of thin and strongly convex cysts. The short rods up to 120 µm thick, intersecting less than 5 cysts. Their length not exceeding 0.8 mm. Pillars irregularly spaced, with areas with numerous, long pillars accompanied by parts of the skeleton composed only of thin, slightly convex cysts. In several specimens transitions between areas of phase 3 with sparse pillars and the phase 1 are present. Long pillars showing internal structure composed of convex cysts, invaginating into central parts of pillars. In other parts of specimens pillars with compact inner structure. In extensive areas of skeleton cone-in-cone structures visible only as thickenings on pillars at junctions with cysts. In tangential sections pillars rounded, long and thickened with concentric structure (Fig. $4C_1$), probably an effect of invagination of cyst plates. Other pillars compact, rarely oval or spool-like. Denticles less common than in skeletons assigned to phases 1 and 2, rising only from flattened cysts. In parts of the skeleton lacking long pillars, with short rods, intersecting less than 3 cyst plates only.

Statistics.—Two sample Kolmogorov-Smirnov and Kruskal-Wallis tests, taken on five skeletal features (height and span of cysts, number of cyst plates intersected by pillars, pillar length, spacing of dissepiments), revealed no statistically significant differences between decribed phases. Therefore all three forms of the skeleton are described as a single species. The null hypothesis was rejected in the case of pillar spacing. Specimens assigned to phase 1 show pillars restricted to mamelon columns and therefore larger values of pillar spacing.

Discussion.—*Stylostroma multiformis* sp. nov. could perhaps be divided into two species, on the basis of different structures of pillars and the absence of mamelons, with phase 3 assigned to genus *Labechia*. However, cone-in-cone structure is not clearly visible in all specimens of this phase. On the other hand, thickenings noticed on pillars at junctions with cysts may be interpreted as recrystallized parts of convex cyst plates. Transitions between the phase 3 and other phases were observed. Thus all phases are considered as belonging to a single species.

Stratigraphic and geographic range.—Southern Poland, Dębnik Anticline, both slopes of the Racławka Valley between Dubie and Paczółtowice villages. Lower part of the Racławka Formation. Upper Famennian.

Order Clathrodictyida Bogoyavlenskaya, 1969

Family Gerronostromatidae Bogoyavlenskaya, 1969

Genus *Gerronostroma* Yavorsky, 1931

Type species: *Gerronostroma elegans* Yavorsky, 1931; Lower Devonian, Kuznetsk Basin, Russia.

Emended diagnosis.—Laminae planar, continuous, reduced in columns; galleries rectangular in longitudinal sections; pillars rodlike, mostly long or superposed, in central part of columns branching and forming meandering vertical walls; mamelons common, sometimes upwardly extended into columns; astrorhizae indistinct.

Discussion.—Species described here reveal amalgamated network of pillars in central parts of mamelons and columns, considered as typical of the *Clavidictyon* Sugiyama, 1939, commonly recognized in Famennian rocks. However, long and superposed pillars are characteristic for genus *Gerronostroma*. The exact taxonomic position of *Clavidictyon* remains unclear. This genus is commonly placed in the order Amphiporida, but Stearn (in Stearn et al. 1999) proposed its moving into the order Clathrodictyida. Specimens of *Gerronostroma raclaviense* sp. nov. from the Raclawka Valley show laminar basal parts with features characteristic for the clathrodictyids (simple laminae, long pillars) and columns with amalgamated central zones, typical of *Clavidictyon*. This supports Stearn's et al. (1999) interpretation that these two genera are closely related, with *Clavidictyon* belonging to order Clathrodictyida.

Specimens of *Gerronostroma cracoviensis* (phases 1, 2) show pillars thickened in upper parts, with conical axial canals. As a result, in longitudinal sections pillars tend to branch dichotomously, resembling species assigned to the genus *Anostylostroma*. However, pillars dividing upward complexly, characteristic for the latter genus, are absent. The species described is therefore assigned to the genus *Gerronostroma*. Specimens described as phase 3 of *Gerronostroma cracoviensis* (Gürich, 1904) show close similarities (thickened pillars and numerous foramina) with "*Actinostroma* cf. *miraculum*" from the Famennian of western Germany (Flügel and Flügel-Kahler 1975). Absence of a hexactinellid pattern in tangential sections suggests that this species should be assigned to the genus *Gerronostroma*. Stearn and Halim-Diharja (1987) referred Famennian species of *Actinostroma* to *Gerronostroma*.

Famennian representatives of the family Gerronostromatidae, with pillars of variable length, short and superposed within single skeleton, are often assigned to genus *Clathrostroma* Yavorsky, 1960. Stearn et al. (1999) put this genus in synonymy with *Gerronostroma*. Thus the species *Gerronostroma sp.* is placed here in *Gerronostroma*, although it reveals short rods appearing together with long, superposed pillars.

Gerronostroma raclaviense sp. nov.

Figs. 4E, 5A–C.

Etymology: From the Racławka Valley, type locality of the species.

Type material: Holotype, UAM RAC-Z1 (a longitudinal thin section) and paratypes UAM RAC-Z51, UAM RAC-Z74, UAM RAC-Z142, UAM RAC-Z145.

Type locality: Western slope of the Racławka Valley, 0.6 km south of Paczółtowice village, 30 meters south of Żarnówczany Dół ravine (Paszkowski 1996; Berkowski 2002), 60 m west from the Racławka stream, 20 m above the valley floor (Fig. 1A, locality 2).

Type horizon: Upper part of the Racławka Formation, Upper Famennian.

Material.—19 fragments from localities 1 and 2. Columns usually broken, slightly abraded, attachments of stems can be traced in tangential sections. A few specimens preserved more completely, with stems rising from encrusting, laminar part of the skeleton.

Diagnosis.—*Gerronostroma* with laminar basal part, consisting of continuous laminae and long pillars; columns erecting as upward-extended mamelons; central parts with long, complexly branching, tripartite pillars, and reduced laminae. *Gerronostroma raclaviense* sp. nov. differs from other species of *Gerronostroma* by the presence of upwardly-extended mamelons and stems, with amalgamated axial zones. Columns of *Gerronostroma raclaviense* sp. nov. differs from *Clavidictyon graciliramosum* Dong, 1964 in the considerably smaller thickness of skeletal elements, from *C. luochengense* Dong, 1964 and *C. regulare* Dong, 1964 in having narrower peripheral parts of columns, and from *C. columnare* Sugiyama, 1939 by the presence of distinct boundaries between axial and peripheral zones of columns. Basal parts of all mentioned species are unknown.

Description.—Skeleton columnar, branching, with laminar basal part, commonly encrusting skeletal fragments of calcareous algae *Parachaetetes* or other stromatoporoids. Columns up to 50 mm long, branching dichotomously. Laminar parts of the skeleton up to 10 mm thick. Their basal parts not exceeding 50 mm in length. Inner structure of the skeleton revealing great variation of structural elements, with three phases being distinguished.

Phase 1 (Figs. 4E, 5A) in the basal part of the skeleton and in peripheral parts of stems, associated with phase 2. Laminae well-defined, continuous, with rare foramina. The thickness of laminae between 50 and 100 μm, not exceeding 150 μm. Laminae single-layered, rarely revealing tripartite structure, with light axial zone resulting from the amalgamation or branching. In peripheral zones of columns interlaminar spaces rectangular, in lower parts of laminar skeletons rounded. Pillars long, crossing three or more laminae. Parts of pillars lying immediately below laminae thickened, with conical axial canal. In vertical sections pillars exhibiting wide variety of shapes, mainly rounded, with upper parts oval, irregular or star-like. Vertical walls uncommon, visible only in parts of the skeleton adjacent to the mamelon columns. Astrorhizae and dissepiments absent.

Phase 2 (Figs. 4E, 5A) in central parts of columns, occupying 50–90% of the stem diameter, and in basal parts of the laminar form of the skeleton. Lateral transitions into phase 1 or phase 3 present. Laminae reduced, only in lateral parts more conspicuous, very thin (not exceeding 30 μm), preserved only as rods between closest pillars, with many foramina. Pillars long, branching complexly, intersecting at least three laminae. Inner structure of pillars usually tripartite, with central light zone.

Phase 3 (Fig. 5B, C) in basal parts of the skeleton, and in the mamelon columns. Skeletal elements strongly thickened. Laminae thick (from 100 to 350 μm), locally interrupted by foramina, single-layered, but sporadically tripartite, with darker lateral zones. In most cases that structure resulting from the amalgamation of closely spaced laminae. In the areas consisting of loosely arranged skeletal elements laminae less conspicuous, with numerous foramina. Pillars long, intersecting at least three interlaminar spaces, thinner than laminae, 150 μm thick in average. In the upper parts pillars thickened, rarely with axial canals, noticed only in loosely packed parts of the skeleton. In tangential sections pillars amalgamated, forming joined, meandering networks. Phase 3 also visible within mamelons and columns (Fig. 5B), if only in lateral parts, then associated with phase 2. Phase 3 in the central zone of columns visible as a mesh of branching, tripartite pillars, and reduced laminae. Within mamelons this phase differs from phase 2 by the strongly thickened pillars (up to 250 μm thick), and by the presence of a short (0.5–1.5 mm) axial canal, completely separated from surrounding interpillar spaces by long, amalgamated pillars (Fig. 5B).

Statistics.—Two sample Kolmogorov-Smirnov and Kruskal-Wallis tests revealed statistically significant differences between specimens assigned to *Gerronostroma raclaviense* sp. nov., *G. cracoviensis* (Gürich, 1904), and *Gerronostroma* sp. Significant differences between skeletons of *G. raclaviense* were detected when considering measurements of pillar and laminar thicknesses (Table 2). This phenomenon is caused by the reduction of laminae in central parts of the columns (phase 2).

Stratigraphic and geographic range.—Southern Poland, Dębnik Anticline, both slopes of the Racławka Valley between Dubie and Paczółtowice villages. Upper part of the Racławka Formation. Upper Famennian.

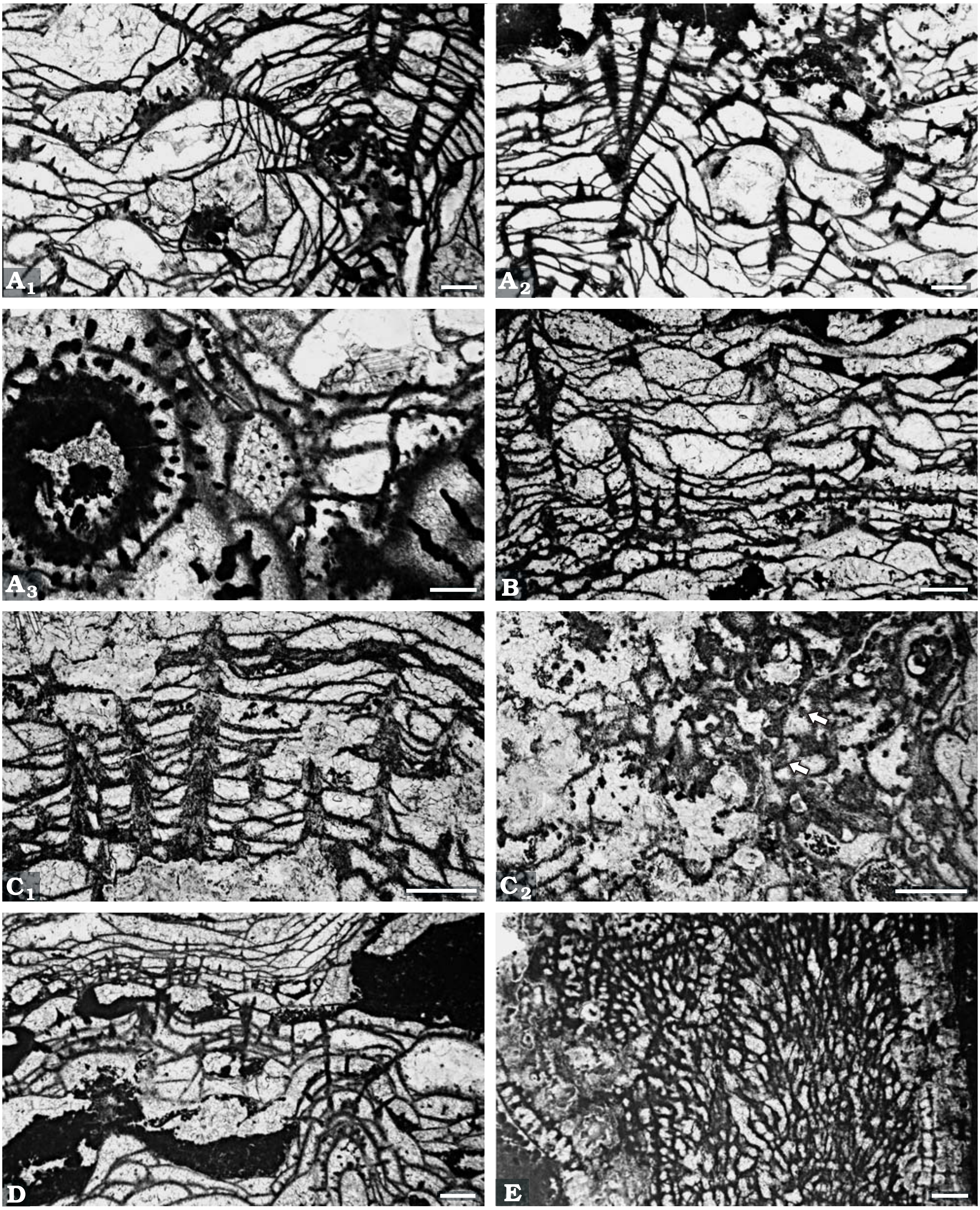

Fig. 4. Famennian labechiid *Stylostroma multiformis* sp. nov. and clathrodictyid *Gerronostroma raclaviense* sp. nov., Dębnik Anticline. **A**. *Stylostroma multiformis* sp. nov., A_1–A_3 Phase 1, holotype UAM RAC-LAB130. Longitudinal (A_1, A_2) and transverse (A_3) sections. Note pillars and short walls adjacent to mamelons (A_3). **B**. Phase 2, paratype UAM RAC-LAB138, longitudinal section. **C**. Phase 3, paratype UAM RAC-LAB133. Longitudinal (C_1) and transverse (C_2) sections. Note significant signs of dolomitisation, cone-in-cone structures (C1), and pillars revealing concentric structure (C_2, arrows). **D**. Paratype RAC-LAB155. Longitudinal section showing phase 1 (at the bottom) overlaid by phase 2 and phase 3 (near the upper margin of the photograph). **E**. *Gerronostroma raclaviense* sp. nov. Holotype UAM RAC-Z1. Longitudinal section of phase 1 (peripheral parts of column, dolomitised) and phase 2 (axial zone). Scale bars 1 mm.

Gerronostroma cracoviensis (Gürich, 1904)

Figs. 5D–G, 6D, E.

1904 *Stromatoporella cracoviensis* sp. nov.; Gürich 1904: 2, pl. 1: 1–3.

Neotype: Specimen UAM RAC29 (two longitudinal and two transverse thin sections) (Fig. 5D, F).

Type locality: Gürich's "Stromatoporoid Rock" (Gürich 1904): western slope of the Racławka Valley, 0.9 km south of Paczółtowice village, 70 m north of Rokiczany Dół ravine (Paszkowski 1996; Berkowski 2002), 100 m west from the Racławka stream (Fig. 1A, locality 3). Góra Żarska Member of the Dubie Formation.

Type horizon: *Quasiendothyra communis–Quasiendothyra regularis* Zone (*Palmatolepis marginifera*–middle *Palmatolepis expansa* conodont zones), Famennian.

Material.—16 specimens from localities 1 and 3, all broken and abraded, often penetrated by the tabulates.

Emended diagnosis.—*Gerronostroma* with mostly thin laminae (30–100 μm), occassionally thickened up to 200 μm. Pillars with conical axial canals, intersecting 2–9 interlaminar spaces, thickened when lying directly below laminae. Mamelons low, commonly composed of long, branching pillars and reduced laminae (Fig. $6A_2$).

Description.—Skeleton laminar or domical, with mamelons showing relief up to 7 mm. Laminar specimens between 4 and 15 mm milimeters thick. Heights of domal skeletons up to 150 mm, and with basal length often exceeding 150 mm. Great variation within skeletons visible, allowing to distinguish three different phases. Each of them could be described as separate species, but with transitions between phases within single specimens.

Phase 1 (Figs. 5D–G, 6E): Skeleton domical, of height up to 150 mm, mammilate. Laminae thin (30–100 μm) and distinct, with rare foramina, one-layered, sometimes dichotomously branching. Spacings between laminae between 200 and 600 μm, but locally interlaminar spaces extremely narrow, allowing adjacent laminae to amalgamate, and forming single thick skeletal elements, usually with a middle lighter zone (Fig. $5D_1$). Foramina more conspicuous in areas adjacent to mamelons. Pillars 80 to 175 μm thick, superposed, intersecting at least two interlaminar spaces, with conical axial canals at tops. In tangential sections pillars cut as dots, rarely as ovals. Next to laminae the axial canals visible in centres of pillars, simulating ring pillars (Fig. 5E). Dissepiments common in most but may nearly absent in others (Fig. $5D_2$), always convex, intersecting laminae and pillars. Mamelons up to 7 mm high, approximately one-third of them associated with indistinct astrorhizae. Axial canals poorly visible (Fig. 5F). Astrorhizae marked rather by long and branching pillars than by the presence of an axial canal. In tangential sections pillars forming short vertical walls radiating from the centre of astrorhizae. In central parts of low mamelons pillars long, branching, in tangential sections forming meandering walls (Fig. 6E), and laminae commonly reduced, closely resembling phase 2 of *Gerronostroma raclaviense* sp. nov.

Phase 2 (Fig. 5G): Skeleton laminar, rarely domical, usually less than 10 mm thick. Mamelons indistinct, associated with astrorhizae, but less common than in phase 1. Laminae up to 300 μm thick, with lighter central zone commonly revealing tripartite structure resulting from amalgamation of adjacent laminae. Foramina very rare, less common than in phase 1. Galleries subrectangular or rounded, joining together through wide foramina in parts of specimens showing strongly thickened skeletal elements, and forming short vertical canals, visible as indistinct astrorhizae in tangential sections. These structures sometimes associated with mamelons. Pillars superposed, intersecting at least 2–3 interlaminar spaces, 80 up to 200 μm thick, thickened in their upper parts. In tangential sections pillars rounded, oval, rarely spool-shaped, in many cases revealing conical axial canal in

Table 2. Univariate analyses of *Gerronostroma cracoviensis*, *Gerronostroma raclaviense* (type and figured specimens), and *Gerronostroma* sp. (specimens UAM RAC 68 and UAM RAC 70). Results of multiple comparison test after Kruskal-Wallis test (Siegel and Castellan 1988). Significant differences are marked by numbers (1, significant differences in pillar length; 2, pillar thickness; 3, laminar spacing; 4, laminar thickness). The 0.05 level of significance was attained.

	UAM	*Gerronostroma cracoviensis*							*Gerronostroma* sp.		*Gerronostroma raclaviense*			
		RAC4	RAC7	RAC9	RAC13	RAC22	RAC29	RAC122	RAC68	RAC70	RAC-Z1	RAC-Z51	RAC-Z74	RAC-Z142
Gerronostroma cracoviensis	RAC4								3	1, 2	3, 4	3		1
	RAC7			2, 4		4	2, 4		3	2			2	
	RAC9		2, 4		4				3, 4	1, 4	4	4	2	1
	RAC13			4					3					
	RAC22		4						3		4			
	RAC29		2, 4						3	4	3, 4	3, 4		1
	RAC122								3	4	1, 2, 4	4		1
Gerronostroma sp.	RAC68	3	3	3, 4	3	3	3	3						
	RAC70	1, 2	2	1, 4			4	4				3	2, 3	3
Gerronostroma raclaviense	RAC-Z1	3, 4		4		4	3, 4	1, 2, 4		3				4
	RAC-Z51	3		4			3, 4	4		3			2	
	RAZ-Z74		2	2						2, 3		2		
	RAC-Z142	1		1			1	1		3	4			

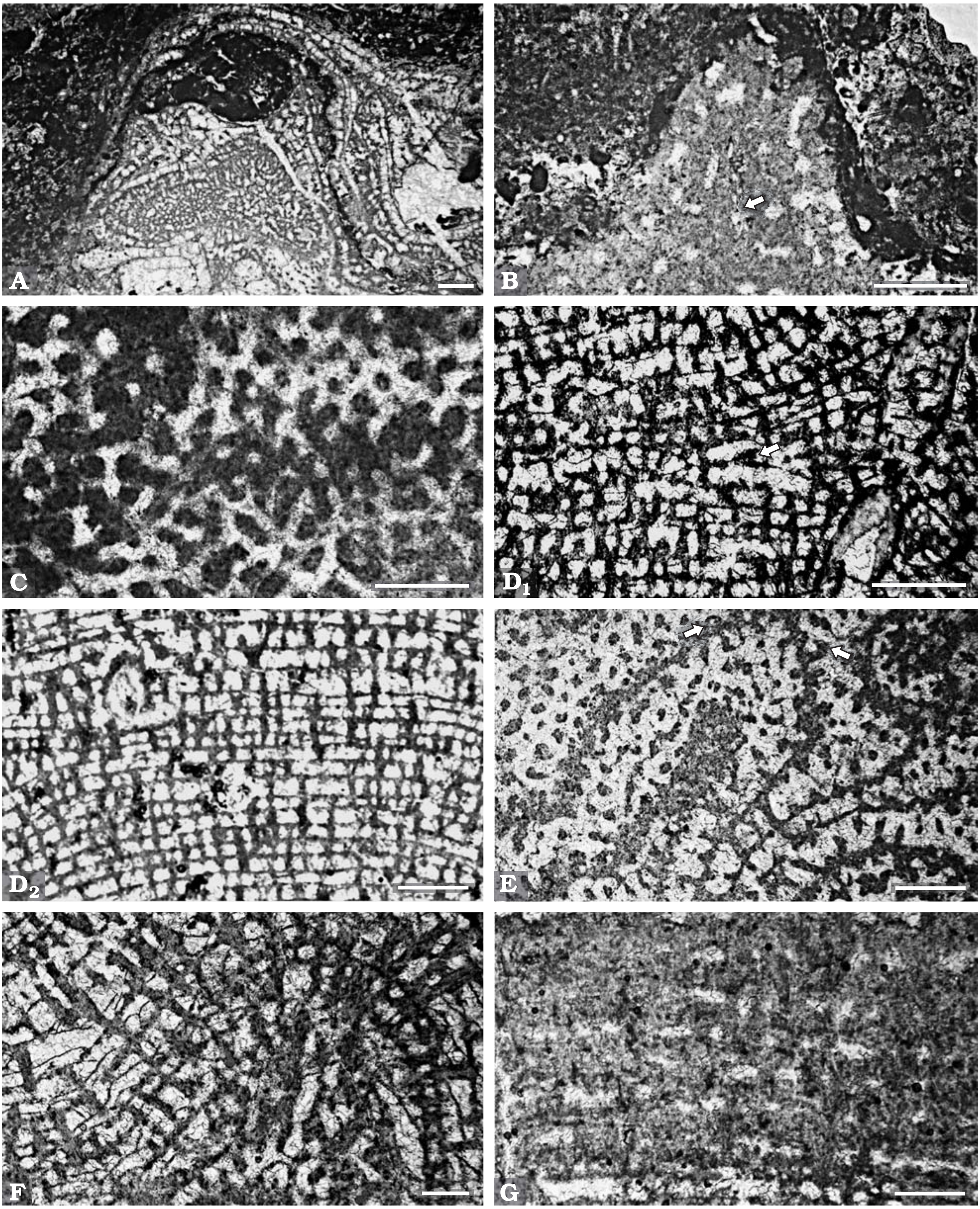

Fig. 5. Famennian clathrodictyids *Gerronostroma raclaviense* sp. nov. and *Gerronostroma cracoviensis* (Gürich, 1904), Dębnik Anticline. **A**, **B**. *G. raclaviense*. **A**. Paratype UAM RAC-Z142. Transverse section through basal part of the skeleton (phase 1), showing upward-extended mamelon (central part, phase 2). **B**. Phase 3, paratype UAM RAC-Z74. Longitudinal section showing low mamelon erecting from laminar part of the skeleton. Note short axial canal in central part of mamelon (arrow). **C**. Phase 3, transverse section of paratype UAM RAC-Z 51. **D**. *G. cracoviensis*. Phase 1, longitudinal sections of neotype UAM RAC29. Note tabulate coral penetrating the stromatoporoid skeleton and amalgamation of surrounding laminae (D_1, arrow). **E**. Phase 1, transverse section of specimen UAM RAC4. Note cross sections of pillars with conical axial canals simulating ring pillars (arrows). **F**. Phase 1, longitudinal section of neotype UAM RAC29. Note astrorhiza with short axial canal and numerous dissepiments, accompanied by foramina (upper left corner). **G**. Phase 2, longitudinal section of specimen UAM RAC7. Note transition between phases 1 and 2 located in the bottom part of the photograph. Scale bars 1 mm.

their upper parts, simulating ring pillars. Dissepiments uncommon, rarely covering foramina. Phase 2 in several specimens overlying phase 1 (Fig. 5G).

Phase 3 (Fig. 6D): Skeleton domical, with a low relief, up to 30 mm. Mamelons numerous, up to 6 mm high. Laminae non-enveloping, one-layered, thin (30–75 μm), with numerous foramina. Spacings between laminae showing great variation, between 200 and 550 μm. In places laminae reduced, visible as short processes of pillars. Pillars long, intersecting at least two, but up to 9 laminae, postlike, simple, immediately below the laminae thickened, rarely dichotomously branching in their upper fragments. Thickness of pillars between 75 and 200 μm, usually larger than laminae. In tangential sections pillars rounded, rarely oval, joining in areas surrounding laminae and forming dense network. Dissepiments common in dense skeleton, absent from areas of light skeleton, with reduced laminae, and numerous foramina. All specimens assigned to phase 3 reveal transitions into and from phase 1 (Fig. 6D, lower part of the photograph).

Statistics.—Data analysis using Kruskal-Wallis test performed on pillar length, pillar spacing, pillar diameter and laminar spacing reveal no significant differences between specimens assigned to *Gerronostroma cracoviensis* (Gürich, 1904). Identical results were also attained when considering measurements collected from the parts of skeletons representing different phases (Table 2).

Discussion.—Gürich (1904) assigned *Gerronostroma cracoviensis* to *Stromatoporella*. However, photographs of specimen described in his paper and the material studied in the present paper do not display features considered diagnostic for that genus. Ring pillars appear on the bottom boundaries of laminae, at the cross sections of pillars with conical axial canals. In the order Stromatoporellida these structures are present above the laminae, and resulted from inflections of the laminae in areas surrounding foramina. Gürich (1904) noticed also tripartite laminae, but they appear to be a result of merging of two adjacent, separate laminae. Thus this species does not exhibit the diagnostic characteristics of *Stromatoporella*.

Gürich's collections deposited at Wrocław (formerly Breslau) and Hamburg Universities were destroyed during World War II (Wolfgang Weitschat and Joanna Haydukiewicz, personal communications 2007). Thus, the type material of *Gerronostroma cracoviensis* is apparently lost. Therefore I decided to designate a neotype selected from material collected at the so-called Stromatoporoid Rock, the original type locality of Gürich (1904). Specimen UAM RAC29 closely matches illustrations in Gürich (1904: pl. 1), and therefore I selected it as the neotype.

Stratigraphic and geographic range.—Southern Poland, Dębnik Anticline, both slopes of the Racławka Valley between Dubie and Paczółtowice villages. Góra Żarska Member of the Dubie Formation. *Quasiendothyra communis*–*Quasiendothyra regularis* Zone (*Palmatolepis marginifera*–middle *Palmatolepis expansa* conodont zones), Famennian. Stromatoporoid assemblage 1.

Gerronostroma sp.

Fig. 6A–C.

Material.—7 specimens from localities 1 and 3, broken, abraded, commonly with stylolitized margins.

Description.—Skeleton laminar or low domical. Laminar specimens up to 50 mm thick, their basal lengths exceeding 100 mm. Heights of domical skeletons up to 70 mm. Laminae well defined, usually planar, with numerous foramina. Laminae sporadically inflecting slightly into pillars, forming zigzag pattern (Fig. $6A_1$). In other areas laminae thick and planar, tripartite, with lighter axial zones (Fig. 6B). Foramina well-developed, but nearly absent from some parts of the skeletons. Laminae spacings between 200 and 500 μm. Laminae up to 250 μm thick, in some parts of skeleton thinner (30–100 μm), making the interlaminar spaces up to 400 μm wide. Pillars stout or crumpled, long, passing through 1–4 interlaminar spaces, perpendicular to laminae or oblique. Most of them 75 to 200 μm thick. Within specimens of phase 2 pillars thinner (30–100 μm), and longer, intersecting at least two interlaminar spaces.

The inner structure of specimens revealing a great range of variation, thus two phases have been distinguished, replacing each other successively, very rarely laterally. Phase 1 forming the dense parts of skeletons, whereas phase 2 appearing in areas consisting of thin skeletal elements.

Phase 1 (Fig. 6A–C) present in bottom and centrals of skeletons, rarely as terminating phase. Laminae thick (up to 250 μm), planar, in some parts of skeletons inflecting into thick pillars or revealing tripartite structure (Fig. 6B). Galleries subrectangular or, more commonly, oval. Foramina present, only in some parts of skeletons numerous. Dissepiments common, flat or slightly convex. Pillars 75–200 μm thick, 0.7–2.5 mm long, superposed, intersecting 1–4 interlaminar spaces, perpendicular to laminae or, less commonly, oblique. In areas neighbouring mamelons pillars longer, of height up to 2.5 mm. Pillars thickened in their upper parts, directly below the overlying laminae, rarely dichotomically branching, mostly in areas adjacent to mamelons. Mamelons numerous, low, with relief up to 2 mm, consisting of thick and long pillars, forming an axial canal, up to 1.5 mm long, intersecting skeletons at distances not exceeding 5 mm.

Phase 2 (Fig. 6A–C) in central and upper parts of skeletons, commonly as a terminating phase. Laminae planar, thin, not exceeding 100 μm, in some areas penetrated by numerous foramina. Galleries rectangular or subrectangular. Pillars thicker than in phase 1, exceeding 100 μm in diameter, simple, postlike, perpendicular or oblique to laminae, oval or irregularly rounded in tangential sections. Pillars long, intersecting at least two interlaminar spaces, thickened in parts lying directly below laminae. Dissepiments rare, of low convexity. Mamelons numerous.

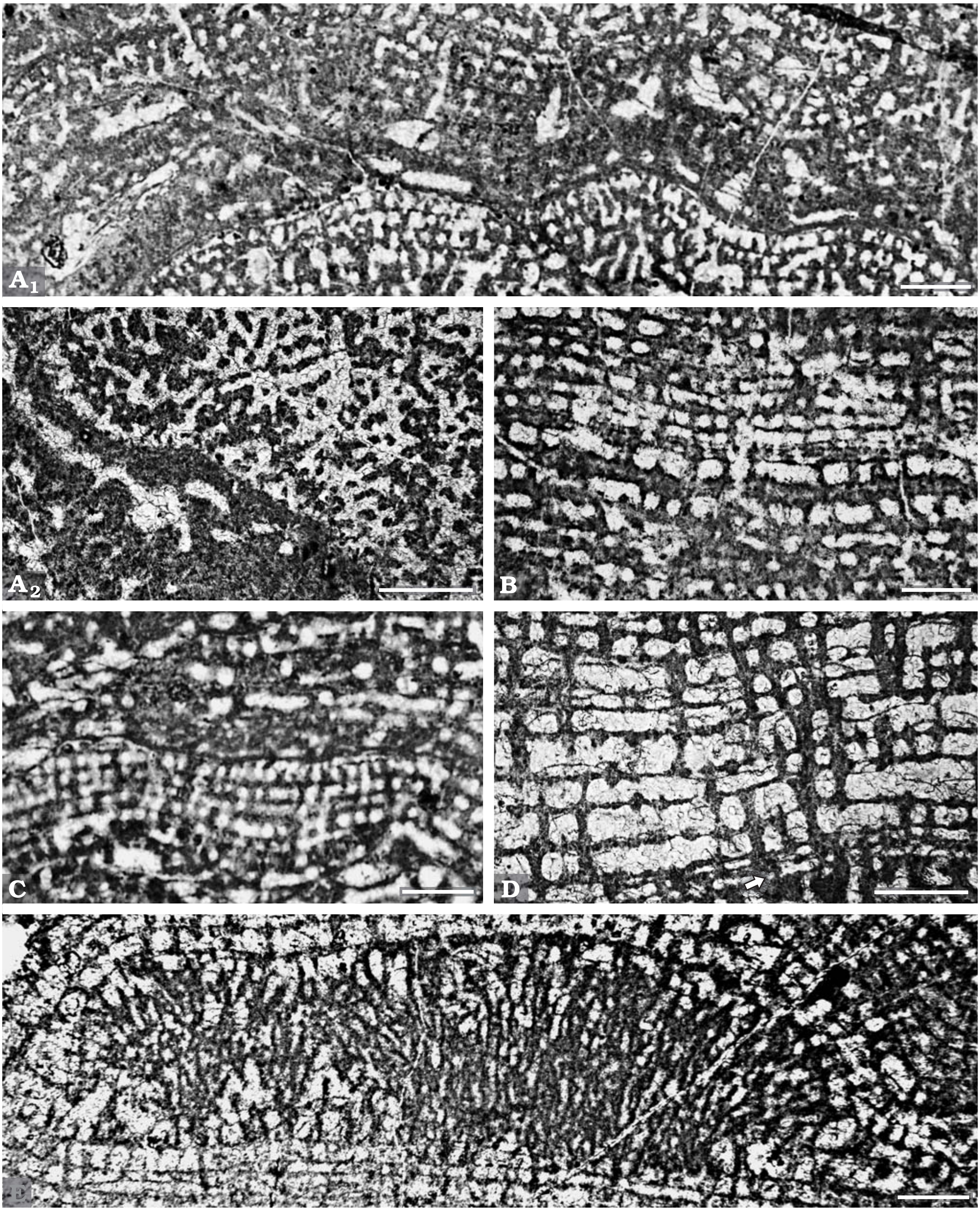

Fig. 6. Famennian clathrodictyids *Gerronostroma cracoviensis* (Gürich, 1904) and *Gerronostroma* sp., Dębnik Anticline. **A**. *Gerronostroma* sp. A_1, phase 2 overlaid by phase 1, longitudinal section of specimen UAM RAC14; A_2, transverse section of the same specimen, phase 2 located in the upper right corner. **B**. Phase 1, longitudinal section of specimen UAM RAC68. Note planar, tripartite laminae. **C**. Longitudinal section of specimen UAM RAC70. Phase 2 (in the middle of the photograph) bounded by denser skeleton (phase 1). **D**, **E**. *Gerronostroma cracoviensis*. **D**. Phase 3, longitudinal section of specimen UAM RAC9. A transition from phase 1 into phase 3 indicated by the arrow. **E**. Phase 1, longitudinal section of specimen UAM RAC62. Low mamelon formed by long, complexly branching pillars resembling phase 2 of *G. raclaviense* sp. nov. Scale bars 1 mm.

Statistics.—Kruskal-Wallis test and multiple comparison test after Kruskal-Wallis test performed on skeletons assigned to *Gerronostroma* revealed significant differences between the specimens of *Gerronostroma cracoviensis* (Gürich, 1904) and *Gerronostroma* sp. (Table 2). Two sample Kolmogorov-Smirnov tests on *Gerronostroma cracoviensis* and *Gerronostroma* sp., were also applied. They revealed differences between these two species (at the 0.05 level of significance), when considering thickness of pillars and laminae, pillar spacing and length.

Discussion.—*Gerronostroma sp.* closely resembles specimens of *Clathrostroma* cf. *jukkense* described by Stearn (1988) from the Famennian of Alberta, Canada. Both species are characterised by two phases replacing each other successively or—only in Stearn's (1988) specimens—contemporaneously. Differences between these two species are visible in tangential sections. Specimens from Famennian of Canada reveal less densely packed skeletal elements, and the pillars are more conspicuous.

Stratigraphic and geographic range.—Southern Poland, Dębnik Anticline, both slopes of the Racławka Valley between Dubie and Paczółtowice villages. Góra Żarska Member of the Dubie Formation. *Quasiendothyra communis*–*Quasiendothyra regularis* Zone (*Palmatolepis marginifera* –middle *Palmatolepis expansa* conodont zones), Famennian.

Remarks on distribution

The latest Devonian stromatoporoids from southern Poland, both labechiids and clathrodictyids, belong to Famennian community 2 sensu Stearn and Halim-Diharja (1987). Upper Famennian assemblage 2 was so far described from North America, eastern Europe, eastern Siberia and China.

The re-occurrence of numerous labechiids in the Famennian was explained by cooling of tropical Frasnian ocean (Stearn 1987). The Labechiida occurred in areas far from palaeoequator, whereas Clathrodictyida dominated in the remnants of warm ocean (Palaeotethys). However, carbonates of the Racławka Formation were suggested by Paszkowski (1995) to be deposited at low palaeolatitudes, in areas adjacent to the Palaeotethys ocean. Nonetheless they contain stromatoporoids of the order Labechiida. Labechiids appear also in the southern Urals and the Russian platform, in areas adjacent to Palaeotethys. Stearn (1987) noticed that the occurence of the order Labechiida in those areas throws doubt on the hypothesis of domination of clathrodictyids in tropical oceans.

The described fauna shows great similarity to eastern European and Siberian stromatoporoids. Labechiids dominated by *Stylostroma* species were described from Famennian of Novaya Zemlya (Gorsky 1938) and from Omolon region (Smirnova 1979). To the contrary, Western European faunas lack the order Labechiida, except for a few specimens found in Belgium and Germany (Weber 1999; Weber and Mistiaen 2001; Mistiaen and Weyer 2007). Eastern European and Siberian affinities of the Famennian faunas of Poland were also noticed in the case of anthozoans (Fedorowski 1981; Berkowski 2002) and conodonts (Baliński 1995).

The presence of columnar stromatoporoid *Gerronostroma raclaviense* sp. nov., showing meandering walls in central parts of columns, characteristic for *Clavidictyon*, also reveals remarkable similarity with Eastern European and Siberian faunas. *Clavidictyon* was first described from Japan (Sugiyama 1939), and it appears frequently in Famennian of China (Dong 1964).

Stromatoporoid assemblages

The presence of three distinct, poorly diversified, successively appearing assemblages is the most striking feature of the Famennian stromatoporoids from the Dębnik Anticline (Fig. 2A). The labechiids and the clathrodictyids occur separately.

Assemblage 1.—This assemblage occurs in at least 20 m thick grainstone unit described by Paszkowski (1995) as Góra Żarska Member of the Dubie Formation. These rocks are well exposed along the eastern slope of the Racławka Valley and in the northern part of its western slope, in the so called Gürich's Stromatoporoid Rock. Foraminifers allows an assignment of this unit to the *Quasiendothyra communis*–*Quasiendothyra regularis* Zone (*Palmatolepis marginifera*–middle *Palmatolepis expansa* conodont zones).

The most important feature of the assemblage 1 is the presence of numerous stromatoporoids identified here as *Gerronostroma cracoviensis* (Gürich, 1904) and *Gerronostroma* sp. They are usually overthrown and abraded, showing distinct signs of redeposition. Only some laminar skeletons remain complete. Stromatoporoids are buried in massive, poorly sorted grainstones.

Assemblage 2.—This assemblage occurs within the lowest parts of the Racławka Formation. This assemblage is composed of large (up to 10-cm thick) skeletons of *Stylostroma multiformis* sp. nov., co-occuring with gastropods in brownish-grey, marly limestones. Foraminifers and conodonts are unknown from the assemblage 2, thus its exact stratigraphic position remains undetermined.

Assemblage 3.—Stratigraphic position of this unit is unclear, since no stratigraphically significant foraminifers were found. This assemblage occurs within the upper part of the Racławka Formation, at least 20 metres above the limestones yielding *Stylostroma multiformis* sp. nov. skeletons. Continuous sections showing succession of both units are not available. A presence of numerous skeletons *Gerronostroma raclaviense* sp. nov. is the most important feature of assemblage 3.

Exposures of the assemblage 3 are present in upper part of the eastern slope of the Racławka Valley. *Gerronostroma* *raclaviense* sp. nov. also appears in dark intrabiosparites collected from the scree on the opposite slope of the valley, north from the Gürich's Stromatoporoid Rock.

Conclusions

Famennian stromatoporoids from southern Poland form a succession of three consecutive faunas, with the oldest being assigned to the *Quasiendothyra communis* Foraminiferal Zone. The exact stratigraphic position of younger assemblages is unclear because no stratigraphically significant foraminifers were found.

Stromatoporoid assemblages are characterized by a presence of both Labechiida (*Stylostroma multiformis* sp. nov.) and Clathrodictyida (*Gerronostroma raclaviense* sp. nov., *Gerronostroma cracoviensis* [Gürich, 1904], *Gerronostroma* sp.) which successively replace each other. The labechiids were described so far exclusively from the Famennian of eastern Europe (Novaya Zemlya, southern Urals, and Donets Basin), whereas they are rare the western Europe Famennian faunas.

Species described in this paper reveal a wide range of variation within individual specimens and the presence of phases. This phenomenon is particularly clearly visible within skeletons of *Gerronostroma raclaviense* sp. nov. The upward extended mamelons and columns (phase 2; complexly branching, tripartite pillars, reduced laminae) erect from laminar basal parts of specimens (phases 1 and 3; continuous laminae, long pillars) and are diagnostic for Famennian *Clavidictyon*. Such an expansion of mamelons is visible also within *Stylostroma* skeletons. Transformation of mamelons into columns might be a response to benthic anoxia, which is recorded in organic-rich, dark grey and black limestones constituting upper parts of the Racławka Formation.

The presence of phases is also visible within skeletons of *Gerronostroma cracoviensis* (Gürich, 1904) and *Gerronostroma sp*. The high level of variability made it difficult to distinguish between these species. In this paper statistical procedures were used for discrimination of *Gerronostroma cracoviensis* (Gürich, 1904) and *Gerronostroma* sp.

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