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Historia evolutiva de los estromatopóridos clathrodíctidos laminados de capa simple

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KEY WORDS: **Ordovician, Silurian, Devonian, Clathrodictyid stromatoporoids, Taxonomy, Phylogeny, Evolution, Faunal dynamics.**

PALABRAS CLAVE: **Ordovícico, Silúrico, Devónico, Clathrodíctidos, Estromatopóridos, Taxonomía, Filogenia, Evolución, Dinámica de faunas.**

ABSTRACT

The order Clathrodictyida is subdivided into five families: Actinodictyidae, Clathrodictyidae, Gerronostromatidae, Atelodictyidae and Tienodictyidae. The name Actinodictyidae has priority over Ecclimadictyidae. The first clathrodictyids *(Clathrodictyon* and *Ecclimadictyon)* with inflected laminae and weakly differentiated pillars appeared at the end of the middle Ordovician. They probably descended from labechiids but the separation could have taken place in a pre-skeletal stage of evolution. During the early Silurian an intense radiation and parallel evolution took place in the families Clathrodictyidae and Actinodictyidae. Later on they were gradually replaced by the clathrodictyids with well differentiated planar laminae and simple (Gerronostromatidae) or complicated pillars (Atelodictyidae, Tienodictyidae), prevailing in the Devonian.

RESUMEN

El orden Clathrodictyida está subdividido en cinco familias: Actinodictyidae, Clathrodictyidae, Gerronostromatidae, Atelodictyidae y Tienodictyidae. El nombre Actinodictyidae tiene prioridad sobre Ecclimadictyidae. Los primeros clathrodíctidos (*Clathrodictyon* y *Ecclimadictyon*), con láminas dobladas y pilares débilmente diferenciados, aparecieron al final del Ordovícico medio. Probablemente descendían de labechiidos pero la separación pudo tener lugar en un estado pre-esquelético de la evolución. Durante el Silúrico inicial se produjo una radiación intensa y evolución paralela en las familias Clathrodictyidae y Actinodictyidae. Más tarde fueron gradualmente reemplazados por los clathrodíctidos con láminas planares bien desarrolladas y pilares simples (Gerronostromatidae) o complicados (Atelodictyidae, Tienodictyidae), que dominaron en el Devónico.

1. INTRODUCTION

Stromatoporoids of the order Clathrodictyida are one of the most common and diverse groups. The skeleton is composed of single-layered, continuous laminae and short or superposed pillars, with a compact microstructure of the skeletal tissue. Representatives of the order Actinostromatida differ in having a reticulate (latticed) skeleton with colliculate ("hexactinellid") laminae, while those of the Stromatoporellida possess tripartite or multi-layered laminae.

2. TAXONOMICAL COMMENTS

Clathrodictyids were separated from actinostromatids by KÜHN (1939) as an independent taxonomic unit of family rank. BOGOYAVLENSKAYA (1969) elevated the group to ordinal rank, defining them as stromatoporoids with inflected laminae. The stromatoporoids with well differentiated planar laminae and rod-shaped pillars were discriminated by her as a separate order Gerronostromatida, but are herein reclassified as gerronostromatids s.s., having family rank within the order Clathrodictyida.

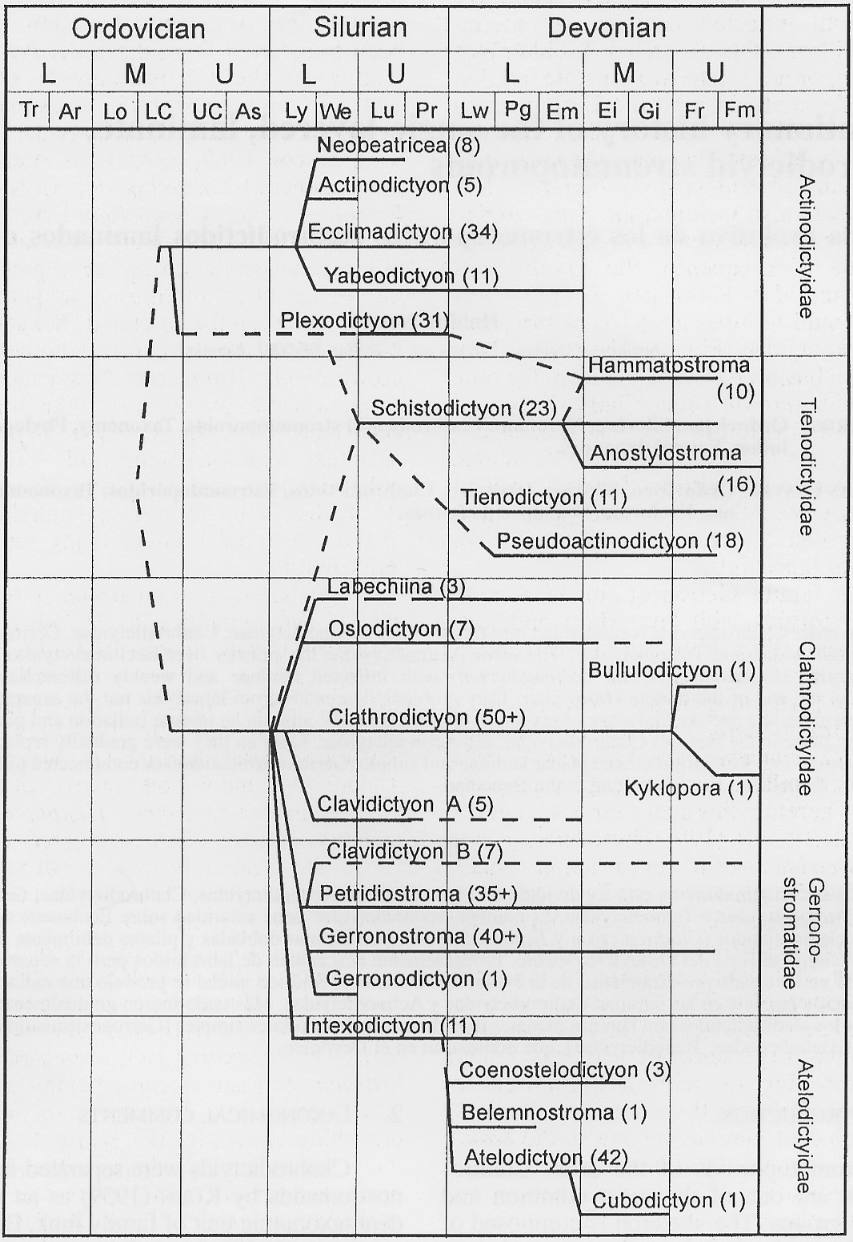


Fig. 1.–Stratigraphical ranges and presumed relationships of the genera of Clathrodictyida The number of confirmed species is given in brackets. Abbreviations: L- Lower, M- Middle, U- Upper, Tr- Tremadoc, Ar- Arenig, Lo- Llandeilo, LC- Lower Caradoc, UC- Upper Caradoc, As- Ashgill, Ly- Llandovery, We- Wenlock, Lu- Ludlow, Pr- Pridoli, Lw- Lochkovian, Pg- Pragian, Em- Emsian, Ei- Eifelian, Gi- Givetian, Fr- Frasnian, Fm- Famennian (including Strunian).

–Distribución estratigráfica y relaciones presumibles de los géneros de Clathrodictyda. El número de especies confirmado se da entre paréntesis. Abreviaturas: L-Inferior, M-Medio, U-Superior.

The author shares the opinion of STEARN (1980) on the division of clathrodictyids with inflected laminae and merged short pillars (the so-called "sublaminate stromatoporoids") into two separate families: the Clathrodictyidae and the Ecclimadictyidae. The former encompasses the forms with irregularly inflected laminae, the latter those with crumpled (zig-zagged), laminae. However, Stearn also included the genus *Actinodictyon* in his newly erected family Ecclimadictyidae. Consequently the family name Actinodictyidae KHALFINA & YAVORSKY 1973 should be used as it has priority over Ecclimadictyidae (Fig. 1). The genus *Bullulodictyon* has been transferred from the order Labechiida into the order Clathrodictyida as the re-examination of the type specimen of the genus has revealed that, while its sublaminar structure resembles *Clathrodictyon*, its numerous zonally developed astrorhizae only simulate the vesicular structure characteristic of labechiids.

The family Gerronostromatidae unites stromatoporoids with both short and long, superposed pillars. YAVORSKY (1960) erected a new genus *Clathrostroma* having partly short and partly long pillars. However, many species traditionally included in *Gerronostroma* (*G. concentricum* YAVORSKY 1931) have short pillars besides long, superposed pillars. Therefore this character has no generic value. STEARN (1991) introduced a new name *Petridiostroma* for a taxon usually referred to *Simplexodictyon.* Type species of *Simplexodictyon* (*S. podolicum* YAVORSKY, 1929) has tripartite, divided laminae and therefore this genus belongs to the order Stromatoporellida.This point of view is accepted here. The genus *Clavidictyon* probably contains species of two different genera of clathrodictyids with a cylindrical or columnar skeleton: those (species group A) with inflected laminae belong to the family Clathrodictydae (*Clathrodictyon cylindricum* YAVORSKY 1955) and the others (group B), with planar laminae, are diagnostic of Gerronostromatidae (Fig. 1).

Clathrodictyids with planar laminae and a complicated interlaminar (pillar) structure have usually been classified in the family Tienodictyidae. NESTOR (1974) demonstrated this subdivision to be rather heterogenous, obviously uniting taxa of different origins. The genus *Atelodictyon*, for a long time considered as a member of the actinostromatids due to the misinterpretation of the interlaminar structure in tangential section, has now been transferred from the order Actinostromatida to the Clathrodictyida (STEARN, 1991). In this connection it seems reasonable to accept the family Atelodictyidae BOGOYAVLENSKAYA, 1969, ascribing to it also some other genera (*Intexodictyon*, *Cubodictyon*, *Belemnostroma*, *Coenostelodictyon*). They have sidewards branching or blade-shaped pillars (coenosteles), forming angular chain-like or net-like structures in tangential section, simulating the so-called "hexactinellid" meshwork of the colliculate laminae of actinostromatids. Transfer of these genera to the Atelodictyidae results in a reduction in the heterogeneity of the family Tienodictyidae: only taxa with mainly upwards furcating or oblique pillars and numerous dissepiments (Pl. II, figs. 3-6), forming a tangled network in the tangential section, being retained in latter family.

The genus *Aculatostroma* is here considered synonymous with *Atelodictyon*. The photos of the type species of *Aculatostroma Syringostroma verrucosum* (KHALFINA, 1961. Pl. D-13, Figs. 3a-b) show clearly that the so-called "hexactinellid" network was developed in the interlaminar space just as in *Atelodictyon* and not on the level of the laminae as in *Actinostroma*. *Tienodictyon* and *Hammatostroma*, often considered as congeneric, are treated here as separate genera because the species commonly included in *Hammatostroma* form a very definite grouping mainly restricted to the Frasnian.

Recently STEARN (1991) revised *Anostylostroma* and related genera. He transferred many species from *Anostylostroma* to *Schistodictyon*. According to his concept *Anostylostroma* contains species having stout pillars, vermiform in cross section, and branching at the tops (Pl. II, fig. 5). *Schistodictyon* has thinner Y-shaped pillars furcating upwards once or twice before reaching the overlying lamina (Pl. II, fig. 3). Having studied the types of the both genera, I fully agree with Stearn´s concept. The re-examination of original colletions has confirmed the need to expand the extent of the genus *Pseudoactinodictyon,* with numerous dissepiments in the comparatively wide interlaminar spaces (Pl. II, fig. 6) assigning it in the tienodictyids. On the basis of this character the type species of the genera *Dualestroma* KHALFINA and *Intexodictyonella* YAVORSKY also prove to be representatives of *Pseudoactinodictyon*.

3. POSSIBLE ORIGINS

GALLOWAY (1957), who gave the first outline of the phylogeny of Stromatoporoidea, regarded clathrodictyids as having evolved from vesicular labechiid stromatoporoids in late Ordovician time by means of replacing the overlapping cysts of labechiids (particularly *Cystostroma*) with side-by-side placing of the cyst plates of clathrodictyids (particularly *Clathrodictyon*). He suggested that the pillars of *Clathrodictyon* were derived from the down-bending cyst edges of *Cystostroma*. The idea was supported by NESTOR (1966), BOGOYAVLENSKAYA (1969), KAZMIERCZAK (1971) and others. NESTOR (1966) stated that the transition from imbricated cysts of a *Cystostroma*-like ancestor to the inflected laminae of the clathrodictyids like *Clathrodictyon* was accompanied by progressive amalgamation of cyst plates, still recognizable in some earlier species of *Clathrodictyon* (*C. vormsiense* from the lowermost Ashgill of Estonia), but totally loosing their independence in more advanced species of *Clathrodictyon*. KHALFINA & YAVORSKY (1967) and WEBBY (1986, 1993) have questioned the opinion arguing that rod- and funnel-shaped pillars, occurring in some clathrodictyids, could not be derived from the cyst plates of labechiids. WEBBY (1969) has described some representatives of the Clathrodictyidae from the middle Caradoc of New South Wales, indicating that derivation of clathrodictyids actually took place earlier than thought previously. This led WEBBY (1993) to doubt the descent of the Clathrodictyida from the Labechiida. STEARN (1994) proposed a new model of skeleton secretion for Clathrodictyida and Stromatoporellida and contrasted it to the secretion mechanism in other groups of stromatoporoids. This also seems to confirm different origins for the Clathrodictyida and Labechiida. However, it is natural that during evolution, a descendent group can develop some new morpho-functional characters lacking or differing from those of its ancestor. Therefore the above-mentioned morphological differences between labechiids and clathrodictyids do not necessarily demonstrate their different origins, but only that divergence of the clathrodictyid and labechiid stocks could start in the pre-skeletal stage of stromatoporoid evolution.

4. EVOLUTIONARY DEVELOPMENT

The order Clathrodictyida had a central position in the evolution of Palaeozoic stromatoporoids. The possible relationships of genera, their stratigraphical ranges and the number of confirmed species are shown in Fig. 1.

The early history of clathrodictyids in the Ordovician has been discussed in detail by WEBBY (1986). The representatives of only three genera, *Clathrodictyon*, *Ecclimadictyon* and *Plexodictyon*, have hitherto been recorded from Ordovician rocks. The last

PLATE I/LÁMINA I

Figs. 1-2.–*Petridiostroma simplex* (NESTOR, 1966). L. Sil., Wenlock, Jaani Stage; Estonia, Saaremaa, loc. Liiva. Holotype, Inst. Geol. Estonian Acad. Sci. (IGEAS) No. Co 3134, Tallinn. 1- vertical section, (x10), 2- horizontal section, (x10).

–*Petridiostroma simplex* (NESTOR, 1966). Silúrico Inferior, Wenlock, Piso Jaani; Estonia, Saaremass, Liiva. Holotipo, Inst. Geol. Academia de Ciencias Estonia (IGEAS) Nº Co3134, Tallinn. 1-sección vertical, (x10), 2-sección horizontal, (x10).

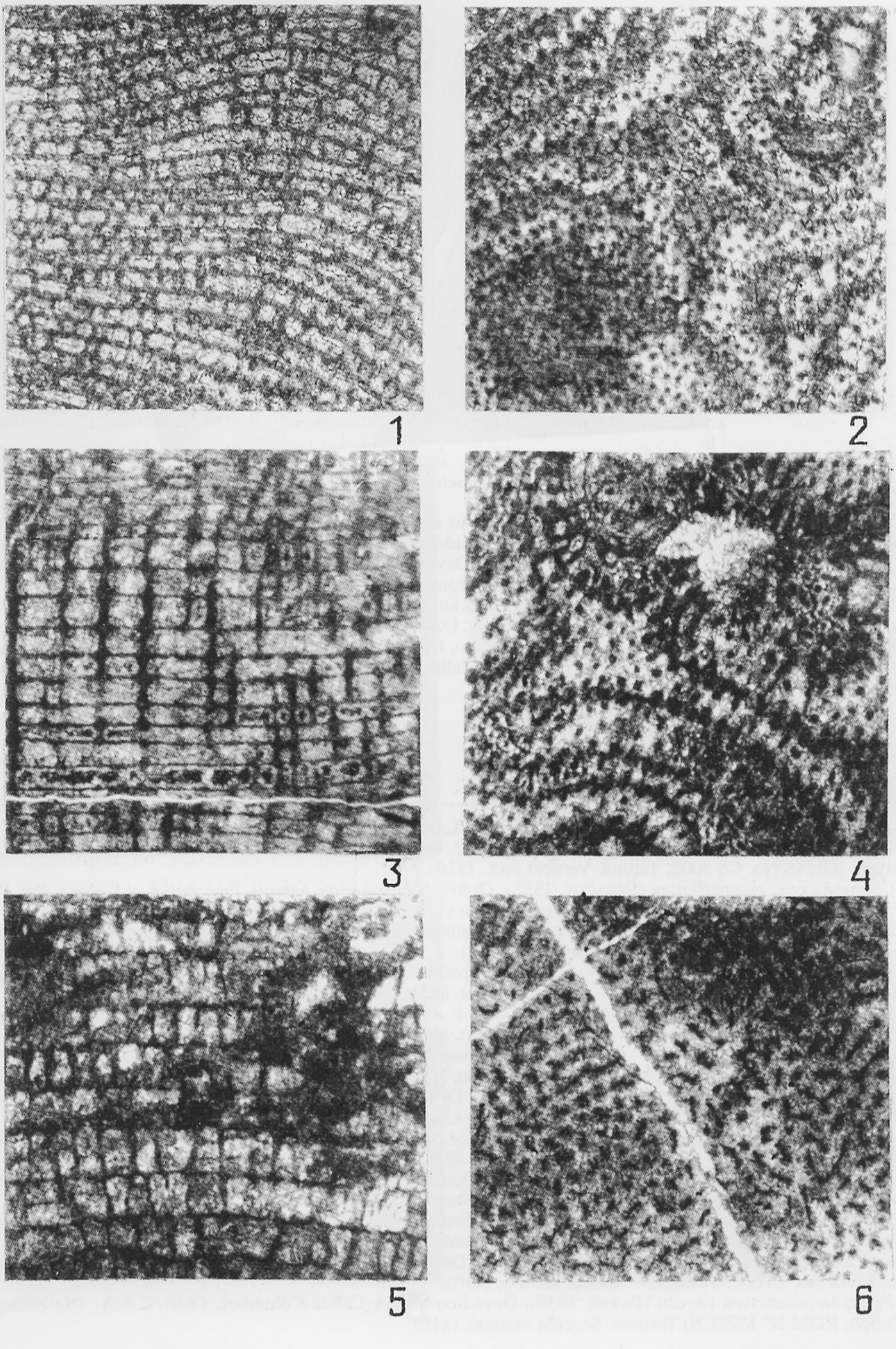
Figs. 3-4.–*Gerronostroma elegans* YAVORSKY, 1931. M. Dev.; Kuznetsk Basin, Russia, loc. Bachat. Holotype, CNIGR Mus. No.3338/3, St. Petersburg. 3- vertical sect., (x10), 4- horizontal sect., (x10).

–*Gerronostroma elegans* YAVORSKY, 1931. Devónico Medio; Cuenca de Kuznetsk, Rusia, loc. Bachat. Holotipo. CNIGR Mus. Nº 3338/3, San Petersburgo. 3-Sección vertical, (x10), 4-Sección horizontal, (x10).

Figs. 5-6.–*Coenostelodictyon krekovi* (YAVORSKY, 1955). L. Dev., Krekov Horizon; Kuznetsk Basin, Russia, Chernevaya Bachat River. Holotype, CNIGR Mus. No. 7351/ 62, St. Petersburg. 5-vertical sect., (x20), 6-horizontal sect., (x20).

–*Coenostelodictyon krekovi* (YAVORSKY, 1955). Devónico Inferior, horizonte Krekov; Cuenca de Kuznetsk, Rusia, río Chernevaya Bachat. Holotipo, CNIGR Mus. Nº 7351/62. San Petersburgo. 5-Sección vertical, (x20), 6-Sección horizontal, (x20).

PLATE I/LÁMINA I



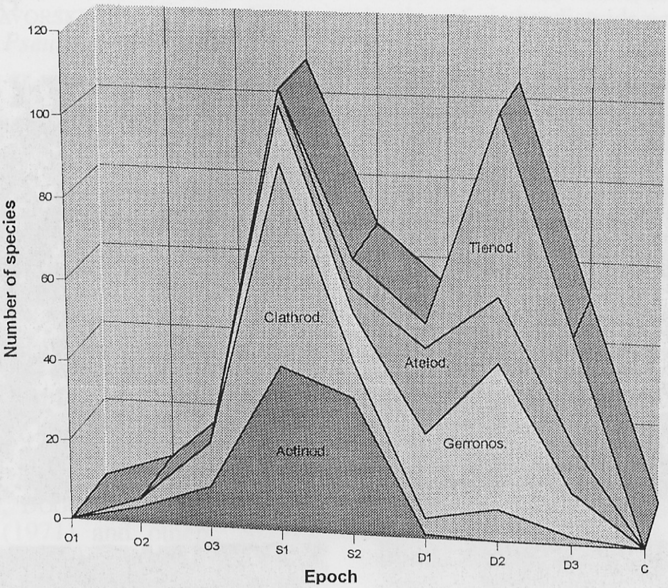


Fig. 2.–Diversity dynamics of species in different families of Clathrodictyida through the Ordovician to Devonian. Stratigraphical indexes: O1- Early Ordovician, O2- Middle Ordovician, O3- Late Ordovician, S1- Early Silurian, S2- Late Silurian, D1- Early Devonian, D2- Middle Devonian, D3- Late Devonian (including Strunian). Abbreviated names: Actinodictyidae, Clathrodictyidae, Gerronostromatidae, Atelodictyidae, Tienodictyidae.

–Dinámica de diversidad de las especies de diferentes familias de Clathrodictyida desde el Ordovícico al Devónico. Índices estratigráficos: O1-Ordovícico Temprano, O2-Ordovícico Medio, O3-Ordovícico Tardío, S1-Silúrico Temprano, S2-Silúrico Tardío, D1-Devónico Temprano, D2-Devónico Medio, D3-Devónico Tardío (incluyendo el Struniense). Nombres abreviados: Actinodictyidae, Clathrodictyidae, Gerronostromatidae, Atelodictyidae, Tienodictyidae.

PLATE II/LÁMINA II

Fig. 1.–*Clathrodictyon mammillatum* (SCHMIDT, 1858). U. Ord., Ashgill, Porkuni Stage; Estonia, loc.Porkuni. Lectotype, IGEAS No. Co 3002, Tallinn. Vertical sect., (x10).

–*Clathrodictyon mammillatum* (SCHMIDT, 1858). Ordovícico Superior, Ashgill, Piso Porkuni; Estonia, loc. Porkuni. Lectotipo, IGEAS Nº CO3002, Tallinn. Sección vertical, (x10).

Fig. 2.–*Plexodictyon katriense* NESTOR, 1966. U. Sil., Ludlow, Paadla Stage; Estonia, Saaremaa, loc. Katri. Holotype, IGEAS No. Co 3134, Tallinn. Vertical sect., (x10).

–*Plexodictyon katriense* NESTOR, 1966. Silúrico Superior, Ludlow, Piso Paadla; Estonia, Saarema, loc. Katri. Holotipo, IGEAS Nº Co3134, Tallin. Sección vertical, (x10).

Fig. 3.–*Schistodictyon posterius* LESOVAYA, 1970. U. Sil., Pridoli, Isfara Horizon; Isfara River, Turkestan Range, Uzbekistan. Holotype, Mus. Ministery Geol. Uzb. No. 3/491 (240/2-9/74), Tashkent. Vertical sect., (x20).

–*Schistodictyon posterius* LESOVAYA, 1970. Silúrico Sup., Pridoli, horizonte Isfara; río Isfara, Cordillera del Turkestán, Uzbekistán. Holotipo, Mus. Minist. Geol. Uzb. Nº 3/491 (240/2-9-74), Tashkent. Sección vertical, (x20).

Fig. 4.–*Hammatostroma albertense* STEARN, 1961. U. Dev., Frasnian, L.-Fairholm Fm., Alberta, Canada, Isaac Creek. Holotype, Geol. Surv. Canada No. 15318 (38-12), Ottawa. Vertical sect., (x10).

–*Hammatostroma albertense* STEARN, 1961. Devónico Sup., Frasniense, Form. Fairholm inf., Alberta, Canada, Isaak Creek. Holotipo, Geol. Surv. Canada Nº 15318 (38-12), Ottawa. Sección vertical, (x10).

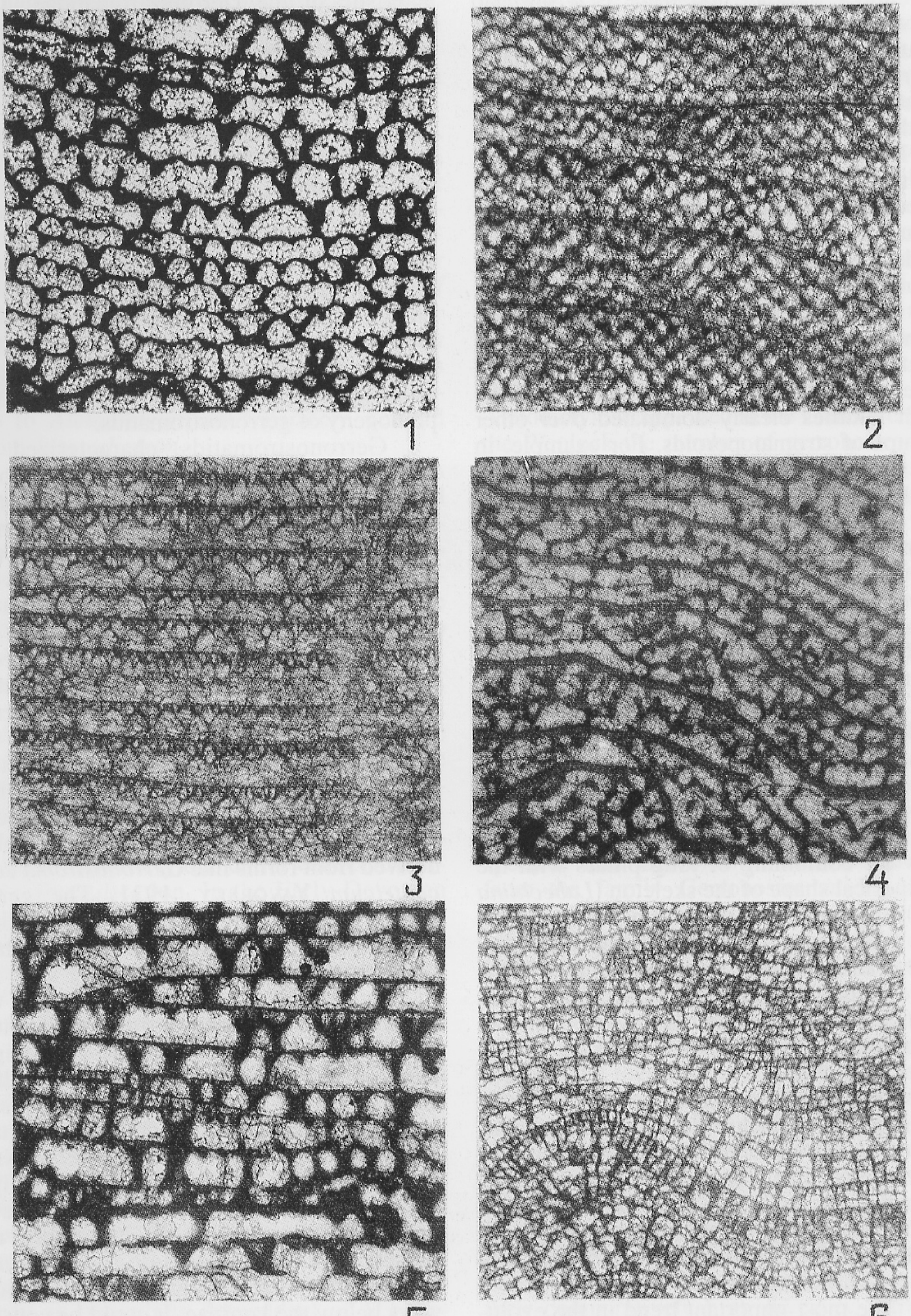
Fig. 5.–*Anostylostroma hamiltonense* PARKS, 1936. M. Dev., Hamilton Fm., Michigan, U.S.A., Long Lake. Diplotype, Royal Ontario Mus. (ROM) No. 2240, Toronto. Vertical sect., (x20).

–*Anostylostroma hamiltonense* PARKS, 1936. Devónico Medio, Form. Hamilton, Michigan, USA., Long Lake, Diplotipo, Royal Ontario Mus. (ROM) Nº 2240, Toronto. Sección vertical, (x20).

Fig. 6.–*Pseudoactinodictyon vagans* (PARKS, 1936). M. Dev. , Columbus Lst., Ohio, U.S.A., Kelley's Island. Cotype, ROM No. 1572CN, Toronto. Vertical section, (x10).

–*Pseudoactinodictyon vagans* (PARKS, 1936). Devónico Medio, Caliza Columbus; Ohio, U.S.A., Isla Kelley's. Cotipo, ROM Nº 1572CN, Toronto. Sección vertical, (x10).

PLATE II/LÁMINA II



genus, distinguished by the alternation of crumpled laminae with planar paralaminae (Pl. II, fig. 2), was originally described from the upper Silurian and there is a big gap between the late Ordovician and typical late Silurian representatives of the genus; the former are only tentatively assigned to that genus. Almost all Ordovician representatives of the clathrodictyids have irregularly inflected laminae and rather weakly differentiated pillars. *Clathrodictyon* and *Ecclimadictyon* appeared in the geological record more or less simultaneously and therefore it is impossible to decide which of them could be the ancestral member for the other clathrodictyids.

During the early Silurian a rapid evolutionary radiation took place in the families Clathrodictyidae and Actinodictyidae. Therefore in the Llandovery, representatives of the both families clearly dominated over other groups of stromatoporoids. For example, in the Estonian sequence they reached up to 2/3 of the number of species and 4/5 of the number of studied specimens. The author has demonstrated that the families Clathrodictyidae and Actinodictyidae underwent parallel development during the early Silurian (NESTOR, 1994: Fig. 3). One trend of evolution in both families was the formation of long additional pillars (*Oslodictyon* and *Yabeodictyon*, the former appearing in the late Llandovery and the latter in the Wenlock). Another tendency was the development of subcylindrical or fasciculate skeletons (*Clavidictyon* sp. group A in the late Llandovery and *Neobeatricea* in the Wenlock). The third direction was the combining of long pillars with the cylindrical shape of the skeleton (*Labechiina* in the early Silurian and *Actinodictyon* in the late Llandovery). In addition, the actinodictyid branch exhibits a special trend with the development of supplementary straight paralaminae in addition to zig-zagged laminae, resulting in derivation of *Plexodictyon* in the late Ordovician.

Only a few representatives of the Clathrodictyidae (*Clathrodictyon*, *Labechiina*, *Oslodictyon*) and only a single species of Actinodictyidae (*Yabeodictyon*) survived into the Devonian. Some clathrodictyids (*Bullulodictyon*, *Kyklopora*) which appeared in the Late Devonian were probably descendants of *Clathrodictyon*.

The most important trend in the evolution of clathrodictyids was the transition from inflected laminae and merged pillars of "sublaminate" Clathrodictyidae to the planar laminae and well-differentiated pillars characteristic of the Gerronostromatidae. This took place in the late Llandovery. *Petridiostroma,* as a primary representative of the family Gerronostromatidae, had only short pillars (Pl. I, figs. 1-2). *Clavidictyon* sp. group B is a cylindrical or fasciculate variety of *Petridiostroma* which evolved probably in the Wenlock. This evolutionary lineage involved the development of superposed long pillars leading to the origination of the genus *Gerronostroma* (Pl. I, figs. 3-4). Typical representatives of *Gerronostroma* are known from the Ludlow. An enigmatic Wenlock form *Gerronodictyon* with unusually thick, somewhat discontinuous laminae and pillars, probably formed a side branch in the phylogeny of gerronostromatids.

Gerronostromatids, characterized by single-layered planar laminae, were obviously ancestors of the order Stromatoporellida. Representatives of the family Stromatoporellidae, characterized by tripartite laminae and prevailingly short pillars, were derived from *Petridiostroma*-like ancestors probably in Wenlock time when the first species of the genus *Simplexodictyon* (redefined by STEARN, 1991) appeared. This latter genus was characterized by the unevenly divided laminae. Another branch of the Stromatoporellida, separated from gerronostromatids in the Pridoli, was the family Hermatostromatidae with tripartite laminae and superposed or long pillars. It was probably derived from forms like *Gerronostroma concentricum* YAVORSKY, 1931. The genus *Amnestostroma* might be an intermediate member between *Gerronostroma* and hermatostromatids.

It is possible that representatives of the family Atelodictyidae with complicated, branching or bladed pillars and thin straight laminae evolved from a *Clathrodictyon*-like ancestor. In the middle Llandovery of Estonia there occurs a very delicate laminate stromatoporoid *Intexodictyon avitum* (NESTOR, 1964: Pl. 29, Figs. 6,7; Pl. 30, Figs. 1,2) which greatly resembles some species of *Clathrodictyon* with comparatively straight laminae (*C. kudriavzevi*, *C. lennuki* etc.) but has pillar substance spreading sideways below the laminae. It could be considered as an ancestral form for the Atelodictyidae. However, during the Silurian the representatives of *Intexodictyon* are rather sparsely distributed and the genus is only tentatively assigned to the Atelodictyidae. An alternative route of origination for the Atelodictyidae could be through the transformation of the rod-shaped pillars of a *Petridiostroma*-like ancestor into the blade-shaped pillars of *Coenostelodictyon* (Pl. I, figs. 5-6). The genera *Coenostelodictyon*, *Atelodictyon* and *Cubodictyon* form a clear evolutionary lineage showing the development from comparatively isolated blade-shaped pillars in *Coenostelodictyon* over laterally merged chain-like coenosteles of *Atelodictyon* to the closed wall-like pillar structures of *Cubodictyon*. *Belemnostroma* with additional megapillars or columns is obviously a side branch of this lineage related to *Atelodictyon*, or separately derived from *Intexodictyon*.

Another group of stromatoporoids with straight (planar) laminae and complicated interlaminar structure, the family Tienodictyidae, is probably derived from clathrodictyids with funnel-shaped pillars (*Clathrodictyon mammillatum*, Pl. II, fig.1). In the Late Silurian such forms could have evolved into *Schistodictyon* which has similar funnel-shaped pillars but straight laminae (Pl. II, fig. 3). An alternative origin for *Schistodictyon*, pointed out by NESTOR (1974), might be reduction of the cassiculate network in the space between the paralaminae of *Plexodictyon* (Pl. II, fig. 2).

During the Devonian the representatives of Tienodictyidae underwent considerable diversification. In the Early Devonian the genera *Tienodictyon* and *Pseudoactinodictyon* appeared. The former is characterized by an irregularly tangled interlaminar network, the latter by numerous dissepiments and comparatively rare oblique pillars (Pl. II, fig. 6). In the Middle Devonian typical representatives of *Hammatostroma* and *Anostylostroma* were added. The former has a highly reduced oblique network in the interlaminar space (Pl. II, fig. 4) which shows signs of derivation from *Plexodictyon* by means of heavy reduction of its cassiculate network. *Anostylostroma* has stout meandroid coenosteles often branching at their tops (Pl. II, fig. 5), and is seemingly an immediate descendant of *Schistodictyon*.

5. FAUNAL DYNAMICS

In the course of the taxonomic revision of the order Clathrodictyida, now in progress, lists of confirmed species of valid genera have been compiled. From these data the relative role of different groups of Clathrodictyida in the geological record can be estimated (Fig. 2). In the Ordovician, only species of Actinodictyidae and Clathrodictyidae were represented in more or less equal numbers (14 and 13 respectively). In the early Silurian Clathrodictyida attained its maximum development. A rapid diversification took place in the families Actinodictyidae (41 species) and Clathrodictyidae (49 species). The dominant genera were *Clathrodictyon* (40 species) and *Ecclimadictyon* (22 species). The first representatives of the Gerronostromatidae and Atelodictyidae appeared in the Llandovery. In the Wenlock the number of gerronostromatids increased mainly owing to the genus *Petridiostroma,* which added 14 species during the Llandovery and Wenlock.

In the late Silurian the number of species of clathrodictyids decreased and their diversity became more or less equal in different families. Only the Actinodictyidae and particularly *Plexodictyon* (20 species) prevailed before their almost total extinction by the end of the Silurian. The first tienodictyids, all belonging to *Schistodictyon*, appeared in the late Silurian.

The Early Devonian was a time of a temporary decline in the evolution of the Clathrodictyida. Only *Petridiostroma* (11 species) and *Gerronostroma* (10 species) from the family Gerronostromatidae were common and a "newcomer" *Atelodictyon* (16 species) prevailed among the clathrodictyids. Only one species of actinodictyid from the genus *Yabeodictyon* has been recorded.

In the Middle Devonian the number of Tienodictyidae (44 species) increased very rapidly and they together with Gerronostromatidae (36 species) gained predominance among clathrodictyids. *Anostylostroma* and *Hammatostroma* appeared as new elements, while *Pseudoactinodictyon* and *Gerronostroma* reached the peak of their development.

In the Late Devonian the final decline in the evolution of the clathrodictyids took place. However, tienodictyids maintained their comparatively high diversity, particularly in the Frasnian. It is worth mentioning that in the very low-diversity stromatoporoid faunas of the Strunian several genera of Clathrodictyida (*Anostylostroma*, *Kyklopora*, *Clavidictyon*, *Atelodictyon*) had been preserved.

6. Conclusions

The main trends in the morphogenetic evolution of clathrodictyids were: 1) progressive differentiation of the laminar and pillar structures, 2) levelling of the laminae, 3) complication of the interlaminar (pillar) structures, 4) recurrent development of long or superposed pillars in different evolution lineages.

During the evolution of the clathrodictyids, the sublaminate stromatoporoids (Actinodictyidae and Clathrodictyidae) dominated in the Ordovician and Silurian. They were replaced gradually by genuine laminate stromatoporoids with simple (Gerronostromatidae) or complicated pillars/coenosteles (Atelodictyidae, Tienodictyidae), which prevailed in the Devonian.

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