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ON GENERATION AND REGENERATION OF CLADIA IN SOME UPPER SILURIAN MONOGRAPTIDS

Abstract. — A description is given of the structure and evolution of Upper Silu-
rian Linograptinae on the base of material etched by chemical treatment of core
samples from deep-boring at Mielnik on Bug (eastern Poland) and from Baltic
erratic boulders. *Neodiversograptus* n. gen., represented by *N. nilssoni* and *N. be-
klemishevi* n. sp., belongs to an earlier evolutionary phase of this subfamily. Their
rhabdosomes are characterized by bipolar growth of thecae, for a sicular cladium
is produced in addition to the primary branch (procladium). *Linograptus posthu-
mus* with multiramous rhabdosomes, comprising several sicular cladia, most pro-
bably descends from such forms. The origin and phylogenetic relations within the
Linograptinae are discussed. The bipolar rhabdosomes of *Diversograptus* and *Neo-
diversograptus* n. gen. in which two branches develop from the sicula in result of
normal astogeny, are distinguished from bipolar „morphoses" — here described in
Lobograptus scanicus parascanicus and *Linograptus posthumus* — which are pro-
duced in result of regeneration of monograptid colonies that had been broken off.
These rhabdosomes are deprived of the sicula at the point of divergence of two
thecal series. The regenerative forms differ fundamentally in their biological sig-
nificance from bipolar forms, produced through normal astogeny, and obviously
they cannot be „taxonomically ranked". An attempt is made to define the morpho-
logical laws that govern the processes of normal astogeny, of the regeneration of
colonies and of the simultaneous growth of thecae on the various branches of one
colony. Using the data now available on the astogeny and evolution of the Mono-
graptidae, a tentative classification is given of the phylogenetic modifications of
astogeny by distinguishing their successive stages. Several new terms and defi-
nitions are introduced relevant to details of structure and development of multi-
ramous monograptids.

INTRODUCTION

The present work has been prepared on the base of observations
made between 1959—1962. The material then collected, though fragmen-
tary, shed some light on the problems connected with the formation and
regeneration of branches in colonies of certain Upper Silurian monograp-
tids. The fossil remains here considered consist of graptolites etched from

Silurian erratic boulders of Baltic origin, collected in north-western Poland, and of material from deep-boring at Mielnik on Bug*, drilled by the Geological Institute (Warszawa).

Both the erratic boulders and the core samples represent argillaceous limestones or marls, from which the graptolites were etched by chemical treatment. Before examining the anatomy of the graptolite specimens, the periderm was bleached in a mixture of potassium chlorate and hydrochloric or nitric acid. The bleached specimens are kept in transparent polystyrene containers filled with glycerine. The drawings were done in transmitted light under the „Lumipan" microscope (Jena, GDR) and with Abbe's (RA-4) drawing apparatus (made in USSR). The specimens here described are housed at the Palaeozoological Laboratory of the Warsaw University (Warszawa, 6, Żwirki i Wigury).

The writer's opinions were first reported at the scientific session of the Palaeozoological Laboratories of the Warsaw University and of the Polish Academy of Sciences in November 1961, and later, in October 1962, at the meeting of the Palaeontological Section of the Geological-Mineralogical Society in Prague.

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* The Silurian succession encountered at Mielnik has been preliminary described in a paper by Tomczyk (1962), where the reader could find a diagrammatical stratigraphic column (fig. 12).

A HISTORICAL REVIEW OF INVESTIGATIONS AND THE PRESENT STATUS OF THE CONSIDERED PROBLEM

Besides monograptids representing the normal monograptid type of development with uniserial and one-directional growth of thecae that has been satisfactorily studied in many species (i.a. Kraft, 1926; Cox, 1934; Eisenack, 1942; Urbanek, 1953, 1954, 1958; Walker, 1953), numerous representatives of this family display modified patterns of this simple and presumably primitive type of development within this family. These modifications are expressed by the formation of secondary branches (cladia; Elles & Wood, 1901-1918) on the main stipe. In some forms, e.g. in certain representatives of the genus *Diversograptus* Manck, the secondary branch constitutes the sicular cladium, i.e. it grows from the apertural part of the sicula in a direction just opposite to that in a normal monograptid stipe (Manck, 1923; Strachan, 1952; Thorsteinsson, 1960, personal comm.). Such a colony may be called biaxial, with bipolar growth. Moreover it has been ascertained that the two main branches in such colonies may be provided with thecal cladia, as e.g. in *Sinodiversograptus* Mu & Chen. Different conditions characterize the genera *Cyrtograptus* Carruthers and *Barrandeograptus* Bouček where the secondary branching occurs owing to the budding of cladia from certain mother thecae of the main stipe (monograptid branch) which are often branched themselves. The knowledge of the process of budding in *Cyrtograptus* was not satisfactorily until Thorsteinsson's recent (1955) investigation, though some earlier descriptions are available (Elles & Wood, 1918; Münch, 1938). Thorsteinsson has recognized the occurrence of most interesting and important regularities which determine the mutual relations of the growing cyrtograptid branches. These regularities are of great significance for the understanding of the morphogenetic mechanisms that govern the development of graptolite colonies (comp. Urbanek, 1960).

Data concerning the development of the Upper Silurian multiramous genera *Linograptus* Frech and *Abiesgraptus* Hundt are relatively meagre, but even in this field considerable progress has recently been made,

chiefly thanks to the most relevant studies of Jaeger (1959) and Teller (in print). In certain aspects these works are complementary, though on some points they disagree. In the light of these investigations it is doubtless that the *Linograptus* colony is multiaxiate (multibrachiate) and that its particular cladia radiate from one common point of divergence, near to the sicula. The nature of certain branches is not, however, quite certain. One of them is undoubtedly the normal monograptid branch (Jaeger, 1959; Teller, in print), while the other constitutes the sicular cladium which buds from the aperture of the sicula in a mode fundamentally resembling that described by Strachan (1952) in *Diversograptus*. The character of all the other branches (cladia) is uncertain. Jaeger (1959) regards all of them as sicular cladia that bud independently, direcly from the sicular aperture, while Teller (in print), on his own observations, postulates that these branches correspond more probably to thecal cladia, but that they bud successively at the base of the first theca of the preceding branch.

Abiesgraptus is apparently a form closely related to *Linograptus* and one that differs actually only in the presence of lateral branches, formed on the two main cladia (Jaeger, 1959). This confirms the correctness of the concepts advanced by Obut (1957) and Teller (in print), postulating that the genera *Linograptus* and *Abiesgraptus* should be placed in a separate family (Obut), or rather subfamily (Teller). Morphologically this suggestion is justified in view of the common type of astogeny and thecal structure in these genera, while stratigraphically it is supported by the presence of a distinct gap between the extinction of the last cyrtograptids and the appearance of the first linograptids. Linograptinae constitute a separate phyletic line of the Upper Silurian Monograptidae, hence their assignment to a new subfamily seems satisfactorily justified.

The picture of the strong astogenetic differentiation in the monograptids has been further complicated by the discovery of enigmatic forms whose thecae grow in two opposite directions from one common point of divergence. The absence of the sicula at the point of divergence in the growth of such colonies seemed particularly strange. There arose also the problem of comparative-anatomical relation of such unusually formed branches to the normal monograptid branches, as well as to thecal and sicular cladia known in other monograptids. The question of the taxonomic position of such forms is thus consequently brought up. This problem is most closely connected with that concerning the nature of the biological processes responsible for the formation of rhabdosomes with bipolar (,,bilateral") growth, and deprived of the sicula.

Such forms were first known only from specimens preserved on the rock surfaces, so that many of their structural details could not be recognized. Bouček and Přibyl (1953) were the first to mention the

occurrence of these forms in connection with their studies of bipolar rhabdosomes of monograptids that they had referred to *Diversograptus* (text-pl. I, fig. *B-D*). Owing to the poor state of preservation of their material, the absence of the sicula at the point of divergence of the two branches of the colony could not always be established with any certainty. It does seem, however, that in a number of cases described by Bouček and Přibyl the lack of the sicula is very probable (comp. p. 223). On this evidence these authors questioned the correctness of the observations of Strachan (1952) who had demonstrated that in *Diversograptus runcinatus* the branches growing in two opposite directions arise from the sicula. In order to explain the most unusual and surprising absence of the sicula at the point of divergence in the growth of colonies they had described, these investigators suggested an interesting and daring conception. It postulated that the bipolar growth of the graptolite colonies under consideration was a biological phenomenon related to regeneration or to agamic reproduction, the latter being associated with division of branches by means of the "oblique septum". The last point of their concept lacks precision and we do not know whether the authors supposed that the graptolite colonies were capable to reproduce by autotomy, subsequently connected with the restoration of the missing parts of the colony. The first point of their hypothesis, that the growth in opposite directions is caused by the regeneration of the branch which had been damaged by being broken off, has been more satisfactorily explained. The breaking up of the rhabdosome owing to some mechanical cause would be followed by secondary growth and the formation of a regenerating branch that would grow in a direction opposite to that of the primary branch. The following facts were regarded by Bouček and Přibyl as adequate evidence in support of their hypothesis:

a) the presence of a sicula could not be soundly shown at the point of divergence of the two thecal series growing in opposite directions, hence the formation of a sicular cladium cannot be taken into account;

b) should both branches bud from the sicula, they would — in Bouček and Přibyl's opinion — have about the same initial size, while actually one of the branches is often from the very beginning distinctly broader (comp. p. 210 and text-pl. I, fig. *C, D*);

c) there is a striking homaeomorphy between certain species with normal monograptid rhabdosomes and associated forms that display bipolar growth. The thecal shape of a monograptid fauna in a given horizon fits with that of the corresponding "diversograptids". Hence it may be supposed that we are dealing here with two biological forms of the same species.

Bouček and Přibyl's interesting hypothesis summarized above re-

quires much attention since there is no doubt that they discovered phenomena which had heretofore failed to attract the attention of other investigators. Interpreting the "diversograptid" type of colonies as the morphological result of the process of colonial regeneration, Bouček and Přibyl stress at the same time the possible phyletic significance of such bipolar forms (1953, p. 551, 574). This point, however, has not been pronounced with sufficient precision and does not seem to be consistent. Moreover, these authors postulate that "bipolar monograptids" constitute a separate evolutionary series and that such forms sufficiently differ from typical monograptids to warrant the erection of a new separate family of the Diversograptidae. They also suggest that several species so far regarded as representatives of the Monograptidae, should be referred to the Diversograptidae on the occurrence of certain specimens which belong to these species, but display bipolar growth[1].

While the "diversograptid" material described by Bouček and Přibyl comes mostly from the Lower Silurian, Jaeger's more recent observations (1959/1960) report the presence also in the Upper Silurian (Lower Ludlovian) of graptolites having a similar structure. At first he ascertained the occurrence of such forms in the material preserved on the surfaces of Lower Ludlovian shales in Thuringia (about 20 rhabdosomes), subsequently he succeeded to etch similar forms from Silurian erratic boulders of Baltic origin. Jaeger's (1959) bipolar monograptid forms were at first only very generally described. That author does not assign them to any particular species, but refers them to the genus *Diversograptus,* though from the typical Lower Silurian diversograptids they differ in having simple thecal type (text-pl. I *A*). The most fundamental point, however, is that in the *"Diversograptus"* from the Lower Ludlovian of Thuringia the sicula is absent at the point of divergence of two thecal series (while its presence was so readily detectable on *Linograptus* specimens in the same state of preservation). In this respect, these forms differ from the Lower Silurian *Diversograptus* described by Strachan (1952), as well as from *Linograptus* whose secondary branches bud from the sicula. Jaeger, however, thought that in thecal structure the *"Diversograptus"* forms discovered by him in the Ludlovian beds resemble *Linograptus* to such an extent, "dass man *Linograptus* gut als Fortsetzung von *Diversograptus* auffassen könnte" (1959, p. 136). The evolutionary series suggested by the writer as leading up to the appearance of *Linograptus* is as follows: *Cyrtograptus carruthersi,* the youngest representative of the cyrtograptids, was transformed by the loss of the thecal cladium into *"Monograptus" nilssoni,*

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[1] Professor B. Bouček (Praha) has informed the writer (personal comm.) that together with A. Přibyl they regarded the strong regeneration ability, leading to the formation of bipolar rhabdosomes, as a feature characteristic of one monograptid group only, and therefore having a diagnostic significance.

a form characterized by a close resemblance of thecal structure with *Linograptus*. This species is also characterized by the presence of an asymmetrical apertural dorsal spine in the sicula. This form might be ancestral to *M.aff.nilssoni*, recorded from the *scanicus* zone, but never described in detail by Jaeger. *M.aff.nilssoni* is closely allied with *M.nilssoni*, but it belongs to a separate species characterized by a symmetrical dorsal spine in the sicula. According to Jaeger (1959, Appendix, p. 178), this form is already referable to the genus *Diversograptus*. It might be stressed here that Jaeger (1959) did not have at his disposal conclusive proofs of the ability of *M.aff.nilssoni* to produce sicular cladia. In his opinion, that form was nearer to *M.nilssoni* and to *Linograptus* than to the Lower Silurian *Diversograptus* which represents a separate phyletic line. Moreover, "die Virgula des zweiten *Diversograptus*-Zweiges könnte man sich dann entstanden denken durch Verlängerung des dorsalen Apertural-Stachels der Sicula" (1959, p. 138).

In Jaeger's opinion, the presence of apertural dorsal spines in monograptid siculae from the *nilssoni* group indicates their ability to produce sicular cladia. These would be two-branched transition forms (*nilssoni — scanicus* zone), grading into the multibrachiate *Linograptus*. According to that author's observations, *Linograptus* had by then made his appearance already in the *scanicus* zone.

Bouček and Přibyl's regeneration hypothesis was at first discarded by Jaeger as not sufficiently substantiated, though he had not at that time accurately examined the causes of the lack of sicula at the point of divergence of the two branches in the *"Diversograptus"* form from the Ludlovian of Thuringia. "Abgesehen von dem ungewöhnlichen Mechanismus, den diese Hypothese annimmt, könnte man etwa fragen, warum von manchen anderen zarten, massenhaft auftretenden Monograptidae (z. B. *M.scanicus* oder *Linograptus posthumus*) niemals ein *"Diversograptus*-Stadium" gefunden wurde? Auch scheinen die in der *scanicus*-Zone bei Stolzenberg in Thüringen sehr häufigen Diversograpten kein entsprechendes *"Monograptus*-Stadium" zu haben, ganz im Gegensatz zu den Diversograpten der *nilssoni*-Zone" (1959, p. 137-138).

In the final stage of his work Jaeger etched some rhabdosomes from an erratic boulder in association with the *scanicus* zone and identified them as *Monograptus* aff.*nilssoni*. In Jaeger's opinion (1959, Appendix, p. 178), these forms with bipolar rhabdosomes reliably warrant the assignment of *M.aff.nilssoni* to *Diversograptus*. He arrived at the conclusion that actually his find — owing to the lack of sicula at the point of divergence of the two branches — rather confirms the regeneration hypothesis of Bouček and Přibyl than Strachan's observations.

In summing up the points of Jaeger's hypothesis (1959) it is but fair to mention that it was an important contribution to our knowledge of the Linograptinae. Nevertheless it does not adequately clarify their

TEXT-PL. I
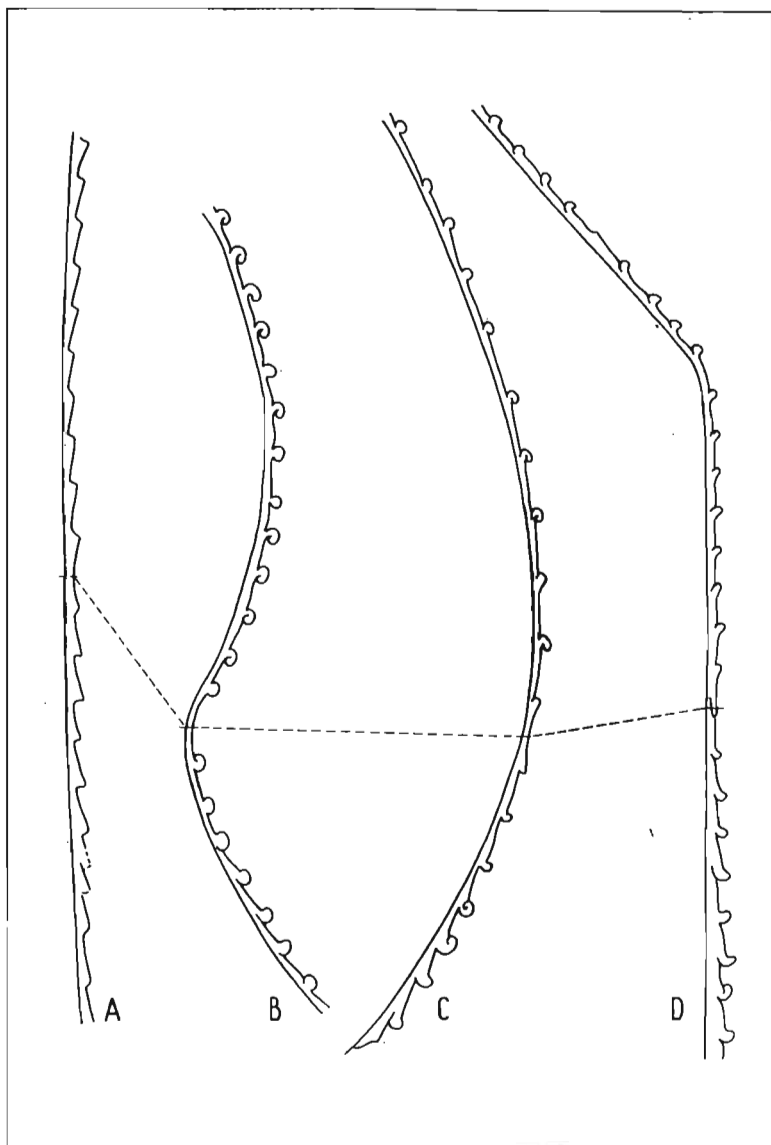
Bipolar monograptid colonies without sicula in region of divergence of two thecal series, described as: A *Diversograptus* sp. (Stolzenberg, Thuringia, Lower Ludlovian; Jaeger, 1959, pl. 8, fig. 10); B *D. globosus* Bouček & Přibyl (Chuchle, Barrandian, Upper Llandoverian; Bouček & Přibyl, 1953, text-pl. 4, fig. 10); C *D. gracilis* (Bouček) (Chuchle, Barrandian, Wenlockian; Bouček & Přibyl, 1953, text-pl. 3, fig. 1); D *D. inexpectatus* Bouček & Přibyl (Chuchle, Barrandian, Upper Llandoverian; Bouček & Přibyl, 1953, text-pl. 5, fig. 1); ca. × 5.

origin and lines of evolution. Particularly doubtful is the relation between *Diversograptus* and *Linograptus,* while the "diversograptid" forms discovered in the Lower Ludlovian have been neither thouroughly investigated nor described by that author. Neither did he elucidate whether the bipolar rhabdosomes lacking a sicula at the point of divergence of branches may nonetheless be referred to *Diversograptus* and what is their taxonomic position in the series of *Linograptus* ancestors. No evidence was put forward by Jaeger in support of the assignment to that genus of the Lower Ludlovian "diversograptid" forms, differing from the typical diversograptids in thecal structure and separated from them by a fairly large stratigraphic gap. Neither did that investigator have at his disposal any direct proof that before acquiring the ability to produce a number of sicular cladia, *Linograptus* had been preceded in its evolution by a two-branched transition form. The presence in the *nilssoni* group — probably closely related with *Linograptus* — of a dorsal spine of the sicula, does not, indeed, provide a conclusive argument in this matter. Moreover, Jaeger did not clear up the relation of these transition forms with two branches, supposedly produced from the sicula, to the peculiar "diversograptid" forms with bipolar colonies, lacking the sicula from the point of divergence and regarded by him as ancestors of *Linograptus,* too.

In an attempt to do away with the inconsistencies and ambiguities in his opinion, Jaeger advanced (1960) another hypothesis explaining the mode of the formation of bipolar rhabdosomes (fig. 1). The new hypothesis — which was presented in the form of a lecture delivered at the 1959 meeting of the Paläontologische Gesellschaft, while its essential points were published in a short note (1960) — is based on the investigation of forms etched from erratic boulders and previously identified as *Diversograptus.* These materials and the information kindly communicated by Dr. Jaeger (1959-1962, in litt.), permit his conception to be recapitulated as follows. In view of the absence of the sicula at the point of divergence it seems reasonable to reject the supposition that one of the branches may represent the sicular cladium. We must also discard the idea that the bipolar growth of these colonies may be explained by regeneration, in the first place on account of the lack of the "oblique septum", whose presence at the point of divergence of two branches was ascertained by Bouček and Přibyl. It has been determined by Jaeger that at the point of divergence of branches the periderm is nearly structureless, i.e. without fusellar structure (fig. 1A). On these facts he infers that the "*Diversograptus*" rhabdosomes were formed through an agamic process by some "multiplication corpuscles" (Vermerungskörper) which later on produced two series of descendent individuals. These "multiplication corpuscles" coated themselves with structureless periderm that persists at the point of divergence of the

rhabdosome. In Jaeger's opinion, this type of bipolar forms may be regarded as an asexual generation of certain monograptids in which alternation of generations (metagenesis) would take place. The graptolite colonies would behave similarly as those of Hydroidea in which the alternation of the jelly fish generation with the polyp generation is of regular occurrence (Jaeger, 1960, *in litt.*). It might reasonably be supposed that the alternation of two generations was fully realized only
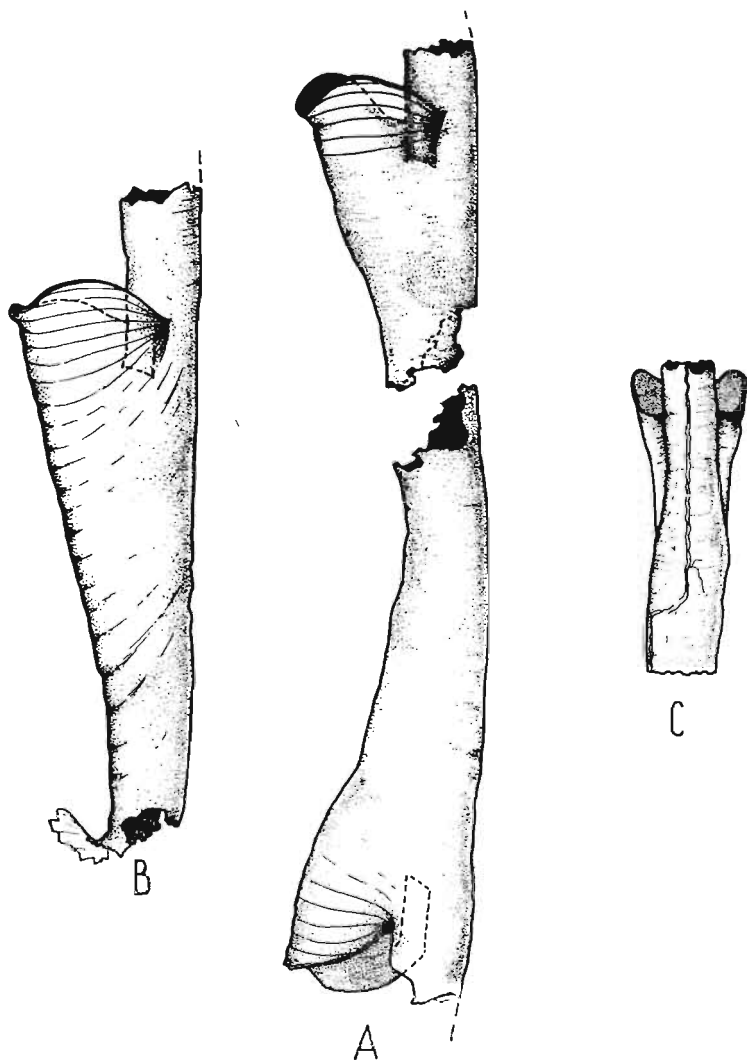

Fig. 1. — Region of divergence of a bipolar rhabdosome without sicula, considered by Jaeger (1950) as a representative of an asexual generation from *nilssoni* group. Baltic erratic boulder, age determined as *scanicus* zone; *A* region of divergence, side view; *B* conspecific distal theca, side view; *C* abnormal course of virgula visible on the dorsal side at the point of divergence; *A-B* ca. × 44, *C* ca. × 26 (on permission of Dr H. Jaeger redrawn from his unpublished figure, 1960).

in certain monograptids, while in others the sexual generation predominated or was even the only one present. Among the graptolites the sexual generation would be represented by colonies started by the sicula and budding from a siculozooid. In what the Lower Ludlovian "*Diversograptus*" forms are concerned, Jaeger stresses their close relationship with *Monograptus nilssoni*. In this species and others closely related, the sicula is provided with a dorsal spine. According to Jaeger's latest interpretation, this spine has some connection with the ability to produce "multiplication corpuscles" or buds which could subsequently be separated from the mother siculozooid and produce bipolar rhabdosomes of the „*Diversograptus*" type that represented the asexual generation. The loss of the ability for the separation of such buds from the mother siculozooid would consequently lead to the formation of sicular cladia of the *Linograptus* type[2].

Should Jaeger's last (1960) far reaching hypothesis — radically changing his previous views on the nature of bipolar rhabsodomes — prove true, it would have a strong bearing on the commonly accepted general views on the organization and biology of graptolite colonies. In order to be accepted or critically evaluated, this concept needs to be examined from all aspects and substantiated by conclusive evidence. Its present status, however, fails to fulfill this pre-requisite as it is based more on theoretical speculation than on concrete observations. No results of Jaeger's anatomic studies have as yet been published, hence his hypothesis must be approached with great caution.

Recently it has been possible to determine with certainty the formation of true sicular cladia, i.e. the budding of branches from the sicular aperture in the Lower Silurian monograptids. This is a result of still unpublished investigations on *Diversograptus runcinatus* from the Arctic Archipelago of Canada (Thorsteinsson, 1960, personal comm.) whose specimens have been etched by chemical treatment. Similar facts have been ascertained by Mu and Chen (1962) in their description of the new genus *Sinodiversograptus* from the Lower Silurian of China. In this genus one of the main branches represents the sicular cladium, while both branches are provided with numerous thecal cladia, too[3].

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[2] It seems that upon accepting this last conception we may dispense with Jaeger's earlier suggestions on the existence in the evolution of Linograptinae of a two-branched (diversograptid) stage. This stage might indeed be reasonably omitted from the suggested evolutionary line (the simultaneous formation of a number of sicular cladia), and thus provide an explanation for the absence at that time of such forms in the Lower Ludlovian fauna. These ideas have not been propounded *expressis verbis* by Jaeger, but are prompted by the line of his considerations.

[3] In A. T. Mu and X. Chen's extremely interesting paper (1962), the forms described by Bouček and Přibyl (1953) are regarded as bipolar rhabdosomes, provided with a sicular cladium (comp. their fig. 5 b, c; foot-note 1 and 2, p. 152), though this is obviously inconsistent with the interpretation given by these Czech authors.

By now, it has been reliably established that certain diversograptids have two main branches: one of them is the sicular cladium, the other a normal monograptid stipe. It is also doubtless that forms described by Bouček and Přibyl (1953), and by Jaeger (1959, 1960) as „diversograptids", and which display bipolar growth and lack of sicula at the point of divergence, represent forms of a different biological significance. There are sound reasons to suppose that such forms cannot provide a basis for the erection of separate taxa. This fact will probably substantially modify the meaning of a number of earlier observations.

Hence, it is thought desirable to publish our observations, based on new Polish material which, though still fragmentary, will probably throw some light on many, previously controversial questions of marked importance for the understanding of the development and the evolution of graptolites.

In summing up the results of previous investigations, it is believed that the solution of the following three fundamental points would be of conclusive importance for the problem here under consideration.

1) Definition of the biological character of bipolar monograptid colonies, without a sicula at the point of divergence — and the establishment of the mode of their formation.

2) Definition of the mode of cladial generation in colonies of Linograptinae and their comparative-anatomical significance.

3) Confirmation whether the transition from normal uniramous monograptids to multiramous Linograptinae was accompanied by the occurrence of intermediate biramous forms, and a definition of their relation to *Diversograptus* Manck.

Our conception as to the ways and modes of evolution of colonies in Upper Silurian monograptids will be based on the solutions of these three fundamental questions.

TERMINOLOGY

The basic terms used in the present paper are those of the standard terminology, commonly accepted (comp. Bulman, 1955). Since, however, the knowledge of multiramous monograptids is as yet rather inadequate, the terminology concerning them is not very complete and is of a descriptive more than of a definitional meaning. Hence some new terms are introduced by the writer, while others, previously accepted but believed as insufficiently explicit, are more precisely defined. The more important of these new or redefined meanings are quoted below, with short definitions.

A. *Anatomic terms*

Adapertural plate — the expanded base of the first theca of the second and following sicular cladia in *Linograptus*, shaped as a subtriangular platform with the true thecal tubule rising on it.

Basal notch — incision of the margin in ventral wall of the basal part of first theca of sicular cladia in *Neodiversograptus beklemishevi* n. sp. and *Linograptus posthumus*.

Cladium — each thecal series in a monograptid colony producing a separate individual branch. Remark: It is proposed to widen the meaning of this definition in relation to that used by its original authors (Elles & Wood, 1918, p. 505) who applied it only for the „so-called branches" in *Cyrtograptus* (pseudobranches, lateral branches = thecal cladia), while the primary branch was in the English literature referred to as a "stipe" or "main branch". Upon the discovery of different kinds of secondary branches, however, a more exact definition of cladia seems indispensible (lateral = thecal, sicular cladia). Therefore it seems more convenient to widen the meaning of cladium, while its particular forms might be expressed by the addition of a suitable prefix. And thus:

Procladium — a cladium produced from the sicula in result of budding and monograptid growth; the only branch present in uniramous rhabdosomes of the Monograptidae.

Metacladium — any other cladium present in the rhabdosome besides the procladium, including the sicular and the thecal cladia.

Sicular cladium — a metacladium whose first theca grows from the sicular aperture by diversograptid and linograptid budding.

Thecal cladium — a cladium whose first theca is produced from the mother theca by means of a cyrtograptid or abiesgraptid budding; thecal cladia may be formed on procladia or on metacladia (thecal cladia of I, II, III, ... order).

Pseudovirgula — a thickened peridermal fibre forming an axis supporting the sicular and thecal cladia; it develops independently of the virgula.

B. *Terms definining structures formed in result of regeneration*

Pseudocladium — secondary branch resulting from the regeneration of a primary branch that had been broken off.

Regenerative virgula — thickened peridermal fibre, secondarily formed, as an axis of the pseudocladium, in result of regeneration.

C. *Terms defining astogenetic stages*

Remark: The terms "monograptid type of development" (Elles, 1922) and "apertural budding" (Kozłowski, 1948), apparently do not now explicitly enough define the various modifications of the basic type of the development of a colony, recently observed among the monograptids.

Hence, similarly as in the case of diplograptids (Bulman, 1936, 1938), it is here proposed to introduce the term "stage" in respect to the several phylogenetic modifications of astogeny, also, to introduce some new terms for closer definitions of the mode of budding in monograptids, describing the particular modifications of the apertural mode of budding, peculiar to this group.

Monograptid stage — a stage of phylogenetic modifications in the development of a colony, in which the process of astogeny produces — by monograptid budding — only a procladium.

Monograptid budding (= subapertural) — non-perforational budding of theca from an opening, subaperturally placed in relation to the definite aperture of the respective mother theca.

Cyrtograptid stage — a stage of phylogenetic modifications in the development of a colony, during which the process of astogeny produces a procladium and at least one thecal cladium that is generated by cyrtograptid budding.

Cyrtograptid budding — the budding of a theca directly from the definite aperture of the mother theca.

Diversograptid stage — a stage of phylogenetic modifications in the development of a colony, in which astogeny results in the formation of a bipolar rhabdosome which consists of a procladium and a sicular cladium, sometimes also of thecal cladia budding from it.

Diversograptid budding — the budding of a theca directly from the definite aperture of sicula, producing only one sicular cladium and not capable of producing more such cladia.

Linograptid stage — a stage of phylogenetic modifications in the development of a colony, in which a procladium and numerous sicular cladia are produced in astogeny.

Linograptid budding — the multiple budding of thecae directly from the sicular aperture, producing several independent sicular cladia.

Abiesgraptid stage — a stage of phylogenetic modifications in the development of a colony, when the procladium and sicular cladium acquire the ability to generate the thecal cladia.

Abiesgraptid budding — a mode of budding of thecal cladia producing two descendent thecae, symmetrically placed on either side of the mother theca, and in turn producing independent cladia.

Astogeny — a complete process of colonial development, comprising the production of the earliest individual and of all the descendent blastozooids, forming one or more branches.

Cladogeny — an astogenetic process, producing more than one cladium, colonial branching (ramification); the term "cladogenesis" — from the Greek words *klados* = a branch, and *genesis* = an origin — is used either to denote the process of colonial branching (Beklemishev, 1952).

or the branching of evolutionary lineages so as to produce new phyloge-
netic lines (Rensch, 1947). The use of this term in the last meaning does
not seem justified in view of the traditional recognition of the term
"phylogenetic line" (phylum), and also insomuch that this term refers to
a phenomenon previously satisfactorily described by the terms "adaptive
radiation" (Osborn, 1902) and „divergence".

ASTOGENY AND PHYLOGENY OF THE LINOGRAPTINAE

Family **Monograptidae** Lapworth, 1873
Subfamily **Linograptinae** Obut, 1957[4]

Diagnosis. — Monograptidae, producing one or more sicular cladia,
on which thecal cladia with bipolar growth may subsequently be formed.
Thecae simple, aperture simple or slightly elaborated with somewhat
elevated apertural margins.

Remark. — In addition to the genus *Linograptus* Frech and *Abies-
graptus* Hundt, the writer proposes to include here *Neodiversograptus*
n. gen., which is closely related to them and probably represents an ear-
lier evolutionary stage of this family.

Stratigraphic range. — Upper Silurian (*nilssoni* zone to the *hercyni-
cus* zone).

Geographical distribution. — Europe, North America, Asia, Austra-
lia. The assignment to this family of the American representatives of
Linograptus is uncertain, owing the thecal characters recorded by
Decker (1935) (Teller, in print).

Neodiversograptus n. gen.

Type species: *Monograptus nilssoni* Lapworth, 1876, sensu Urbanek 1954.
Derivation of name: Gr. *neos* — new, geologically younger than the typical
Diversograptus Manck.

Diagnosis. — Rhabdosomes consisting of a normal monograptid stipe
(procladium), able to produce, at least sporadically, one (or more?) sicu-
lar cladia, and then producing bipolar rhabdosomes by diversograptid
budding. Sicula provided with a dorsal apertural spine whose prolonga-
tion in bipolar forms produces a virgula of the sicular cladium (pseudo-
virgula). Thecae tubular, with apertures either straight or with slightly
elevated margins.

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[4] Obut's statement (1957, 1960) that the family Linograptidae had been esta-
blished by him in 1950, does not seem quite correct since in that paper he hesita-
tes to place *Linograptus* among the Diversograptidae, but does not formally esta-
blish a new taxonomic unit. In Obut's later works the status of this unit was
more correctly, but by no means exhaustively determined; its definition is not gi-
ven, but the name Linograptidae is used and the genera it comprises are specified.
The group in question has been properly defined and ranked as subfamily in a pa-
per by Teller (1962).

Species. — *Neodiversograptus nilssoni* (Lapworth, 1876), sensu Urbanek, 1954, and *Neodiversograptus beklemishevi* n. sp.

Stratigraphic range. — Upper Silurian, Lower Ludlovian (from the *nilssoni* zone to the *leintwardinensis* zone).

Differences and affinities. — *Neodiversograptus* n. gen. represents in the adult stage a type of colony that generally corresponds to the bipolar rhabdosomes of *Diversograptus* Manck (comp. p. 239). A number of morphological differences, however, prevent the inclusion into the same genus of forms from the Lower Ludlovian and the Lower Silurian. These differences primarily concern the structure of the thecae; in *Diversograptus* these are hooked, provided with an apertural lobe, while in *Neodiversograptus* n. gen. they are always simple or straight, practically without apertural differentiation. Thecal cladia, encountered on the main branches of *Diversograptus*, have not so far been found in *Neodiversograptus* n.gen. Stratigraphic data suggest a stratigraphic gap between the last representatives of *Diversograptus* and the earliest representatives of *Neodiversograptus*. This gap probably involved at least the *Cyrtograptus lundgreni* and *Pristiograptus vulgaris* zones, as well as the transition beds, the so-called ''*Gothograptus nassa* — *Pristiograptus dubius* band''.

These facts indicate that *Neodiversograptus* n.gen. represents a separate phylogenetic lineage, not connected with the Lower Silurian *Diversograptus* and justifying its generic separation. On the other hand, the forms assigned to *Neodiversograptus* n.gen. are doubtless very closely allied with the geologically younger *Linograptus*, and they are reasonably referable to the subfamily Linograptinae Obut (comp. discussion on p. 198). These forms represent a distinct evolutionary lineage with regular morphological sequence, characterized by certain transitional forms. Their relationship with *Linograptus* is expressed in strong resemblance of thecal structure and a tendency to the formation of a compound rhabdosome that consists of a procladium and a sicular cladium. *Linograptus* thecae may be regarded as modifications of the thecae of *Neodiversograptus*, while in the astogeny of the former genus there is a "diversograptid stage" in which the rhabdosome approaches the bipolar rhabdosome of *Neodiversograptus* n.gen. (comp. p. 181).

Neodiversograptus nilssoni (Lapworth, 1876), sensu Urbanek, 1954
(text-pl. II — IV)

1900. *Monograptus nilssoni* (Barr.); E. M. R. Wood, The Lower Ludlow..., p. 482, fig. 24 (?pl. 25, fig. 28 A, B).
1918. *Monograptus nilssoni* (Barr.); G. E. Elles & E. M. R. Wood, British graptolites..., p. 369-371, fig. 241a (? 241, b, c).
1954. *Pristiograptus (Pristiograptus) nilssoni* Barr.; A. Urbanek, Some observations..., p. 300-302 (Polish text), p. 83-84 (Conspectus), fig. 13-16.

1958. *Pristiograptus nilssoni* (Lapworth); A. Urbanek, Monograptidae..., p. 80-83, fig. 52-55, fig. 56 C (non fig. 56 A, B).
1959. *Monograptus nilssoni* (Lapworth); H. Jaeger, Graptolithen und Stratigraphie..., p. 138, fig. 22, b_1 (? fig. 22, b_2).

Material. – Well over ten siculae or fragments of siculae, also numerous fragmentary rhabdosomes collected from:

1) deep-boring of the Geological Institute (Warsaw) at Mielnik, from a depth between 1044,3 and 1035, 9 m; marls and calcareous intercalations of Lower Ludlovian, *nilssoni* zone;

2) Baltic erratic boulders or marly limestones, numbered S. 19 and S. 20 (Poznań), and S. 38 (Jarosławiec), in the collection of the Palaeozoological Laboratory of the Warsaw University;

3) a small fragment of a limestone concretion from an outcrop at Borek near Lejškov in the Bohemian Barrandian.

All these specimens have been etched by chemical treatment. Their fairly satisfactory state of preservation allows the reconstruction of astogenetic stages and the analysis of the fusellar structure.

Remarks on nomenclature and taxonomy. - The species here discussed is one of the most common Lower Ludlovian forms and it is an important index fossil. Nevertheless, the concept of this species was markedly controversial and the history of its investigations may be regarded as rather unfortunate. The name *Graptolithus nilssoni* was used by Barrande (1858, p. 31, pl. 2, figs. 16-18) with reference to the fragmentary cyrtograptid rhabdosomes, and this has been recognized by Perner (1899, p. 14-15) and Bouček (1936, p. 5). Hence the priority of the species name belongs to Lapworth (1876, p. 315, pl. 10, fig. 7 a-c) who used it for one of a "thin" Lower Ludlovian monograptid.

More recent investigations call for redefinition of the concept of the species in question. Investigations on the morphology and stratigraphy of graptolite material from the deep-boring at Mielnik show that we are dealing here with two separate forms, very similar in outer morphological details and in size, but differing in structural details, trend of specialization and stratigraphic occurrence. There is sound evidence to suppose that both forms, which cannot always be readily distinguished in a flattened state, have been identified as *Monograptus nilssoni* by the majority of authors. Actually, however, they are more likely separate species, tentatively referred here to „*nilssoni* A" and "*nilssoni* B".

The "*nilssoni* A" type is characterized by the following features: a) presence of dorsal apertural spine on the sicula, suggesting a linograptid trend of specialization; b) straight thecae, devoid of apertural differentiation; c) older geological age, preceding the appearance of the "*nilssoni* B" form, in deep-boring Mielnik this form is encountered between the depth of 1044, 3 — 1035.9 m.

The "*nilssoni* B" type is characterized as follows: a) absence of a dorsal apertural spine on sicula and its replacement by a normal, round apertural process; b) proximal thecae straight, medial and distal thecae with slight, symmetrical elevations on the apertural margin, which suggest a tendency to form apertural lobes indicating the cucullograptid trend of specialization; c) younger geological age: appearance after the extinction of the "*nilssoni* A" type, but before the incoming of the earliest representatives of typical *Lobograptus (L.simplex)*. In deep--boring Mielnik this form is encountered between the depth of 1035.0--1008,40 m, however, higher up to depth of 980 m, the occurrence of similar but fragmentary thecae has been observed which may eventually be also assigned to the species in question.

The two forms-"*nilssoni* A" and "*nilssoni* B"- have many features in common, i.a. the dorso-ventral curvature of the rhabdosome, the shape and proportions as well as dimensions of thecae. The form defined as "*nilssoni* A" is conspecific with that identified by Urbanek (1954, 1958) as *Pristiograptus (Pristiograptus) nilssoni* Lapworth. Hence the writer proposes to call it *nilssoni* Lapworth, sensu Urbanek, and to restrict the use of the specific name *nilssoni* only to that form. It is geologically older and is reported both from deep-boring Mielnik and from the fauna of erratic boulders. In the latter occurrence it is associated with a graptolite assemblage which is commonly regarded as typical of the *nilssoni* zone *(Colonograptus colonus, Monograptus uncinatus)*. The British forms of *nilssoni* (Wood, 1900; Elles & Wood, 1918, fig. 241a) appear to be provided with a dorsal apertural spine on the sicula (comp. Urbanek, 1954). This fact speaks in favour of this rather arbitrary taxonomic suggestion.

The above considerations also point out that the assignment of this species either to the genus *Monograptus* (e.g. Lapworth, 1876; Elles & Wood, 1918; Bouček, 1936; Jaeger, 1959) or to *Pristiograptus* (Přibyl, 1948; Urbanek, 1954, 1958, e.a.) has now lost its ground. The presence of the dorsal apertural spine in the sicula and the ability to produce bipolar rhabdosomes — already established in this paper — allow the writer to assign it to the subfamily Linograptinae. At the same time, it represents the two-branched "diversograptid" evolutionary stage of the Linograptinae for whose representatives the writer proposes to erect a new genus: *Neodiversograptus* n.gen. (comp. p. 199).

The form referred to as "*nilssoni* B" is a separate species that belongs to a cucullograptid trend of specialization. It probably derives from the „*nilssoni* A" form or perhaps it may have evolved somewhat later from their common, as yet unknown ancestor. Its different specialization trend not only justifies the introduction of a separate specific name, but also its assignment to another genus. This species will be described by the writer as a new *Lobograptus* in his forthcoming pa-

per dealing with the Cucullograptinae. *"Nilssoni* B" is a form which by its morphological development and stratigraphic occurrence preceded the appearance of the first true lobograptid, and initiated the development of the Cucullograptinae. These, surely, must have had ancestors in common with Linograptinae.

The differentiation of these two species which most often have so far been tentatively assigned to *nilssoni*, will result in important taxonomic and stratigraphic consequences. From the standpoint of taxonomy this calls for a decision as to the position of species (*"nilssoni* A" or "B"?) that have previously been described as *Monograptus nilssoni*, but which lacks the dorsal apertural spine on the sicula[5] (e.g. Kühne, 1955, p. 384-86, fig. 10). From the standpoint of stratigraphy this calls for a careful revision of earlier sections that should lead to the redefinition and a narrower concept for the proper *nilssoni* zone, by separating from it the overlying *"nilssoni* B" zone.

Description. - One-branched rhabdosome, consisting only of a procladium, or two-branched, with an additional sicular cladium. Thus, two astogenetic stages may be distinguished: 1) the monograptid stage, involving the formation of sicula of the first branch (procladium); 2) the diversograptid stage, involving the formation of the sicular cladium. Thecae straight, lacking apertural differentiation. Sicula provided with a peculiar asymmetrical dorsal process at the aperture.

Monograptid stage

Sicula (text-pl. II, fig. A-D) nearly straight or slightly ventrally curved, strongly expanding in the adapertural region. Total sicular length in the measured specimens ranges from 1.25 to 1.55 mm, exceptionally being even up to 1.65 mm. At the point of budding of the first theca, the width is from 0.24 to 0.28 mm, near the aperture of metasicula from 0.25 to 0.37 mm, exceptionally attaining 0.40 mm.

Prosicula (text-pl. II, fig. A, *psi*) is approx. 0.40 mm in length, exceptionally 0.50 mm. Thus it is relatively short, being about one-third of the total length of sicula. On most specimens the periderm of prosicula is very much wrinkled and partly damaged, so that the spiral thread is scarcely detectable. Longitudinal ribs are faintly indicated only on one specimen (text-pl. II, fig. A). The width of the prosicular aperture is 0.13 - 0.15 mm. The apex, prolonged into the virgula (nema), reaches to about two-thirds or three-fourths of the length of first theca.

Metasicula (text-pl. II, fig. A-C, *msi*) ranges from 0.85 to 1.00 mm in length, exceptionally 1.15 mm. Towards the aperture the metasicula generally expands strongly so as to attain there a diameter from 0.25

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[5] According to the information kindly sent by Dr H. Jaeger, Kühne's specimen is damaged in the apertural part of sicula and the presence or absence of a dorsal spine cannot be reliably established.

TEXT-PL. II
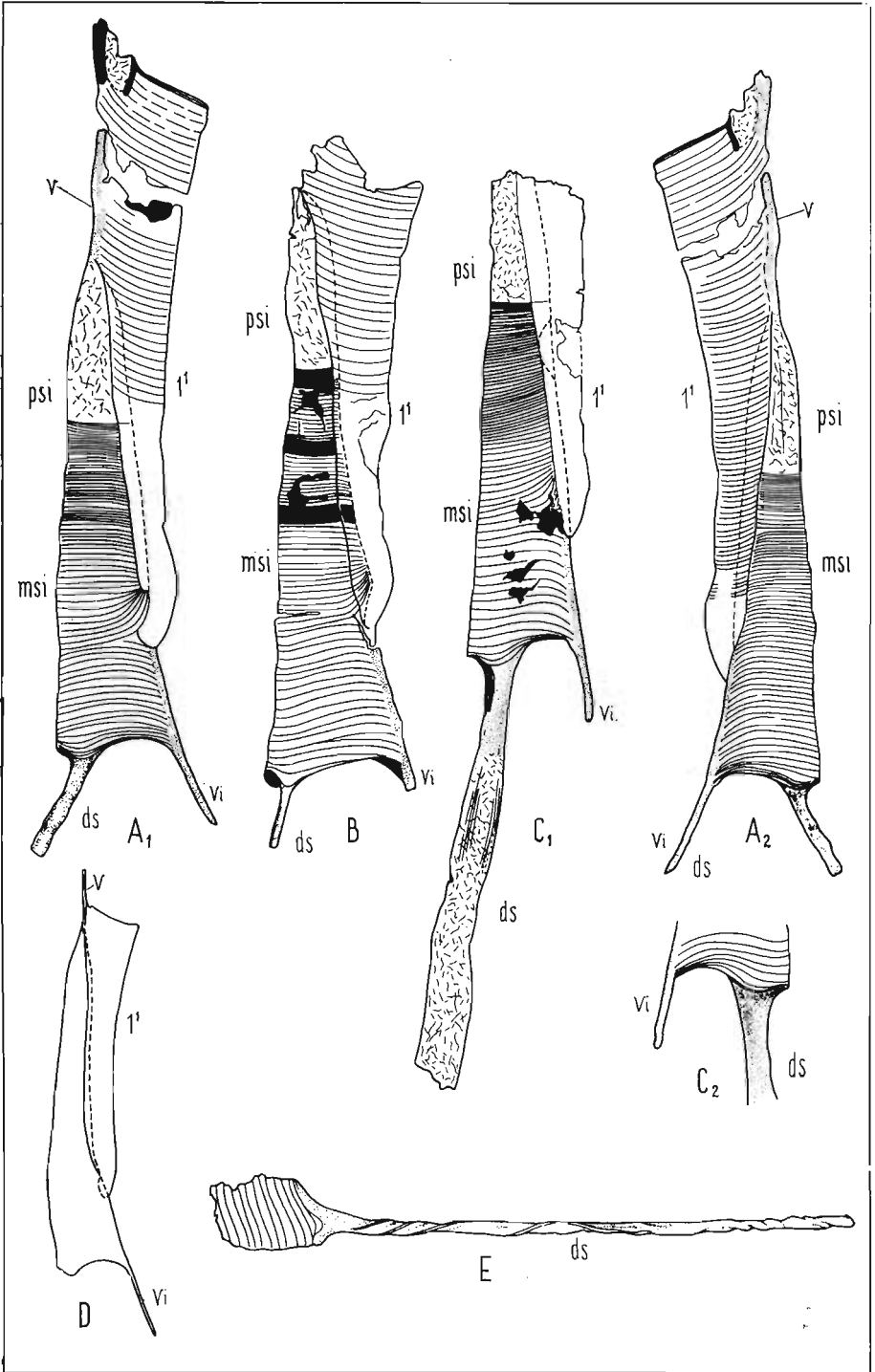
to 0.40 mm. Two separate forms of metasiculae may be distinguished, sometimes occurring together in the same population (e.g. in the assemblage from erratic boulder S. 38). One form lacks the metasicular rings (ringless form). The other is provided with rings which consist of internal thickenings on the periderm (comp. text-pl. II, fig. B). The number of rings varies from 3 to 4, the first ring being formed on the boundary of the prosicula with the metasicula. At a distance of about 0.55 to 0.75 mm from this boundary, occurs the anterior margin of theca 1^1 whose development must have been realized after a monograptid pattern by the occurrence of the "*sinus*" and "*lacuna*" stages (Eisenack, 1942). The metasicula continues to grow for some time after the budding of theca 1^1, until the formation of its definitive aperture. The margin of metasicula is differentiated. A normal virgella is present ventrally, not differing from other monograptid virgellae either in length or in thickness. Dorsally the margin of the aperture has two slight symmetrical elevations, separated by a small notch lying in the plane of symmetry. Both these elevations, at first poorly developed (text-pl. III, fig. A), are gradually emphasized by the addition of short, slightly arched fuselli, whose number ranges from 2 to 5. The elevations may attain a height of 0.05 — 0.07 mm (text-pl. III, fig. B, C). On the obverse side the elevation stops at this stage of development, while an asymmetrical apertural spine is initiated on the margin of the elevation on the opposite side (text-pl. III, fig. D). The formation of this apertural spine is probably preceded by a fairly long interval, during which the mature sicula still lacks this spine.
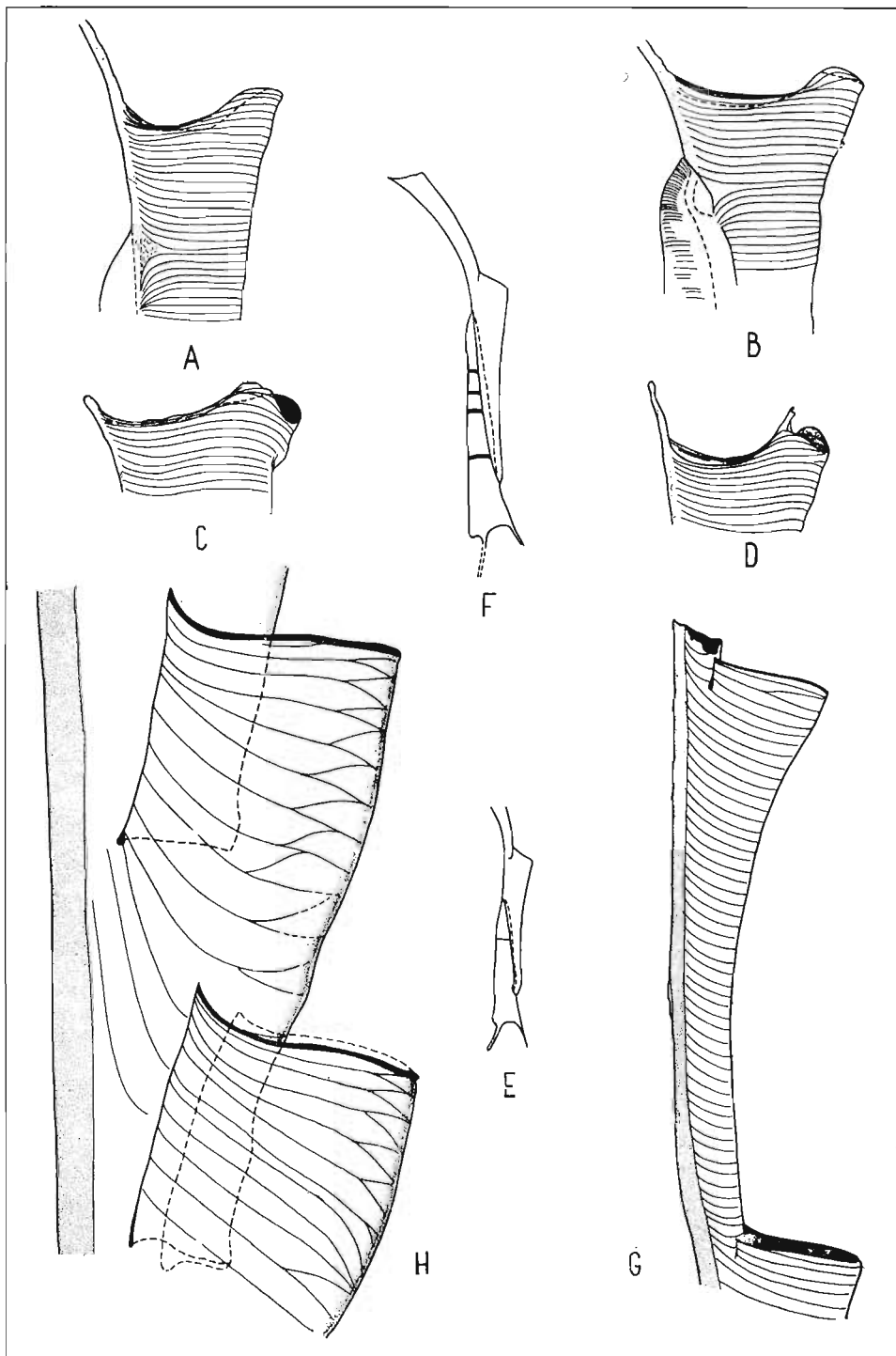
Figure D of text-pl. II shows a sicula with theca 1^1 whose growth is nearly completed, but which lacks even an onset of the apertural dorsal spine. Its formation may have occurred later, after that of several proximal thecae, as is suggested by the presence of relatively numerous mature siculae, lacking even an initial spine of this kind. This spine, first having the shape of a short appendage, may subsequently grow longer, attaining the lenght of 1.45 mm, i.e. nearly equal to the lenght of the sicula itself (text-pl. II, fig. E). Moreover, it is quite possible that this spine is not completely preserved and that originally it may have been still longer. Sometimes it is relatively thin, not differing in this

TEXT-PL. III

respect from the virgella (text-pl. II, fig. *E)*; in other specimens it may be much thicker (text-pl. II, fig. *C*), and sometimes takes on the appearance of a strong, robust rod that gradually expands and — at a distance of 1.05 mm from the metasicular aperture — attains a width of approx. 0.11 mm. Longitudinal striae are observable at the base of the rod; they probably correspond to the growth lines of the periderm. Occasionally, this spine shows distinct traces of spiral twisting, but this feature may be lacking and then the spine resembles a relatively wide and laterally somewhat flattened band. Sometimes its position is nearly straight, but more often somewhat antero-dorsally inclined.

The slightly smaller size of the ringless siculae is very noticeable as compared with the ringed siculae (comp. text-pl. III, fig. *E, F*). Marked contrasts are seen in extreme cases, but owing to the scarcity of material it is hardly possible reliably to correlate these differences concerning size with the presence or absence of rings.

Together with several proximal thecae, theca 1^1 forms the initial dorsally curved part of the rhabdosome (text-pl. III, fig. *F*), while the next part of the rhabdosome is ventrally curved. Thus in *Neodiversograptus nilssoni* the rhabdosome has a double, dorso-ventral curvature.

Theca 1^1 is approx. 1.50 — 1.70 mm long, at the apex of the prosicula it attains a width of 0.20 — 0.35 mm, near the aperture it is not less than 0.25 — 0.27 mm in diameter. The apertural margin is placed obliquely to the ventral margin — at an angle of 60—70°. The metatheca is extremely short, approx. 0.08 — 0.10 mm in length. In more distal thecae which have a length of 1.75 mm and are 0.30 mm in apertural diameter, the apertural margin is nearly straight (text-pl. III, fig. *G*). Distal thecae, approx. 1.85 — 1.87 mm in length and 0.62 mm in apertural diameter, have a perfectly straight aperture. The metatheca is here not more than 0.70 mm long. Its ventral wall is straight or nearly straight. Thus during astogeny the lenght ratio of protheca/metatheca changes fundamentally, since in theca 1^1 it is about 150 : 10 (nearly 93 per cent of the thecal length being taken up by the protheca), while in distal thecae it is 115:70 (only 63 per cent of thecal length being represented by protheca).

Diversograptid stage

This stage is expressed by the formation of the sicular cladium, owing to which the rhabdosomes take on the appearance of a two-branch-

Text-pl. III
Neodiversograptus nilssoni (Lapworth) sensu Urbanek
Formation of the dorsal apertural spine of sicula and structure of thecae. *A–C* aperture of metasicula in different growth stages (Mielnik, depth 1044.30 m); *D* incipient dorsal apertural spine of metasicula (Lejškov, loc. „Borek", Barrandian); *E* proximal part of rhabdosome in a ringless form (Mielnik, depth 1035.90 m); *F* proximal part of rhabdosome in a ringed form (Lejškov, loc. „Borek", Barrandian); *G* proximal theca; *H* distal theca; *A–D, G, H* ca. × 50, *E, F* ca. × 15

ed bipolar colony. In the writer's material this stage is represented only
by a single specimen. It is a short fragmentary rhabdosome (approx.
2 mm long) consisting of a fragmentary sicula and theca 1^1, and of
a complete theca 1^2, with a short fragment of theca 2^2 (text-pl. IV, fig.
$A_1 — A_2$). This specimen was etched out of the erratic boulder S. 19
(Poznań). The periderm is partly damaged, but allows the examination
of the essential details of the fusellar structure.

The fragmentary sicula approx 0.90 mm in length, represents a
nearly complete metasicula. The metasicular ring is visible very near to
the margin along which the sicula was broken off. Toward the aperture,
the sicula is strongly expanded. On the ventral margin the metasicular
aperture is provided with a strong virgella, about 0.70 mm in length.
The virgella meets the ventral margin of the sicula at an angle of
approx 30°. Near the dorsal margin, on the „reverse" side of the me-
tasicular aperture, there is a slight elevation. From it protrudes a long
spine, whose continuation forms a pseudovirgula, that runs afterwards
along the middle of the dorsal wall of the sicular cladium. On the „obver-
se" side, in reflected and transmitted light, it was possible to ascertain
the lack of such a spine, hence it may be assumed that its position is
asymmetrical, shifted from the symmetry plane onto the "reverse" side.
The interval between the base of the dorsal spine of sicula and the
dorsal margin of theca 1^2 is filled in with strongly carbonized and dark
periderm (cp), with the margin of the dorsal spine distinctly visible on
the surface of theca. These observations indicate that the spine is
unpaired and that probably it runs somewhat asymmetrically along the
greater part of theca 1^2.

Theca 1^1, of which only the earliest part of protheca is preserved,
starts at a distance of 0.35 mm from the apertural margin of metasicula.
Owing to the poor state of preservation, neither the fusellar structure
of this theca, nor structure of metasicula near the primary notch, could
be examined. The shape of the preserved fragment of theca 1^1 suggests
that its width was considerably smaller than the width of theca 1^2.

Theca 1^2 starts in the prolongation of the margin of the sicular
aperture and attains a length of approx. 1.0 mm. The earliest part of
protheca consists of relatively narrow fuselli that somewhat arcuately
overlap the margin of the sicular aperture. Though the course of the
fuselli could not be very closely followed owing to the poor state of
preservation of the periderm, it is probably less regular than in the
remaining part of theca. The ventral wall of the earliest part of protheca
forms a slight convexity which passes into the straight ventral wall.
The initial width of theca 1^2 is 0.45 mm, increasing to approx. 0.60 mm
in the metathecal area. The metatheca is short, about 0.25 mm in length,
approx. 0. 75 mm being thus occupied by the protheca. The margin of
the thecal aperture is nearly straight, slightly depressed on either side.

The base of theca 1^2 nearly completely overlaps the sicular aperture, hence the internal cavity of the sicula passes into the internal cavity of theca 1^2. The lack of any opening in the ventral wall of protheca 1^2 reasonably suggests that the cavity of the metasicula was connected with the outer environment only by thecae 1^2 and 1^1.

A thick peridermal membrane ("web") extends from the ventral margin of the basal part of protheca 1^2 to the virgella. This membrane has a strongly wrinkled surface, without any distinct traces of fusellar structure (text-pl. IV, fig. A_1-A_2, m).

Theca 2^2 is preserved as a very short fragment of the initial part of protheca; its width suggests that in dimensions it approaches theca 1^2, i.e. that it was relatively broad.

Doubtless this specimen represents a fragment of rhabdosome which consisted of two branches that were produced independently from the sicula. One branch, of which only a small fragment of theca 1^1 is preserved, represents the normal procladium; the other cladium, with preserved theca 1^2 and the beginning of theca 2^2, was the sicular cladium budding from the sicular aperture. It is noteworthy that already the first thecae of this cladium attained the dimensions and proportions characteristic rather of distal than of proximal thecae in *nilssoni* group (text-pl. IV, fig. B).

The shape and size of the preserved fragment of sicula and thecae reliably indicate that the fragment of the colony here described is referable to *Neodiversograptus nilssoni* (Lapworth), sensu Urbanek.

Of particular interest is the shape of the sicular aperture provided with an asymmetrical dorsal spine. This sicula does not in any respect differ from typical siculae of this species, already described. Without doubt, the presence of a dorsal sicular spine, shifted to the "reverse" side, is a constant character of mature siculae of this species. In shape and structure theca 1^2 likewise closely resembles the distal thecae of *Neodiversograptus nilssoni*. The occurrence of this form in an assemblage of many typical siculae and thecae of *Neodiversograptus nilssoni* that represent fragmentary rhabdosomes of the monograptid stage, speaks in favour of the assignment of this bipolar form to this species. We are most likely dealing here with the rhabdosome of a species, in which an additional sicular cladium was evolved during astogeny. Jaeger (1959) put forward an interesting concept that such a dorsal spine could be transformed into the virgula of the second branch, supposedly representing the sicular cladium of the evolutionary more advanced descendents of "*Monograptus*" *nilssoni* and closely relatives of *Linograptus*. That author did not, however, have in his possession any sound evidence to prove either the occurrence in these forms of a sicular cladium or that such cladium develops on a virgula, representing a continuation of the dorsal spine. The specimen just described, however, proves

TEXT-PL. IV
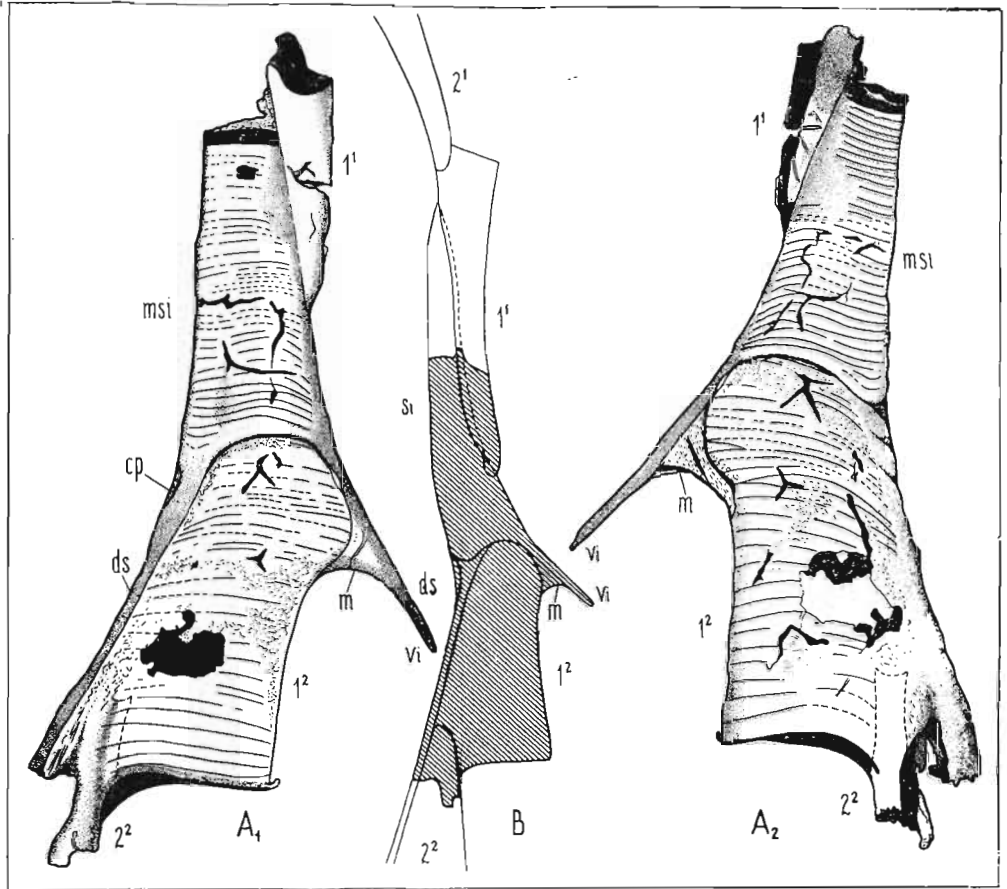
Neodiversograptus nilssoni (Lapworth) sensu Urbanek
Fragment of a sicular part in a bipolar rhabdosome. A_1-A_2 specimen from reverse and obverse sides (boulder S. 19, Poznań); B diagrammatical reconstruction of structure in region of divergence of both branches in bipolar rhabdosome, based on specimen figured A_1 (stippled), and other specimens (unstippled); A_1-A_2 ca. $\times$ 55

cp small protuberance at the base of dorsal spine made up of carbonized periderm, ds dorsal apertural spine of metasicula, m membrane of the base of virgella, msi metasicula, vi virgella

without doubt that a sicular cladium could be produced on the dorsal spine as a support. Owing to the rarity of specimens presenting this phenomenon, it is hardly possible to establish whether the sicular cladia were formed sporadically, or whether they represented a normal developmental stage of each rhabdosome in this species. The frequency of bipolar forms in populations of *Neodiversograptus nilssoni* was, however, probably rather low (comp. discussion on p. 202)[6].

On the above facts it may be inferred that the presence of an asymmetrical dorsal spine of the sicula in normal rhabdosomes of *Neodiversograptus nilssoni* indicates its linograptid trend of specialization. At the same time it suggests a predisposition to the formation of a sicular cladium, so that the dorsal spine may be regarded as the incipient pseudovirgula. All this is inconsistent with Jaeger's (1960) later hypothesis, postulating that not a true sicular cladium, but hypothetical "multiplication corpuscles" could be formed on the dorsal spine (comp. p. 225).

The dimensions of the preserved part of theca 1^1 and its assignment to the species *Neodiversograptus nilssoni* doubtless indicate that the proximal thecae of the procladium were long and slender. The dimensions and shape of theca 1^2, in this respect approaching nearer to distal thecae (comp. p. 212), are in contrast with the above conditions.

Stratigraphic range. — In deep-boring Mielnik this species is encountered between a depth of 1044.3 and 1035.9 m. In this series, though not always directly associated, it is accompanied by the following species: *Colonograptus* cf. *colonus* (Barrande) sensu Perner, *Monograptus uncinatus* Tullberg, *Spinograptus spinosus* (Wood), *Holoretiolites* sp., and *Dalmanites* cf. *vulgaris* Salter.

In erratic boulders the *Neodiversograptus nilssoni* occurs in the following association: S. 20 (Poznań) — with *Monograptus uncinatus* Tullberg, *Pristiograptus bohemicus* (Barrande) and *Pr. dubius* (Suess); S. 38 (Jarosławiec) — with *Colonograptus colonus* (Barrande) *sensu* Perner and *Monograptus uncinatus* Tullberg; in the concretion from Lejškov (Borek) from the Barrandian of Czechoslovakia — with *M. uncinatus* Tullberg and *Colonograptus* sp.

The bipolar form etched from the erratic boulder S. 19 (Poznań) occurred in an assemblage of the following graptolites: *Neodiversograptus nilssoni* (Lapworth) sensu Urbanek (numerous monograptid stages), *Monograptus uncinatus* Tullberg, *Colonograptus colonus* Barrande sensu Perner and *Pristiograptus dubius* (Suess).

All the assemblages just mentioned indicate the *nilssoni* zone as currently defined.

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[6] Dr H. Jaeger (Berlin) has informed the writer that bipolar *nilssoni* forms with rhabdosomes provided with sicular cladia have been encountered by him in erratic boulders from the Baltic coast, but that so far he had failed to etch any such specimens.

Systematic position. — The structure and stratigraphic distribution of *Neodiversograptus nilssoni* suggest that all the other Linograptinae may derive from it. In the structure of this species, this supposition is justified by the presence of an asymmetrical dorsal spine of the sicula and by the ability to produce the sicular cladium. These two characters indicate the linograptid trend of evolution. The simple structure of thecae supports the supposition that the remaining Linograptinae derive from that very species, unspecialized in this respect.

By its stratigraphic distribution *Neodiversograptus nilssoni* may also be regarded as the oldest representative of this subfamily (comp. discussion on p. 198).

Neodiversograptus beklemishevi n.sp.
(text-pl. V, VI; fig. 2)

Holotype: Text-pl. V, fig. C; deep-boring at Mielnik n.B., depth of 1000,9 m.
Paratypes: Text-pl. V, fig. D-F.
Stratum typicum: Greenish-blue mudstones and marls in the core of the deep-boring at Mielnik, between 1000.9 and 966.9 m, corresponding to the *scanicus* zone as currently defined.
Derivation of name: In honour of the recently deceased Professor W. N. Beklemishev, an outstanding Russian zoologist. His works betraying a keen insight into problems concerning the evolution of colonies in higher invertebrates were the direct stimulation for the writer's studies on the organization of graptolite colonies.

Material. — More than 10 siculae in different growth stages among them several mature thecae 1^1, one theca 1^2. Some few proximal and distal thecae. The specimens are mostly flattened, but the fairly satisfactory state of preservation of the periderm allows one the examination of the fusellar structure. The specimens come from the deep-boring of the Geological Institute (Warszawa) at Mielnik. They have been etched from marls and limestone intercalations at a depth between 1000.9 and 934.5 m. The specimen with the sicular cladium comes from erratic boulder S. 32 (Gdańsk-Wrzeszcz).

Diagnosis. — One-branched rhabdosome consisting of 1 cladium supposedly able to attain the two-branched stage by the formation of the sicular cladium. This is suggested by the presence of a symmetrical dorsal spine on the aperture of sicula and the occurrence of fragmentary sicula with a structure typical of this species and provided with a sicular cladium. Proximal thecae straight, in distal thecae the apertures are with a slight marginal elevation which forms two small, symmetrical lateral lobes.

Monograptid stage
Sicula (text-pl. V, fig. A-D; fig. 2) nearly straight and relatively narrow, but slightly expanded in the adapertural area. Entire length of

sicula of the measured specimens from 1.15 to 1.36 mm. Width at point
of budding of theca 1^1 approx. 0.19—0.20 mm, at the aperture of meta-
sicula 0.20—0.27 mm. The youngest known stage already represents the
sicula with a large portion of protheca 1^1 (text-pl. V, fig. A).

Prosicula relatively short *(psi)*, ranging from 0.45 to 0.55 mm in
length on the examined specimens; the periderm is in most cases
partly damaged so that sometimes the only detectable details are thin
longitudinal threads (ribs), whose number is 1 or 2 (text-pl. V, fig. D).
The longest measured prosiculae (approx. 0.55 mm) occur in the highest
leintwardinensis zone. Since, however, the whole material consists of
only 2 siculae, it is not certain whether we are dealing with some evolu-
tionary progression or an accidental change in intraspecific variation.
The prosicula is invariably provided with the prosicular ring which
does not occur on the apertural margin, as is usual in all the described
cases for monograptids, but in the middle of prosicula (text-pl. V, fig.
A-D). The width of the aperture of the prosicula is approx. 0.14—0.15
mm. Some specimens bear traces of the prosicula being damaged during
lifetime, also of the formation of regenerating nema (virgula) (text-pl.
V, fig. B).

Metasicula (text-pl. V, fig. A-D) is 0.60—0.84 mm in length. Toward
the aperture the metasicula expands gradually to attain its maximum
diameter there. The first fuselli are extremely thin, occasionally they
are condensed, forming a darker band. It is striking, however, that the
first metasicular ring does not lie exactly on the contact of the prosicula
and the metasicula, but at a some distance off. Within the metasicular
area the number of rings varies from 1 to 3. In forms with 3 rings the
third ring may be sometimes rather faintly marked, incomplete (not
fully closed) and lighter (text-pl. V, fig. A). The anterior margin of
theca 1^1 occurs at a distance of approx. 0.39—0.50 mm from the margin
of prosicula. Its budding was realized according to a normal monograp-
tid pattern through the *"sinus"* and *"lacuna"* stages. The final aperture
of sicula is formed at a considerable distance from the bud of theca 1^1.
A strong dorsal spine is present along with a long and relatively well
developed virgella on the ventral side of the aperture. The dorsal spine
lies in the symmetry plane of the sicula and it forms on the zigzag
dorsal suture (text-pl. V, fig. A, ds). The base of the spine is often pro-
vided with a rather small but characteristic fragment of the periderm
in the form of a swelling (text-pl. V, fig. D, cp). Even in a young sicula,
in a stage before theca 1^1 reaches the apex of prosicula, the dorsal spine
is approx. 0.20 mm long (text-pl. V, fig. A). In later growth stages it
may be up to 0.70 mm long, but during lifetime probably much longer.

A comparison of the mode of its formation with that of the dorsal
spine in *Neodiversograptus nilssoni* shows distinct acceleration in rela-
tion to the growth of theca 1^1. The biological significance of this sym-

TEXT-PL. V
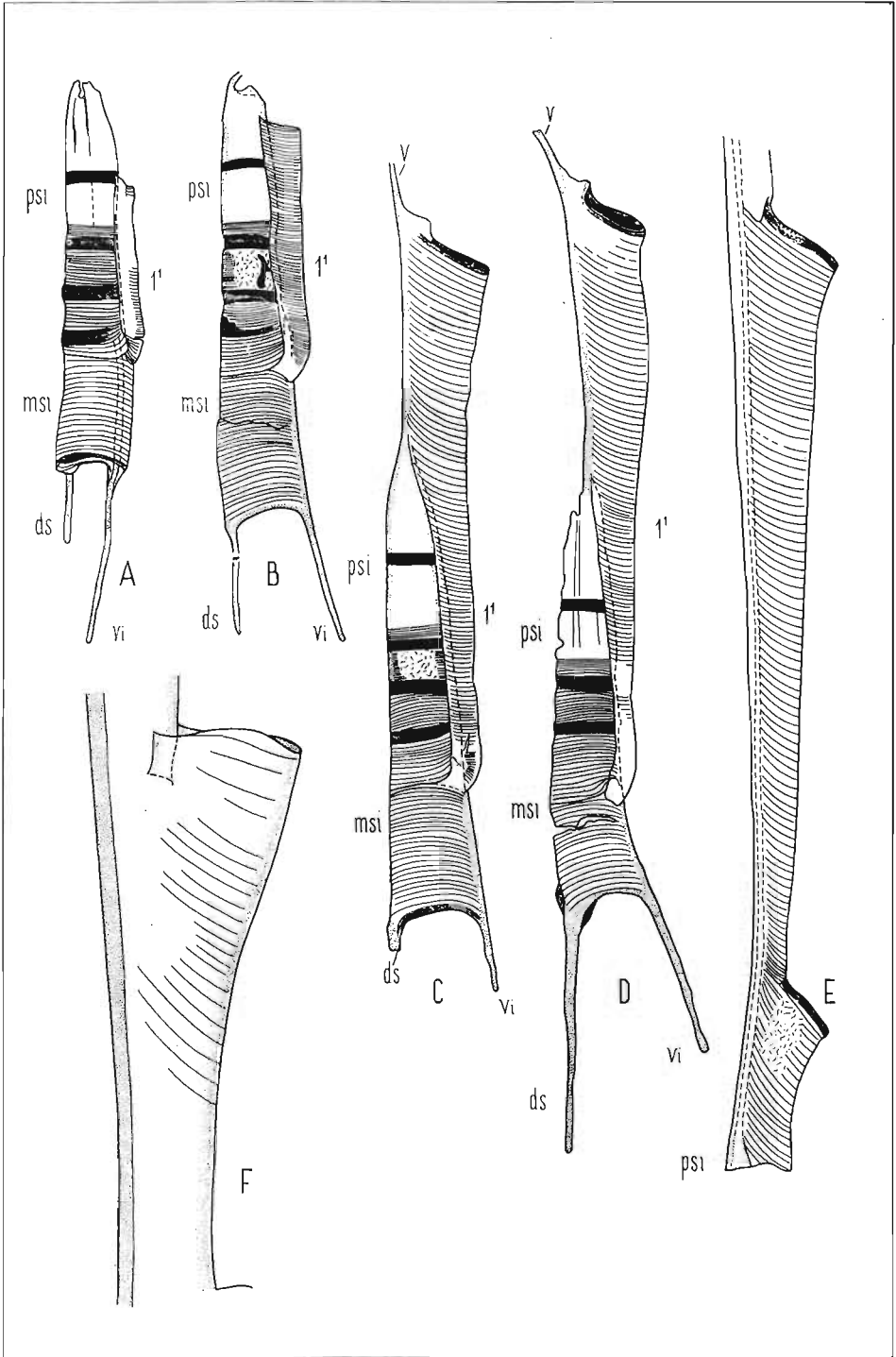
metrical dorsal spine must have been analogous with the role of the dorsal spine in *Neodiversograptus nilssoni*. Its continuation was probably the pseudovirgula forming the skeletal axis on which the growth of the sicular cladium occurred.

Thecal structure and morphological succession may be established only on short rhabdosome fragments. Theca 1^1 (text-pl. V, fig. *C, D*) attains a length of 1.40—1.80 mm, while its width at the apex of the sicula is approx. 0.16—0.18 mm. The thecal aperture is oblique, at an angle of about 50°—60° in relation to the dorsal margin of this theca. The width of the thecal aperture is about 0.20—0.22 mm. Theca 2^1 is up to 2 mm in length (text-pl. V, fig. *E*), its basal width is approx. 0.7—0.10 mm, the width of the aperture 0.20—0.26 mm. The metathecae of these thecae are very short (about 0.03 mm long), so that practically the thecae consist only of prothecae. In the medial thecae the apertural margin is nearly perpendicular to the dorsal wall of thecae, moreover it is distinguished by slight side elevations. It appears that the true distal thecae are not represented in our material. The most distal of the examined thecae are about 1.70 mm long, their basal width is approx. 0.26 mm, the width of the thecal aperture is approx. 0.45 mm. The metatheca is 0.13 mm long, the ratio of protheca to metatheca is 157:13 (i.e. nearly 92 per cent of thecal length is represented by the protheca). These thecae display a slight curvature of the ventral wall. The side elevations on the apertural margin are more conspicuous, but consist of one fusellus only (text-pl. V, fig. *F*).

Diversograptid stage

The diversograptid stage is represented by 1 fragmentary rhabdosome, about 2.60 mm long, consisting of a fragment of the sicula with thecae 1^1 and 1^2, and of a short fragment of theca 2^2 (text-pl. VI, A_1-A_3). This specimen was etched from a Silurian erratic boulder S. 32 (loc. Gdańsk-Wrzeszcz). Its state of preservation is satisfactory and allows one the examination of the fusellar structure.

The sicular fragment preserved, about 0.65 mm long, represents a considerable part of metasicula (*msi*) together with its aperture and the "sinus" area for theca 1^1. The sicula is relatively narrow, up to 0.25 mm in apertural diameter. The apertural margin nearly straight, pro-


Text-pl. V
Neodiversograptus beklemishevi n.sp.
Structure of sicula and thecae. *A* young sicula with incipient theca 1^1, showing the symmetrical position of dorsal apertural spine of sicula; *B* young sicula with theca 1^1 in somewhat more advanced growth stage; *C* sicula with complete theca 1^1; *D* sicula and complete theca 1^1 with better preserved dorsal apertural spine of sicula; *E* apertural part of theca 1^1 and complete theca 1^2; *F* more distal theca (Mielnik, *A-C, E* depth 1000.90 m, *D* — 973 m, *F* — 974.90 m); ca. $\times$ 50

ds dorsal spine of sicula, *msi* metasicula, *psi* prosicula, *v* virgula, *vi* virgella.

TEXT-PL. VI
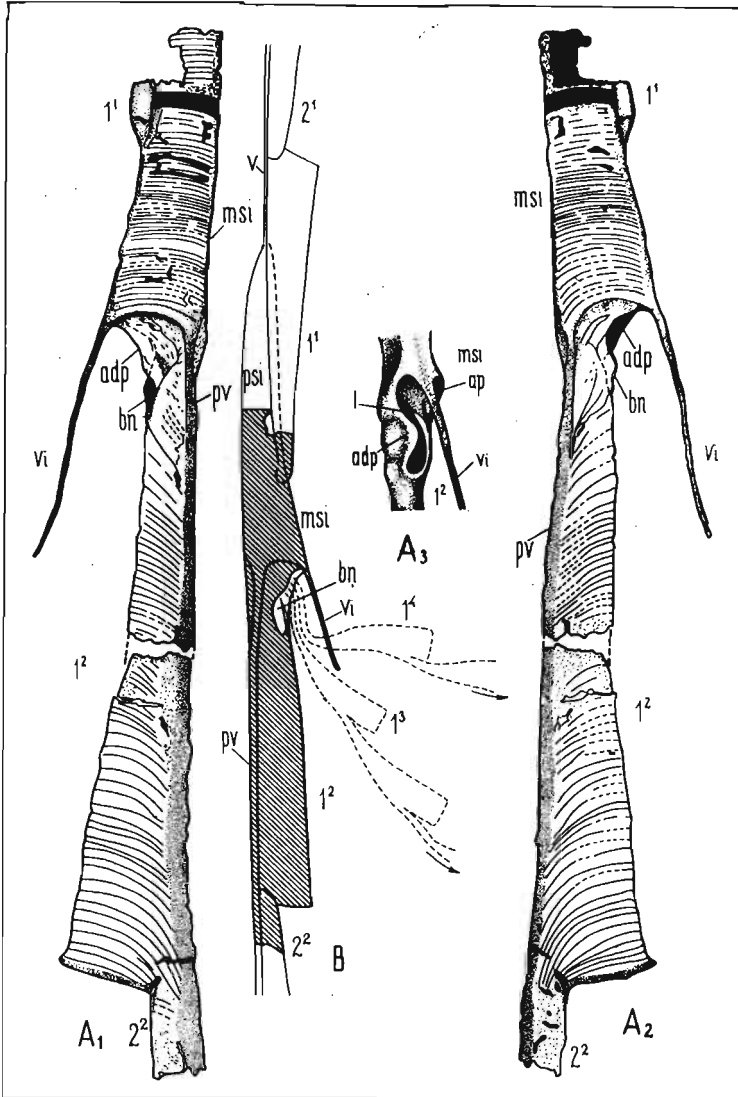
Neodiversograptus beklemishevi n.sp.

Fragment of sicular part of a bipolar rhabdosome. A_1-A_2 same specimen from obverse and reverse side; A_3 ventral view of apertural part of a sicula and the base of theca 1^2 (boulder S. 32, Gdańsk-Wrzeszcz); B diagrammatical reconstruction of the structure of compound rhabdosome in region of divergence of both branches, based on specimen A (stippled) and other specimens (unstippled). Broken lines indicate the course of hypothetical additional sicular cladia; A_1-A_3 ca. $\times$ 52

adp adapertural plates, *ap* aperture of sicula, *bn* basal notch, *l* list penetrating inside the basal notch, *msi* metasicula, *psi* prosicula, *pv* pseudovirgula, *v* virgula, *vi* virgella.

vided with a barely detectable dorsal spine. The pseudovirgula which constitutes the base of the sicular cladium, develops in the prolongation of this spine. As far as it was possible to establish, the pseudovirgula has a symmetrical or nearly symmetrical course from its very beginning. Owing to the unsatisfactory state of preservation, the fusellar structure in the vicinity of the primary notch could not be accurately examined. One of the sicular rings occurs in the proximity of the "*sinus*".

Theca 1^1 has been preserved as an extremely short fragment. It starts at a distance of 0.40 mm from the apertural margin of the sicula.

The sicular cladium is produced from the sicular aperture; only theca 1^2 is well preserved. This theca develops in the continuation of the apertural margin and grows on its straight prolongation. The angle of the initial divergence is about 180°, but later the sicular cladium displays a tendency to slight dorsal curvature.

Theca 1^2 is up to approx. 1.75 mm in length, the width at the base of the protheca is about 0.12—0.13 mm, attaining 0.30 mm at the base of metatheca. Hence this theca is relatively long and thin. The structure of the base of theca 1^2 is very interesting. The base itself does not take up more than 1/2 of the diameter of sicular aperture, but subtriangular peridermal plates whose one margin is attached to the base of theca 1^2, the other to the apertural margin (*adp*), are formed on either side of it at the base of protheca. They resemble initial, incomplete adapertural plates in *Linograptus*, filling up most of the remaining diameter of the aperture of sicula. Ventrally the base of protheca 1^2 does not start with a straight margin, but is provided with a notch that resembles the basal notch of theca 1^2 in *Linograptus*. This basal notch (*bn*) is up to about 0.25 mm long (text-pl. VI, fig. A_3). The adapertural plates are attached to the lateral margins of this basal notch. Moreover, the right wall of protheca forms a list that enters the interior cavity of the basal notch (text-pl. VI, fig. A_3, *l.*). The adapertural plates have a fusellar structure, the fuselli are oblique and probably run irregularly. The reverse of them has a distinct incision on its free margin, faintly indicated on the opposite plate (text-pl. VI, fig. A_1-A_2). The margins of protheca are quite distinctly delimited from the surface of plates by a thickened border, hence they must be independent structures. The whole theca 1^2 practically consists exclusively of the prothecal segment, the metatheca being exceptionally short. Along its whole length the walls are very thin, nearly membraneous owing to which they break off during bleaching. The fuselli are strongly oblique in relation to the thecal axis. The aperture is similarly oriented, being provided with straight margins. Theca 2^2 is represented only by a very short fragment, about 0.20 mm in length.

It is evident that the specimen here considered represents a fragmentary rhabdosome which primarily consisted of two branches (pro-

cladium and a sicular cladium) (comp. reconstruction on text-pl. VI, fig. B). It seems likely, however, that it belongs to the early growth stage of a multiramous colony, since the mode of the budding of theca 1² and the presence of adapertural plates closely resembles the early ontogenetic stages of colonies in *Linograptus*. The presence of a basal notch likewise characterizes theca 1² in *Linograptus*. These characters place our form close to genus *Linograptus*. On the other hand, the direction of the growth of theca 1² differs distinctly from the direction observed in other known representatives of *Linograptus* (Jaeger, 1959; Teller, in print). It corresponds to that in *Neodiversograptus*, in which the angle of divergence of the branches is approx. 180°. The fact that the base of theca 1² occupies only 1/2 of the surface of the sicular aperture, together with the presence of adapertural plates — one of which is provided on its free margin with a characteristic incision (possibly the incipient of the thecal tube of theca 1³) — reasonably suggest, potential ability to produce a greater number of sicular cladia (comp. reconstruction, text-pl. VI, B).

The bipolar colony here described may be reliably referred to *Neodiversograptus beklemishevi* n.sp. The structure and dimensions of the preserved fragment of the sicula do not differ from the structure and size of the apertural segment of siculae in this species. In the assemblage accompanying this form there are also many fragments of rhabdosomes whose thecae fully agree with thecae of *Neodiversograptus beklemishevi* n.sp.

Stratigraphic range. — In the core of deep-boring at Mielnik this species is encountered between 1000.9 and 934.5 m. Its first appearance (at 1000.9 m) is in association with a fauna suggesting the *scanicus* zone, as currently defined (i.e. *Lobograptus scanicus parascanicus* (Kühne), *L.* cf. *expectatus* Urbanek, *Monoclimacis micropoma* (Jaekel), *Saetograptus chimaera* (Barrande) (scarce), *Pristiograptus dubius* (Suess), *Pr. bohemicus* (Barrande)). The latest appearance of this species indicates the *leintwardinensis* zone, as it is accompanied by *Saetograptus leintwardinensis* (Lapworth) and *Pristiograptus* cf. *dubius* (Suess). These data point out that the occurrence of the species here considered is confined to the middle part of the *scanicus* zone (as currently defined), and the *leintwardinensis* zone.

The two specimens etched from the *leintwardinensis* zone represent — in some structural characters of sicula — morphological transients between typical siculae of *N. beklemishevi* n.sp. from *scanicus* zone and *Linograptus* siculae. The dorsal apertural spine of sicula shows a greater deviation (fig. 2), however the sicula is provided with sicular rings which are not recorded for *Linograptus* populations at Mielnik. Proximal thecae have oblique apertural margins without any elaboration. Prosicula is, however, longer than in *N. beklemishevi* n.sp. from

Fig. 2. — *Neodiversograptus beklemishevi* n.sp. (Mielnik, depth 934.50 m). Sicula and proximal thecae from the *leintwardinensis* zone; ca. × 50

db dark bands of sicula, *ds* dorsal apertural spine of sicula, *msi* metasicula, *psi* prosicula, *v* virgula, *vi* virgella.
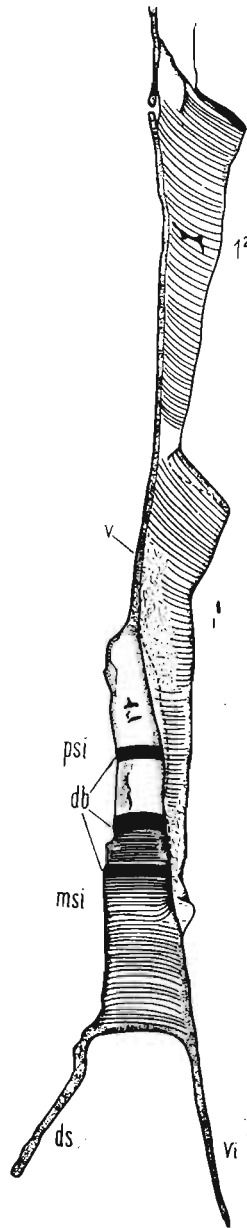
scanicus zone. The material is too scarce for a nearer evaluation of observable variation (comp. p. 163).

No representatives of Linograptinae are recorded from the core of the deep-boring between the last appearance of *Neodiversograptus nilssoni* (at 1035.9 m) and the first appearance of *N. beklemishevi* n.sp. (at 1000.9 m). Over this 35 m thick band of the section, the successive appearance of the following forms is noted: "*nilssoni B*" (at approx.

1035 m; comp. p. 152), *L. simplex* Urbanek (at 1021 m). *L. scanicus para-scanicus* (Kühne) (at approx. 1017 m), *L. exspectatus* Urbanek (at 1016 m), *Cucullograptus pazdroi* Urbanek (at 1002.5 m) and another undescribed species of *Lobograptus*. The appearance of *Neodiversograptus beklemishevi* precedes that of *L. scanicus scanicus* (Tullberg) sensu Bulman, which appears at 989 m.

Within the series here mentioned the occurrence of this species is not continuous. It has been found in several samples, whose sites are separated by intervals of several up to a score of metres where it is absent. Since it is nowhere a frequent form, it may be inferred that in Lower Ludlovian assemblages it was rather scarce, too.

The sicula provided with the sicular cladium, referred here to *Neodiversograptus beklemishevi* n.sp., comes from the erratic boulder numbered S. 32 (Gdańsk-Wrzeszcz). It is associated there with a rich assemblage containing i.a.: *Lobograptus scanicus parascanicus* (Kühne), *Cucullograptus pazdroi* Urbanek, *Saetograptus chimaera* (Barrande), *Pristiograptus bohemicus* (Barrande) and *Pr. dubius* (Suess). In this assemblage there are also rather numerous thecae and fragmentary rhabdosomes, closely resembling the rhabdosomes of *Neodiversograptus beklemishevi* n.sp. On this assemblage it is perfectly sure that we are dealing with the *scanicus* zone as currently defined. The same age seems reasonably assignable to other erratic boulders, containing probably conspecific thecae and siculae, but which are not described here owing to their fragmentary state of preservation.

Systematic position. — The structure and stratigraphic occurrence of *Neodiversograptus beklemishevi* n.sp. reasonably suggests that it is derived from *N. nilssoni,* being at the same time morphologically intermediate between *Neodiversograptus* n.gen. and *Linograptus.* This is proved by its later appearance than that of the ancestral species just mentioned, since it occurs in higher horizons (the *scanicus* and *leintwardinensis* zones), and moreover, an earlier appearance, preceding *Linograptus.* The thecal structure of this species may be readily traced to the thecae of *N. nilssoni,* while the presence of a symmetrical apertural spine of the sicula, the mode of budding of the first sicular cladium — possibly expressing its potential ability to produce a greater number of sicular cladia — bring it nearer to *Linograptus.* On the other hand, the direction of the growth of the first sicular cladium remains the same as in *N. nilssoni* and in this it differs from typical linograptids. The species in question evidently displays certain characters intermediary between the two genera mentioned above. The "diversograptid" direction of growth of the first sicular cladium is, however, a diagnostic character readily seen even in a flattened state of preservation, hence the writer believes that its assignment to the genus *Neodiversograptus* n.gen. is at present well justified, though future investigations may

show that it is referable rather to *Linograptus* (comp. discussion on p. 200).
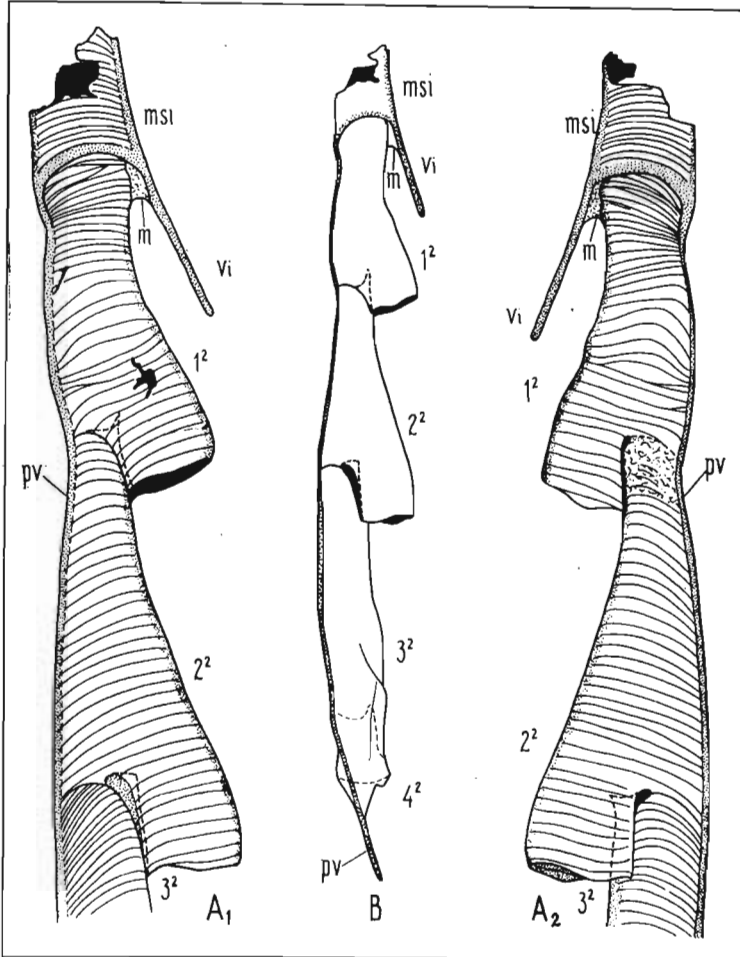
Neodiversograptus? sp.
(text-pl. VII, fig. *A, B*)

Material. — One specimen, about 3.7 mm long, representing an apertural fragment of sicula, also a sicular cladium with 3 thecae (1^2—3^2). The excellent state of preservation allows a close examination of the fusellar structure. The material has been etched from the core of a deep-boring of the Geological Institute (Warszawa) at Mielnik. The sample was collected from a depth of approx. 903.6 m; it consists of grey-bluish marls or marly limestones.

Description. — The preserved fragment of sicula represents only the adapertural (*msi*) segment, and its maximum length is about 0.30 mm. The aperture of the sicula, approx. 0.30 mm in diameter, is provided with a virgella (*vi*) up to 0.50 mm in length. Dorsally, the apertural margin of the sicula developed a dorsal spine whose continuation forms the pseudovirgula of sicular cladium. A triangular peridermal membrane, with rough and structureless surface (text-pl. VII, *A-B, m*) spans the virgella and the ventral wall of the base of protheca 1^2.

The first theca of the sicular cladium 1^2 starts in the continuation of the apertural margin of sicula, the aperture being completely concealed by its base. This theca is up to 0.93 mm long. The initial part of protheca 1^2, 0.25 mm in width, consists of relatively narrow fuselli whose width increases toward the aperture. These fuselli are first irregularly arranged, at a varying angle to the direction of thecal growth; the presence of several shorter intercalary fuselli, terminating on the lateral walls of theca, was also noted. In the remaining part of protheca and in the metatheca the ventral thecal wall is slightly sigmoid. The metatheca is approx. 0.20 mm in length. The apertural margin of theca 1^2 has slight lateral elevations, each consisting of one fusellus. The width of theca 1^2 at the base of metatheca is up to 0.30—0.33 mm. Theca 2^2 attains a length of about 1.1 mm. In shape theca 2^2 resembles theca 1^2, but the fusellar structure is regular along the whole length of theca. The elevations on the apertural margin of theca 2^2 are somewhat less conspicuous than that in theca 1^1. Theca 3^2 is up to approx. 1.35 mm in length. The apertural margin is practically without elevations, suggesting its incomplete growth (immaturity). Moreover, this theca was subjected to secondary deformation which is expressed by the twisting of the apertural segment of theca to the obverse side. Behind theca 3^2 appears the short initial part of theca 4^2, which represents the end of a growing tip of the sicular cladium.

Systematic position. — Doubtless, our specimen represents a fragmentary rhabdosome which consisted originally of two branches budding

TEXT-PL. VII

?*Neodiversograptus* n.sp. or teratological colony of ?*Linograptus* sp.
Apertural fragment of sicula and 3 thecae of sicular cladium. A_1-A_2 proximal
part of preserved specimen from reverse and obverse sides; B complete appearance
of preserved specimen, aperture of theca 3^2 has been secondarily deformed and
twisted (Mielnik, depth 903.60 m); A_1-A_2 ca. $\times$ 50, B ca. $\times$ 28,3

m membrane at the base virgella, mst metasicula, pv pseudovirgula, vi virgella.

independently of the sicula. In result of damage the procladium was broken off, while the initial part of the sicular cladium was preserved. The close relationship of this form with *Neodiversograptus beklemishevi* n.sp. is indicated by the shape of sicular aperture, the presence of a symmetrically placed apertural dorsal spine that continues as the pseudovirgula of the sicular cladium, as well as the structure of thecae preserved on this cladium. Details of the development of the sicular cladium, however, are different and in this respect the form here described comes nearer to *Neodiversograptus nilssoni*. The irregularity of the fusellar structure in theca 1^2 suggests, however, that maybe we are dealing here with a teratological anomaly in the process of astogeny, since this specimen deviates from the regular structural time-sequence, represented by the remaining Linograptinae. Hence, the details of the development of the sicular cladium are not of systematic significance, but merely express anomalies in the process of astogeny. The last concept is perhaps supported by the stratigraphic occurrence of this form, recorded from a series that is distinctly younger than the latest occurrence of *Neodiversograptus beklemishevi* and *N. nilssoni*. Therefore, this specimen may possibly represent an abnormally developed *Linograptus* colony which had secondarily lost its ability to produce more sicular cladia.

Stratigraphic range. — The specimen here considered occurs in an assemblage with *Pristiograptus dubius* (Suess) and *Pr. bohemicus* (Barrande). The bed containing this assemblage lies more than 30 m above the *leintwardinensis* zone, i.e. 30 m above the last appearance of *Neodiversograptus beklemishevi* n.sp. and 18 m above that of *Cucullograptus aversus rostratus* Urbanek. The series to which the bed just mentioned belongs is characterized by a qualitative scarcity of the graptolite fauna (fewer species) and simultaneously by rather great quantitative abundance of *Pr. bohemicus* (Barrande). This applies to both the typical form and its certain varieties which probably represent separate but closely related new subspecies or species[7]. Hence, at present, the mentioned series is not directly comparable with Upper Silurian graptolite sequences from other countries, since the faunas from the corresponding series abroad are either inadequately known, or they are very incompletely developed, as compared with the sequence encountered in the deep-boring at Mielnik. There is no doubt, however, that this series corresponds with the horizon of the mass occurrence of *Pristiograptus bohemicus* that was recognized by Tomczyk in the lower part of the so-called "Siedlce beds" (a series between the *leintwardinensis* and the *ultimus* zones) from deep-borings in the western framing of the Eastern European Platform (Polish Lowland) (Mielnik, Żebrak, Pasłęk, Lębork).

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[7] A description of these forms will be given in the writer's next papers which will deal with the monograptids from the deep-boring at Mielnik.

Linograptus posthumus (Reinh. Richter, 1875)
(text-pl. VIII—XII; fig. 3)
Synonymy: see Jaeger, 1959, p. 143—144; Teller (in print).

Material. — A dozen or so of nearly complete siculae with proximal ends of branches 1 and 2; 8 siculae with fragment of theca 1³, numerous fragments of proximal and distal parts of branches. Most specimens are readily bleached. Although strongly flattened they allow a detailed examination of the fusellar structure. All the stages of astogeny are represented including the five-branches stage. The material etched from the core of a deep-boring of the Geological Institute (Warszawa) at Mielnik. The samples have been collected from, a depth of 837,60—820,0 m, and consist of grey-bluish or greenish marls, or impure limestones.

Description. — The development of a multiramous *Linograptus* passes through the formation of the primary branch (procladium), and next that of the first, and following sicular cladia. Several stages may be distinguished in *Linograptus* astogeny, i.e. the monograptid stage — formation of sicula and procladium, the diversograptid stage — formation of the first sicular cladium beside the procladium, and the linograptid stage — formation of following sicular cladia.

Monograptid stage.

Sicula (text-pl. VIII, fig. *A-C*) nearly straight and relatively narrow; its length in measured specimens ranges from 1.3 to 1.7 mm, its width — from 0.18 to 0.25 mm at the point of origin of theca 1¹, and from 0.3 to 0.35 mm at the metasicular aperture. *Prosicula* (text-pl. VIII, fig. *A-C, psi*), from 0.75 to 1.05 mm in length, hence relatively long and representing nearly two thirds of the total length of sicula. On most specimens the periderm of prosicula is strongly wrinkled and partly decomposed, so that the helical line was undetectable. Relatively long longitudinal threads (ribs) are visible all along the length of the prosicula. There may be 1-3 in number, but sometimes there are none (text-pl. X, fig. *C*). The width of the prosicular aperture is from 0.15 to 0.22 mm, its apex passes into a robust and relatively thick virgula. The prosicula extends to about the middle of theca 1¹.

Metasicula (text-pl. VIII, fig. *A-C, msi*) is 0.45—0.65 mm long. Toward the aperture it gradually expands to attain there a width of 0.30—0.35 mm. At the boundary of pro- and metasicula the fuselli are somewhat crowded and under a slight magnification they have the appearance of a dark band. Occasionally this band takes on the appearance of a normal metasicular ring, lying at the boundary of pro- and metasicula (text-pl. VIII, fig. *A*). The low position of the primary notch is a striking feature of the metasicula in *Linograptus*, and occasionally only 4 or 5 of the first fuselli are normal, while the next 6—7 fuselli

form a characteristic inflexion or sinus on the reverse side, thus providing a notch for the bud of theca 1^1. The adapical margin of this notch most commonly occurs very near the margin of prosicula (at a distance of 0.04—0.07 mm from it). Only exceptionally the distance rises up to 0.15 mm. This suggests a very early formation of bud 1^1, which leaves the metasicula almost immediately after its formation. In this respect *Linograptus* differs from other Monograptidae in which bud 1^1 is generally produced much nearer to the aperture of the metasicula. Similarly, the formation of the virgella occurs very early. It has been established that it develops directly on the margin of the prosicula and consists of the first fuselli, which form the base of the virgella owing to a characteristic modification of its margin, contacting with the zigzag ventral suture. In the majority of the monograptids that have been examined in this respect, the virgella is formed farther from the margin of the prosicula: in *Saetograptus chimaera* at a distance from 0.18 to 0.32 mm, in *Pristiograptus dubius* 0.24—0.36 mm, and only exceptionally it is formed nearer (Urbanek, 1953). In *Linograptus* the virgella is a robust, relatively broad peridermal rod, which subsequently protrudes far out of the metasicular aperture.

The aperture of the metasicula has a dorso-ventral diameter, 0.30—0.35 mm long, and nearly straight margins with a slight thickening. A characteristic feature is the lack of the dorsal apertural process, which is replaced by a dorsal apertural spine which forms very early. This spine lies in the plane of symmetry of the sicula and is sometimes placed at a right angle in relation to its axis (the angles between ventral wall of cladia, actually measured, range between 270° and 240°).

The inception of the dorsal apertural spine of sicula is already visible at the stage when theca 1^1 is only 1 mm long (text-pl. VIII, fig. *A, ds*). Most likely, this spine, then approx. 0.22 mm in length, was originally longer, but was secondarily broken off. There is no doubt that the dorsal apertural spine constitutes the inception of the pseudovirgella, i.e. of the peridermal axis, along which later grows the first sicular cladium.

Ventrally the metasicular aperture is provided with a long and strong virgella, whose free end protrudes outside of the aperture, and may be over 1 mm, even up to 2 mm long. In most cases the end of virgella is not preserved, being broken off. On two specimens the virgella is not damaged. On this basis it may be established that the *Linograptus* virgella was provided with a peculiar structure, without analogy in other monograptid siculae so far described. This peculiarity consists in the presence on the virgella of a terminal organ which the writer proposes to call the *"virgellarium"* or the "virgellar organ" (fig. 3, *vg*). This name seems more appropriate than the earlier term — "ter-

TEXT-PL. VIII
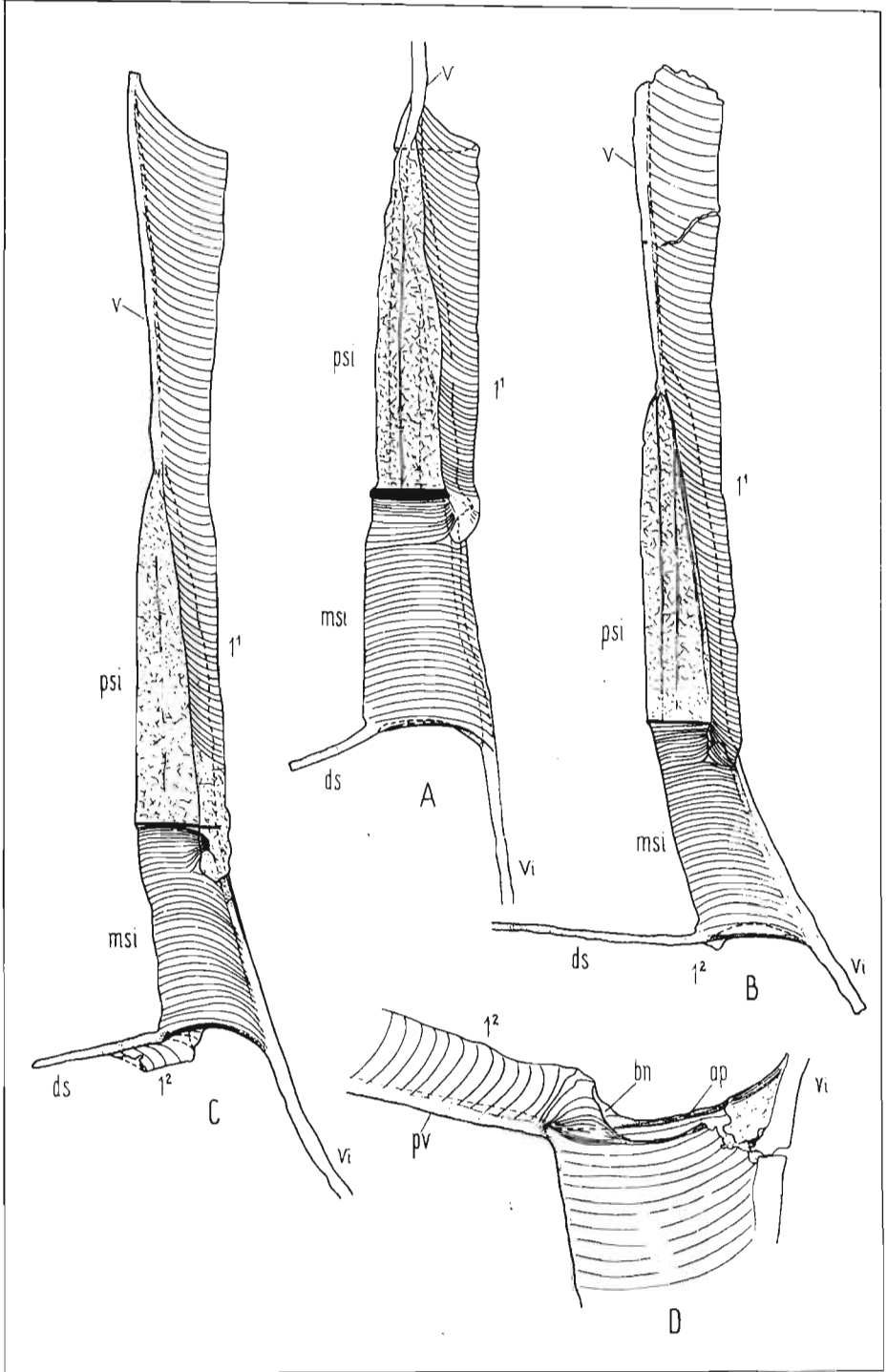
minal disc", introduced by Teller (in print) which does not well enough show off its appearance and position. The virgellarium is secondarily strongly flattened and partly coated by the sediment, so that it can with some difficulty be restored to its original appearance. Most likely, primarily, before being secondarily flattened in result of the compaction of sediments, it had the shape of a cone, a calice or an upturned umbrella. Its base is attached to the apex of the virgella, while the walls consist of a membraneous periderm. This periderm formed on its free margins probably 4 triangular processes, each of which was supposedly provided with a finger-like trabecular outgrowth. Our specimen bears two only of these processes, approx. 0.30—0.38 mm long, the other two being probably broken off.

The specimen shown in text-pl. XII, fig. B_1-B_2, and pl. I, fig. 2a-b represents an isolated, broken off virgellarium, preserved with a longer fragment of virgella, about 1.25 mm in length. It is less flattened out and better preserved. After bleaching, it was possible to determine the presence of 4 triangular processes of the peridermal membrane, each provided with a finger-like, sharply terminated outgrowth. The peridermal membrane is structureless, except for numerous longitudinal striae. As a whole, the organ can rather be compared with the calyx of a tetrameric flower, with a maximum width of approx. 0.55 mm, with petals grown together and the apexes prolonged into finger-like outgrowths, 0.25—0.32 mm long.

The third specimen of a preserved virgellarium is shown in text-pl. XII, fig. A, and pl. II, fig. 1. Originally this organ was connected with the sicula, provided with 5 cladia, after bleaching, however, it broke off. The virgella is developed as a strong rod, approx. 2 mm long, terminally provided with the virgellar organ. In spite of its rather strong flattening, it has been determined that its structure does not differ from that just described, since it also consists of a cone formed by peridermal membrane resembling the calyx of a flower, and provided with 4 finger-like outgrowths.

Teller (in print) was the first to note the peculiar virgellar organ in *Linograptus*. Before that it never attracted the attention of any investigators, e.g. Jaeger (1959) does not mention such a structure in

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Text-pl. VIII

Linograptus posthumus (Reinh. Richter)

Structure of sicula and early stages of astogeny. *A* sicula and young theca 1^1; *B* sicula with nearly complete theca 1^1 and incipient theca 1^2; *D* apertural part of sicula and base of prothecal segment of theca 1^2 (Mielnik, *A-C* depth 830,90 m, *D* — 840.60 m); *A-C* ca. $\times$ 52, *D* ca. $\times$ 100

ap aperture of sicula, *bn* basal notch, *ds* dorsal apertural spine of sicula, *msi* metasicula, *psi* prosicula, *v* virgula, *vi* virgella.

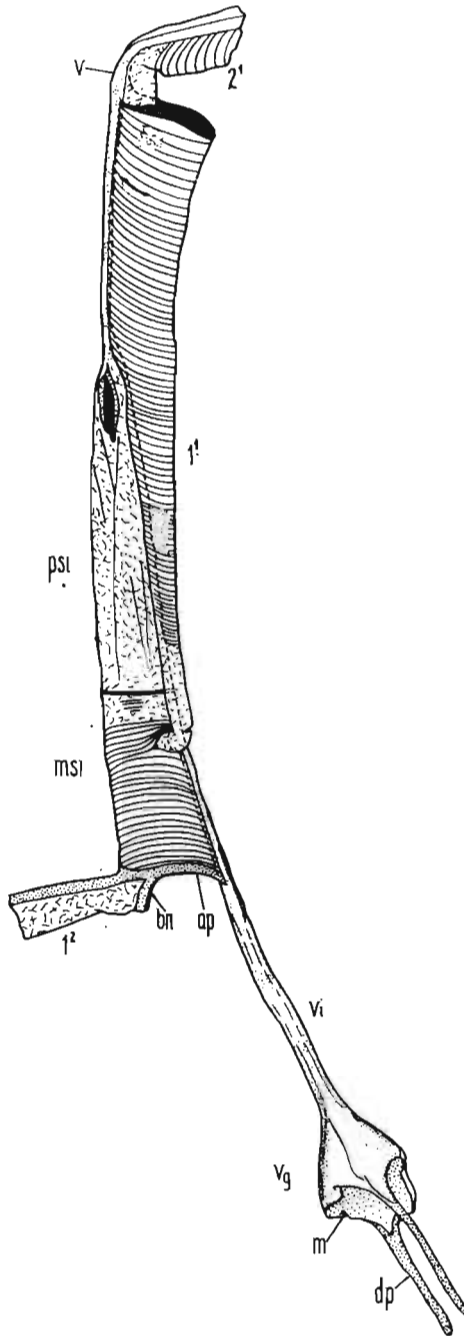Fig. 3. — *Linograptus posthumus* (Reinh. Richter) (Mielnik, depth 821.70 m). Si-
cula provided with virgellarium and complete theca 1¹; ca. × 50

ap aperture of sicula, *bn* basal notch, *dp* finger-like outgrowth of virgellarium, *m* membra-
ne of virgellarium, *msi* metasicula, *psi* prosicula, *v* virgula, *vi* virgella, *vg* virgellarium.

Linograptus; perhaps it was not preserved or was interpreted as an artefact[8].

Although the virgellarium has been preserved on 3 specimens only in the material here described, it is doubtless a constant element of structure, characteristic of the *Linograptus* sicula, and this is likewise suggested by the development of the virgella as a very robust rod.

Teller (in print) supposes that this organ served as an attachment for the multiramous *Linograptus* colonies, which suspended themselves centrally, not by means of the virgula or the pseudovirgulae, but by means of a modified virgella. According to our current knowledge on *Linograptus,* this hypothesis seems a very reasonable one as it accounts for the functional significance of this most peculiar organ. Additional observations are, however, needed for its conclusive justification. Without doubt, the virgellar organ, as preserved in the fossil state, represents only a skeletal part of a more complex structure which was made up of soft extrathecal tissues, too. Together they constituted an apparatus for attaching the colony, or perhaps also a hydrostatic apparatus for the floating of the colony.

The last concept merits special consideration in view of the presence in a North-American *"Linograptus" phillipsi multiramosus* (Decker, 1939) of "a central ringlike disc", Decker supposes that this disc is the flattened remains of a "pneumatocyst", a buoyant apparatus on which this multiramous colony floated. It is interesting to note the presence on the surface of such a pneumatophor of certain ribs radiating from its apex. The *Linograptus* virgellarium might be the skeleton of a similar apparatus, while the pneumatocyst ribs might be compared with the finger-like outgrowths of its peridermal membrane. Decker's (1939) and Ruedemann's (1947) interpretations which compare these structures with gonothecal sacs in some diplograptid synrhabdosomes, seem too far reaching, while the concept that we are dealing here with bladder-like structures, appears sound enough to the present writer.

The first theca of procladium is formed from the sicula by way of normal monograptid budding, the only difference being the low position of the primary notch. This theca is straight, slender and relatively long. Its width at the apex of prosicula is from 0.11 to 0.15 mm, and up to 0.20 mm at the aperture. The length of theca 1^1 ranges from 1.3 to 2.1 mm. The margins of the aperture may be nearly straight, obliquely placed in relation to the long axis of theca, or they may have a slight elevation of the apertural margin, consisting of one fusellus (text-pl. X, fig. B.).

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[8] Quite recently the presence of such an organ on some specimens of *Linograptus* etched from erratic boulders has been established also by Dr H. Jaeger (personal comm.).

TEXT-PL. IX
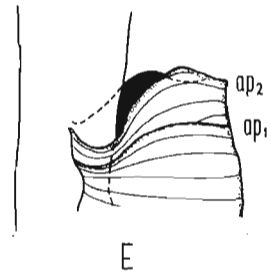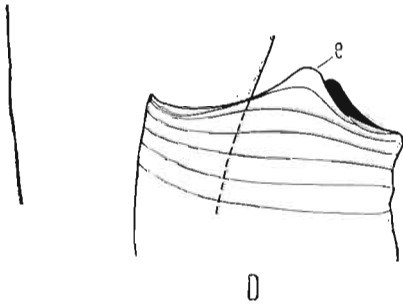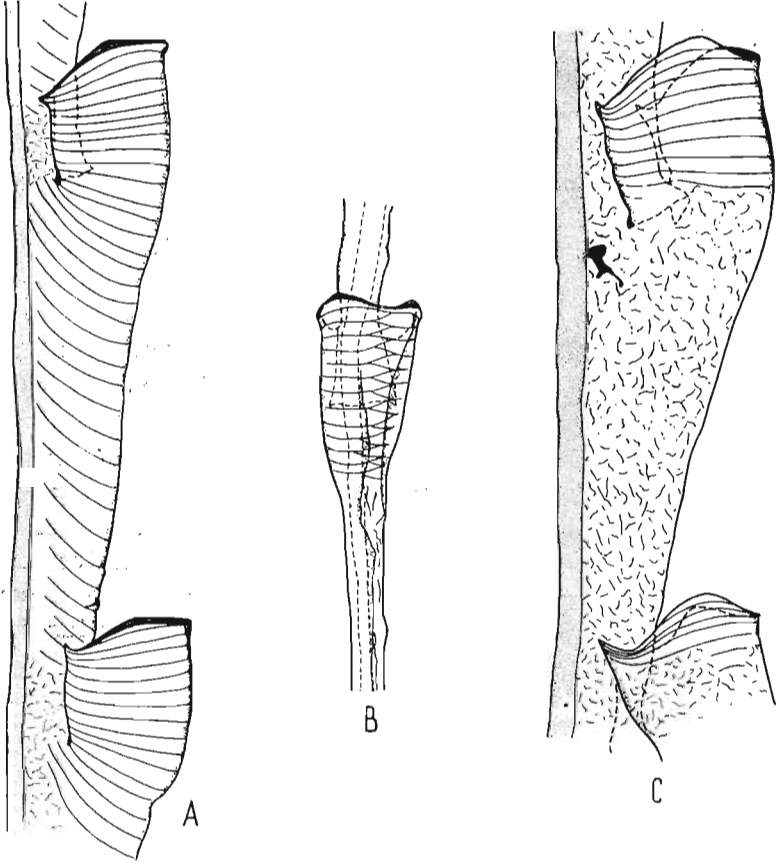
The longest isolated fragment of a cladium preserved in the material is about 30 mm long, the longest fragment of the procladium connected with sicula consists of only 3 thecae. The astogenetic changes must be therefore restored on the base of preserved short fragments. Text-pl. IX, fig. A shows a medial theca whose length is approx. 1.80 mm, of which the prothecal segment represents 1.45 mm, and the metathecal 0.35 mm. The width at the base of protheca is 0.21 mm, at the base of metatheca 0.30 mm, and the width of the branch at the level of the aperture of theca is 0.40 mm. The ventral wall of the theca shows a slight sigmoid curvature and its apertural borders are provided with small lateral elevations, separated by slight ventral incision (text-pl. IX, fig. B). The more distal theca is shown on text-pl. IX, fig. C. It attains some 1.88 mm in length of which the prothecal segment takes 1.38 mm, the metathecal 0.50 mm. The width at the base of protheca is approx. 0.28 mm, at the base of metatheca 0.35 mm, the width of the branch at the apertural level is approx. 0.55 mm. The fusellar structure is well visible only in the metathecal segment being not discernible on the prothecal one, where the periderm is strongly wrinkled and partly decomposed. The sigmoid curvature of the ventral wall and the apertural elevations are more expressed as compared with medial thecae. On etched specimens the mentioned characters are on the whole more stressed than in flattened specimens described previously (comp. Jaeger, 1959, fig. 22, A_1-A_2, p. 137). In most distal and probably senile thecae the lateral elevations could be especially strongly developed forming rather pointed processes (text-pl. IX, fig. D). Some thecae preserved traces of secondary growth, with thickenings marking the position of old and new apertural levels (text-pl. IX, fig. E). On certain branches some abnormalities in the development of thecae had been noted.

Diversograptid stage

By the time the first theca of procladium has reached the apex of prosicula, the dorsal spine on the aperture of metasicula is at least 0.2 mm long. Thus the prolongation of this spine progresses simultaneously with the growth of theca 1^1. At the same time the spine constitutes the initial stage of the formation of the first sicular cladium. Theca 1^2 of this cladium is preceded by the formation of a corresponding apertural spine which also represents the incepting pseudovirgula of the first sicular cladium. The basal part of theca 1^2 growing along
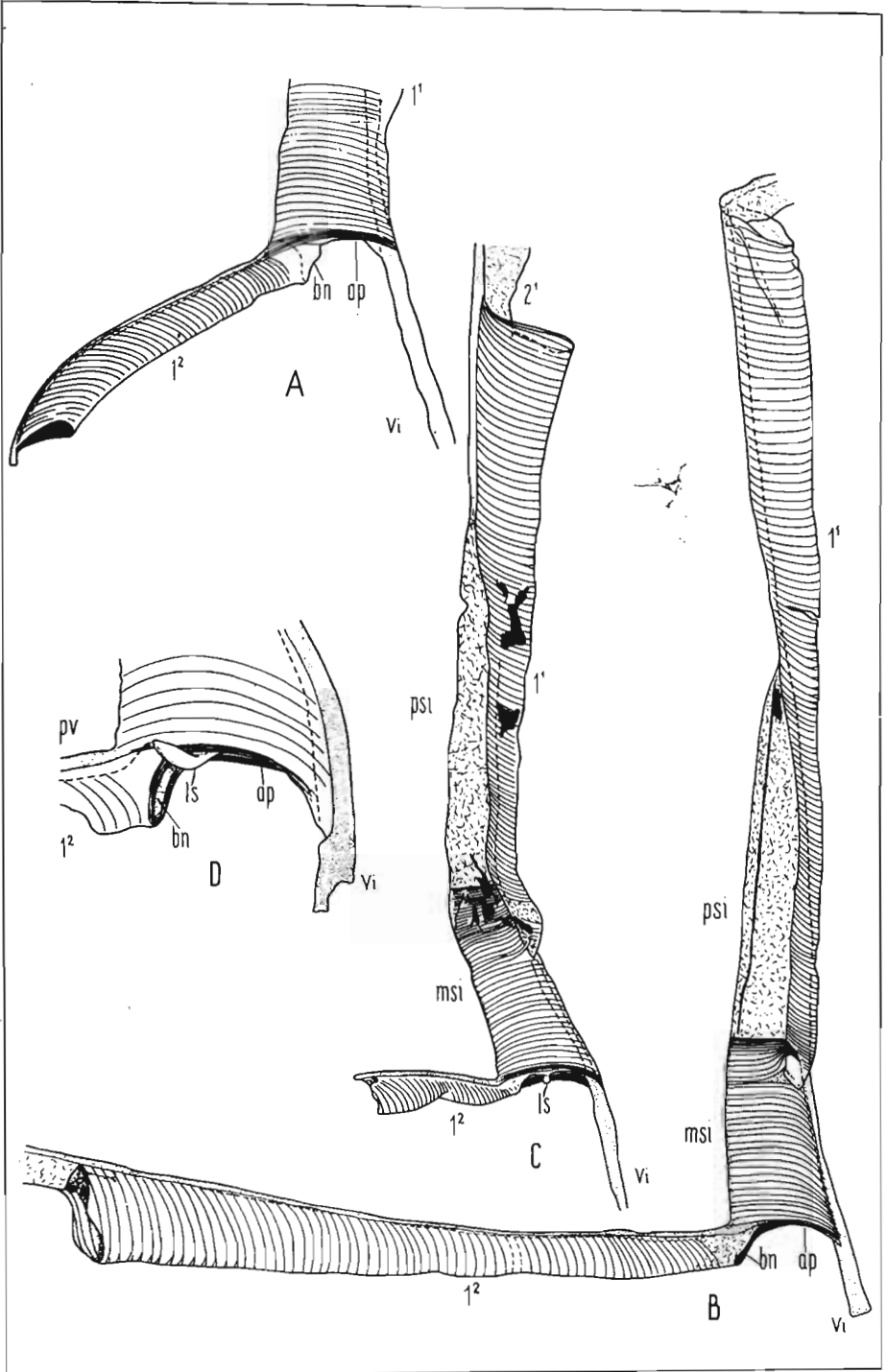

Text-pl. IX
Linograptus posthumus (Reinh Richter)
Structure of thecae. A lateral view of a more proximal theca; B ventral view of a similar theca; C lateral view of a more distal theca, fusellar structure of protheca not discernible; D apertural border of a mature distal theca with strongly developed elevations; E apertural border of a theca showing traces of secondary growth (Mielnik, A-C, E depth 821.10 m, D — 820.10 m); ca. × 50
ap_1, ap_2 former and new level of apertural border.

TEXT-PL. X

the pseudovirgula (text-pl. VIII, fig. B) is initiated when theca 1^1 has attained its nearly entire length, but has not yet formed its definite aperture. The fusellar structure of the basal part of theca 1^2 is usually effaced so that it may be restored only on the basis of the specimen shown in text-pl. VIII, fig. D, in which some conjectural elements have been added.

The first fuselli consist of narrow bands arcuately overlapping the apertural margin and dorsally fused with the rod of the pseudovirgula, while ventrally they terminate on the free margin set at a certain angle to the apertural margin of metasicula. Thus a basal notch, with a length of 0.13—0.16 mm in the plane of thecal symmetry, is formed at the base of theca 1^2. After that, on the ventral side of theca, the fuselli start to produce their oblique sutures so as to form a complete thecal tubule. The base of theca 1^2 occupies approx. 1/3 of the diameter of the aperture of metasicula. The next segment of protheca 1^2 is made of fuselli oriented obliquely toward the direction of growth of theca (text-pl. X, fig. A). The ventral wall of theca 1^2 is straight, the aperture has distinct lateral elevations on the margin. At the base of protheca it is about 0.10—0.12 mm in width, near the aperture the width ranges from approx. 0.22 to 0.25 mm. Theca 1^2 is from 1.4 to 1.7 mm in length. Its metatheca is extremely short. The longest fragment of the first sicular cladium within the writer's material consists only of two thecae. Theca 2^2 does not differ much from theca 1^2. It is up to about 1.4 mm long, when the width of the base of protheca is about 0.10 mm, and that of the aperture of metatheca — 0.25 mm. Owing to partial deformation of the speci-mens, the last mentioned measurement is only approximate.

Linograptid stage

The material here investigated allows one to elucidate the mode of the formation of the second, third and fourth sicular cladium. As far as it was possible to determine, the second cladium begins through the inception of the corresponding pseudovirgula as a lateral apertural spine (text-pl. X, fig. C-D, *ls*), which occurs on the margin of the sicular aperture at the base of theca 1^2. Specimens of this astogenetic stage have the lateral apertural spine on the reverse side, but other specimens distinctly suggest that theca 1^3, together with the corresponding pseudo-


Text-pl. X
Linograptus posthumus (Reinh. Richter)
Diversograptid stage and beginning of linograptid stage in astogeny. A apertural part of sicula with growing first sicular cladium; B sicular part of rhabdosome in diversograptid stage of astogeny; C late diversograptid stage with incipient pseudo-virgula of second sicular cladium; D apertural part of sicula showing the lateral apertural spine (Mielnik, A depth 839.60 m, B — 830.90, C — 821.10 m, D — 820.30 m); A-C ca. × 52, D ca. × 100
ap aperture of sicula, *bn* basal notch, *ls* lateral apertural spine of sicula, *msi* metasicula, *psi* prosicula, *pv* pseudovirgula, *v* virgula, *vi* virgella.

TEXT-PL. XI
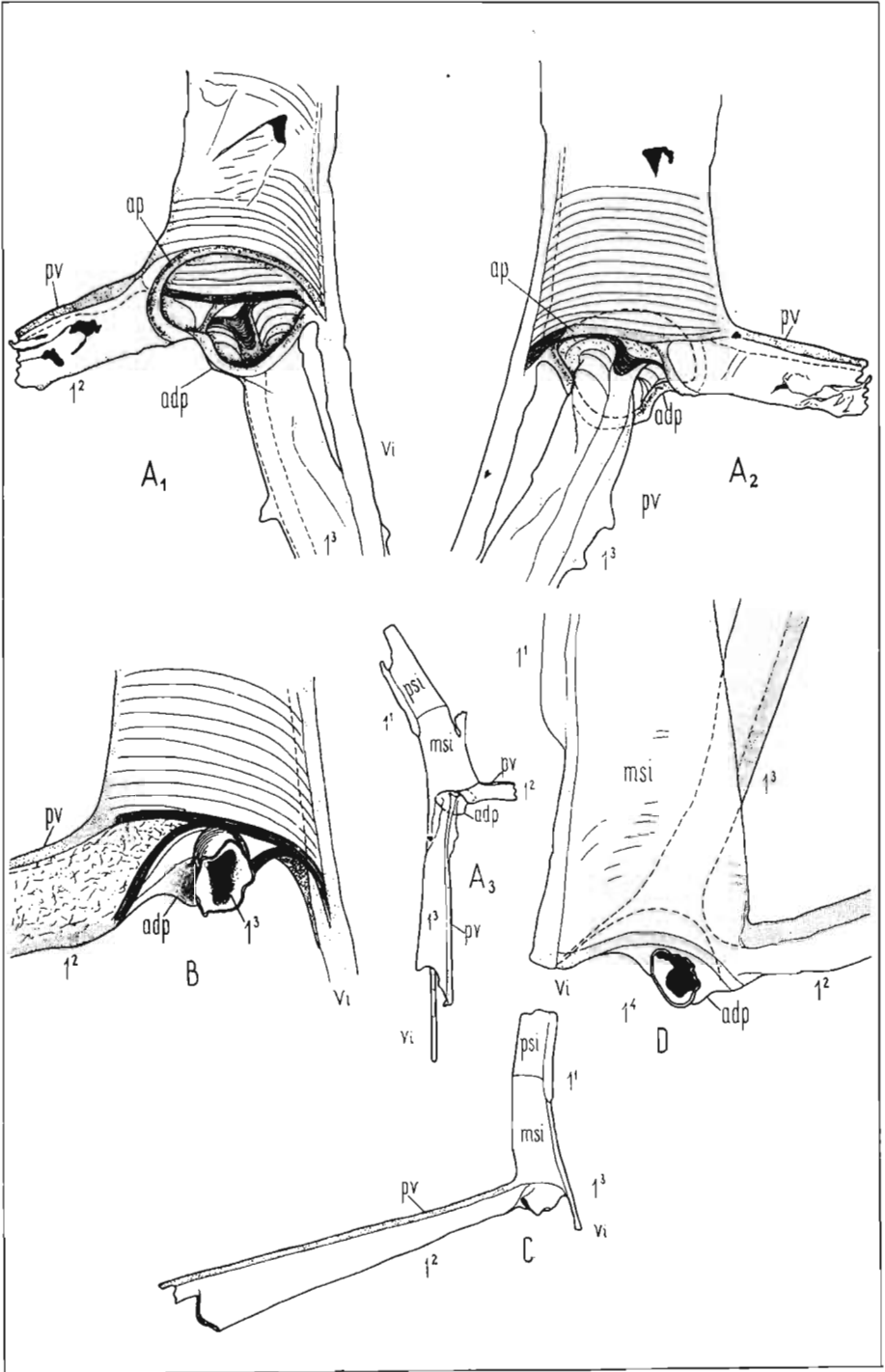
virgula, may be connected either with the reverse or the obverse margin of the aperture of metasicula. Out of the eight specimens with preserved proximal part of the second sicular cladium or with initial part of theca 1^3, four come out from the reverse margin, four from the obverse margin. Hence the position of the theca 1^3 in relation to the plane of symmetry of the sicula is not constant, but subject to variation. Consequently, the position of theca 1^4 must also be subject to analogous variations since it is determined by the position of theca 1^3 which takes up a corresponding area of the aperture.

The next stage in the development of theca 1^3 is associated with the formation of a thecal tubule, at first consisting of fuselli that are but faintly indicated (text-pl. XI, fig. A_1-A_2). On one side the fuselli terminate freely and form a thickened margin at the thecal base, on the other side they meet, at a certain angle, the corresponding pseudovirgula which is developed as a broad rod. This results in an expanded base of theca 1^3 which the writer proposes to call the adapertural plate (text-pl. XI, fig. A-C, adp) and from which the true thecal tubule arises. The adapertural plate of theca 1^3 on one side adheres to the margin of the basal notch of theca 1^2, on the other side to the margin of the metasicular aperture, reaching up to the virgella. The free margin of the adapertural plate is conspicuously thickened, thus forming the marginal thickening by which the base of theca 1^3 is framed. The true thecal tube arises on the adapertural plate; it is antero-laterally oriented in relation to the sicula, but with a slight dorsal or ventral deviation. Only incomplete specimens of theca 1^3 are present in the writer's material, so that its shape and size cannot be properly described.

The mode of the formation of the third sicular cladium could be studied on one specimen only. Besides the sicula and complete thecae 1^1 and 1^2, this specimen also represents the proximal end of theca 1^3 and the adapertural plate with a fragment of the broken off margins of the thecal tubule of theca 1^4 (text-pl. XI, fig. D). In the specimen here considered the adapertural plate is connected with the apertural margin on the obverse side, but it is quite obvious that its position may vary depending on the position of theca 1^3 and that it may have occurred on the reverse side, as well.


Text-pl. XI
Linograptus posthumus (Reinh. Richter)
Linograptid stage in astogeny. A_1-A_2 apertural part of sicula and initial parts of first and second sicular cladia; A_3 general appearance of same specimen; B apertural part of sicula and base of theca 1^2 with adapertural plate and beginning of thecal tubule 1^3 visible; C fragment of sicula and theca 1^2 with base of theca 1^3; D apertural part of sicula with basal parts of thecae 1^2, 1^3, and adapertural plate of theca 1^4 (Mielnik, A, D depth 820.10 m, B, C — 837.60 m); A_1-A_2, B, D ca. $\times 100$, A_3, C ca. $\times 25$

adp adapertural plate, ap aperture of sicula, msi metasicula, psi prosicula, pv pseudovirgula, vi virgella.

TEXT-PL. XII
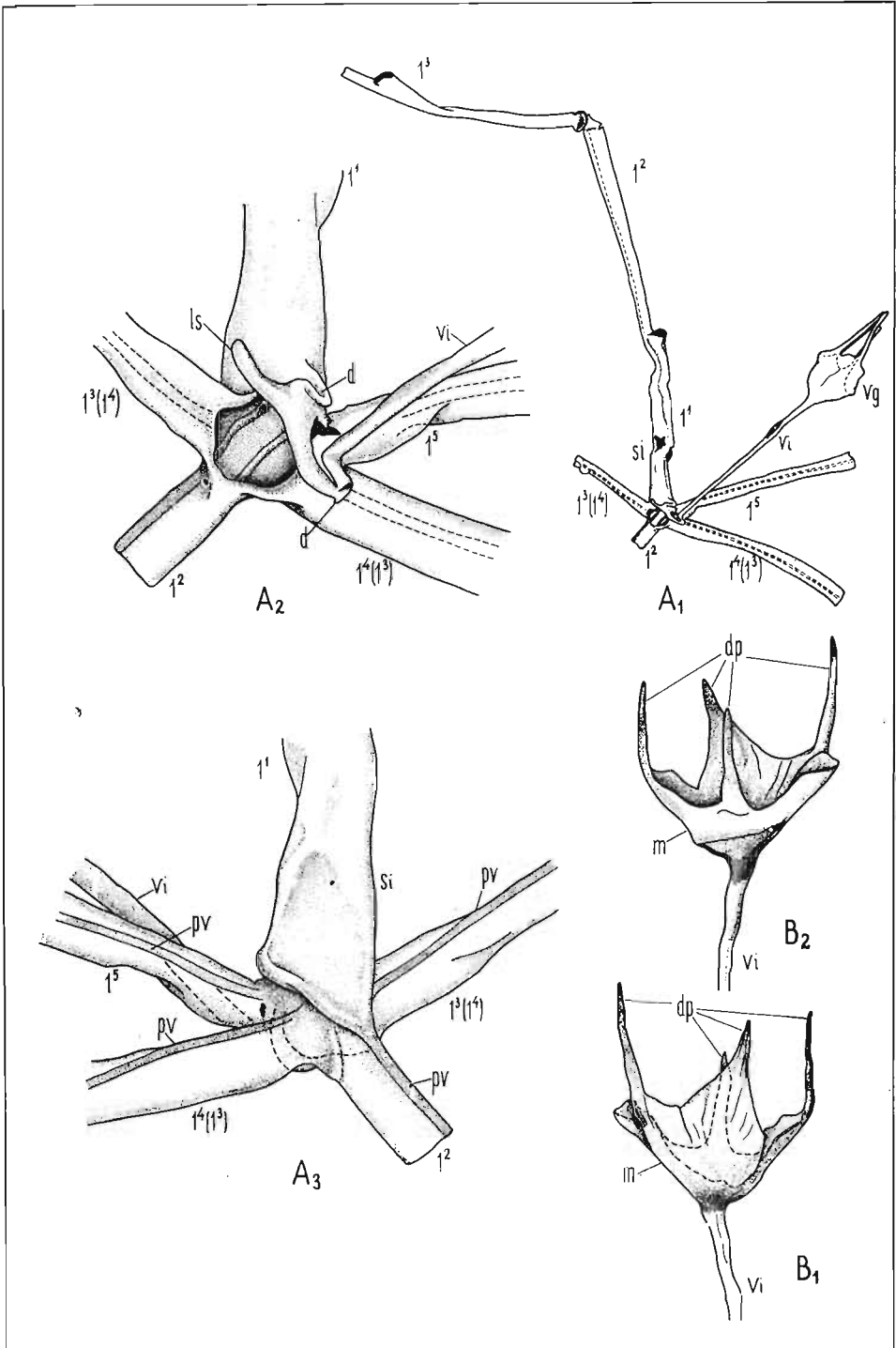
The adapertural plate of theca 1^4 in the writer's material has an analogous position with that in theca 1^3. The margins only of the broken off thecal tube 1^4 are preserved. Doubtless, the third sicular cladium developed analogously with the second sicular cladium and was probably preceded by the formation of the lateral apertural spine that represented the inception of its pseudovirgula. In relation to the preceding cladium, the second cladium grew symmetrically, in the opposite direction.

Within the material here investigated, only one specimen represents a more advanced stage of cladogeny (text-pl. XII, fig. A_1-A_3; pl. II, fig. 1). It consists of a sicula provided with a long virgella in which the virgellarium is excellently preserved, of a procladium with three preserved thecae, and of 4 fragmentary sicular cladia (fig.A_1). These are represented by apertureless fragments of thecae 1^2, 1^3, 1^4 and 1^5 The definition of thecae 1^3 and 1^4 is merely arbitrary in view of the variability of their position in relation to the plane of symmetry of the sicula. These thecae occur on the opposite sides of the metasicular aperture. As far as it could be established, theca 1^5 buds on the obverse side of the metasicular aperture, from an angle enclosed by the virgella, the margin of the aperture and the base of thecae 1^4 (1^3?) (text-pl. XII, fig. A_3). Hence it lies ventrally in relation to this theca. Unfortunately, the base of virgella and partly also the aperture of sicula, as well as the base of theca 1^5, are secondarily deformed (d) so that the exact position of theca 1^5 in relation to the sicular aperture could not be established. Most likely, similarly as in the earlier specimens already mentioned, the formation of the true thecal tube 1^5 was preceded by the formation of the lateral apertural spine which must have attached itself to the sicula in the angle between the margin of the aperture and the base of virgella. This spine, growing on the obverse side, later initiated the pseudovirgula of the fourth sicular cladium which in turn supported the thecal tube 1^5. The above mode of the formation of the fourth sicular cladium is reliably indicated by the presence of a peculiar spine, occurring on the reverse side in an angle between the sicular aperture and the virgella (text-pl. XII, fig. A_2, ls). This process is most probably

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Text-pl. XII

Linograptus posthumus (Reinh. Richter)

Advanced linograptid stage in astogeny and structure of virgellarium (the virgellar organ). A_1 sicular fragment of a five-branched rhabdosome with virgellarium attached to it; A_2 same specimen showing details of structure in apertural part of sicula and relations of initial parts of sicular cladia from reverse side; A_3 same specimen from obverse side; B_1-B_2 details of structure of completely preserved but isolated virgellarium from both sides (Mielnik, A depth 823 m, B — 820.10 m); A_1 ca. $\times$ 15, A_2-A_3 ca. $\times$ 70, B_1-B_2 ca. $\times$ 50

cdp adapertural plate, d compressed due to state of preservation and secondarily deformed base and initial parts of virgella, dp finger-like outgrowth of membrane in virgellarium, ls lateral apertural spine of sicula forming the incipient pseudovirgula of theca 1^6, msi metasicula, pv pseudovirgula, vg virgellarium, vi virgella, m peridermal membrane of virgellarium.

nothing else than the inception of the pseudovirgula of theca 1^3 whose development was analogous and which is symmetrically placed to theca 1^5. In this way the specimen here considered illustrate also the mode of formation of the fifth sicular cladium (6th branch).

The writer's material does not contain any specimens of *Linograptus* with more than 5 sicular cladia, therefore the mode of formation of the following cladia could not be investigated[9]. It may, however, be reasonably supposed that their formation was associated with the formation of new adapertural plates that gradually concealed the apertural opening of the metasicula. In multiramous colonies of *Linograptus* the bases of the first thecae of the successive sicular cladia may even have fully closed up the aperture of the metasicula. This process was probably accompanied by a certain morpho-physiological depreciation (partial degeneration) of the siculozooid, which was transformed into a tissue node spanning the proximal zooids of all the colonial cladia. A similar process of the reduction of the mother zooid which constituted a budding centre for a greater number of descendent blastozooids, is also encountered in *Cephalodiscus*. Occasionally it may be reduced there to a mere sterile peduncle devoid of the true zooid, as e. g. in *Cephalodiscus gracilis* (after Harmer, 1905, *fide* Kozłowski, 1948/1949). Hence the cladia in *Linograptus*, radiating from a sicula, formed a complex colony. In the aspect of its biological organization such a colony resembled diplograptid synrhabdosomes, though the structure of the central elements of diplograptid compound colonies (Ruedemann, 1895) seem to differ fundamentally from that in *Linograptus* colonies.

General remarks on the formation of sicular cladia

The development of *Linograptus* colonies, so far investigated only on material preserved on the rock-surface (Jaeger, 1959; Teller, in print) represents a strongly controversial problem, particularly with regard to the interpretation of the mode of formation of sicular cladia. Jaeger (1959) thought that all branches, except the first one, are budded directly and independently from the sicular aperture, and represent true sicular cladia. This concept supports the earlier suppositions of Bulman (1938) who very correctly called them sicular cladia (also Bulman, 1955). Teller, however (in print), believes that only the first additional cladium buds directly from the aperture of the sicula, while the next ones bud successively from the base of the first theca of the preceding cladium, thus: 1^3 from the base of 1^2, 1^4 from the base of 1^3

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[9] In the material described by Jaeger (1959), the maximum number of branches in *Linograptus posthumus* was 15 (!), but the 4-branched forms were statistically the most common ones. In Teller's material (in print) the greatest number of branches is 6, with a relatively small predominance of the 4-branched forms over the 2- and 5-branched forms.

and so on. Should these observations be correct, all the particular cladia, the first two excepted, would be merely a kind of thecal cladia, budding however, subaperturally in relation to the aperture of the mother theca.

The material here described indicates quite reliably that all the *Linograptus* metacladia follow the same mode of budding, i.e. independently from the aperture of sicula, so that the internal cavities of their first thecae do not communicate directly from one another, but all join the cavity of the sicula. Obviously, the relations of the soft parts of stolons that presumably connected the zooids of proximal thecae of the corresponding cladia with the siculozooid can hardly be reconstructed. Nevertheless the structure of the preserved peridermal parts suggests that they budded independently and directly from the siculozooid and this coincides with the concepts of Bulman and Jaeger.

It also means that the siculozooid here was able to bud several descendent blastozooids, one of which was formed during an early stage of growth of the siculozooid (theca 1^1), others in later stages. These got out of the sicula through its aperture giving rise to the corresponding sicular cladia. The process of repeated budding is apparently somewhat analogous with the mode of budding in certain Cephalodiscidae, e.g. *Cephalodiscus gracilis* Harmer. The zooid of this pterobranch is able to bud nearly simultaneously a number of descendent individuals, resulting in the formation of a stellate group of zooids in but slightly different growth stages. Doubtless, similarly as in other multiramous monograptids, *Linograptus* colonies constituted integrated biological units, whose development followed a certain regular plan. This may e. g. be expressed by a definite rhythm in the formation of the successive sicular cladia. The material here investigated is, however, too fragmentary to establish, even approximately, the number of thecae successively produced on the preceding cladia up to the moment of the formation of the inception of the next sicular cladium. In this respect, material obtained from the rock surface, consisting of longer branches, is, so far, more reliable though this material too, may lead to contradictory conclusions. In Jaeger's opinion (1959) the *Linograptus* astogeny occurs after the following pattern: the first two branches (procladium and first sicular cladium) are formed simultaneously and at least initially they grow step by step. Also the third and fourth branches bud nearly simultaneously at the moment when the first two branches have already produced a supposedly constant number of thecae (6-7?), after that all branches grow step by step. This mode of growth of the particular *Linograptus* cladia roughly coincides with the regular plan of the growth of thecal cladia in *Cyrtograptus*, as postulated by Thorsteinsson (1955).

Other conclusions have been drawn by Teller (in print) who sug-

gests the following sequence in the formation of branches: theca 1^2 starts budding at the moment when theca 1^1 has reached the apex of the sicula (comp. p. 181), while thecae 1^2 and 2^2 grow quicker than the corresponding thecae of the first branch, so that by the time 2 thecae have been produced by either branch, the number of thecae on the procladium and sicular cladium is balanced. Subsequently both cladia grow step by step. Theca 1^3 buds after the cladia have produced 4—5 thecae. Theca 1^4 buds after the formation of no more than two thecae on the second sicular cladium and its growth completes at the 6—7 thecae stage of the procladium. In addition to the relatively fast succession in the formation of the particular cladia, it is interesting to note the more rapid growth of the proximal segments of each cladium, as compared with the rate of growth of thecae, simultaneously growing on the preceding cladia. In this way the number of thecae on the particular branches is soon even and the later growth progresses step by step. As is quite rightly suggested by Teller (in print), this process of the compensation of the number of thecae, caused by differences of the growth rate, deviates from the regular growth pattern of cladia, established in *Cyrtograptus* by Thorsteinsson (1955) (comp. p. 206).

Teller's observations call for further checking on the basis of etched material, since in a flattened state it is indeed hardly possible to ascertain whether the termination of a branch is primary or secondary due to damage by breaking off. The moment of the formation of theca 1^2, as suggested by Teller, may be confirmed on the material here considered. The budding of theca 1^3 may be supposed to take place after the formation of no less than 2 thecae on the procladium and first sicular cladium, while differences in the growth rate of cladia, causing the equilibrium in the number of thecae, cannot be checked on the present material. If true, it would indicate a characteristic feature of the astogeny of *Linograptus*.

No contrasts in structure and size of proximal thecae in the particular cladia are encountered in *Linograptus*, though the budding of some of them was considerably delayed in relation to the development of procladium; e. g. according to Teller, theca 1^4 grew simultaneously with the theca 7^1 of procladium. Obviously the differences in *Linograptus* are so slight that they are not discernible neither on the material preserved on the rock surfaces (Jaeger, 1959; Teller, in print), nor on the incomplete etched material here described. A marked acceleration in the rate of budding of the sicular cladia of *Linograptus*, all of them being formed during the early growth stages of procladium, is probably responsible for this situation. In *Neodiversograptus nilssoni*, in which the formation of the sicular cladium was most likely much delayed as compared with the procladium, these differences are considerable and readily discernible (comp. p. 161).

Physiological orientation of the colony

The recognition of the virgellarium as an organ for the epiplank-
tonic attachment of the colony or for its holoplanktonic floating may
provide a basis for the establishment of its probable physiological orien-
tation. Thus the virgellarium might represent the apex of the rhabdo-
some from which the several cladia were suspended in a position ap-
proaching to a "deflexed" condition of growth.[10]

An analysis of the structure of specimens, shown in text-pl.: XI,
fig. *D*, XII, fig. *A*, plainly indicates that the sicular cladia, radiating
from the sicula, marked — together with the procladium — the corners
of a four- or five-rayed pyramid (text-pl. XII, fig. *A*). Hence more or
less constant growth directions must have been followed by the succes-
sive branches. The *Linograptus* colonies, however, differed from the
suspended colonies of the Dichograptidae in that their apertural side of
cladia was upturned. The drawings in this paper show *Linograptus*
colonies mainly in an anatomic position for more convenient comparison
with one-branched monograptid colonies.

Systematic position. — The European representatives of *Linograp-
tus* are all referred to the same species — *L.posthumus* (Reinh. Rich-
ter). Besides a typical subspecies, this form also comprises its variety —
tenuis Jaeger, which in the first place differs in smaller distal width
of the rhabdosome (according to Jaeger, 1959, it is 0.25 — 0.40 mm, in-
cluding the aperture). Specimens from deep–boring at Mielnik distally
attain a maximum width of approx. 0.50 — 0.70 mm (the width of the
thecal aperture together with the prothecal width of the next theca),
while at the base of distal thecae the width is 0.21—0.35 mm, whereon
it is referable to *L. posthumus posthumus*. In width the rhabdosomes
from Mielnik come closer to specimens of this subspecies from Thurin-
gia (after Jaeger, 1959, their distal width being 0.7—1.0 mm), than to
specimens from the boring of Chełm, whose distal width, according to
Teller (in print), ranges from 0.40 to 0.50 mm. On the other hand, the
number of thecae over 10 mm of the lenght of cladium is from 7.5 to
8.5 This comes closer to conditions recorded for *Linograptus posthumus*
from the boring at Chełm, than to the Thuringian forms for which 6 — 7
thecae in 10 mm are claimed by Jaeger (1959).

As regards its structure, *Linograptus posthumus* may be considered
as the relative of *Neodiversograptus beklemishevi* n.sp. on the suppo-
sition of further progressive changes in the ability to produce sicular
cladia, as well as of a change in the growth direction of the first sicu-
lar cladium in order to make place for the following buds. We might

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[10] Before the presence of the virgellar organ in *Linograptus* had been esta-
blished, Jaeger (1959) thought that its orientation during life-time was the other
way about, and he defined it as "reflexed".

also reasonably suppose simultaneous modifications in the structure of sicula, expressed by the elongation of prosicula and altered position of the original bud. In thecal structure both these forms differ but very slightly. The only change supposedly consists in certain modifications of the aperture of proximal thecae of *L. posthumus*, represented by lateral elevations of the apertural margins that are similar to those present in the more distal thecae of *N.beklemishevi* n.sp. It is reasonable to explain this difference as an expression of ancestral feature which spread here farther proximally. Hence we would be dealing with a feature introduced distally in this lineage (comp. discussion on p. 203)[11].

It is well to stress here that in the deep-boring at Mielnik there is a gap of 97 m between the earliest appearance of *Linograptus posthumus* and the last occurrence of *Neodiversograptus beklemishevi* n.sp., in which none of these forms are present. Possibly however, either this is a gap of local significance or it may be due to the peculiar properties of material from the borings. In view of the diameter of the respective boreholes the samples are often inadequate to determine the stratigraphic ranges. The stratigraphic distribution of *L. posthumus* in other areas suggests, however, that it may have been the descendant of *N.beklemishevi* n.sp. (comp. discussion on p. 201).

Stratigraphic range. — Within the Mielnik borehole, the first fossil remains referable to *Linograptus?* sp. occur at a depth of approx. 921 m, that is 13 m above the *leintwardinensis* zone. These remains consist of single thecae which are not accompanied by siculae so characteristic of *Linograptus*, hence their assigment to this genus seems rather uncertain.

Siculae and thecae characteristic of *Linograptus posthumus* occur within a series that begins at a depth of 837.6 m, approx. 97 m above the *leintwardinensis* zone. The exact stratigraphic position of these series cannot be readily recognized owing to absence of index forms in the assemblage, associated here with *L.posthumus* (*P.dubius* (Suess), beyrichiid ostracods, unidentifiable Eurypterida and brachiopods). Below these layers occurs a barren unfossiliferous series, partly incompletely cored of containing unidentifiable remains (at a depth between 842.6 and 853.9 m). Yet, directly below these layers, at a depth of 854.6 m and deeper down, the presence has been noted of a monograptid, probably conspecific with "*Monograptus*" *inexpectatus* Bouček (Bouček 1932). Somewhat lower down this species is accompanied by new species or subspecies, closely related with it. Therefore, we are probably dealing here

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[11] The North-American forms described as *Linograptus*, and the European *L. remeši* Bouček, supposedly represent separate evolutionary lineages, probably not directly connected with *L. posthumus* (comp. also Teller, in print).

with a so far not fully investigated series from the Upper Silurian sequence[12].

Among the representatives of *Linograptus posthumus* here described, the youngest occur at a depth of approx. 820 m, where they are accompanied by *"Monograptus" formosus* Bouček and *Monoclimacis ultimus* (Perner). The occurrence of these forms does not, however, mark the upper range of this species in the borehole here considered, since the overlying beds have not as yet been fully investigated there (the etching of samples in now under way). Doubtless, the range of this species is much wider.

In its other occurrence areas *Linograptus* s.str. is supposedly confined to the *leintwardinensis* and *hercynicus* zones (Teller, in print). Records of the earlier appearance of representatives of this genus were due either to inaccuracy in recognizing the zone (Jaeger, 1959), or they are probably incorrect and need checking. According to Sherrard (1952) and Jaeger (1959), the Australian *Linograptus* is encountered in the *nilssoni — scanicus* zone[13].

TENTATIVE MORPHOLOGICAL ANALYSIS OF EVOLUTIONARY CHANGES IN COLONIES OF LINOGRAPTINAE

The morphological and stratigraphic analysis of the Linograptinae, described in the present paper, shows that species here belonging form evolutionary series with regular stratigraphic sequence of structural changes. As may be reasonably supposed, the particular species must have represented relatively more stabile stages of certain phases of morphological changes. Indeed, just in this meaning the term *phase* may be used when speaking about the evolution of the Linograptinae. Each particular morphological phase has been determined by the association of some features characterizing the structure and development of the colonies. Five such evolutionary phases may be distinguished in the group here investigated: 1) the praeneodiversograptid phase, 2) neodiversograptid phase, 3) praelinograptid phase, 4) linograptid phase, 5) abiesgraptid phase.

These several phases at the same time constitute the intermediate stages grading from the preceding into the following evolutionary phase.

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[12] The stratigraphic range established in previous papers for *M. inexpectatus* Bouček as the *nilssoni-scanicus* zone seems quite incorrect and this form is undoubtedly much younger. This species is neither synonymous with „*Monograptus*" *scanicus,* as was for a time recognized (Bouček, 1936; Přibyl, 1948), nor does it belong even to a group of species, separated into *Lobograptus* Urbanek.

[13] According to Dr H. Jaeger's (Berlin) personal communication, recent data indicate that the appearance of *L. posthumus tenuis* is not referable to the *scanicus* zone, but to the *leintwardinensis* zone.

The representatives of particular phases actually display certain in-
termediate features between more and less advanced forms (text-pl.
XIII).

The *praeneodiversograptid phase* is largely a hypothetic evolutio-
nary phase of the Linograptinae, immediately preceding the appearance
of *Neodiversograptus nilssoni*. It is during this phase that must have
occurred the differentiation of the group just mentioned, and started
the main trends of its evolution. These processes must have taken place
in the lowermost zone of the Lower Ludlovian (*Pristiograptus vulgaris*
zone) and at the Wenlockian-Ludlovian boundary, in beds directly un-
derlying this zone.

The absence from these zones in Europe of any monograptids what-
soever, that might be looked upon as the ancestral form of the Lino-
graptinae, is rather puzzling. Moreover, in these zones a marked impo-
verishment of the monograptid fauna, leading to a crisis in the evolu-
tion of this group, is observed. The monograptids are represented by
extremely few species whose number in most described European pro-
files does not exceed 1—2. Moreover, these species represent only one
morphological type and all belong to the same genus (*Pristiograptus*).

The existence of such an evolutionary crisis in the development of
the graptolite fauna on the Wenlockian-Ludlovian boundary was long
ago recognized in the Ludlovian of Great Britain by Wood (1900). Accor-
ding to that author, the faunal changes there are expressed by the follow-
ing features: although there are but 1—2 species in common for these
two stages, the faunal gap between them is less extensive than it might
at first be supposed, for further faunal development points out that
most of the species-groups (genera in the present meaning) are com-
mon for the Wenlockian and the Ludlovian. In Wood's opinion, the spe-
cies- groups that are new for the Ludlovian, developed probably from
Wenlockian ancestors. In the light of the most recent studies, this con-
cept seems only partly correct (comp. p. 196), while the reduction of the
number of species on the Wenlockian-Ludlovian boundary merits full
consideration.

A faunal crisis, on the Wenlockian-Ludlovian boundary, has indeed
been observed by many investigators in the Silurian of Great Britain
(Alexander, 1936; Boswell, 1949; Holland, Lawson & Walmsley, 1959).
Within the Ludlovian Alexander even distinguished as a lowermost se-
ries the so-called "Barren Beds of the Lower Ludlow Shales". The nu-
merical reduction of monograptid species, as indicated by Elles and
Wood (1918), has been most suggestively illustrated by Bulman (1933)
in a frequency distribution curve of species in the particular graptoli-
tic zones. This curve strongly emphasizes the numerical decrease of
species on the boundary of the Wenlockian and the Ludlovian.

Analogous or very similar conditions have been found on the Wenlockian-Ludlovian boundary in other European areas. An abrupt faunal impoverishment as a rule occurs in the uppermost zones of the Wenlockian *(testis-lundgreni* zone); higher up the occurrence is frequently noted of passage beds of considerable thickness, these are characterized by maximum specific impoverishment, often associated with a common or even mass occurrence of *Pristiograptus dubius* and *Gothograptus nassa. Pristiograptus vulgaris* appears still higher up, first also in a meagre association. The number of species accompanying Pr. *vulgaris* gradually increases, leading up to progressively stronger differentiation of the graptolite fauna within the *nilssoni* and *scanicus* zones.

In Poland, especially in the southern region (Kielce) of the Holy Cross Mountains (Góry Świętokrzyskie), these facts have been well studied by Tomczyk (1960, 1962), who suggests the establishment of the *nassa* zone as the lowermost graptolite zone of the Lower Ludlovian in Poland, preceding the *vulgaris* zone. In the *nassa* zone, the extreme numerical reduction of graptolite species is accompanied by a rich non--graptolite fauna.

A similar situation apparently occurs in Scandinavia (Island of Gotland) (Hede, 1942). The mass occurrence there of *Gothograptus nassa* in a distinct horizon is associated only with *Pristiograptus dubius*

The most recent research work in Czechoslovakia has led to a more thorough recognition of the graptolite sequence of the lowermost Ludlovian; a zone of the monotonous occurrence of *P.* ex grege *dubius* and *Gothograptus nassa* has been distinguished there by Horný (in: Horný, Prantl & Vaněk, 1958) below the *Pr. vulgaris* zone.

In Thuringia, Jaeger (1959) established above the *Cyrtograptus lundgreni* zone the presence of passage beds; these are often characterized by thin layers of carbonized organic remains, containing also graptolites, which allow their assignment to the uppermost Wenlockian. These beds are overlain by a zone, characterized only by the presence of *Pr. dubius* and *Gothograptus nassa* (*"dubius-nassa* Interregnum" according to Jaeger's terminology), while *Pr. vulgaris* appears later on. The probably all-European significance of this faunal crisis has been very strongly emphasized by Jaeger.

It may reasonably be supposed that analogous conditions in this respect will be recognized in other European areas, as their knowledge progresses. These facts apparently indicate a mass extinction of the autochtonous monograptid fauna in the Silurian seas of Central and Western Europe at the boundary of the Wenlockian and the Ludlovian. Out of all the known Wenlockian lineages, only that represented by *Pristiograptus (Pr. dubius — Pr. vulgaris)* occurs continuously within this area, all the others disappear and have no representatives in the lowermost Ludlovian of Europe. Within the higher zones, however

(the *nilssoni* and the *scanicus* zones), there is a rapid enrichment of the fauna in representatives of several new lineages not recorded from the lowermost Ludlovian. Only some of them may have developed through evolutionary modifications from the European (autochtonous) monograptids of the Lower Ludlovian. These are namely genera traceable to pristiograptids (*Colonograptus, Saetograptus*[14]).

Representatives of other lineages (*Monograptus*, e.g. *M. uncinatus*), probably also *Monoclimacis* (e.g. *M. micropoma*), seem to be the continuation of lineages present already in the Wenlockian. They must, however, represent a strange geographical element from other areas of the Silurian seas where, at the Wenlockian-Ludlovian boundary, the development of the monograptid fauna must have been continuous.

Moreover, some monograptid lineages may hardly be regarded as the direct continuation of any of the earlier lineages. These monograptid lineages were probably differentiated during the early Ludlovian, and their ancestors appear most likely as the allochtonous immigrants in Europe. Linograptinae belong to these lineages in the very first place, as they are not traceable to any of the known European monograptids of the earliest Ludlovian. Our inadequate knowledge concerning the correlation and sequence of the Silurian graptolites from most of the areas outside Europe does not now allow a more exact determination neither of the direct ancestors of *Neodiversograptus nilssoni* — the oldest known representative of Linograptinae — nor of the region where the differentiation of the mentioned evolutionary line was realized. For the time being, the Linograptinae should be regarded in this respect as a cryptogenic group.

The data available supply certain suggestions concerning the oldest pre-Ludlovian ancestors of the Linograptinae. Namely, cyrtograptids encountered in the uppermost Wenlockian zones very closely resemble the primitive Linograptinae in thecal structure and general appearance of the rhabdosome, the presence of thecal cladia excepted. These are the representatives of *Barrandeograptus* Bouček.

The various authors who have taken part in the discussion on the origin of *Neodiversograptus nilssoni* or of *Linograptus*, all fully agree in that the ancestors of these forms must be searched for among the "pauciramous" representatives of *Barrandeograptus*. Although the views of these investigators may differ on particular details, their general standpoints agree and may be regarded as the "cyrtograptid theory" on the origin of the Linograptinae.

Wood (1900, p. 453, 483) was the first to advance this opinion by pointing out the close relationship of *Cyrtograptus* (= *Barrandeograptus*)

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[14] The derivation of *Colonograptus* from progressive pristiograptids seems now a more reliable supposition than the older conceptions tracing these forms back to *Monograptus* (Elles, 1922; Urbanek, 1958, 1959).

carruthersi with *Monograptus* (= *Neodiversograptus*) *nilssoni*. These forms resemble so much that "*Cyrtograptus*... may perhaps be regarded rather as a temporary reversion, than a constant biological genus, seeing that in one instance at least — namely that of *Cyrtograptus carruthersi* and *Monograptus nilssoni* — the two forms appear to be identical in all respects, except in the matter of branching" (Wood, 1900, p. 453). Later, this view was more clearly presented by Elles and Wood (1901—1918, p. 70): "The nearest relation of *M. nilssoni* is undoubtedly *Cyrtograptus carruthersi* of the Upper Wenlock Beds, fragments of which are indistinguishable from similar fragments of *M. nilssoni*, the only distinguishing feature being the presence of branches in the *Cyrtograptus* form". According to the English authors just mentioned, in *Barrandeograptus carruthersi* "thecae both on the stipe, and on the cladia are in all respects like those of *M. nilssoni*" (p. 513).

Recently, Jaeger (1959) confirmed this opinion concerning the origin of *Neodiversograptus nilssoni*. He does not, however, refer to the earlier and completely analogous views of the British authors, though naturally he must have been familiar with them. At the same time, Jaeger developed this hypothesis by correctly supposing that, owing to the structure of thecae, and particularly that of siculae (as described by Urbanek, 1954), *N. nilssoni* should be regarded as one of the links in the evolutionary line that leads to *Linograptus* (comp. p. 140). Hence, consistently with the views of Jaeger, the origin of *N. nilssoni* from *Barrandeograptus carruthersi* confirms the cyrtograptid origin of *Linograptus*.

Similar views have been advanced previously. Bouček's (1933) conception represents another hypothesis as to the cyrtograptid origin of *Linograptus*. That author attempted to prove direct connections between representatives of *Barrandeograptus* and *Linograptus* by pointing to the close similarities between *B. pulchellus* (Tullberg) and *Linograptus*. This hypothesis, however, has met considerable difficulties owing to the large stratigraphic gap separating the occurrence of these two forms, and the lack of morphologically and stratigraphically intermediate forms.

The cyrtograptid theory is now doubtless the most acceptable concept of the origin of the linograptids. The distinct stratigraphic gap between the occurrence of *Barrandeograptus carruthersi* (Lapworth) — the supposed ancestor of this group (the *lundgreni* zone) — and the appearance of *Neodiversograptus nilssoni* (the *nilssoni* zone) which geologically is the oldest linograptid, — may be explained by the general discontinuity in the development of the graptolite fauna on the Wenlockian-Ludlovian boundary in Europe. Hence, though the direct ancestors of *Neodiversograptus* are not known, it seems quite probable that the roots of this group may be traced down to certain representatives of *Barrandeograptus*. This might be indicated not only by fairly strong

affinities in thecal structure, but also by the presence of a double cur-
vature of the rhabdosome (dorso-ventral) and strongly reduced number
of thecal cladia in the youngest representatives of *Barrandeograptus*. This
hypothesis, though very likely, cannot however be regarded as entirely
proved. *Barrandeograptus carruthersi* is a relatively little known spe-
cies; the structure of the proximal part of the rhabdosome and sicula
has hardly been investigated, while the thecae — though on the whole
resembling those in *Neodiversograptus* yet in fig. 359 of Elles and Wood
(1918) — are shown with an obliquely oriented apertural margin, ven-
trally higher than dorsally. A knowledge of etched specimens of this
cyrtograptid is needed to reach a conclusive decision whether it is this
species or another closely allied form that represents the ancestor of
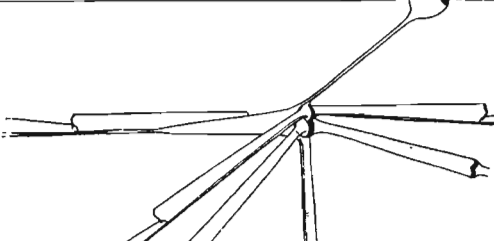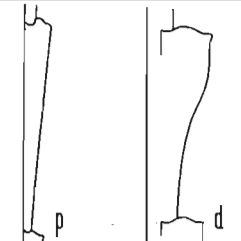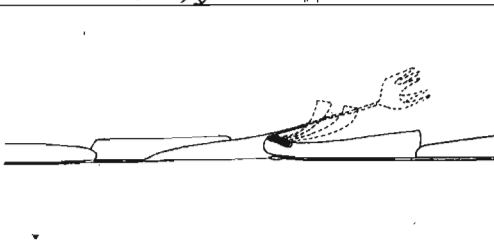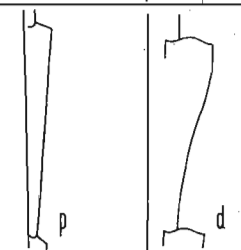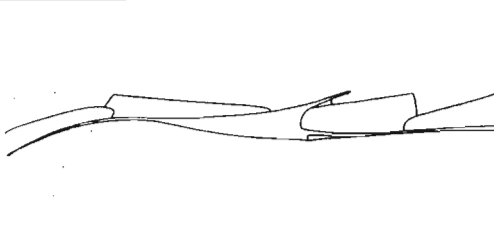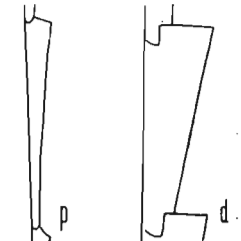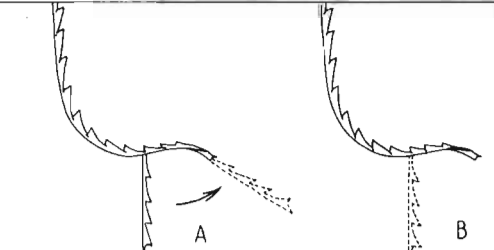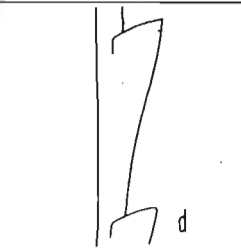Linograptinae.

Still the hypothesis on the cyrtograptid origin of the Linograptinae
is sound enough to be used as a tentative interpretation of the evolutio-
nary processes realized during the praeneodiversograptid phase. Older
authors and, recently Jaeger, too, claim that the chief modification is
expressed by the disappearance (reduction) of thecal cladia, resulting
in the development of a form (*Neodiversograptus nilssoni*) that consis-
ted only of the main stipe. The ability to produce a sicular cladium was
acquired by this form later (text-pl. XIII, fig. *B*). In the light of the
most recent investigations of the present author, suggesting that already
N. nilssoni was capable to produce sicular cladia (comp. p. 157) and em-
phasizing the essential homology between thecal and sicular cladia (comp.
p. 209), another conception of this process seems reasonable enough. Du-
ring a phase here named the praeneodiversograptid, evolution might
merely consist in a change in the position of the mother theca of meta-
cladium into which, by way of evolutionary modifications, the meta-
sicula was transformed (text-pl. XIII, fig. *A*). Obviously nothing certain
is known as to whether this shifting occurred gradually during a num-
ber of intermediate stages or, omitting them, in the way of some salta-
tion. The very exceptional presence in *N. nilssoni* of the sicular cladia
may possibly indicate that the new feature was at first a morphogene-
tically non-stablilized character or that its formation has been strongly
delayed in astogeny, resulting in the low frequency of bipolar forms in
linograptid populations that represent the neodiversograptid phase of
evolution.

The evolutionary processes realized during the praeneodiversograp-
tid phase might be very briefly summarized as follows:

1) the reduction of the number of metacladia to a single one;

2) the proximal shifting of the mother theca of metacladium, gra-
dually leading to its replacement by the sicula, and the transformation
of the thecal cladium into the sicular one.

TEXT-PL. XIII

Structural changes in earlier phases of evolution of Linograptinae. Praeneodiverso-graptid phase based on data of Elles and Wood (1918). *A, B* two theoretically possible modes of changes preceding the neodiversograptid phase of evolution (change in position of mother theca of metacladium or its reduction). Further explanations — in text.

The neodiversograptid phase is represented by *Neodiversograptus nilssoni*, the oldest known linograptid which occurs, in the *nilssoni* zone. The main morphological features of this form, that are the index characters of this evolutionary phase, are as follows:

1) relatively long sicula (1.25 — 1.65 mm) with a rather short prosicula (0.40 — 0.50 mm) and a long metasicula (0.85 — 1.05 mm).

2) aperture of metasicula rather strongly expanded and provided with an asymmetrical dorsal spine, which appears relatively late in the astogeny and is subsequently modified into the pseudovirgula of the sicular cladium;

3) presence of a dorsal curvature in the proximal part of procladium, resembling the curvature in *Barrandeograptus carruthersi*;

4) probably delayed budding of the sicular cladium and the marked resulting contrast between thecæ l^1 and l^2;

5) aperture of the sicula is completely concealed by the base of theca l^2, suggesting that during this evolutionary phase the Linograptinae were potentially able to produce but one sicular cladium;

6) sicular cladium grows in the prolongation of the metasicula in a direction opposite to that of the growth of procladium;

7) thecae of both branches are straight, without apertural differention, so that they resemble the thecae in *Barrandeograptus*.

The *praelinograptid phase* represents that evolutionary stage during which certain neodiversograptid characters (direction of growth of first sicular cladium) are combined with certain linograptid features (supposed ability to produce a greater number of sicular cladia). Hence, this phase might be called the „advanced neodiversograptid'' phase. It is represented by *Neodiversograptus beklemishevi* n.sp., encountered in the *scanicus — leintwardinensis* zones. This evolutionary phase lasted longer than the neodiversograptid phase. Its fundamental features are as follows:

1) as compared with *N. nilssoni* the sicula was reduced, being 1.15 — 1.36 mm in lenght. Its reduction resulted from the shortening of the metasicula which is only 0.66—0.84 mm long, i.e. less than the minimum length of the metasicula in *N. nilssoni*. The length of the prosicula, however, is practically unchanged, being 0.45 — 0.55 m;

2) aperture of the metasicula expands to a smaller degree than that in *N. nilssoni*, and is provided with a symmetrical apertural dorsal spine. Most likely the at first asymmetrical dorsal spine of the metasicula was modified, during this evolutionary phase, into a spine lying in the plane of symmetry. Hence, in this respect conditions already resemble those characteristic of *Linograptus*. The spine here displays astogenetic acceleration and is formed at an earlier growth stage than in *N. nilssoni*, namely before theca l^1 attains the apex of the prosicula. Later this spine is modified into the pseudovirgula of the sicular cladium;

3) dorsal curvature probably disappears from the proximal part of procladium, and in this the conditions resemble those in *Linograptus;*

4) first sicular cladium, during this evolutionary phase, probably budded at an earlier stage of astogeny than that in *N. nilssoni*. This results from the fact that theca 1^2 has the appearance of a proximal theca and does not much differ from theca 1^1;

5) metasicular aperture is only partly concealed by the base of theca 1^2, a considerable part of its surface still remains to be open. This fact as well as the presence of the basal notch at the base of theca I^2 indicate at least a potential ability to produce more than one sicular cladium. These conditions differ from those described in the neodiversograptid phase and, with the exception of the direction of growth of first sicular cladium, analogous with *Neodiversograptus*, they resemble the conditions in *Linograptus;*

6) first sicular cladium grows in the prolongation of the metasicular aperture, in a direction opposite to that of the growth of procladium. The divergence angle here is about 180°, as in *N.nilssoni;*

7) proximal thecae are straight, their apertures undifferentiated (as in *N. nilssoni*), while the median and distal thecae have lateral elevations on the apertural margin (as in *Linograptus*).

The *linograptid phase* is represented by *Linograptus posthumus.* The first appearance of this species calls for more precise determination. In the deep-boring at Mielnik this form makes its appearance approx. 97 m above the *leintwardinensis* zone, in a Silurian series in the western framing of the Eastern European Platform, for which Tomczyk (1962) introduced the name: Siedlce Beds. Fragments of rhabdosomes, however, encountered lower down, some 13 m above the zone just mentioned, strongly resemble *L. posthumus.* Yet the specific assignment of these forms is still an open question since their remains do not occur in association with siculae characteristic of *Linograptus.* On the whole, it is quite reasonable to suppose, after Teller (in print), that *Linograptus* is confined between the zones *Saetograptus leintwardinensis* — "*Monograptus*" *hercynicus,* but in the present writer's opinion, may probably appear above the *leintwardinensis* zone.

The main features of the linograptid stage are as follows:

1) sicula displays secondary elongation up to 1.3 — 1.7 mm. This extension is due to the elongation of the prosicula which attains a length from 0.75 to 1.05 mm. As compared with *N. beklemishevi* n. sp., the length of the metasicula is only slightly changed, being 0.45—0.65 mm. The extension of the prosicular segment possibly suggests a kind of embryonization of the siculozooid, expressed by delayed metamorphosis. The secondary elongation of the sicula cannot be regarded as regressive evolution and a return to the ancestral state, since it is realized by an

extension of the prosicula accompanied by a reduction of the metasi-
cula, i.e. according to another pattern than in *N. nillsoni;*

2) metasicular aperture expands but little and is provided with
a dorsal spine lying in the plane of symmetry. This spine is produced
during early astogeny, before theca 1^1 attains the apex of the prosicula.
The virgella of the sicula is provided with a characteristic terminal or-
gan — the virgellarium — which probably constitutes either the hydro-
static apparatus or the attachment apparatus of the colony. No such,
even an incipient organ has ever been found in the earlier linograptids.
The fossil remains of this apparatus probably represent only the ske-
letal framework of a more complex organ that consisted of soft parts,
too. It is quite possible that an incipient organ of this kind existed al-
ready during the praelinograptid stage when it consisted of soft parts
only which could not be preserved;

3) similarly as in *N. beklemishevi* n.sp., there is no dorsal curvature
in the proximal part of procladium;

4) sicular cladia are formed early in astogeny and follow one an-
other rather quickly (accelerated formation of cladia). This may account
for lack of contrast in the structure of first thecae of the particular
cladia (1^1, 1^2, 1^3, 1^4.....) which are all of the proximal type and do not
really differ in size or structure;

5) base of theca 1^2 only partly overlaps the metasicular aperture,
hence a great number of sicular cladia may be formed — up to 15, ac-
cording to Jaeger (1959). In the evolution of the Linograptinae, the sta-
bilization of the ability to produce multiramous colonies was perhaps
realized as a rapid shift in the genetic structure of populations. In ear-
lier populations bipolar colonies would not at first be very numerous
(the diversograptid and the praelinograptid phases), while low expres-
sivity (the presence of one or of a small number of sicular cladia) would
be associated with the low frequency of a given character. A subsequent
development of expressivity (ability to produce many sicular cladia)
would be accompanied by markedly increased frequency of multiramous
colonies in the populations, resulting in their numerical predominance.
The formation of multiramous *Linograptus* colonies, provided with
a virgellarium, was probably an expression of fundamental, morphologi-
cal and ecological evolutionary changes;

6) first sicular cladium does not grow in the prolongation of the me-
tasicular aperture, but at a certain angle to its axis. Thus the base of the-
ca 1^2 is shifted away from the surface of the metasicular aperture, pro-
viding a free space and hence making possible the production of more
numerous buds which are the incipient successive cladia of the sicula.
The divergence of sicular cladium in *Linograptus* seems to be a special
astogenetic adaptation for multiple budding and for producing multira-

mous colonies, such as develop during this evolutionary phase of the Linograptinae;

7) thecae, mostly as early as theca 1^1, have symmetric elevations on the apertural margins, in this respect representing a more advanced stage than *N. beklemishevi* n. sp.

The *abiesgraptid phase* is represented by forms belonging to the genus *Abiesgraptus (A. tenuiramosus, A. multiramosus)*, relatively little known, though Jaeger's paper (1959) is an important contribution to their knowledge. This genus is confined to the *uniformis* and *praehercynicus* zones in Thuringia, but probably also occurs in Czechoslovakia and Poland (Jaeger, 1959; Tomczyk, 1960; Teller, in print).

Geologically this is the youngest evolutionary phase of the Linograptinae. The *Abiesgraptus* rhabdosome may be interpreted as a colony of linograptids which had acquired the ability to produce thecal cladia on the procladium and on one of the sicular cladia (so-called main stipes). The new thecal cladia grow in pairs on either side of the mother theca which, after Jaeger (1959), buds two thecae that are the first thecae of each thecal cladium. This paired and bilateral mode of the growth of new thecae has not so far been observed in any other monograptid. Therefore, if Jaeger's observations (1959) are correct, it merits some special attention as the abiesgraptid type of budding, characteristic of the abiesgraptid stage of astogeny, distinguished by the formation of peculiar "paired" thecal cladia on the procladium and the sicular cladium.

According to Jaeger (1959), during the astogeny, and, probably, during the phylogeny, *Abiesgraptus* passes through a four-branched linograptid stage of development, hence *A. tenuiramosus* cannot during this astogenetic stage be distinguished from the four-branched *Linograptus posthumus*. The last named species is probably the direct ancestor of *A. tenuiramosus*, and this is confirmed by their astogeny and thecal structure. Jaeger's hypothesis (1959), postulating a close phylogenetic relation between *Linograptus* and *Abiesgraptus*, appears soundly substantiated, though some of its points call for better knowledge. For example, the structure of the sicula is not sufficiently elucidated since the presence of the virgellarium — an organ typical of the *Linograptus* — has not as yet been established in the *Abiesgraptus*, though it is reasonable to expect it there. Its absence might suggest secondary reduction, but this is hardly probable. The early stages of astogeny of *Abiesgraptus* are inadequately known. Particularly the mode of development of sicular cladia calls for more examining. The astogeny of *Abiesgraptus* is by Jaeger (1959) interpreted as follows: two main branches grow simultaneously in two opposite directions from the sicula, and display a slight spiral coiling. One branch is the procladium, the other the sicular cladium budding from the aperture of the sicula. The divergence

angle of the two main branches is approx. 180°, thus markedly differing
from the direction of growth of the first sicular cladium in *Linograptus*.
Jaeger thinks that "wahrscheinlich erfolgt im Laufe des Wachstums
sehr bald eine zunehmende Streckung des Rhabdosoms, d.h. Verringe-
rung des Divergenzwinkels auf dem endgültigten Wert von 180°, der
mechanisch am vorteilhaftesten erscheint" (p. 161). After a certain length
has been attained by the stipes, two further thecae are simultaneous-
ly budded from the aperture, giving rise to lateral branches that are
perpendicular to the main branches. The further development of the
rhabdosome consists in the formation of thecal cladia on the main bran-
ches. If Jaeger's interpretation of the mode of formation of the first si-
cular cladium is correct, the formation of *Abiesgraptus* would be connec-
ted with rather considerable modifications in the pattern of cladogeny.

According to Jaeger (1959), the four-branched *L. posthumus* would
be the ancestral form of the primitive abiesgraptids, as the "abiesgrap-
tid addition" represented by thecal cladia was realized on the founda-
tion of such forms. With reference to this hypothesis it is interesting to
note Teller's (in print) original observations that in the Linograptinae
the thecal cladia may also be produced in three-branched forms. *Abies-
graptus?* sp., described by him from a borehole at Chełm (southern
Poland), in a zone determined by the new species of *Pristiograptus* and
lying above "*M.*" *formosus*, consists of a procladium and two sicular
cladia. One of the cladia is provided with a pair of symmetrical thecal
cladia, analogous with those in a typical *Abiesgraptus*. Teller assigns to
this form a certain phylogenetic significance on the supposition that
they may have given rise to the true abiesgraptids. Since, however, his
material consists of a single specimen we might, quite as well, be dea-
ling here with an infraspecific variation of a non-prospective charac-
ter, i.e. one without any phyletic significance. Nevertheless this fact
indicates the ability of linograptids to produce thecal cladia even during
early evolutionary stages. It is also noteworthy that the first sicular
cladium displays here the normal linograptid divergence, while
the sicula was provided with an incompletely preserved virgellarium.

In the writer's opinion, Bouček's (1933, p.74) observations also sug-
gest an equally early appearance of similar forms. Bouček described
from the *ultimus* zone a fragmentary rhabdosome, consisting of a short
branch provided with thecae, resembling those of *Linograptus*, but dis-
playing thecal divergence in two opposite directions. The sicula is lack-
ing from the point of divergence, there is a thecal cladium on one of
the branches. This form originally described by Bouček (1933) as *Lino-
graptus?* sp. was later referred by Bouček and Přibyl (1953) to the genus
Diversograptus under the name of *D. mesoludlovensis* Bouček & Přibyl.
Jaeger has suggested that this is a synonym of *Linograptus tenuis* Jae-
ger, but should this be so, the absence of the sicula from the point of

divergence cannot be explained. In the present knowledge of this problem, it seems more reasonable to suppose that we are dealing here with a regenerating fragment, showing bipolar growth, belonging to a "prae--abiesgraptid" form resembling Teller's specimen.

The evidence just mentioned reasonably indicates the relatively early appearance of the tendency to produce compound colonies of the abiesgraptid type, considerably preceding the appearance of the true representatives of *Abiesgraptus*.

The evolutionary series of the Linograptinae described above probably consist, therefore, of the following links which have all been more or less accurately investigated:

1) *?Barrandeograptus carruthersi* — 2) *Neodiversograptus nilssoni* — 3) *Neodiversograptus beklemishevi* n.sp. — 4) *Linograptus posthumus* — 5) *Abiesgraptus tenuiramosus*. It is now still too early to state even tentatively whether each of these links directly gave rise to the next one, or whether they graded into another by transition forms. The first alternative seems particularly probable in relation to links 1-2 and 3-4. In spite of a stratigraphic gap *N. nilssoni* does seem to be the direct ancestor of *N. beklemishevi* n.sp. The transition from link 4 to link 5 calls for further investigation, particularly concerning *Abiesgraptus* and its astogeny. Some of the species gave rise to certain side lineages. These were, however, merely blind branches of the main evolutionary line of Linograptinae which is expressed by the sequence of the 5 above species. These side branches were supposedly short and very few.

The present state of the knowledge on the Lower Ludlovian monograptids does not clarify the relation of the Linograptinae to other subfamilies. On the data available it is reasonable to suppose particularly close connection of the Linograptinae with the Cucullograptinae. The two groups evolved during the early Ludlovian from common ancestors, possibly the unknown descendants of *Barrandeograptus corruthersi* or another similar species. The stratigraphic distribution of the forms thus far investigated also suggests that forms with a linograptid trend of specialization (*Neodiversograptus nilssoni*) appeared earlier than forms with a cucullograptid type of structure (comp. p. 169). If we recognize that the cucullograptid line evolved from *N. nilssoni,* the evolutionary changes in the sicular structure would express a certain despecialization (secondary reduction) of the apertural dorsal spine, characteristic of the linograptids. The slight tendency to differentiate the apertural margins, as observed during the evolution of the linograptids, is conspicuously stronger expressed among the cucullograptids. It is not excluded, however, that both these lines evolved from a common ancestor, still lacking the characters of specialization and still unknown for such reasons, as e.g. its occurrence within another geographical area. In this case the stratigraphic sequence of forms so far investigated would

not indicate the succession in which these forms were differentiated, but the successive immigrations into central and western Europe of forms having common ancestors. This hypothesis, though certainly difficult to prove, should not be disregarded at the present state of knowledge of the problem here considered.

The *"Pristiograptus" bohemicus* (Barrande) group of species is the third one probably more closely allied with the two groups mentioned above. These species, though formally referable to *Pristiograptus* Jaekel (straight tubular thecae), seem to come nearer to the linograptids and cucullograptids than to the typical pristiograptids such as *P. dubius*. This is expressed not only by the structure of thecae and of the rhabdosome, but in the evolutionary trend, too. The relatively conservative group of *P. bohemicus* becomes distinctly progressive in zones directly overlying the *leintwardinensis* zone, while some characters realized in *"Monograptus" inexpectatus* Bouček — closely allied with the *bohemicus* group — strikingly resemble features that were realized independently and in an earlier zone by the cucullograptids.

MORPHOLOGICAL REGULARITIES OF CLADOGENY

The data available on the astogeny of multiramous monograptid colonies are extremely few. Practically, they consist of the papers by Thorsteinsson (1955), Bulman (1958), Jaeger (1959), and Urbanek (1960), the latter being an attempt at a biological interpretation of previous observations.

The development of multiramous cyrtograptid colonies, which consist of a procladium and of a certain number of thecal cladia, has been thoroughly investigated by Thorsteinsson. He has established that thecae, budded simultaneously both on the procladium and on the thecal cladia, agree in size and shape. Since the formation of thecal cladia is somewhat delayed in relation to the growth-of the procladium, their proximal part consists of thecae that correspond closely to the thecae on the distal part of the simultaneously developing procladium. The further growth both of the procladium and of the corresponding thecal cladia occurs step by step, i.e. the appearance of each theca on the procladium is accompanied by the formation of a corresponding theca, of the same size and shape, on the thecal cladium.

Our knowledge of the relations between the procladium and the sicular cladium in diversograptids is more limited. Anatomically, the thecal cladia may not be too sharply opposed to the sicular cladia. The latter bud from the metasicula, and — from a comparative-anatomical standpoint — the metasicula fully corresponds to the thecae (autothecae) of the remaining zooids. The existing differences may be regarded

as modifications that do not affect the structural pattern which, in graptolite colonies, is followed both by the metasicula and the remaining thecae. Indeed, two distinct segments may be distinguished both in the metasicula and in thecae of blastozooids of graptolite colonies. The more basal segment is called the protheca (*pth*), the more distal one is referred to as the metatheca (*mth*). In the metasicula the prothecal segment
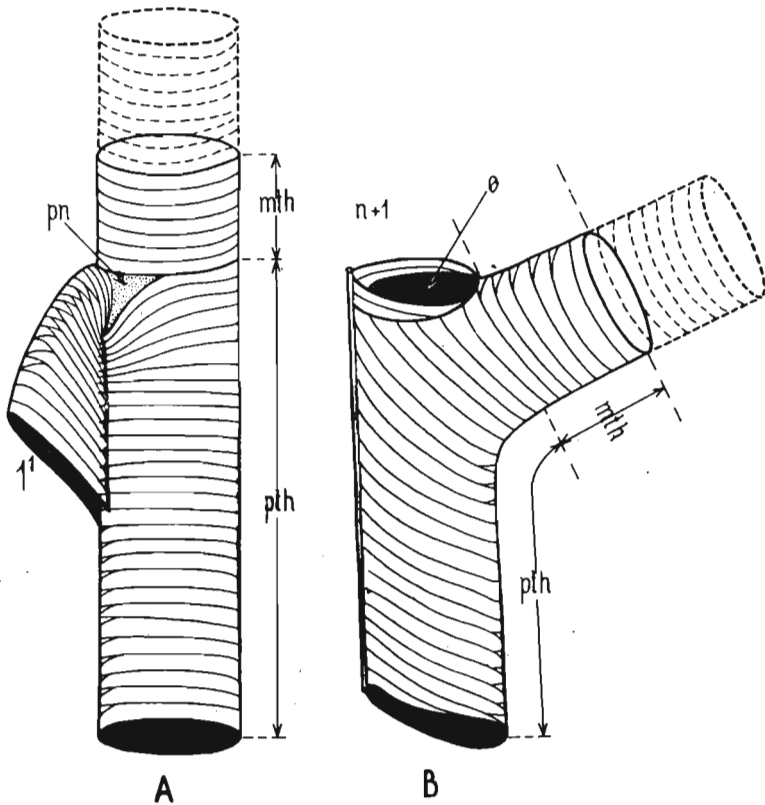

Fig. 4. — Diagram comparing the thecal segments in a generalized metasicula (*A*) and blastozooid theca (*B*) in monograptids. Broken lines indicate the relation of a descendant thecae produced by supraapertural budding to corresponding mother thecae

mth metathecal segment, *n* + 1 beginning of next blastozooid theca, *o* opening for the bud of theca *n* + 1, *pn* primary notch (opening for the bud of theca 1¹), *pth* prothecal segment

corresponds to that portion contained between its base and the point of the formation of the pore (Eisenack's *lacuna*), i.e. the primary notch for the bud which produces the first theca of the colony (1¹) (fig. 4A). The metathecal segment is situated between the upper margin of the pore and the margin of the definitive aperture of the metasicula (fig. 4 A). In each blastozooid theca the prothecal (*pth*) segment analogously constitutes the part which is situated between the base of the theca and the point of the formation of the opening for the bud of the next blasto-

zooid. The metathecal segment is placed at a certain angle to the preceding segment and is situated between the upper margin of the protheca and the margin of the definitive aperture of a mature theca (fig. 4 B). For the sake of simplification we disregard here the cases suggesting that the metathecal segments of the metasicula and of the remaining thecae may consist of two distinct parts: the subapertural, previously defined, and the apertural, represented by various apertural structures raised above the apertural margin (spines, apertural lobes, etc.; Urbanek, 1960). These differentiations do not fundamentally modify the morphological relations which are identical both in the metasicula and the thecae of all the blastozooids.

The mode of budding of the successive zooids, which form a series of thecae of the procladium, is stable. In the metasicula as well as in the remaining thecae the new bud is produced on the margin of the aperture of the mother theca, hence it is formed by non-perforation. Independently of the position of such an opening, it is, however, invariably subaperturally placed in relation to the definitive aperture of a mature mother theca, and delimits the prothecal segment from the metathecal segment. Such a mode of budding is characteristic of all the thecae in one-branched monograptids and it may be called subapertural or monograptid budding[15].

The existing differences in the mode of budding of the first theca (shifting of the bud from the plane of symmetry to the left in relation to the sicula), as compared with the pattern followed by the remaining thecae (position of the bud in the plane of symmetry), do not introduce any significant morphological changes.

Conditions are quite different when thecal cladia are produced on blastozooid thecae of the procladium (e.g. in cyrtograptids). There the bud is formed on the level of the aperture of the mother theca, rising above the margin of its subapertural or apertural part (fig. 4 B, broken lines). This mode of budding might be called supra-apertural. It is interesting to note that the formation of the sicular cladium follows the same relation to the metasicula, i.e. that it buds supra-aperturally (fig. 4 A, broken lines). Hence there is a striking analogy between the mode of budding of the thecal cladia and that of the sicular cladium. A marked difference, however, exists between the mode of budding of thecae on the procladium, and the budding of first thecae on the two mentioned types of secondary cladia which, together, may hence be referred to as the metacladia.

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[15] The use of the term "monograptid budding" is justified only with reference to the Monograptidae whose genus "*Monograptus*" has only a procladium in which all the thecae bud after this pattern. The same mode of budding is, however, encountered probably in all graptoloid thecae, the multiramous forms excepted.

There are other analogous details in the formation of both the thecal and the sicular cladia. In both cases a pseudovirgula precedes the formation of a secondary branch and is attached to one of the apertural margins of the mother theca. The next to be formed is the thecal tubule of the first theca of a given cladium.

All possible transitions are encountered in the position of the typical thecal cladium and that of the sicular cladium. In cyrtograptids the mother theca of the first thecal cladium may vary in position. As a rule, however, it is not formed in the close vicinity of the sicula, but at a certain distance from it. In *Cyrtograptus mancki* this is theca 7 or theca 8, in *C. rigidus* theca 8 or theca 10 of the procladium, while in other species the position of the mother theca of the first thecal cladium may be still more distal, being that of theca 30 or theca 40 of the procladium. Very interesting relations have been established in this respect in *Sinodiversograptus* (Mu & Chen, 1962). In this form the development of a colony, after the formation of some number of thecae on the procladium, is followed by a gradual development of the sicular cladium and then next of the thecal cladia budding on both primary branches. The first to be formed is the thecal cladium budding from theca 1 of the procladium, followed by the next thecal cladia budding from the successive thecae (thecae 2^1, 3^1, 4^1, and so on). After seven thecal cladia have been produced on the procladium, the first thecal cladium starts, budding from theca 3^2 of the sicular cladium. The following thecal cladia are produced on the successive thecae (4th, 5th, 6th, and so on) of the sicular cladium. In mature *Sinodiversograptus* colonies the total number of thecal cladia is up to 20 and even more. Moreover, the thecal cladia form here (particularly so on the procladium) a continuous morphological series, leading from the most proximal thecae (1st, 2nd, 3rd) to the most distal ones (15th, 16th, 17th) (fig. 5). The more proximal thecal cladia are formed earlier than the distal ones. The sicular cladium does not in any respect deviate from that series and buds from the sicula which, consistently with our previous considerations, may be called the zero theca of the procladium (0^1), and the formation of a cladium on it precedes the thecal cladium of theca 1^1. The presence of a continuous series of cladia budding from theca 0^1 (the sicula), thecae 1^1, 2^1, 3^1, and so on of the procladium, allows the sicular cladium to be regarded as a peculiar case of the thecal cladium of theca 0^1 (fig. 5). The same fact is obviously suggested by the mode of budding of the sicular cladium. Hence, the thecal cladia on the procladium are homologous with the sicular cladium, while the latter is not a morphological equivalent of the procladium. Therefore, it might reasonably be supposed that the regularities encountered in the development of the diversograptid thecal cladia will also be expressed in the development of the diversograptid sicular cladia.

Data available clearly indicate that the monograptids which develop a bipolar rabdosome during the mature stage of astogeny (procladium +sicular cladium), in their early stage pass through a monograptid stage, characterized by the presence of the procladium alone (Strachan, 1952; Mu & Chen, 1962). Hence the formation of the sicular cladium is somewhat delayed and occurs together with the growth on the growing tip of the procladium. The latter consists of thecae of the distal type, differing from the proximal thecae in size, and mostly also in structure. Thus it would be reasonable to suppose that — in contrast to the proximal thecae of the procladium — the sicular cladium of diversograptids would produce from the very beginning thecae of the distal type.
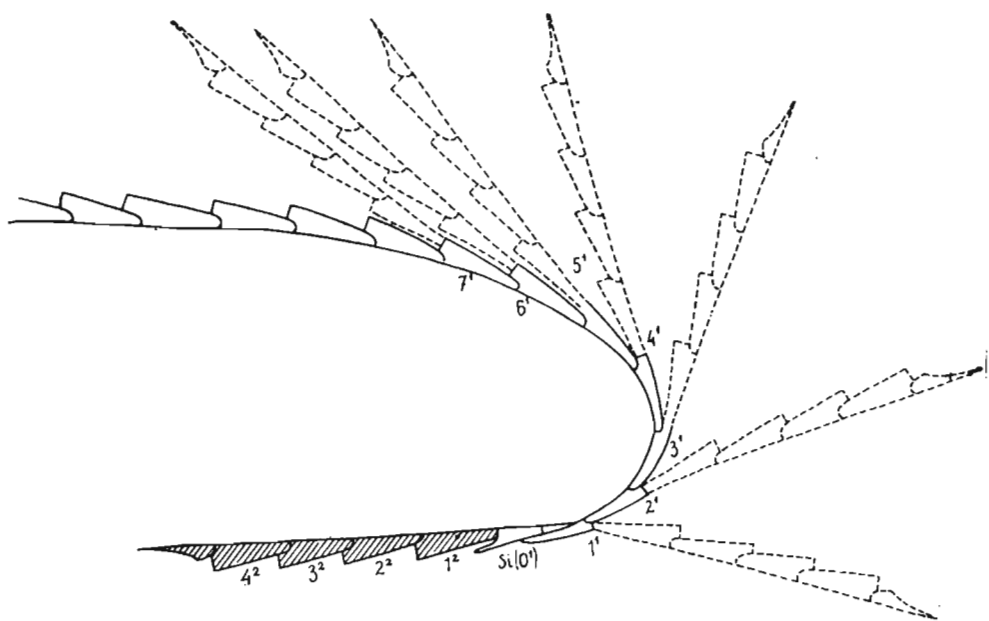

Fig. 5. — Diagram showing the relation of typical thecal cladium to sicular cladium, based on conditions recognized in cyrtograptids and *Sinodiversograptus*. Sicular cladium (stippled) may be considered as the thecal cladium of metasicula (theca 0^1) as indicated by continuous morphological series of metacladia representing transients. Further explanations — in text.

si sicula

Indeed, in a form that Strachan (1952) described as *Diversograptus runcinatus* (Lapworth) (fig. 6), the proximal thecae of the sicular cladium are seen to be distinctly wider and displaying a general resemblance to the distal thecae, in contrast to the proximal thecae of the procladium. This has not been described by Strachan, but is clearly enough figured in his drawings. Moreover, it is confirmed by Thorsteinsson's observations, who etched a specimen of *D. runcinatus* (Thorsteinsson, 1958, p. 97) from the Silurian limestones of Cornwallis Island in the Ca-

nadian Arctic Archipelago. According to a personal communication of Dr Thorsteinsson (1960), in the diversograptids examined by him the sicular cladium starts with thecae of the distal type. This fact is regarded by him as an expression of the same regularities that he had previously encountered in the thecal cladia of *Cyrtograptus*. The same
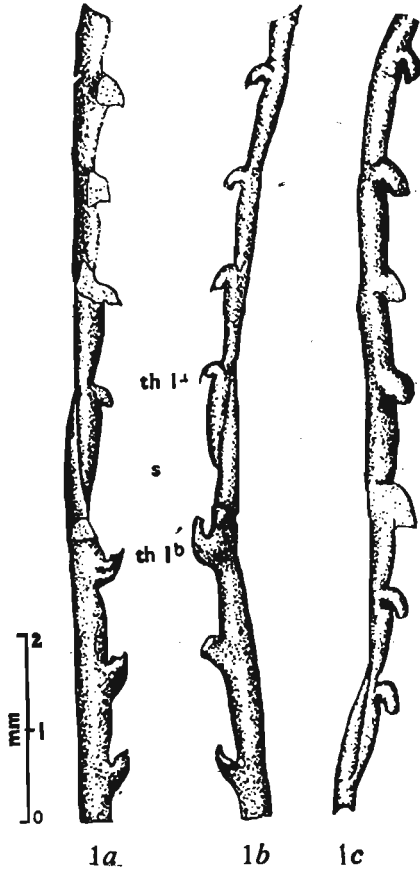

Fig. 6. — *Diversograptus runcinatus* (Lapworth), bipolar rhabdosomes showing differences in size of thecae on procladium and sicular cladium (*A, B*) and monograptid stage in astogeny (C). Glenkiln Burn, Dumfriesshire (from Strachan, 1952).

conditions probably occur in *Sinodiversograptus* in which Mu and Chen (1962, p. 153) found the procladium and the sicular cladium to "have an uniform width of 0.8 mm, except the proximal portion of the main stipe where the thickness is slightly smaller".

Doubtless the same conditions also characterize *Neodiversograptus nilssoni*, described here (comp. text-pl. IV, fig. A_1, A_2). Theca 1^2 in this form resembles the distal thecae of its procladia, but is in extreme contrast with the appearance of the proximal thecae. Similarly, though less distinctly, theca 1^2 in *Neodiversograptus beklemishevi* n.sp. (comp.

text-pl. VI, fig. A_1, A_2) differs in appearance from the proximal thecae of procladia, common to this group of species, in the presence of a certain sigmoid curvature of the ventral metathecal wall.

In both cases, the proximal thecae of the sicular cladium in size and shape agree with thecae which were formed simultaneously with them in the distal part of the procladium. This indicates that the development of the sicular cladium was considerably delayed as compared with that of the procladium, while the regularities observed in the development of cyrtograptid thecal cladia are expressed also in the development of sicular cladia in diversograptid forms[16].

The above facts permit to extrapolate these regularities on the processes of the formation of all cladia in colonies of multiramous monograptids and to regard the relations first described by Thorsteinsson in cyrtograptids as the general and fundamental law of cladogeny.

It is here suggested to call this law the *"Thorsteinsson rule"*, in honour of Dr R. Thorsteinsson, the outstanding Canadian geologist and palaeontologist, who was the first to emphasize the presence of these regularities. The Thorsteinsson rule may also be described as "the law of morphological equivalence of simultaneously budding thecae of the same rhabdosome", which states that the simultaneously budding thecae of the same graptolite colony have the same size, shape and structure, independently of their position in the rhabdosome.

EXAMPLES OF PROCESSES OF REGULATION OF COLONIES (PSEUDOCLADOGENY)

The facts described above may have some value for the elucidation of the development of multiramous monograptid colonies produced by the formation of sicular cladia. These processes, which are a part of the complicated astogeny of such colonies, may be termed cladogeny. They express the normal processes of colonial development in the group of Linograptinae.

Here below the writer reviews facts that may be distinctly referred to quite another group of phenomena. They concern the regulation or regeneration of graptolite colonies which, in an attempt to reconstruct the lost parts of the rhabdosome, give rise to the formation of pseudocladia, i. e. regenerative branches.

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[16] The determination of definite relations of the astogenetic succession of thecae on the particular cladia of *Linograptus* meets with greater obstacles owing to the inadequacy of the material now available and in view of the character of its cladogeny. In *Linograptus* we are dealing most probably with an accelerated formation of branches, which are produced in a rather short time. In this connection the structural differences between the first thecae of the successive branches are very slight and not readily established (comp. p. 190).

Up to now the particular investigators were in most cases unable to correctly distinguish the morphological results of these processes, which were often described under common anatomic terms (bipolar or "bilateral" rhabdosomes), or even regarded as representing the same taxon (*Diversograptus*), as formally they complied with certain diagnostic features (bipolar growth from a common point of divergence).

This taxonomic usage is not, however, justified by the result of anatomic-comparative analysis. It is now beyond doubt that bipolar rhabdosomes may be produced by two different modes, either in result of the regeneration of damaged branches (text-pl. XIV, fig C, D) or through normal astogeny that leads to the formation of sicular cladia (text-pl. XIV, fig. A, B). The colonies that are formed in result of either of these processes display certain superficial analogies, but there is no doubt that they differ fundamentally in their biological and taxonomic significance.

Lobograptus scanicus parascanicus (Kühne, 1955)
(text-pl. XV, fig. A—F)

Material. — A fragmentary rhabdosome consisting of two thecae that probably belong to a primary branch, and of one theca of a secondary branch that is being formed most likely by way of regeneration (specimen A). Also 5 short fragments supposedly representing various stages of regeneration of the cladia (specimens B—F). The material has been etched from erratic boulder S. 181 from Czarnogłowy, in western Pomerania, probably a fragment of a flat marly concretion. Hence all specimens belong to the same population and the same zone (chronodeme).

Description. — Specimen A (text-pl. XV, fig. A_1, A_2) represents a fragmentary rhabdosome in which the growth of thecae was bipolar from a common point of divergence. One of the branches, about 2.30 mm long, is represented by two thecae (theca n, $n+1$). The more distal one $n + 1$) is 1.55 mm in length, as measured from the aperture of theca n, the total length being approx. 2.20 mm. It is nearly complete, with the exception of the left metathecal wall which is broken off. This damage appears to have occurred *in vivo*, since the peridermal margins are almost smooth and slightly thickened. On the other hand, the breaking up of the rhabdosome above theca $n+1$ is probably incidental, due to its state of preservation. The more proximal theca (n) is only partly preserved as a metathecal fragment, approx. 0.65 mm in length. The apertural lobes and the ventral wall of this theca have been destroyed and only the side walls, protruding freely as short plates, have been preserved. The lower margin of the right plate probably results from a breaking up of the rhabdosome which has taken place during the life-time. It has been very characteristically smoothed out and slightly swollen, and

TEXT-PL. XIV
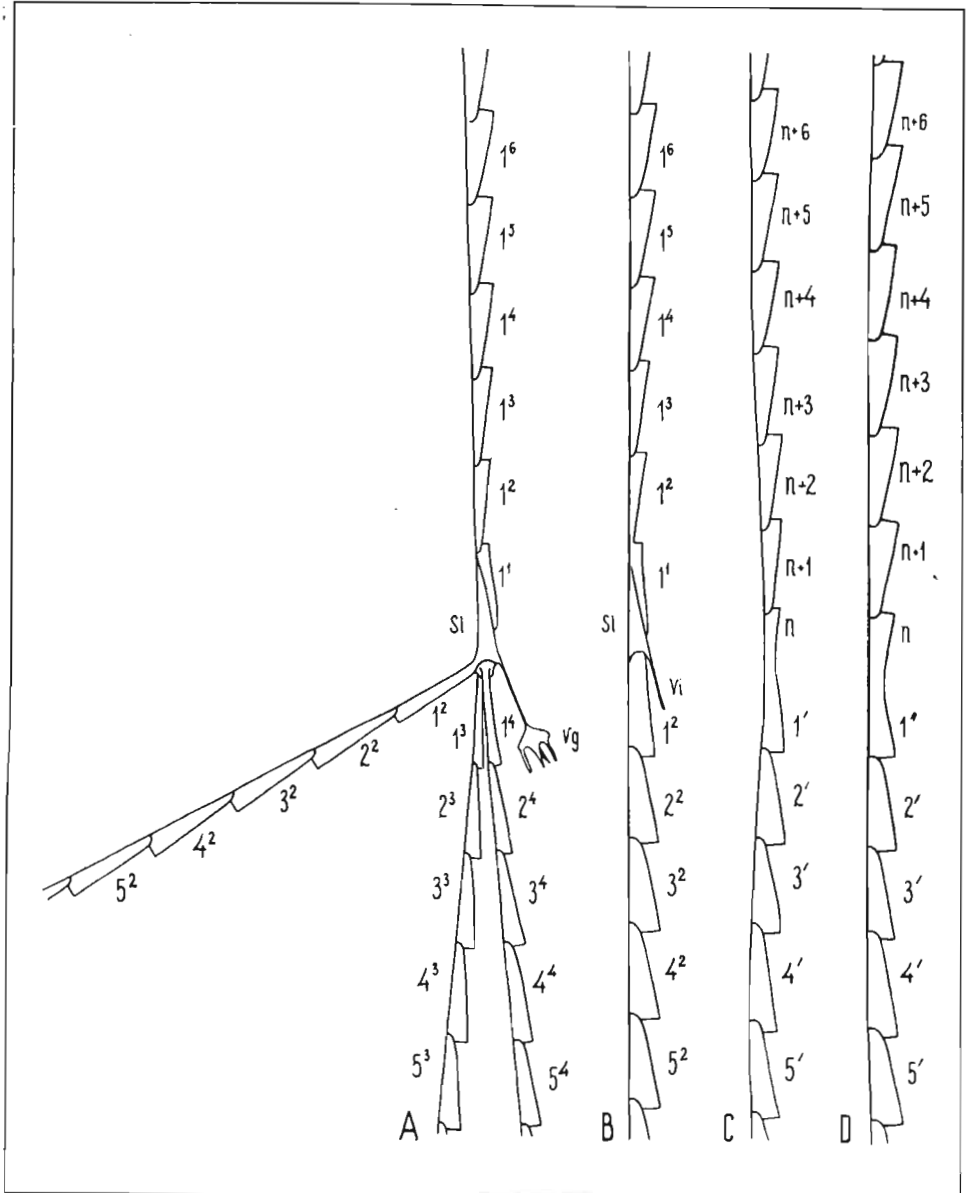
Comparison of structure of multiramous (A) and bipolar (B) rhabdosomes formed in process of normal cladogeny, with bipolar morphoses formed owing to regeneration and showing contrast in size of initial thecae on primary and secondary branches (C) or without such a contrast (D). Further explanations — in text.

n, $n + 1$ successive thecae on primary branch, $1'$, $2'$ successive thecae on regenerating branch.

thus bears signs of healing up. On the shape of both thecae, and most particularly on the structure of the apertural lobes, it is quite doubtless that the specimen represents a fragment of a *Lobograptus scanicus* rhabdosome, and probably of its subspecies *parascanicus* (Kühne) whose mass occurrence in this association has been observed.

Below theca n occurs the base of the theca of the secondary branch which grows in an opposite direction to the growth of the primary branch. This theca ($1'$) attains a length of approx. 2.10 mm, and in relation to the primary branch it is slightly more ventrally directed. The base of this theca, approx. 0.20 mm in width, has a strongly wrinkled, uneven periderm. A distinctly protruding margin or rib (d) that probably indicate the discordance between the periderm of theca n and that of theca $1'$, is visible on both sides, but particularly so on the left side (for zooid) (fig. A_2). In its position this obliquely placed rib resembles the so-called "oblique septum", frequently described from bipolar diversograptid rhabdosomes, preserved on the surface of rocks (Bouček & Přibyl, 1953). While the contact of the fusellar system of theca n with that of theca $1'$ was realized along that oblique rib, the prothecal tubule is ventrally quite flat and partly produced by a fragment of the interthecal septum of theca n of the primary branch, onto which the fuselli of theca $1'$ have been superposed.

The structural conditions at the point of divergence, particularly the mode of connection of the inner cavities of the primary branch with those of the secondary branch, reasonably suggest that this joining up was effected directly by the theca $n + 1$ to theca $1'$ outside of the inner cavity of theca n.

It is not excluded that in result of the breaking up of the primary branch at the level of metatheca n, the corresponding zooid had been subjected to necrosis or degeneration. Owing to the primary branch being broken off this theca became "uninhabited". The zooid of theca $n + 1$ may possibly also have experienced similar processes and this is suggested by lack of distinct sign of repairing of the damaged metathecal periderm.

In some aspects theca $1'$ differs from the shape of theca n and theca $n + 1$. Near the aperture its width is 0.35 mm, while in theca $n + 1$ it is 0.42 mm. The metatheca seems shorter, too. It is about 0.32 mm long and its apertural lobes have a shape not typical of this species. This might suggest certain morphological disturbances connected with the regeneration of theca $1'$.

The next theca of the secondary branch ($2'$) is in an incipient stage, being represented only by a very short fragment of the protheca. The termination of the secondary branch indicates that it was still growing. It is extended as a long thread, the virgula — probably regenerative, which here protrudes to a distance of approx 3 mm. Owing to

TEXT-PL. XV
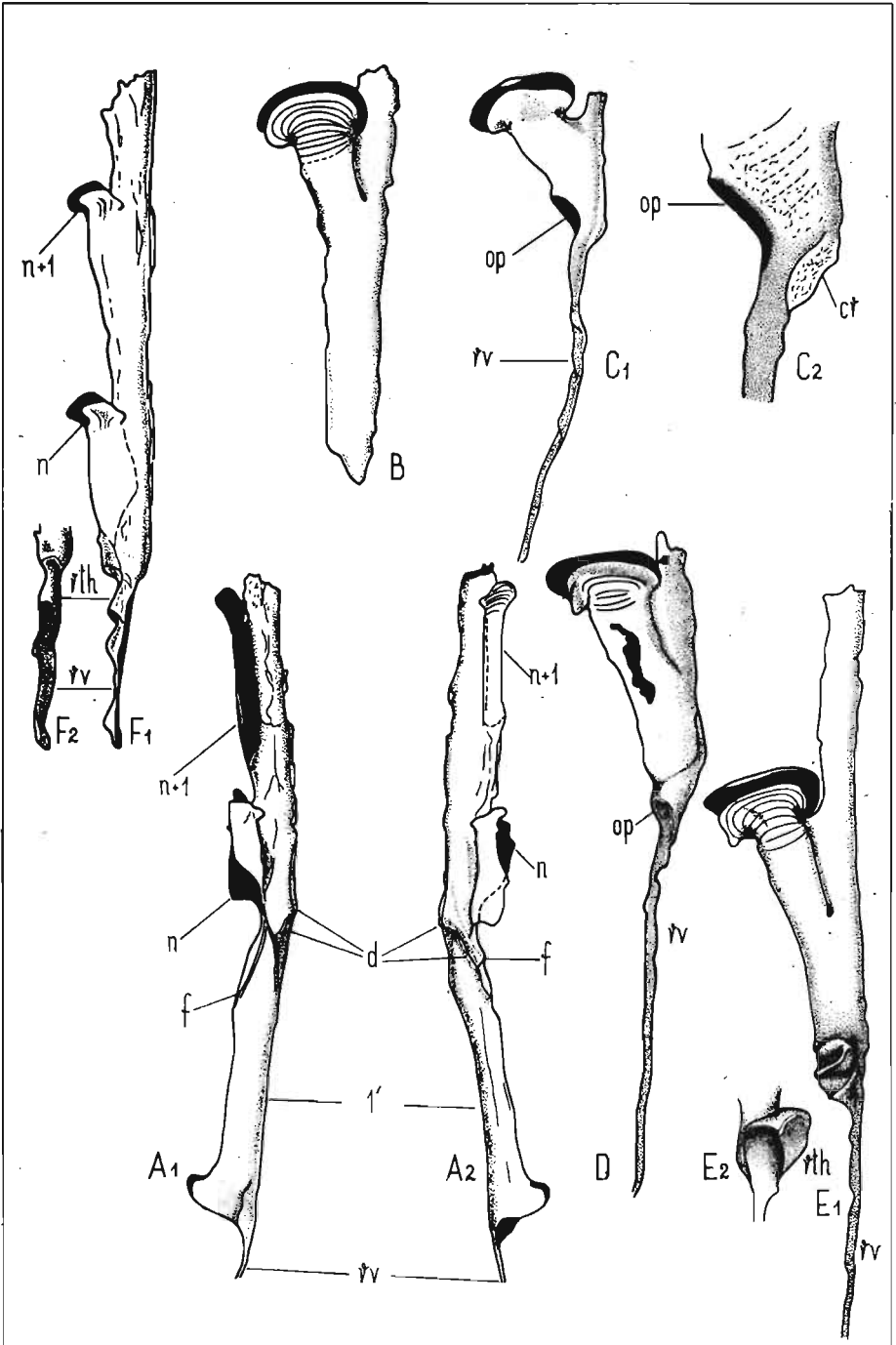
the strong carbonization of the periderm it is not possible reliably to establish the mode and place of its formation or its relation to the virgula of the primary branch.

Interpretation of specimen A. — This specimen represents a bipolar rhabdosome with no sicula at the point of divergence, but bearing distinct signs of a breaking up of the primary rhabdosome. This is suggested by the damage of the specimen and by the presence of discordance between the periderm of theca n and theca $1'$. Most probably, thecae n and $n + 1$ belonged to the primary branch, while theca $1'$ was part of a secondary branch in an early stage of growth. It is, however, hardly possible quite conclusively to establish which of the thecae belonged to the primary branch and which ones to the regenerative branch.

The process of development of theca $1'$ budded from theca n that had probably been previously broken up, is not comparable with the formation of thecal cladia or of sicular cladia in multiramous forms. It may rather be correlated with the phenomenon of regeneration or colonial regulation. A secondary branch thus formed may well be called the "pseudocladium" (comp. p. 147). Specimen A, however, is too short to provide sound evidence concerning the morphological sequence of thecae on the pseudocladium, particularly in view of the signs on theca $1'$ of the existence of a certain morphogenetic disturbance.

Description of specimens B—F. — These specimens represent probably successive stages of the regeneration of a cladium. The structure of the well preserved apertural lobes indicates quite reliably that these thecae belong to *Lobograptus scanicus*, probably to its subspecies *parascanicus* (Kühne).

Specimen B (text-pl. XV, fig. B) is the fragment of single theca, approx. 1.40 mm in length, probably once a part of a larger fragment of the rhabdosome from which it was broken up *post mortem*. Hence the breaking up of the above theca seems accidental and due to the state

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Text-pl. XV
Lobograptus scanicus parascanicus (Kühne)
Regeneration of rhabdosome. A_1-A_2 region of divergence of a rhabdosome with bipolar growth, from both sides; B theca, probably in early stage of regeneration of rhabdosome; C_1 more advanced stage of same process showing regenerative virgula; C_2 same specimen, details of structure of basal part of theca; D primary theca with regenerative theca and virgula in incipient stage of formation; E_1 regenerative theca visible as protuberance of periderm; E_2 ventral view of same specimen; F_1 fragment of rhabdosome with incipient regenerative theca; F_2 same specimen, ventral view of basal part (boulder S. 181, Czarnogłowy, western Pomerania); A_1-A_2, F_1-F_2 ca. × 22.5, C_1, D, E_1-E_2 ca. × 43, C_2 ca. × 95
cr crest-like outgrowth at the base of regenerative virgula, *d* line of discordance between fusellar system of primary and regenerative thecae, *f* secondary folds of periderm, *n*, *n + 1* successive thecae of primary branch, *1'* completely formed regenerative theca (first theca of pseudocladium), *op* opening formed due to damage of theca, *rth* regenerative theca, *rv* regenerative virgula.

of preservation. On the lower part of the protheca, however, there are distinct signs of a breaking up of the theca, probably still during the life-time. This is suggested by the characteristically smoothed up margin of the opening thus formed, whose longer diameter is approx. 0.10 mm. The margins of this opening are secondarily thickened, most likely owing to the deposition of the additional peridermal material, and they seem darker than the remaining part of the periderm. On the left the margin of the opening bears a small triangulate projection with strongly thickened periderm. Specimen B probably represents a theca that had been broken up basally *in vivo*, while the first attempts toward a regeneration of the theca, indicated by the thickening of the basal foramen and the presence of a projection, had already been made by the zooid.

Specimen C (text-pl. XV, fig. C_1-C_2) also represents but one fragment of a theca, approx. 0.45 mm in length, which was a member of the proximal part of the rhabdosome. The breaking up of the thecal tubule above the thecal aperture seems secondary and due to the state of preservation, while the damage of the lower part of theca is undoubtedly primary. This resulted in the formation of an opening, approx. 0.14 mm in longitudinal diameter, and approx. 0.11 mm in transverse diameter. The margins of the opening are perfectly smooth, thickened, and dark owing to the secondary deposition of the peridermal substance. Dorsally the theca continues downward as a relatively long virgula (1.12 mm long) whose irregular course and variable thickness (greatest at the base of theca) indicate that it did not constitute the virgula of the primary cladium, but that it is of regenerative nature. This is likewise suggested by a crest-like excrescence at the base of the theca and the regenerative virgula near the opening (fig. C_2). Specimen C, similarly as specimen B, probably represents a theca that had been broken up *in vivo* at the boundary of the protheca with the metatheca, while before burial in the deposit the zooid had already succeeded partly to heal up the margins of the opening and to regenerate a fragment of the virgula. Obviously we are not dealing here with an ordinary healing up of the theca, but with a more advanced process. This is moreover indicated by lack of a cicatrice in the opening and by the reconstruction of the virgula. The traumatic impulse probably liberated here the ability of regeneration, permitting the budding of a new zooid from the mother zooid, growing along the fibre of the regenerative virgula.

Specimens D-E on the whole closely resemble specimen C, though they probably represent a slightly more advanced stage (text-pl. XV, fig. D).

Specimen D, approx. 1 mm long, has already produced a kind of short thecal tubule which may constitute the base of the regenerating

theca that grows in an opposite direction to that of the growth of the mother theca along the here present fibre of the regenerative virgula.

Specimen E (text-pl. XV, fig. E_1-E_2) consists of a fragment, 1.70 mm in length. At the very base, close to the broken up margin, it has produced an incipient wall, seen from the left side, which probably represents the beginning of a regenerating theca, too. This young regenerating theca has the appearance of a distinct protuberance of the periderm (fig. E_2).

Specimen F (text-pl. XV, fig. F_1-F_2) is a fragmentary distal part of the rhabdosome, approx. 3.5 mm long, and consists of two thecae (n and $n+1$). The upper portion of protheca n is abnormally developed; it bears traces of a cicatrice of the opening that must have been caused owing to a *in vivo* breaking up at a distance of approx. 0.50 mm from the metatheca. This opening is but partly cicatrized, since at the lower end it continues as a thin tubule, approx. 0.25 mm long, terminating in a free opening (rth) and resting on a groove-like peridermal process with irregular margins, up to approx. 1.13 mm in length and 0.09 mm in width. This process is probably an equivalent of the regenerating nema (fig. F_2 rv). The tubule just mentioned probably communicates with the inner cavity of theca n — though this could not be quite certainly recognized — and constitutes the incipient regenerative theca that grows in an opposite direction to that of the growth of the primary cladium.

Interpretation of specimens B-F. — These specimens may most likely be interpreted as the early stages of the formation of theca 1 of the regenerative cladium (pseudocladium) which starts at the place where the primary branch had been broken off. Specimen A may represent a more advanced stage of a similar process, after the formation of theca 1 of the pseudocladium. Specimens A-F, which have all been etched from the same sample, probably belong to a population whose colonies have often been exposed to damage and hence the regeneration of the cladium was a common phenomenon there.

Systematic position. — Specimens A-F are supposedly conspecific; their apertural lobes display a distinct but small degree of asymmetry and partly overlap. In view of the lack in the associated assemblage of the characteristic distal thecae of *L. scanicus scanicus,* all these forms most probably belong to *L. scanicus parascanicus* Kühne.

Stratigraphic range. — All the specimens here considered have been etched from an erratic boulder S. 181 from Czarnogłowy (western Pomerania), kindly presented to the writer by the late Professor R. Kongiel and Dr A. Wilczyński. This boulder is probably a fragment of a marly ashy-bluish concretion. *Lobograptus scanicus parascanicus* (Kühne), which occurs in great abundance, is the dominant fossil. It is

associated with: *Cucullograptus pazdroi* Urbanek, *Pristiograptus dubius*
(Suess), *Saetograptus chimaera* Barrande (very rare), and *Holoretiolites
mancki* (Münch). This fauna leaves no doubt that the boulder comes
from the *scanicus* zone as currently defined.

Linograptus posthumus (Reinh. Richter, 1875)
(pl. III, fig 1-2)

Material. — Two specimens, representing bipolar rhabdosomes, but
deprived of the sicula at the point of divergence of two thecal series.
The specimens are preserved on the rock surface and their periderm,
only partly damaged, permits a thorough examination of the outline and
relation of the internal cavities of thecae. These specimens belong to
the collection of Dr L. Teller (Geological Laboratory of the Polish
Academy of Sciences, 6, Żwirki i Wigury, Warsaw). The specimens have
been prepared by Dr Teller from the core of a deep-boring at Chełm
(central Poland) drilled by the Geological Institute (Warsaw). In a paper
by Teller (in print) they are described as result of the regeneration of
branches in *Linograptus posthumus*. These specimens have been turned
over to the writer for closer investigations. Specimen *A* has been col-
lected at a depth of approx. 1553.5 m, specimen *B* — from approx.
1554.9 m.

Description. — Specimen *A* represents a fragmentary cladium, con-
sisting of two thecal series that grow in an opposite direction from the
same point of divergence. The first series consists of 12 thecae of a total
length of approx. 15 mm, practically agreeing in size and shape. This
series represents a thecal type more common in the distal parts of
cladia of *Linograptus posthumus*. The thecae are 1.1 to 1.2 mm long.
Their basal width is 0.25—0.30 mm, up to 0.50 mm near to the aperture.
The ventral walls of thecae are slightly geniculated, while the dorsal
margin of thecae is straight.

At a distance of approx. 1.1 mm from the aperture of theca 1 of
this series, there is a certain discontinuity of the peridermal structure.
The ventral wall is irregularly thickened, the dorsal wall slightly con-
vex. The point of divergence of both thecal series occurs here. The
aperture of theca 1 of the second thecal series, growing in an opposite
direction, is lying at a distance of 1.2 mm from the peridermal thicken-
ing on the ventral wall. The second thecal series, of a total length of
approx. 3.2 mm, consists only of two thecae provided with an aperture,
and of a fragment of third theca, of which the base only is preserved.
The thecae of this series have slightly larger dimensions than those of
the first series. Theca 2 of the second series is approx. 1.3 mm long,
0.40 mm in basal width, while at the aperture it is approx. 0.60 mm
wide. The terminations of the two thecal series do not seem original;

they may have been longer, but have perhaps been secondarily damaged.

Specimen *B*, similarly as specimen *A*, is a fragmentary cladium consisting of two thecal series that grow in two opposite directions from the same point of divergence. The first series consists of approx. 15 thecae, practically agreeing in size and shape. This series is about 20 mm long. The thecae represent a morphological type, common in distal or median parts of the cladium of *L. posthumus*. The thecae are 1.5—1.6 mm in length, 0.25 mm in width at the base, and approx. 0.50 mm wide near the aperture. The ventral walls of thecae form a distinctly sigmoid curvature ("geniculum"), while the dorsal margin of theca is straight. At the point of divergence of two thecal series, the ventral wall is provided with two protrusions. The upper one probably corresponds to the aperture of the most proximal theca of the first series (pl. III, fig. 2), while the lower one may be merely a tattered fragment of the periderm of the same theca. At this point the theca was either broken off, or it represents a somewhat abnormally developed aperture of the most proximal theca of the second series. In any case, the partly preserved periderm of the theca, and the continuity at the point of divergence of both the ventral and the dorsal wall, reasonably exclude the supposition that these protrusions are merely tattered fragments of the periderm of another specimen, underlying it similarly as the object lying next to it (pl. III, fig. 2 *p*).

The second series consists of three well preserved thecae and two other ones, distinctly outlined on the specimen. Originally this series probably contained more thecae. In size the thecae of the second series hardly differ from the neighbouring thecae of the first series. Theca 2 of this series is approx. 1.3 mm long, 0.20 mm wide at the base, and about 0.50 mm wide at the aperture.

Systematic position. — The structure and dimensions of the preserved fragments reasonably refer them to *Linograptus posthumus* (Reinh. Richter). In spite of the lack of the characteristic proximal part of the compound rhabdosome, the specific identification is facilitated by Dr L. Teller's observation (1963, personal comm.) that the assemblage in the layers which yielded the specimens here considered contained solely *L. posthumus*.

Stratigraphic range. — The specimens here described were collected from the borehole at Chełm, at a depth of 1553.5—1554.9 m. These layers belong to a zone determined on the occurrence of a new species that will be described in Dr Teller's paper under the name of *Pristiograptus bugensius* Teller and which occurs directly above the "*Monograptus*" *formosus* Bouček zone. According to the most recent terminology, introduced by Tomczyk for the western framing of the East-European Platform, this zone occurs within the lower part of the "Podlasie Beds" (Tomczyk, 1962).

TAXONOMICAL AND BIOLOGICAL SIGNIFICANCE OF THE PHENOMENA
OF REGULATION OF COLONIES

In the present writer's opinion, the only reasonably probable and acceptable interpretation of rhabdosomes showing bipolar growth, which lack a sicula at the point of divergence of two thecal series, is the concept that these rhabdosomes result from the process of regeneration (regulation) of the rhabdosome. Most probably, the primary branch — in the case of *Lobograptus scanicus parascanicus:* the procladium (comp. p. 213), and, in the case of *Linograptus posthumus*: the procladium or one of the metacladia (comp. p. 220) — had been broken off with the result that its more proximal (sicular) part was detached from the distal fragment. A secondary zooid, growing in an opposite direction to that of the growth of zooids of the primary branch, was produced by way of regeneration from that distal fragment where the soft tissues of the zooids had been damaged. From this regenerative zooid, by way of budding, a whole series of descendent blastozooids, forming the secondary regenerative branch, was subsequently produced. This secondary branch was characterized by its growth in opposite direction to the growth of thecae on the primary branch. In view of its peculiar mode of formation, this branch merits special attention and must be distinguished from the other cladia, formed in the process of astogeny. It is here suggested to call it the "pseudocladium" (comp. p. 147).

A confirmation of the formation of the bipolar rhabdosome of *Lobograptus scanicus parascanicus* in connection with the breaking up of the primary branch, is provided by the presence at the point of divergence of the two thecal series of a distinct discordance of the fusellar systems. On specimen *A* these are visible as a ribbed elevation placed obliquely in relation to the thecal walls. Other specimens of this species, previously described, have also retained at the point of divergence more or less distinct traces of discordance between the periderm of the primary and that of the secondary branch. Thus the formation of colonies with bipolar growth must have obviously been preceded by the breaking up of the primary branch. Hence, it should be accepted that the formation of the secondary branch of the rhabdosome consists in a process of the regeneration (regulation) of colonies.

Graptolite colonies, particularly those consisting of long and thin thecae, must have been particularly susceptible to damage by breaking up, due to various physical or biological factors. This is particularly true of such groups as the Cucullograptinae and the Linograptinae. The rhabdosomes in the mentioned groups produce long thread-like or hair-like branches, during the life-time probably extremely elastic. Traces of this elasticity have persisted in the fossil state in that the longer fragments of etched rhabdosomes are very flexible in glycerine when

touched with a brush or a hair. Nevertheless, the colonies of these grap-
tolites must have been frequently damaged by being broken off. Hence
it is not surprising that the first doubtless occurrence of the breaking
off and regeneration of the rhabdosome is encountered in graptolites
with this type of colonies.

In view of their fragmentary nature, examples of the regeneration
of the branches in *Lobograptus scanicus parascanicus* here described are
not sufficient for a more detailed investigation of the growth relations
between the primary and the secondary branch. The specimens of *Lino-
graptus posthumus*, with longer preserved fragments of the two bran-
ches, do, however, suggest certain inferences concerning the mutual
relation of astogenetic succession on both branches. While in specimen
B the two thecal series hardly differ in dimensions, in specimen *A* one
of the series has thecae distinctly larger than those in the other series.
Hence the cladia display a slightly different astogenetic succession.

It seems soundly justifiable to suppose that some of the previously
described rhabdosomes, which have a bipolar growth of the thecae and
lack the sicula at the region of divergence of the two branches, were
formed by regeneration, too. Certain forms described by Bouček and
Přibyl (1952) as various "species" of *Diversograptus*, seem particularly
referable to this category of bipolar rhabdosomes. This material con-
sists of a number of forms, among which the most significant speci-
mens are supposedly those belonging to three "species": *Diversograptus
globosus* Bouček & Přibyl (text-pl. I, fig *B*), *D. inexpectatus* Bouček &
Přibyl (text-pl. I, fig. *C*), *D. gracilis* Bouček (text-pl. I, fig. *D*). These
three forms are relatively well represented and better preserved, thus
permitting a more thorough investigation of the structure of the region
of divergence of the branches.

It is a well known fact that Bouček and Přibyl (1953) (comp. p. 139)
have established the lack of the sicula at the point of divergence of the
two branches. After examining the original material described by these
authors, the writer was able personally to ascertain that the presence
of the sicula at the region of divergence of the growth of branches can-
not be established in any one of their specimens. This cannot, however,
be regarded as quite doubtless owing to the unsatisfactory state of pre-
servation of most specimens, in which the periderm is often replaced
by a silvery film of mineral substance, or else is badly damaged. *D. glo-
bosus* described by Bouček and Přibyl occurs in association with *Mono-
graptus sartorius* (Bouček & Přibyl, 1953, text-pl. 4, fig, 10, 11) (whose
proximal parts seem to be provided with the sicula). On the specimens
of *M. sartorius* here considered, however, the sicula is very indistinct.
It is not clearly delimited from theca 1^1, and its virgella is hardly dis-
cernible, too. Hence, it may reasonably be supposed that it would hardly
be possible to establish the presence of the sicula in the region of diver-

gence in *D. globosus* which displays a similar state of preservation. Specimens of *D. inexpectatus* are better preserved, particularly so its holotype (Bouček & Přibyl, 1953, text-pl. 5, fig. 1—3; pl. 3, fig. 3). This specimen and its counterpiece are somewhat compressed; the periderm is partly preserved, and partly visible on the rock as an impression on the surface impregnated by pyrite. The region of divergence is most satisfactorily preserved in the counterpiece of the holotype occurring as a shallow depression on the rock with the structural details of the periderm visible. The oblique septum is here seen as a low rib, probably corresponding to the primary furrow of the periderm.

Considerable significance was ascribed to the presence of this oblique septum by Bouček and Přibyl, who pointed out to its occurrence in a number of other forms (comp. p. 139). The writer has, however, been able to establish that most of these structures are extremely indistinct, hardly discernible and not well identifiable (comp. Bouček & Přibyl, 1953, *D. globosus*, text-pl. 4, fig. 10, 11; *D. gracilis*, text-pl. 3, fig. 1). Moreover, in some specimens such an oblique septum was not discernible. Apparently we are dealing here with a strongly variable structure, possibly merely a superficial discordance of the periderm, such as that of the fusellar system between the primary branch and the pseudocladium, indicating the line of the breaking up of the rhabdosome. Hence the "oblique septum" would correspond with the peridermal discordance observed in *Lobograptus scanicus parascanicus*, suitably modified owing to the state of preservation of the Bohemian specimens (comp. p. 215). This would practically cancel the only sound justification in support of Bouček's and Přibyl's concept connecting the "oblique septum" with the hypothetical asexual reproduction of graptolite colonies, realized through the separation (autotomy) of branches by means of such a septum. On the other hand, those authors' second conception postulating that bipolar rhabdosomes are produced by regeneration, is well applicable in these cases. An additional argument advanced by Bouček and Přibyl in confirmation of the latter concept is that one of the branches of such bipolar rhabdosomes is often, from its very beginning, thicker and broader than the other branch. This can be readily seen on those authors' specimens redrawn on our text-pl. I, fig *C, D*). In the light of the data now available, this fact cannot be regarded as conclusive evidence that such branches resulted from regeneration. Indeed, the initial width of the procladia and of the sicular cladium may differ radically (comp. p. 210) also during processes of normal cladogeny.

Hence, though Bouček and Přibyl's material does not provide completely doubtless evidence as to the presence or absence of the sicula in the region of divergence of the two branches, still it seems reasonably probable that at least some of these specimens developed through the regeneration of rhabdosomes. Some indirect facts confirm this supposi-

tion. The strong homaeomorphism between the thecae of *M. sartorius* and those of the bipolar rhabdosomes of *Diversograptus globosus* has been stressed already by Bouček and Přibyl. The inference that the latter thecae are referable to the regeneration of branches of *M. sartorius*, seems sound enough. They cannot, however, be regarded as forms produced by the budding of the sicular cladium, since, according to the writer's observations, near the point of divergence the two branches are wider than the most proximal (sicular) rhabdosome fragments in *M. sartorius*. This seems also applicable to other forms.

It seems doubtless that also other forms with bipolar rhabdosomes result from the process of regeneration. They were described by Jaeger (1959) from the Lower Ludlovian of Thuringia as *Diversograptus* sp. (redrawn on our text-pl. I, fig. A); later they were etched from erratic boulders and identified by the same author, first (1959) as *Diversograptus* too, but subsequently as representatives of an asexual generation of a monograptid from the *nilssoni* group, characterized by alternation of generations (1960) (redrawn on our fig. 1, p. 144). The latter forms are of particular interest as they have been more closely studied by Jaeger who believed that their formation is connected with the alternation of generations.

The material here considered justifies a critical approach to some of Jaeger's arguments. There is no conclusive evidence for his recognition that such bipolar rhabdosomes were produced from the hypothetical multiplication corpuscles or free-living buds. That author's observation of the presence in the region of divergence of the two branches of only a structureless membrane, supposedly protecting the multiplication corpuscles, is hardly a confirmation of his theory of the origin of bipolar rhabdosomes. Even if the absence of the fussellar structure is not secondary, i.e. due to the state of preservation[17], it should be remembered that the structureless peridermal membrane is often produced in graptolites during processes of thecal regeneration in the vicinity of damaged areas (Kozłowski, 1948/1949; Urbanek, 1958). It might also be stressed here that no free peridermal coatings of the multiplication corpuscles have so far been described, neither do we know the growth stages of such multiplication corpuscles, showing symmetrical and bipolar growth. If we are dealing with a process of astogeny realized after Jaeger's suggestion, these growth stages may be expected to accompany the more advanced forms of astogeny. Neither does the lack at the point of divergence of the oblique septum — in Jaeger's opinion an argument against the regeneration theory of the formation of bipolar rhabdosomes — seem to possess the significance assigned by Bouček

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[17] In the basal parts of thecae the fusellar structure is indeed frequently effaced owing to the partial decomposition of the periderm (comp. conditions described here for *L. posthumus*, text-pl. IX, fig. C).

and Přibyl. These structures do, by no means, occur in all the regenerating rhabdosomes and their absence in specimens described by Jaeger does not deny the concept that their formation, too, resulted from regeneration.

There are, however, certain facts which do suggest that such forms may have been caused by regeneration. One of them is the abnormal course of the virgula at the point of divergence, as is observable on Jaeger's (1960) specimens and, to a certain extent, resembling the anomalies in the course of the virgula in *L. scanicus parascanicus* (see specimen C — text-pl. XV). This course of the virgula may be due to its primary breaking off and to the formation of a new regenerating virgula along which the growth of the pseudocladium was taking place.

In Jaeger's opinion, the restriction of bipolar rhabdosomes to a certain species only speaks against the regeneration theory of their formation. Should this concept be true, such rhabdosomes would — according to that author — occur in many other monograptids whose thin rhabdosomes are very susceptible to damage by breaking off. At present, upon the discovery among the Linograptinae and the Cucullograptinae of doubtless cases of regeneration, this argument has evidently lost its significance.

Hence, the regeneration theory seems the most acceptable one also in the case of forms discovered by Jaeger (1960), since the facts described by that investigator may be more readily interpreted by the regeneration theory than by the more complex and not soundly substantiated concept concerning the alternation of generations in monograptid colonies. Additional confirmation of the regeneration theory of the formation of similar bipolar rhabdosomes is provided by the description of the growth stages of *Diversograptus gracilis* (Bouček) (Bouček & Přibyl, 1953, pl. 3, fig. 9; text-pl. 3, fig. 3—5). It is clearly seen there that one of the branches is distinctly longer and consists of a number of thecae, while the other branch is much shorter and may consist only of 1 or 1 $1/4$ theca. This indicates that the growth of the two branches was from the beginning neither simultaneous nor symmetrical, but asymmetrical owing to the earlier formation of one branch in relation to the other.

The recognition that bipolar rhabdosomes, lacking the sicula at the point of divergence, were produced through regeneration, does not evidently imply that they are — according to the views of Bouček and Přibyl (1953), and of Jaeger (1959) — representatives of the same strictly defined taxonomic unit. Such rhabdosomes are merely the expression of a certain type of morphosis, resulting from the process of regeneration and their formation is not due to the phylogenetic processes. The phylogenetic lineages comprising such forms (e.g. Jaeger's earlier hypothesis on the origin of Linograptinae, 1959), — are fictitious, while

the taxa, in which such forms are grouped, are merely more or less incidental assemblages of species, whose most frequent feature in common is the presence of a thin rhabdosome. In *"Diversograptus"* — such as now currently understood by the majority of investigators — are indeed in the first place assembled the "thin" monograptids whose rhabdosomes are most readily damaged and which produce the most frequent bipolar forms due to regeneration. The erection of a separate family of the Diversograptidae for the group of such forms, or the assignment of the particular species to the genus *Diversograptus* merely on their ability to produce bipolar regenerating rhabdosomes, is evidently unjustified. A suggestion of this kind (proposed by Bouček and Přibyl, 1953) disagrees distinctly with the principles of the regeneration theory, claimed by these authors for the formation of such forms.

Facts indicating that bipolar rhabdosomes may also be produced by way of regeneration call for an investigation of the systematic status of the genus *Diversograptus* Manck in which, according to Manck (1923): "die Entwicklung des Tieres geht vom breiten Ende der Sicula aus. Die Hauptzweige wachsen nach entgegensetzter Richtung, und zwar entweder fast geradling nach beiden Seiten verlaufend..." (p. 283).

Diversograptus ramosus Manck, 1923, was selected by Bulman (1929) as the lectotype species of this genus. It has not so far been established that one branch of this type species truly represents the sicular cladium. Strachan (1952) writes that "the material studied by Manck was all rather poorly preserved (the graptolites being found as silvery films on the black shales) and he was unable to say how two main stipes arose from the sicula" p. 365).

Among the rich *Diversograptus* material described by Bouček and Přibyl from Bohemia and Germany, *D. ramosus* is likewise well represented. The presence or absence of the sicula in the region of divergence cannot, however, be established in these specimens. Hence, the occurrence of a sicular cladium in *D. ramosus* is still an open question. Should the absence of the sicula in the region od divergence in *D. ramosus* be conclusively proved by future studies, it would not then fit into the generic diagnosis given by the author of the genus. A complete elimination, however, of the name and concept of *Diversograptus* does not seem purposeful inasmuch that the existence has been proved of similar bipolar monograptids provided with a sicular cladium, showing, however, some differences in the thecal shape as compared with *"D."* ramosus group (Strachan, 1952; Thorsteinsson 1960, personal comm.). In this case, this generic name should be connected with the species *D. runcinatus* Lapworth, one of whose branches was first shown by Strachan (1952) to represent the sicular cladium. Evidently, the priority of the correct generic definition would then belong to Strachan.

The presence of either the sicular part or the sicula has not so far been found in any bipolar rhabdosomes whose formation may be referred to regeneration. Most likely, in all the specimens so far considered we are dealing with the process of regeneration of the distal part of the rhabdosome (text-pl. XVI), the sicula not being reproduced on the secondary branch in result of regeneration. A biological comparison
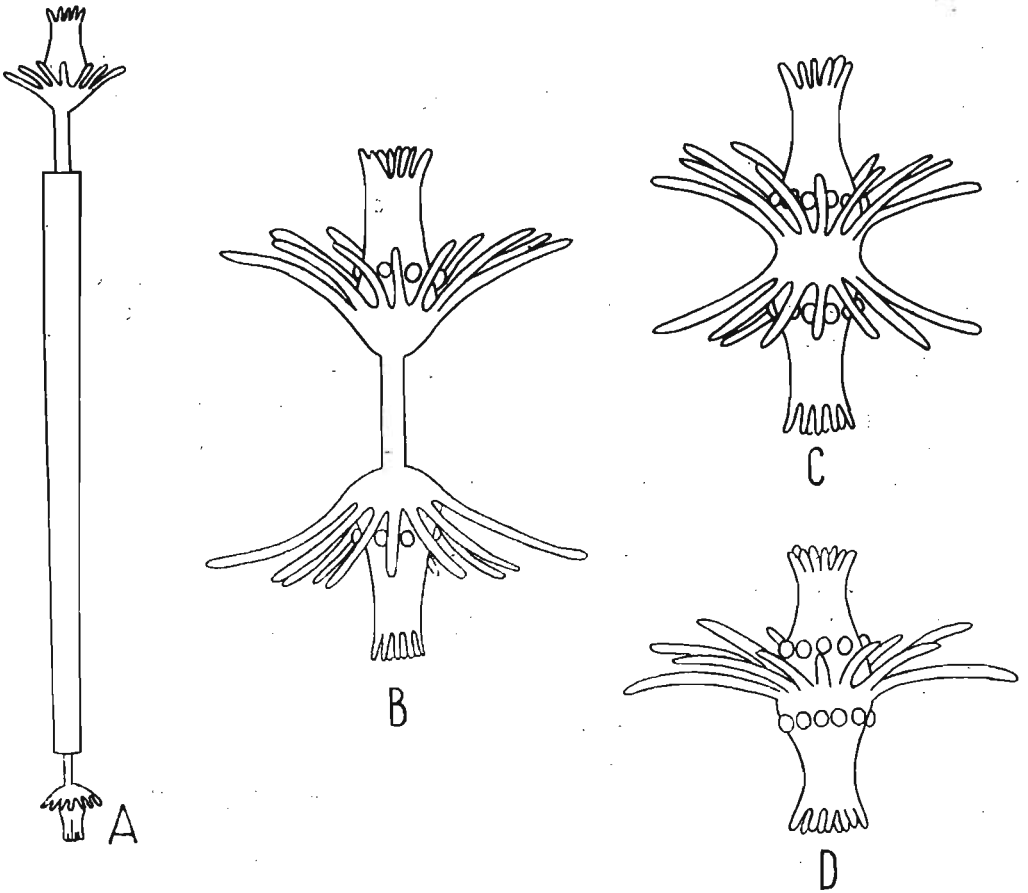

Fig. 7. — A-D Formation of bipolarly growing twin-individuals due to regeneration in Tubularia (after Child, 1941).

of this process of regeneration in the branch of a graptolite colony with that in recent animals suggests certain analogies with atypical regeneration i.e. heteromorphosis, in which the lost part is only partly reproduced. This process is easily understood since regeneration is simply a multiplication of the zooids, realized by way of budding while the formation of the sicula is connected with a process of sexual reproduction (Kozłowski, 1948/1949). All these cases are also connected with the change in the direction of growth of the secondary branch in respect to the

primary one. In the recent animals, analogous processes have been ob-
served during regeneration of hydrozoans. For example, in *Tubularia* the
regeneration of damaged branches often results in the formation of bi-
polar colonies, the twin zooids produced by way of regeneration being
at a varying distance one from the other (Child, 1941) (comp. fig. 7).
A closely similar phenomenon of the reversal of growth direction
has been observed on the hydrocaulia of a colonial hydrozoan *Pennaria*

Fig. 8. Formation of bipolarly growing colony in *Pennaria* after regeneration
of a cut off fragment of main stem (hydrocaulion). Regenerative part in solid black
(after Gast & Godlewski, 1903).

cavolinii (Gast & Godlewski, 1903). The cutting up of a fragment from the
main axis of the colony, from which lateral branches were produced at
a certain angle, results in regeneration of the removed part, which in
turn produces side branches that grow in an opposite direction to that
of the side branches of the primary stipe (comp. fig. 8). Hence, the
formation of bipolar colonies may also be spoken of when referring to

the regeneration of colonies in *Pennaria*. It may be supposed that such processes as the incomplete regeneration of the lost part of a colony, changes in astogenetic succession of the regenerating branch, reversal of the direction of growth, — all represent in the process of colonial regeneration analogous phenomena to those expressing the reversal of polarity during individual regeneration of recent animals.

TENTATIVE DETERMINATION OF THE FUNDAMENTAL REGULARITIES IN ASTOGENY

A study of the regeneration processes in damaged branches may probably just as importantly contribute to the knowledge of regularities in monograptid astogeny as the investigation of their normal astogenetic development. Examples illustrating this process of regeneration may be, indeed, a kind of experiments of Nature. Their appropriate investigation and interpretation may provide important information concerning the biological organization of graptolite colonies.

The general applicability of the law of morphological equivalence of simultaneously budding thecae, established by Thorsteinsson (1955), reasonably suggests that this regularity is expressed in every phenomenon of cladogeny, hence including the regeneration processes of the rhabdosome (pseudocladogeny), too. This would reliably explain the differences in the astogenetic succession of both branches (comp. p. 223), established in the regeneration of colonies. The larger size of the initial thecae of one branch might be interpreted as an expression of the law of morphological equivalence of simultaneously budding thecae. In the case of regeneration of the distal fragments of the rhabdosome, to which all the examples of colonial regeneration here considered may be referred, the initial thecae of the pseudocladium would develop simultaneously with the more distal, terminal thecae, on the growing tip of the primary branch. Hence, that branch which may, with great probability, be regarded as the secondary, regenerative branch, starts at once with thecae of the distal type.

These phenomena also throw some light on the factors responsible for the normal course of astogeny. In the astogenetic development of the Monograptidae a regularity is generally recognizable in the morphological succession, that is expressed by changes in the size and proportion of thecae, and in their structure (text-pl. XVI, fig. *A*). These changes occur after a very gradual and regular, as well as directional pattern suggesting that they are caused by the occurrence of a morphophysiological gradient (Urbanek, 1960). Most probably, the mechanism of this process may perhaps consist within each colony in the production and distribution of suitable morphogenetic substances. These substances

might be produced by the oozooid (siculozooid) and gradually used up by the stock of the budding individuals along with the growth of the colony. Thus the morphogenetic substances, responsible for the development of certain features, would gradually and regularly decrease with the growth of the colony. The regular gradient of the morphogenetic substances would also give rise to gradual and directional morphological changes in the successively budding individuals of a colony. These changes would at the same time express the decreasing potential of morphogenetic induction, i.e. an increasing physiological isolation of the successive blastozooids from the centre of induction (siculozooid) (Urbanek, 1960).

On the other hand, it may be supposed that the physiological activity of blastozooids was not expressed by the use of morphogenetically active substances (,,competition theory"), but, on the contrary, by their production[18]. This would lead up to the gradual increase of the amount and concentration of such substances in colonies whose regular growth, along with the budding of new zooids, would, through the increasing induction, give rise to morphophysiological gradients. The distal type of thecae, characterized by appropriate dimensions and proportions, or by the presence of definite morphological characters, would in this case result from an increased induction of the morphogenetic substances and not from their decrease.

The present status of the knowledge of fossil material does not warrant an undisputed exclusion of the second alternative. All the examples of the normal astogeny and of regeneration, so far examined, may reasonably be interpreted in the light of the first, as well as of the second hypothesis. There is a complete lack, however, of any "experimentum crucis" that would suggest a preference for either one or the other alternative.

Still some indirect arguments do speak in favour of the first rather than of the second alternative. In the first place it is the fact that the increase in physiological integration of invertebrate colonies is commonly connected with the formation of some centres of dominance. An increase here occurs not only of the interdependence of individuals one from the other, but also of that from the common centre of colonies. In the light of data available, the siculozooid (Urbanek, 1960, p. 150—154) probably represented such a centre in graptolite colonies. Another argument is provided by the fact that the astogenetic succession in graptolites is subject to relatively small infraspecific variations. The morphogenetic substances, therefore, must have been produced in rather precisely defined amounts. If it is accepted that these substances were produced by

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[18] The writer's attention to this fact was drawn by Dr Leigh Van Valen's (New York, USA) most valuable suggestions (in litt.).

TEXT-PL. XVI
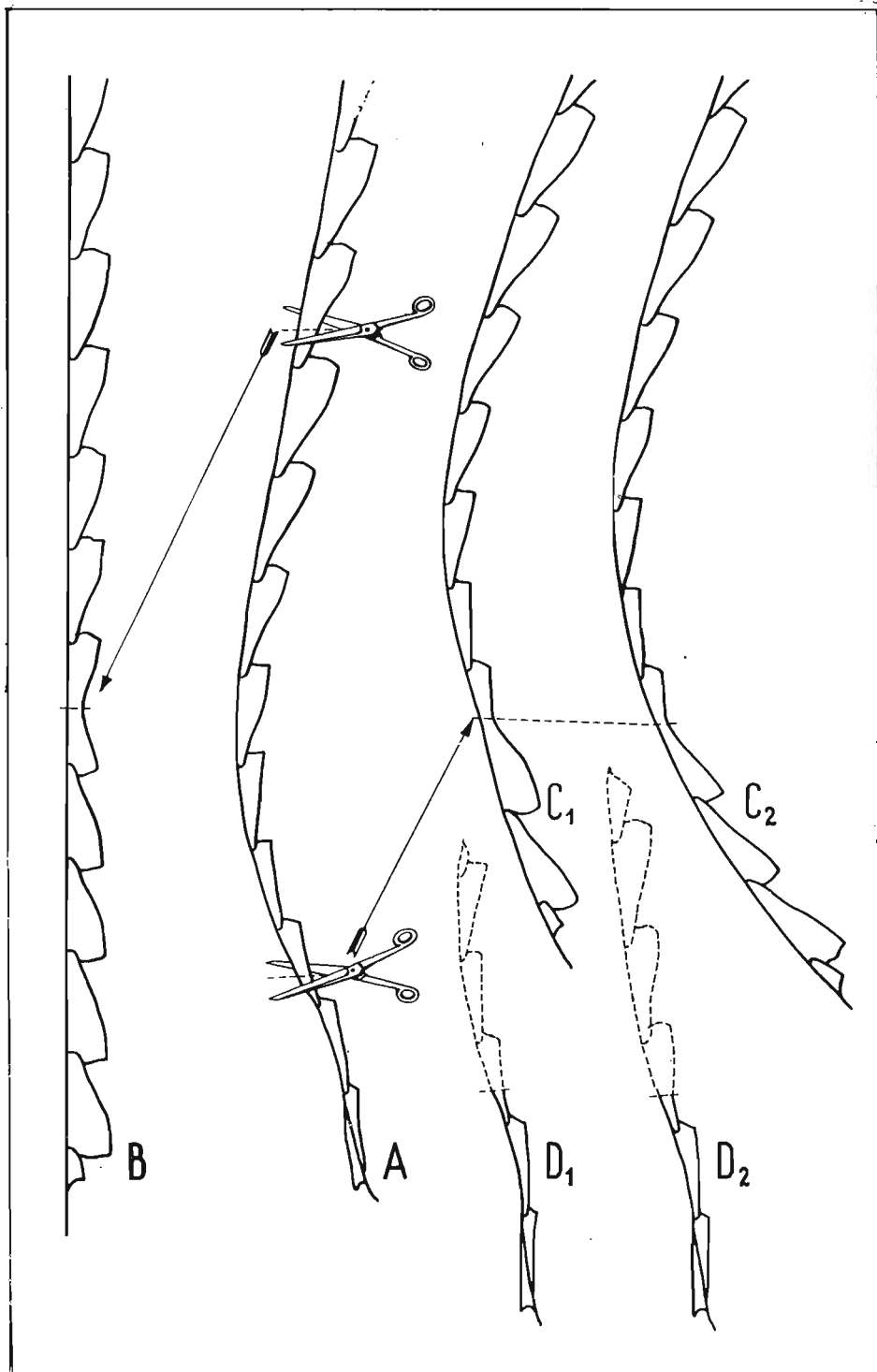
all blastozooids, they cannot be regarded as simple products of metabolism. These are, indeed, inhibitors of growth, while during the astogeny of all the Graptoloidea, a distinct increase of the thecal dimensions occurs along with the growth of the colonies. Hence, these substances should be regarded as peculiar hormone-like secretions, stimulating growth, but their amount also largely depends on the physiological activity of the individuals within each colony, therefore, on their nutrition, too. Such conditions would result in a great lability of the astogeny, which is not observable on fossil material. Indirectly these facts indicate that the amount of the produced substances would have to be rather precisely genetically controlled. The sexual process resulting in the formation of the oozooid (siculozooid) may possibly be the regulator of this production. Thus this point of view, too, apparently supports the concept that the siculozooid occupied a very special position in graptolite colonies. The above speculations reasonably suggest that the most probable hypothesis is the previously advanced one, that the astogenetic succession is due to the process of induction by the siculozooid.

In the light of this hypothesis, the morphological effects that accompany the process of the breaking off and subsequent regeneration of rhabdosomes, are easily understood. If the colony is broken off around the more distal part of the rhabdosome (text-pl. XVI fig. A, the upper shears), it might be expected that, after this hypothesis, the regenerating distal part will produce, at the place of the breaking off, at first a regenerative bud and then a pseudocladium growing in an opposite direction to the growth of the primary branch. The formation of the pseudocladium, however, occurs from the very beginning, under conditions of complete isolation from the inductive influence of the sicular centre which had been subjected to amputation. Hence, all the thecae formed on the pseudocladium, beginning with the earliest ones, are of the distal type and do not differ from the distal thecae of the primary branch. This phenomenon is readily understood in view of the conditions accompanying the formation of the distal type of thecae. Also on the primary branch these were formed under relative physiological isolation from the inductive influences of the sicular centre (partial exhaustion of the inductive substances by the preceding zooids, or perhaps great distance from the siculozooid). Thus, both in the normal

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Text-pl. XVI

Astogenetic succession of thecae in course of normal development of the monograptid colony (A) and in the case of breaking off and regeneration of rhabdosome (B-D). The shears indicate the place of cutting off the primary rhabdosome; B expected effects of regeneration of distal fragment of primary stipe after its breaking up in distal part; C_1-C_2 expected effects of regeneration of distal fragments of primary stipe after its breaking up in proximal part; D_1-D_2 supposed affects of regeneration of sicular fragments of a primary stipe. Further explanations — in text.

astogeny and in regeneration of colony, physiological isolation from the influence of the inductive centre results in the formation of the distal type of thecae.

During the regeneration of the distal part of a colony (text-pl. XVI fig B) both branches will along their complete length bear thecae of the same size and shape. These conditions fit well into the picture of regeneration observed in *Linograptus posthumus* (comp. p. 221; pl. III, fig. 2), "*Diversograptus*" sp. described by Jaeger (comp. text-pl. I, fig. A), "D." *globosus* Bouček & Přibyl (comp. text-pl. I, fig B). A complete physiological isolation here is responsible for the disappearance of the polarity within the rhabdosome.

Different conditions might be expected to follow the cutting off of the rhabdosome in a more proximal part (text-pl. XVI, fig. A, lower shears), since the regenerating branch develops under completely different condition than the primary branch. It is namely produced in complete isolation from the influence of the sicular centre, while the directly adjacent thecae of the primary branch developed under the inductive stimulus of the siculozooid. A structural contrast of the neighbouring thecae at the point of divergence has been caused through differences in the developmental conditions of the two branches. From the very beginning the regenerating branch produces larger and proportionately wider thecae.

In theory, a very sharp contrast might be expected between these branches (text-pl. XVI, fig C_1), actually however, the more common phenomenon is that the first few thecae of the pseudocladium display an intermediate structure, not altogether of the distal type, which is realized by the following thecae (text-pl. XVI, fig. C_2). Thus the procladium displays a, so to say, abbreviated, strongly accelerated astogenetic succession in relation to that of the primary branch. Hence, the contrast between the two branches is less sharp, but none the less distinct. These conditions are observed on specimens identified as "*Diversograptus*" *inexpectatus* Bouček & Přibyl (text-pl. I, fig. C) and "D." *gracilis* (Bouček) (text-pl. I, fig D). The supposedly shortened astogenetic succession may be due to the action of the remainder of the morphogenetic substances, which persisted in the proximal part of the primary branch. The contrast between the primary and the regenerative branch is, however, stronger in *Linograptus posthumus*, specimen A (comp. p. 220; pl. III, fig. 1).

The examples of regeneration in monograptid colonies, so far recorded, concern exclusively the regeneration of the distal portion of the branches. The question, therefore, arises what was the fate of the broken off proximal fragments of the rhabdosomes, including the sicula. One might suppose that at least potentially the sicular parts also had the ability to produce regenerative branches. The greater rarity of this

phenomenon might be explained by a supposition that in most cases such colonies, deprived of their attachment organ and passively floated by currents, were soon destroyed. Moreover, the results of the regeneration of the sicular part, where the regenerating branch retains its original growth direction, are not readily distinguished from other, teratological disturbances of the astogeny. A reliable conclusion as to the existence of peridermal damage calls for an adequate knowledge of the fusellar structure.

The eventual morphological effects that might be expected during the regeneration of the sicular part of the rhabdosome may be foreseen on the basis of the gradient theory concerning organization of graptolite colonies. In case of the amputation of the sicular part of a young colony, in which the morphogenetic substance had been used up in a small extent only, the astogenetic succession of the regenerating branch should not much differ from that of normal astogeny (text-pl. XVI, fig. D_1). On the other hand, in case of the amputation of the sicular part of an older colony, in which the major part of the morphogenetic substance had already been used up in the processes of growth of the zooids, the process of regeneration will be characterized by sharper contrasts between the primary and the secondary thecae which are produced in isolation from the inductive factors (text-pl. XVI, fig. D_2).

The sharp contrast in size and shape of thecae formed on the regenerating branch, thus far lacking causal interpretation, may be now understood on the recognition that the organization of monograptid colonies was characterized by the presence of respective morphophysiological gradients. These facts provide additional support for the above hypothesis, originally based on phenomena connected with normal astogeny and cladogeny. At the same time, phenomena of regeneration in colonies provide convincing proofs of the universal applicability of Thorsteinsson's rule. The example illustrated both in pl. III, fig. 1, and in text-pl. XVI fig. C_1 indicate that the pseudocladial thecae probably correspond to the thecae in the terminal part of the primary branch which are developed simultaneously with them. These conditions very much resemble the regularities accompanying the formation of the sicular cladium in diversograptids and they arise from similar causes (decrease or lack of the inductive factor).

It may, therefore, be concluded that certain, general, and at the same time closely mutually related causal regularities occur during normal astogeny and cladogeny, as well as during processes of the regeneration of graptolite colonies (pseudocladogeny). They are:

1) During the normal astogeny and cladogeny, i.e. the development of the colony from a siculozooid, and always in the presence in a colony of the siculozooid, there is invariably a regular and directional morphological succession of thecae, which is responsible for the occurrence of

the polar organization of cladia, i.e. for their differentiation into the proximal and distal parts, differing in the structure and size of thecae.

2) During the process of pseudocladogeny, i.e. the regeneration of colonies lacking the sicula, and always in the absence in the colony of the sicula, there is invariably a lack of morphogenetic succession of thecae, responsible for the disappearance of polar organization on the growing cladia that grow by way of simple multiplication of the distal type of thecae.

3) During the development of any colony, both in the presence or the absence of the siculozooid, there is invariably a morphological equivalence of the simultaneously budding thecae, independently of their position, which determines their analogous size, structure and shape (Thorsteinsson's rule).

A TENTATIVE CLASSIFICATION OF PHYLETIC CHANGES IN THE DEVELOPMENT OF MONOGRAPTID COLONIES

In respect to the pattern of development of colonies, the monograptids may be classed as a group displaying the monograptid type of astogeny. The monograptid type of development may be defined as that with uniserial and scandent growth of thecae, directed toward the apex of the sicula ("upwards"), beginning with the primary bud produced by way of apertural budding (Kozłowski, 1948/1949). Recent investigations indicate that, though the quoted definitions retain their correctness for the majority of monograptids, still the astogenetic differentiation realized during the evolution of this group calls for some emendations to supplement the classic definitions in respect of some evolutionary lineages.

In most monograptids the process of astogeny gives rise to a colony consisting of a single branch only. The development of this branch is completely stabile in all the forms so far investigated. The primary bud is produced by the siculozooid by way of apertural budding and in this the Monograptidae differ from the Diplograptidae which display a perforational type of budding (Kozłowski, 1948/1949). The remaining blastozooids, too, have fundamentally the same mode of budding (comp. p. 208). Hence, the primary single branch of a monograptid colony is a uniform morphological structure which may justifiably be called the *procladium* (comp. p. 147). In many other forms, however, the process of astogeny does not stop at this stage, but continues to produce additional branches which are the phylogenetic "novelties" acquired in some lineages. The name proposed here for these branches, independently of the place and mode of their formation, is *metacladia* (comp. p. 147). The characteristic pattern in the evolution of astogeny in the Monograptidae

is that, while the mode of the development of the procladium is stabi-
lized, a tendency is displayed in many phylogenetic lineages to produce
additional branches as a kind of superstructure, based on the founda-
tion of the primary branch of the colony. These additional branches arise
in different ways in the particular evolutionary lines and thus suggest
the distinction within the monograptid type of development of certain
stages that correspond to the stages of phylogenetic modifications of the
astogeny of Monograptidae (text-pl. XVII).

The use of the term "stage" with reference to the particular devel-
opmental phases of a definite compound colony is self evident. In this
meaning Strachan (1952) speaks of the "monograptid stage" in the devel-
opment of colonies of *Diversograptus* and *Cyrtograptus*. Mu and Chen
(1962) have gone further by calling the various astogenetic stages of
Sinodiversograptus the 1) "streptograptid stage", 2) "diversograptid stage",
and 3) "sinodiversograptid stage". The term "stage" is used in the
same meaning in the present work in descriptions of the successive
periods of development of compound colonies of *Neodiversograptus*
n. gen. and of *Linograptus*. Yet an analysis of changes in the evolutio-
nary lines so far investigated indicates that they consist in the phylo-
genetic modification of astogeny, realized by the gradual appearance,
development and spreading of new characters that alter the pattern of
colonial development. This applies both to phylogenetic phenomena in
structural modifications of thecae (Urbanek, 1960), and to the evolutio-
nary process of the compound rhabdosome (cladogeny). In this meaning
we may speak here about *phylastogeny,* analogous to processes of phy-
lembriogeny (Severtzoff, 1931), and indicating the existence of mutual
relations between phylogeny and astogeny. Therefore, it seems well
justified to use "stage" also with reference to the particular phases of
phylogenetic modifications of the astogeny (stages of phylastogeny). The
respective phylogenetic stages, thus understood, would. at the same time,
determine the maximum degree of complexity, attainable during the
development of a colony of a given species or genus. All of them would,
however, pass through a monograptid stage of varying duration, provi-
ding a phylogenetic and astogenetic foundation for the development of
compound colonies. In the astogeny of the compound colonies there is
a distinct parallelism to the morphological processes that occur in the
phylogeny of a given group. This is reliably indicated by the develop-
ment of a *Linograptus* colony, previously described, which passes through
the monograptid and the diversograptid stage. Additional suggestions in
this respect are provided by Jaeger's (1959) observations on the paralle-
lism in the development of *Abiesgraptus* and *Linograptus*, also those by
Mu and Chen (1952) on the development of *Sinodiversograptus*, which
"possibly reflects the evolutionary series of *Streptograptus — Diverso-
graptus — Sinodiversograptus*" (p. 152).

The names used by the writer for the particular stages of the phylogenetic modifications in astogeny are based on names of genera in which the given stage is most completely expressed. It is believed that these terms should be rather of comparative-anatomical than phylogenetic meaning. Hence, it seems more appropriate to use one name to define the same structural and developmental type of colonies, independently of differences that may occur, e.g. in thecal structure or in origin of the given forms. The writer, therefore, only speaks of the "monograptid stage" and does not consider it necessary to introduce the terms "pristiograptid stage", "streptograptid stage"[19], "lobograptid stage" etc. Similarly only the "diversograptid stage" is mentioned, with the exclusion of the "neodiversograptid stage", for the last names seem to refer more justly to actual phases in the evolution of the particular phylogenetic lineages, than to morphological stages in the evolution of colonies (comp. p. 193).
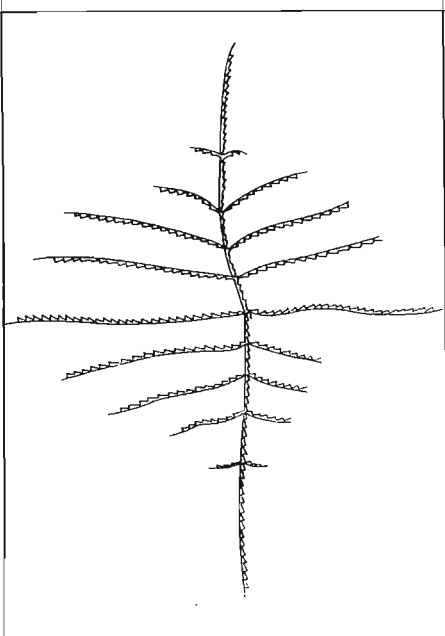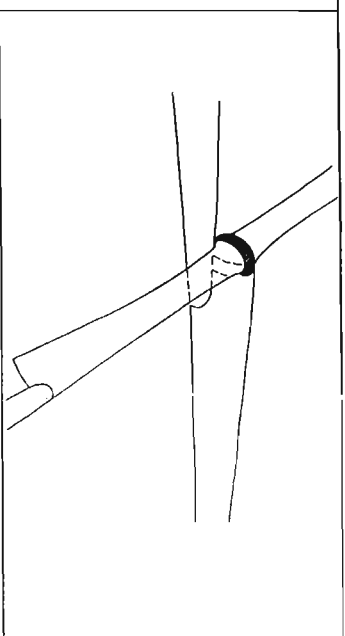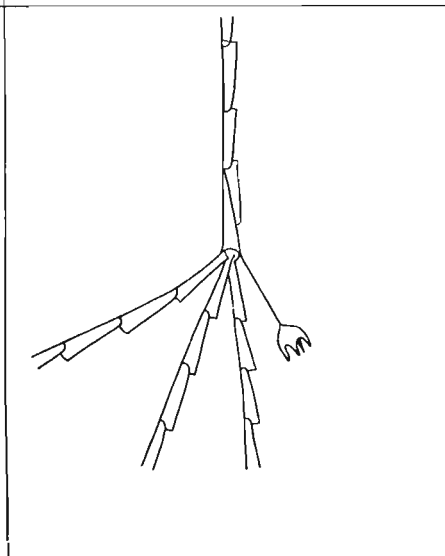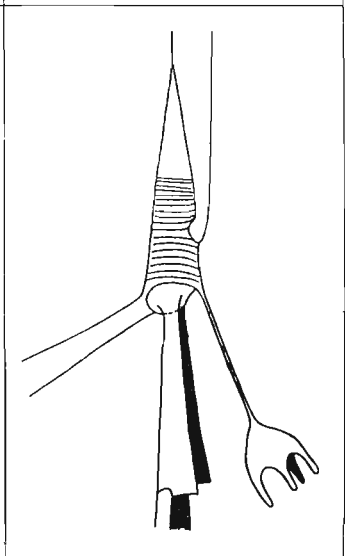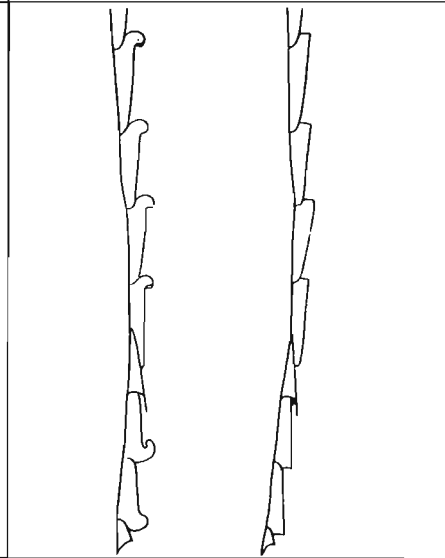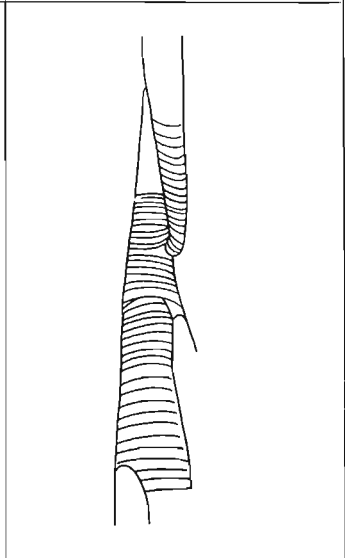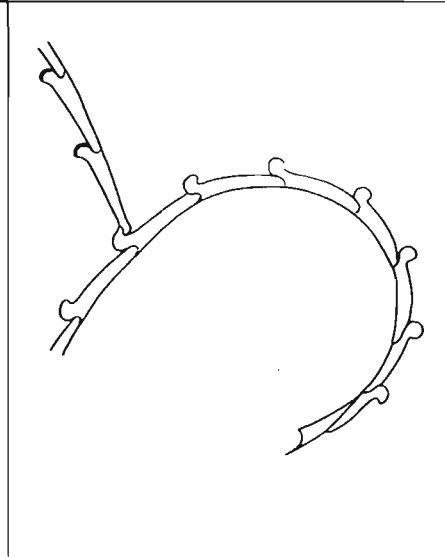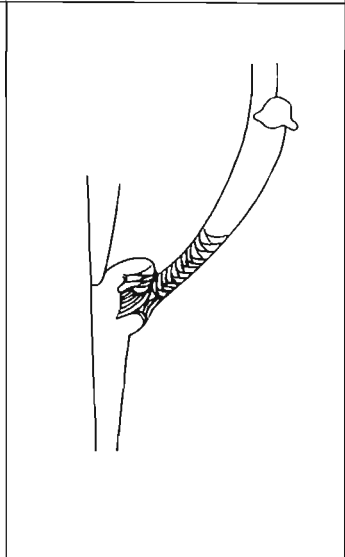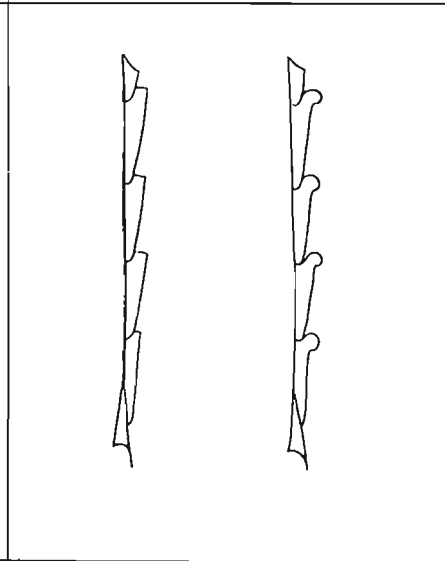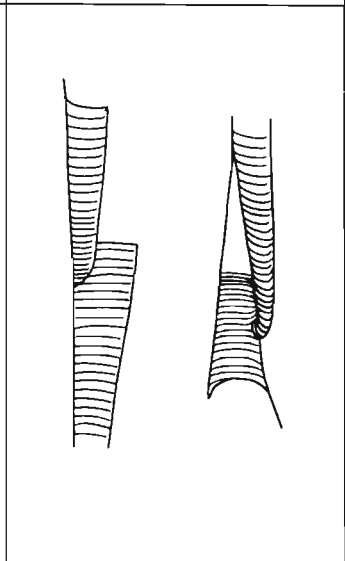
The particular stages of the monograptid type of evolution would differ from the analogous stages distinguished by Bulman (1936, 1938) in the diplograptid type of development, in that they do not express the modifications in the mode of formation of the primary branch which retains a constant pattern of development throughout this group. They merely express the various modes of formation of the secondary branches. Differences in the morphological meaning of the term "stage" result, in both cases, from differences in the evolutionary trends, which have divergent tendencies in these two families.

Most likely the primitive stage of astogeny is represented by one--branched colonies, having only the procladium. Though this type of development characterized various monograptid genera, the writer proposes to call it the "monograptid stage", for it is characteristic of *Monograptus* — the type genus (text-pl. XVII).

A closer examination of the mode of budding of thecae in the monograptid stage shows that the primary bud and all the other thecae are formed aperturally, but below the definitive aperture of the respective mother theca (comp. p. 208). Hence, a certain restriction of the meaning of apertural budding, as suggested by Kozłowski (1948/1949), seems advisable. The budding of all thecae on the procladium would then represent a variety of that mode of budding for which it is here proposed to

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[19] The use of the name „streptograptid stage" and the distinction of *Streptograptus* now meets certain difficulties. The type species (*M. nodifer* Törnquist), for which Yin claimed a coiled apertural lobe of the theca, actually displays a perfectly different structure. On the basis of well preserved Swedish forms, Dr B. Waern (Uppsala) (personal comm.) arrived at the conclusion that, contrary to Yin's suggestion, the apertural lobe in this species is not spirally curved, but that its structure had been correctly described by Törnquist (Undersökningar öfver Siljansområdets Graptoliter", 1892, pl. 2, fig. 27, 28). In this connection the erection of a separate genus on the established morphological differences seems doubtful.

Stage of development	General appearance of rhabdosome	Characters of budding
abiesgraptid		
linograptid		
diversograptid		
cyrtograptid		
monograptid		

Stages of phylogenetic modifications of astogeny within the monograptid type of development (stages of phylastogeny). The abiesgraptid type of budding restored largely conjecturally on its supposed analogy to multiple budding of sicular cladia in *Linograptus*. *Abiesgraptus* colony redrawn form Jaeger (1959, fig. 25). Further explanations — in text.

introduce the name of "subapertural" or "monograptid budding" (comp. p. 148).

The cyrtograptids are a group of forms probably belonging to several phylogenetic lineages, which display a tendency to produce metacladia represented in this group by the thecal cladia. The latter develop on the mother thecae, i.e. on the appropriate thecae of the procladium (comp. p. 148). In certain cases thecal cladia of a "higher order" may have been formed, and their mother thecae would be the corresponding thecae of the thecal cladium of a "lower order". The term "cyrtograptid stage" — after the genus *Cyrtograptus* representing this stage — is proposed for such a stage of phylogenetic modifications in the astogeny (text-pl. XVII). The budding of the first theca on the thecal cladium from the corresponding mother theca of the procladium differs in its style of budding from that of the thecae on the procladium. The descendant theca buds here directly from the definitive aperture of the corresponding mother theca (Thorsteinsson, 1955). This mode of budding, characterizing the first theca of the thecal cladium, should be distinguished as a variety of the apertural type of budding under the name of „supraapertural" or „cyrtograptid budding" (comp. p. 148).

A separate group of forms comprises the Monograptidae in which the metacladium is represented by a single sicular cladium, e.g. in *Diversograptus runcinatus* and *Neodiversograptus nilssoni*. Such forms, though doubtless belonging to separate phylogenetic lineages, morphologically represent the same phylogenetic stage of modifications of the astogeny, for which the name of the "diversograptid stage" is here suggested (text-pl. XVII). The formation of the first theca of the sicular cladium occurs by way of direct budding from the definitive aperture of the metasicula. The writer proposes to introduce for this case the term "diversograptid budding" which is actually equivalent with the supraapertural budding, though the mother theca is here represented by the metasicula (comp. p. 148).

In certain diversograptids (*Sinodiversograptus*) two types of metacladia may have been realized: the sicular cladium and the thecal cladia produced on the two main cladia of rhabdosome. This type of astogeny may be called the "cyrtograptid stage, attained on a diversograptid foundation". Perhaps it would be correct to recognize it as a particular stage of the monograptid type of astogeny, but in principle it does not express new modes of the formation of cladia or of budding, but merely a combination of those previously described. Hence it seems more justifiable to accept it as the evolutionary phase of a defined phylogenetic lineage than as a stage of phylogenetic modifications in the astogeny of the whole group of Monograptidae.

The Monograptidae which have the ability to produce a number of sicular cladia (*Linograptus*) would represent the "linograptid stage" in the

evolution of colonies. In this stage of development, a number of descendant thecae, initiating the particular cladia, are budded independently from the aperture of the metasicula. This mode of budding may be distinguished as the "linograptid mode of budding". It is connected with a change in the growth directions of the first sicular cladium, which does not grow in the continuation of the procladium, but displays a certain divergence from it (text-pl. XVII).

Abiesgraptus displays a mode of colonial development which permits to regard it as a representative of a separate stage of astogeny. The rhabdosome here consists of the procladium and a certain number of sicular cladia. During later development thecal cladia are successively formed on the two main cladia, one of which represents the procladium, the other — one of the sicular cladia. However, in what regards the degree of astogenetic modifications, this stage is not merely a simple combination of the linograptid and cyrtograptid stages of development, for the thecal cladia here are produced in pairs, on either side of the aperture of the mother theca (Jaeger, 1959). This style of formation of thecal cladia is not recognized in any other monograptid, though it does constitute a certain analogy with the budding of sicular cladia of the metasicular aperture in *Linograptus*[20]. This type of cladogeny may be distinguished as the ,,abiesgraptid budding", a variety of apertural budding. It characterized the "abiesgraptid stage" of astogeny.

Stratigraphic data reasonably suggest that the astogenetic stages, here distinguished, represent the successive phases of progressive complications in the structure and development of colonies. The oldest known monograptids (from the *Orthograptus vesiculosus* and *Pristiograptus cyphus* horizons) are all one-branched, and therefore represent the monograptid stage. This basic and ancestral type of colony has been not only simple, but also extremely stabile, persisting to the highest horizons of occurrence of Monograptidae. It would seem that the earlier phases in monograptid evolution consisted rather in modifications of thecal structure, expressed by the occurrence during the Lower Silurian of a number of evolutionary trends. The earliest trend of thecal elaboration starts to operate already in the *cyphus* zone by the appearance of some forms, showing hooked thecae in proximal part of rhabdosome. In overlying horizons the number of thecal elaboration trends quickly increases. A tendency to produce compound rhabdosomes was manifested somewhat later. The determination of the stratigraphic distribution of forms representing the diversograptid stage meets some difficulties in that some of the forms here referred are merely bipolar morphoses due to regeneration (comp. p. 226). Forms which have been

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[20] Details of the formation of thecal cladia in *Abiesgraptus* are not yet adequately known. The are tentatively figured in text-pl. XVII, on the base of the same analogy with the multiple budding of sicular cladia in *Linograptus*.

shown to produce the sicular cladium occur, however, already in the *"M."sedgwicki* and *"M." turriculatus* zones (Strachan, 1952; Thorsteinsson, 1958). *Sinodiversograptus* occurs in the *turriculatus* zone, too (Mu & Chen, 1962). Thus the diversograptid forms would precede the appearance of cyrtograptid forms, whose first representatives are encountered in the *Monoclimacis crenulata* horizon, while the last ones become extinct in the *Cyrtograptus lundgreni — "Monograptus" testis* horizon. Should *Barrandeograptus*, representing the cyrtograptid stage, constitute a single evolutionary line, it would illustrate the secondary reduction in the number of thecal cladia, for the first representatives have rhabdosomes consisting of a great number of thecal cladia, while in the younger ones they are but very few (comp. *B. pullchellus — B. carruthersi*). Between the first and the second of the mentioned species there is, however, a considerable stratigraphic gap. Doubtless, forms representing the diversograptid stage belong to various phylogenetic lineages, too. *Neodiversograptus* occupies a particularly separate position, it is not directly related with Lower Silurian diversograptids, though it represents the same stage of complications of the development and structure of rhabdosome, which has been realized quite independently. Monograptids representing the linograptid stage of evolution appear above the *leintwardinensis* zone and persist to the *hercynicus* horizon, while forms representing the abiesgraptid stage appear still later and are confined, according to data now available, to the *uniformis-praehercynicus* zone.

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Warszawa, November 1962

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ADAM URBANEK

O ROZWOJU I REGENERACJI GAŁĄZEK W KOLONIACH PEWNYCH
GÓRNO-SYLURSKICH MONOGRAPTIDAE

Streszczenie

W pracy niniejszej — na podstawie materiałów wypreparowanych metodami
chemicznymi, pochodzących z głębokiego wiercenia wykonanego przez Instytut
Geologiczny (Warszawa) w Mielniku n. Bugiem oraz z sylurskich głazów narzuto-
wych — zbadano budowę, rozwój kolonii i występowanie stratygraficzne górno-
-sylurskiej grupy monograptidów należących do podrodziny Linograptinae. Opie-
rając się na tych faktach przedstawiona została analiza przebiegu ich ewolucji.
W ewolucji Linograptinae można wyróżnić kilka faz morfologicznych. Naj-
prymitywniejszą z poznanych faz reprezentuje *Neodiversograptus* n.gen., którego
przedstawicielami są opisane tu *N. nilssoni* (Lapworth) sensu Urbanek i *N. bekle-
mishevi* n.sp. Jak wykazano, pierwszy gatunek występujący w poziomie *nilssoni*
miał zdolność do sporadycznego tworzenia kladium sikularnego, które pojawiało
się w późnym okresie astogenezy, wskutek czego powstawał rabdozom bipolarny,
o dwu gałązkach niezależnie pączkujących z sikuli w dwu przeciwnych kierunkach.
Kladium sikularne tworzyło się na podstawie asymetrycznego kolca apertural-
nego sikuli. *N. beklemishevi* n.sp., występujący w poziomach *scanicus-leintwardi-
nensis*, reprezentuje bardziej zaawansowaną fazę ewolucji Linograptinae. Wyraża
się to przede wszystkim w potencjalnej zdolności do tworzenia więcej niż jed-
nego kladium sikularnego, w pewnym przyśpieszeniu tworzenia się kladiów, jak
też w pewnym zróżnicowaniu apertur w tekach medialnych i dystalnych. Kladium
sikularne rozwija się na podstawie aperturalnego kolca dorsalnego sikuli, który
położony jest już symetrycznie. Jeszcze wyższą fazę ewolucji tego szczepu repre-
zentuje *Linograptus posthumus* (Reinh. Richter), który nabył zdolności do two-
rzenia kolonii wielogałązkowych. Na materiale zbadanym można było ustalić spo-
sób rozwoju gałązki pierwotnej i 5 kladiów sikularnych. Te ostatnie pączkują nie-
zależnie z apertury sikuli, która opatrzona jest długą wirgellą; na jej końcu znaj-
duje się swoisty organ, dla którego proponuje się zastosować termin „wirgel-
larium". Zachowane w stanie kopalnym wirgellarium stanowiło prawdopodobnie
tylko część szkieletową bardziej skomplikowanego utworu, złożonego za życia

również z tkanek miękkich. Stanowił on funkcjonalnie aparat, służący do przytwierdzania lub, być może, do hydrostatycznego unoszenia kolonii.

W pracy omawia się zagadnienie pochodzenia Linograptinae i stosunek rodzaju *Linograptus* do *Abiesgraptus*.

Ewolucja Linograptinae prześledzona na zbadanym materiale pozwala stwierdzić, że wielogałązkowy *Linograptus* poprzedzony był przez formy skąpogałązkowe, których przedstawicielami były przede wszystkim dwugałązkowe formy bipolarne, jak *Neodiversograptus nilssoni*.

Zbadanie procesów tworzenia się gałązek kolonii w wyniku normalnej astogenezy (kladogenezy) pozwoliło na sprecyzowanie, że podlegają one ogólnej prawidłowości, dla której proponuje się nazwę „reguła Thorsteinssona"[1]. Reguła ta określa, że równocześnie pączkujące teki danej kolonii monograptidów mają tę samą wielkość, kształt i budowę, niezależnie od tego, czy tworzą się na gałązce pierwotnej, czy też na kladium tekalnym lub sikularnym.

Bipolarnie rosnące *morfozy*, powstające w wyniku regeneracji (regulacji) kolonii, należy przeciwstawić bipolarnym rabdozomom stanowiącym rezultat normalnej astogenezy. Rabdozomy takie złożone są z dwu serii tek rosnących w przeciwne strony, przy czym w miejscu dywergencji obu serii tek brak sikuli, która uległa widocznie oderwaniu. W zbadanym materiale takie regeneracyjne formy bipolarne opisano dla *Lobograptus scanicus parascanicus* (Kühne) i *Linograptus posthumus* (Reinh. Richter). W pierwszym przypadku udało się ustalić występowanie okazów reprezentujących poszczególne stadia regeneracji gałązki — aż do utworzenia się kompletnej teki regeneracyjnej, rosnącej w kierunku przeciwnym do wzrostu tek na gałązce pierwotnej. Większość badaczy nie odróżniała dawniej kolonii bipolarnych, tworzących się w wyniku normalnej astogenezy, od bipolarnych postaci regeneracyjnych, które również opisywano jako przedstawicieli rodzaju *Diversograptus*.

Zbadany materiał nie uzasadnia tej praktyki taksonomicznej, natomiast stanowi poparcie dla jednej z hipotez wysuniętych już wcześniej przez Boučka i Přibyla (1953), a mianowicie dla hipotezy regeneracyjnego pochodzenia pewnych form bipolarnych. Na podstawie zbadanych faktów poddano natomiat krytyce hipotezę Jaegera (1959, 1960), który wiązał występowanie bipolarnie rosnących rabdozomów, pozbawionych sikuli w miejscu dywergencji tek, ze zjawiskiem przemiany pokoleń.

Powstająca w wyniku regeneracji gałązka, dla której proponuje się nazwę „pseudokladium", jest w początkowej swej części znacznie szersza, niż gałązka pierwotna w części proksymalnej. Początkowe teki pseudokladium przypominają morfologicznie teki tworzące się w dystalnej części gałązki pierwotnej. Fakty te znajdują wyjaśnienie w świetle hipotezy, przypisującej koloniom graptolitów organizację polarną, wywołaną występowaniem gradientów morfo-fizjologicznych (Urbanek, 1960). W normalnej astogenezie, teki dystalne tworzą się w wyniku

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[1] Reguła nazwana na cześć wybitnego geologa i paleontologa kanadyjskiego R. Thorsteinssona, który pierwszy wykrył występowanie ogólnych zależności w rozwoju tek w złożonych koloniach monograptidów (1955).

osiągnięcia przez odpowiednią część kolonii względnej izolacji fizjologicznej od sikulozoida, który był przypuszczalnie ośrodkiem dominującym i indukującym w koloniach monograptidów. Natomiast teki gałązki regenerującej od samego początku mają postać tek dystalnych, gdyż tworzą się w warunkach zupełnej izolacji od wpływów sikulozoida, który uległ oderwaniu wraz z częścia sikularną gałązki pierwotnej i nie jest w takich koloniach obecny. W pracy tej czyni się próbę sformułowania bardziej ogólnych prawidłowości, rządzących zarównu procesami astogenezy i kladogenezy, jak i regeneracji gałązek (pseudokladogenezy). Prawidłowości te wynikają z polarnej organizacji kolonii graptolitów.

Zbadany materiał i badania poprzednio już wykonane przez innych autorów dają pewien obraz modyfikacji procesu astogenezy, jakie dokonały się w ewolucji Monograptidae. Posłużyły one do wyróżnienia 5 stadiów w obrębie monograptidowego typu rozwoju, analogicznych do stadiów wyróżnionych w obrębie diplograptidowego typu rozwoju. Stadia te różnią się ilością i sposobem tworzenia się kladiów, których zróżnicowanie — obok procesów różnicowania tek — zdaje się stanowić nić przewodnią ewolucji kolonii Monograptidae.

Ponieważ istniejąca terminologia anatomiczna, odnosząca się do wielogałązkowych monograptidów, była bardzo uboga, wprowadzono szereg nowych terminów i pojęć, lub uczyniono próbę bliższego zdefiniowania pojęć, używanych dotychczas w sposób nie zawsze konsekwentny.

OPISY NOWYCH JEDNOSTEK TAKSONOMICZNYCH

Rodzina **Monograptidae** Lapworth, 1873

Podrodzina **Linograptinae** Obut, 1957

Rodzaj *Neodiversograptus* n.gen.

Gatunek typowy: *Monograptus nilssoni* Lapworth, 1876 sensu Urbanek, 1954.

Pochodzenie nazwy: *Neodiversograptus* — gr. *neos* = nowy, geologicznie młodszy od typowego *Diversograptus* Manck.

Diagnoza. — Rabdozomy składające się z normalnej gałązki monograptidowej (prokladium), ze zdolnością do przynajmniej sporadycznego tworzenia co najmniej jednego kladium sikularnego i przyjmujące wtedy, w drodze pączkowania diwersograptidowego, charakter rabdozomów bipolarnych. Sikula opatrzona dorsalnym kolcem aperturalnym, w którego przedłużeniu tworzy się u form bipolarnych wirgula kladium sikularnego (pseudowirgula). Teki rurkowate, o aperturach prostych lub opatrzonych słabą elewacją krawędzi.

Gatunki: *Neodiversograptus nilssoni* (Lapworth) sensu Urbanek i *Neodiversograptus beklemishevi* n.sp.

Występowanie stratygraficzne. — Górny sylur, dolny ludlow (od poziomu *nilssoni* do poziomu *leintwardinensis*).

Neodiversograptus beklemishevi n.sp

(text-pl. V, VI; fig. 2)

Holotyp: Text-pl. V, fig. C, wiercenie Mielnik n.B., głębokość 1000,90 m.

Paratypy: Text-pl. V, fig. D-F.

Poziom typowy: Zielonkawo-niebieskie mułowce i margle w rdzeniu wiert-
niczym Mielnik n.B., głębokość 1000,90—966,90 m, odpowiadające poziomowi *sca-
nicus* w dotychczas przyjętym znaczeniu.

Pochodzenie nazwy: beklemishevi — na cześć niedawno zmarłego wybitnego
zoologa radzieckiego Prof. W. N. Beklemiszewa, którego pełne głębokich idei prace
nad zagadnieniem kolonijności u wyższych bezkręgowców stanowiły dla autora
bezpośredni bodziec do badań nad organizacją kolonii graptolitów.

Diagnoza. — Rabdozom jednogałązkowy, składający się z jednego kladium,
mógł przypuszczalnie osiągać stadium dwugałązkowe przez tworzenie się kladium
sikularnego. Świadczy o tym obecność symetrycznego dorsalnego kolca apertu-
ralnego sikuli oraz występowanie fragmentów sikul, mających budowę właściwą
dla tego gatunku i opatrzonych kladium sikularnym. Teki proste w części proksy-
malnej, w części zaś dystalnej apertury ich opatrzone są nieznaczną elewacją kra-
wędzi, tworzącą dwa symetryczne wyrostki boczne.

OBJAŚNIENIA DO ILUSTRACJI

Fig. 1 (p. 144)

Region dywergencji rabdozomu bipolarnego pozbawionego sikuli i uważanego
przez Jaegera (1960) za przedstawiciela pokolenia bezpłciowego gatunku z grupy
nilssoni. Bałtycki głaz narzutowy, wiek określony jako poziom *scanicus; A* region
dywergencji widziany z boku; *B* teka dystalna tegoż gatunku, z boku; *C* anormalny
przebieg wirguli widziany na stronie dorsalnej w miejscu dywergencji; *A-B* ca. x
44, *C* ca. x 26 (przerysowane za zezwoleniem z nieopublikowanego rysunku
Dr H. Jaegera, 1960).

Fig. 2 (p. 169)

Neodiversograptus beklemishevi n.sp. (Mielnik, głęb. 934,50 m); sikula i teki
proksymalne z poziomu *leintwardinensis; db* ciemne pierścienie sikuli, *ds* dorsalny
kolec aperturalny sikuli, *msi* metasikula, *psi* prosicula, *v* wirgula, *vi* wirgella;
ca. x 50.

Fig. 3 (p. 178)

Linograptus posthumus (Reinh. Richter) (Mielnik, głęb. 821,70 m); sikula opa-
trzona wirgellarium i kompletną teką 1^1; *ap* apertura sikuli, *bn* wcięcie bazalne,
dp palczaste odrostki wirgellarium, *msi* metasikula, *psi* prosikula, *v* wirgula, *vi*
wirgella, *vg* wirgellarium; ca. × 50.

Fig. 4 (p. 207)

Diagram porównawczy przedstawiający stosunki segmentów tekalnych meta-
sikuli (*A*) i teki blastozoida (*B*) u Monograptidae. Liniami przerywanymi zazna-
czono stosunek tek powstających przez pączkowanie supraaperturalne do odpo-
wiednich tek macierzystych; *mth* metateka, *n*+1 początek teki następnego blasto-
zoida, *o* otwór dla pączka teki *n* + 1, *pn* otwór dla pączka pierwotnego, *pth* proteka.

Fig. 5 (p. 210)

Diagram przedstawiający stosunek typowego kladium tekalnego do kladium
sikularnego, oparty na budowie *Cyrtograptus* i *Sinodiversograptus*. Kladium siku-
larne (zakreskowane) można uważać za kladium tekalne metasikuli (teki 0^1), na
co wskazuje obecność serii form przejściowych o różnym położeniu tek macie-
rzystych; *si* sikula. Dalsze objaśnienia — w tekście.

Fig. 6 (p. 211)

Diversograptus runcinatus (Lapworth), rabdozomy bipolarne z różnicą w wiel-
kości i budowie sąsiednich tek prokladium i kladium sikularnego (*A, B*) oraz sta-

dium monograptidowe w ich astogenezie (C). Glenkiln Burn. Dumfriesshire (wg Strachana, 1952).

Fig. 7 (p. 228)

A-D Tworzenie się rosnących bipolarnie bliźniaczych osobników Tubularia w wyniku regeneracji (wg Childa, 1941).

Fig. 8 (p. 229)

Tworzenie się rosnących bipolarnie kolonii stułbiopława *Pennaria* w wyniku regeneracji odciętego fragmentu gałązki głównej. Części odtworzone regeneracyjnie zaczerniono (wg Gasta i Godlewskiego, 1903).

Text-pl. I (p. 142)

Bipolarne kolonie monograptidów pozbawione sikuli w miejscu dywergencji dwu serii tek i opisane jako: A *Diversograptus* sp. — Stolzenberg, Turyngia, dolny ludlow (Jaeger, 1959, pl. 8, fig. 10); B *D. globosus* Bouček & Přibyl — Chuchle, Barrandien, górny llandowery Bouček & Přibyl, 1953, text-pl. 4, fig. 10); C *D. gracilis* (Bouček) — Chuchle, Barrandien, wenlok (Bouček & Přibyl, 1953, text-pl. 3, fig. 1; D *D. inexpectatus* Bouček & Přibyl — Chuchle, Barrandien, górny llandowery (Bouček & Přibyl, 1953, text-pl. 5, fig. 1); ca x 5.

Text-pl. II (p. 154)

Neodiversograptus nilssoni (Lapworth) sensu Urbanek. Sikula i teka 1^1. A_1-A_2 sikula i teka 1^1 widziane od strony „reverse" i „obverse" (Mielnik; głęb. 1035,90 m); B sikula opatrzona pierścieniami sikularnymi (Lejškov, loc. „Borek", Barrandien); C_1-C_2 sikula opatrzona niezwykle grubym kolcem aperturalnym od strony „reverse", C_1 fragment aperturalny od strony „obverse" (Mielnik; głęb. 1044,30 m):, D młoda sikula pozbawiona zaczątku kolca aperturalnego i rosnąca teka 1^1 (głaz narzutowy S. 38, Jarosławiec, Pomorze Zach.); E izolowany kolec dorsalny apertury sikuli (głaz narzutowy S. 20, Poznań); *ds* kolec dorsalny, *msi* metasikula, *psi* prosikula, *v* wirgula, *vi* wirgella; *A-C, E* ca. × 50, *D* ca. × 32.

Text-pl. III (p. 156)

Neodiversograptus nilssoni (Lapworth) sensu Urbanek. Tworzenie się kolca dorsalnego sikuli i budowa tek. *A-C* apertura metasikuli w różnych stadiach wzrostowych (Mielnik; głęb. 1044,30 m); D zaczątek kolca dorsalnego apertury metasikuli (Lejškov, loc. „Borek", Barrandien); E proksymalna część rabdozomu formy bezpierścieniowej (Mielnik; głęb. 1035,90); F proksymalna część rabdozomu formy pierścieniowej (Lejškov, loc. „Borek", Barrandien); G teka proksymalna; H teka dystalna; *A-D, G, H* ca. × 50, *E, F*, ca. ×15.

Text-pl. IV (p. 160)

Neodiversograptus nilssoni (Lapworth) sensu Urbanek. Fragment części sikularnej rabdozomu bipolarnego A_1-A_2 okaz widziany od strony „reverse" i obverse" (głaz narzutowy S. 19, Poznań); B schematyczna rekonstrukcja stosunków morfologicznych w miejscu dywergencji obu gałązek rabdozomu, oparta na fragmencie rabdozomu okazu A_1 (zakreskowane) i innych okazów tego gatunku (niezakreskowane); *cp* zwęglona błona perydermalna u podstawy kolca aperturalnego sikuli, *ds* kolec dorsalny apertury metasikuli, *m* błona u podstawy wirgelli, *si* metasikula, *vi* wirgella; A_1-A_2 ca. × 55.

Text-pl. V (p. 164)

Neodiversograptus beklemishevi n.sp. Budowa sikuli i tek. A młoda sikula z zaczątkową teką 1^1 oraz widocznym symetrycznym położeniem dorsalnego kolca aperturalnego; B młoda sikula z teką 1^1 w nieco bardziej zaawansowanym stadium wzrostowym; C sikula i kompletna teka 1^1; D sikula i kompletna teka 1^1 z lepiej zachowanym dorsalnym kolcem aperturalnym sikuli; E część aperturalna teki 1^1

i kompletna teka 1^2; F teka bardziej dystalna; ds aperturalny kolec dorsalny sikuli, msi metasikula, psi prosikula, v wirgula, vi wirgella (Mielnik; A-C, E — głęb. 1000,90 m, D — głęb. 973 m, F — głęb. 974,90 m); A-F ca. $\times$ 50.

Text-pl. VI (p. 166)

Neodiversograptus beklemishevi n. sp. Fragment części sikularnej rabdozomu bipolarnego. A_1-A_2 okaz widziany od strony „obverse" i „reverse", A_3 część aperturalna sikuli i podstawa teki 1^2 widziane od strony wentralnej (głaz narzutowy S. 32, Gdańsk-Wrzeszcz); B schematyczna rekonstrukcja stosunków morfologicznych w miejscu dywergencji obu gałązek rabdozomu, oparta na okazie A (zakreskowane) i innych okazach tego gatunku (niezakreskowane). Liniami przerywanymi zaznaczono przypuszczalny przebieg hipotetycznych dodatkowych kladiów sikularnych. adp płytka adaperturalna, ap apertura sikuli, bn wcięcie bazalne, l listewka wnikająca do wnętrza wcięcia bazalnego, msi metasikula, psi prosikula, pv pseudowirgula, v wirgula, vi wirgella; A_1-A_3 ca. $\times$ 52.

Text-pl. VII (p. 172)

?Neodiversograptus n.sp. lub teratologiczna kolonia *?Linograptus* sp. Fragment aperturalny sikuli i 3 teki kladium sikularnego. A_1-A_2 proksymalna część zachowanego fragmentu od strony „reverse" i „obverse"; B ogólny widok zachowanego obrazu, apertura teki 3^2 uległa wtórnemu skręceniu (Mielnik; głęb. 903,60 m); błona u podstawy wirgelli, msi metasikula, pv pseudowirgula, vi wirgella; A_1-A_2 ca. $\times$ 50, B ca. $\times$ 28,3.

Text-pl. VIII (p. 176)

Linograptus posthumus (Reinh. Richter). Budowa sikuli i wczesne stadia astogenezy. A sikula i młodociana teka 1^1; B sikula z prawie kompletną teką 1^1 i zacząktiem teki 1^2; C sikula z prawie dojrzałą teką 1^1 i początkową częścią teki $1'$; D aperturalna część sikuli i podstawa proteki 1^2; ap apertura, bn wcięcie bazalne, ds kolec dorsalny, msi metasikula, psi prosikula, v wirgula, vi wirgella (Mielnik A-C — głęb. 830,90 m, D — głęb. 840,60 m); A-C ca. $\times$ 52, D ca. $\times$ 100.

Text-pl. IX (p. 180)

Linograptus posthumus (Reinh. Richter). Budowa tek. A teka bardziej proksymalna, z boku; B teka bardziej proksymalna, od strony wentralnej; C teka bardziej dystalna, z boku; D krawędź aperturalna teki ze szczególnie silnie rozwiniętymi elewacjami; E krawędź aperturalna teki z zaznaczającym się wtórnym przyrostem fuzellusów; ap_1 — ap_2 poprzedni i wtórny poziom krawędzi aperturalnej (Mielnik; A-C, E — głęb. 821,10 m, D — głęb. 820,10 m); ca. $\times$ 50.

Text-pl. X (p. 182)

Linograptus posthumus (Reinh. Richter). Stadium diwersograptidowe i początek stadium linograptidowego w rozwoju kolonii. A część aperturalna sikuli i rosnące pierwsze kladium sikularne; B część sikularna rabdozomu w stadium diwersograptidowym; C późne stadium diwersograptidowe z widocznym zaczątkiem pseudowirguli drugiego kladium sikularnego; D część aperturalna sikuli z widocznym lateralnym kolcem aperturalnym; ap apertura sikuli, bn wcięcie bazalne, ls kolec lateralny apertury sikuli, msi metasikula, psi prosikula, pv pseudowirgula, v wirgula, vi wirgella (Mielnik; A — głęb. 239,60 m, B — głęb. 830,90 m, C — 821,10 m, D — 820,30 m); A-C ca. $\times$ 52, D ca. $\times$ 100.

Text-pl. XI (p. 184)

Linograptus posthumus (Reinh. Richter). Stadium linograptidowe w rozwoju kolonii. A_1-A_2 część aperturalna sikuli i początek piewszego i drugiego stadium sikularnego; A_3 ogólny wygląd tegoż okazu; B część aperturalna sikuli z podstawą teki 1^2 i dobrze widoczną płytką aperturalną oraz początkiem rurki tekalnej 1^3;

C fragment sikuli z teką 1^2 i podstawą teki 1^3; *D* część aperturalna sikuli, początek tek 1^2, 1^3 oraz płytka adaperturalna teki 1^4; *adp* płytka adaperturalna, *ap* apertura sikuli, *msi* metasikula, *psi* prosikula, *pv* pseudowirgula, *vi* wirgella (Mielnik; *A*, *D* — głęb. 820,10 m, *B*, *C* — głęb. 837,60 m); A_1-A_2, *B*, *D*, ca. $\times$ 100, A_3, *C* ca. $\times$ 25.

Text-pl. XII (p. 186)

Linograptus posthumus (Reinh. Richter). Zaawansowane stadium linograptidowe w rozwoju kolonii i budowa wirgellarium (organu wirgellarnego). A_1 Część sikularna rabdozomu 5-gałązkowego z zachowanym wirgellarium; A_2 ten sam okaz, szczegóły budowy części aperturalnej i początkowe części kladiów sikularnych od strony „reverse"; A_3 to samo od strony „obverse"; B_1-B_2 szczegóły budowy kompletnie zachowanego wirgellarium, widzianego z dwu stron; *adp* płytka adaperturalna, *d* zdeformowana wtórnie nasada i początkowa część wirgelli, *dp* odrostki palczaste wirgellarium, *ls* lateralny kolec aperturalny sikuli, stanowiący zawiązek pseudowirguli teki 1^6; *msi* metasikula, *pv* pseudowirgula, *vg* wirgellarium, *vi* wirgella, *m* błona perydermalna wirgellarium (Mielnik; *A* — głęb. 823 m, *B* — głęb. 820,10 m); A_1 ca. $\times$ 15, A_2-A_3 ca. $\times$ 70, B_1-B_2 ca. $\times$ 50.

Text-pl. XIII (p. 199)

Zmiany strukturalne we wcześniejszych fazach ewolucji Linograptinae. Faza praeneodiwersograptidowa oparta na danych Elles i Wood (1918). *A*, *B* dwa teoretycznie możliwe sposoby zmian ewolucyjnych, poprzedzających fazę neodiversograptidową (zmiana położenia teki macierzystej metakladium lub jego redukcja). Dalsze objaśnienia — w tekście.

Text-pl. XIV (p. 214)

Różnice i podobieństwa morfologiczne w budowie wielogałązkowych (*A*) i dwugałązkowych (*B*) form, tworzących się w rezultacie normalnej astogenezy i bipolarnych morfoz, powstających wskutek regeneracji z zaznaczeniem różnicy w wielkości tek obu gałązek (*C*) i braku takiej różnicy (*D*) *n*, *n* + 1 kolejne teki gałązki pierwotnej; *1'*, *2'* kolejne teki gałązki regeneracyjnej. Dalsze objaśnienia — w tekście.

Text-pl. XV (p. 216)

Lobograptus scanicus parascanicus (Kühne). Regeneracja rabdozomu. A_1-A_2 miejsce dywergencji rabdozomu o wzroście bipolarnym, widziane z dwu stron; *B* teka znajdująca się przypuszczalnie we wczesnym stadium regeneracji rabdozomu; C_1 bardziej zaawansowane stadium, wraz z wirgulą regeneracyjną, C_2 szczegóły budowy bazalnej części teki C_1; *D* teka pierwotna wraz z zaczątkiem teki regeneracyjnej i wirgulą regeneracyjną; E_1 podobnie jak *D*, regenerat wyrażony w postaci uwypuklenia perydermy ; E_2 bazalna część teki widziana od strony wentralnej; F_1 fragment rabdozomu z zaczątkiem teki regeneracyjnej, F_2 bazalna część tego fragmentu od strony wentralnej; *cr* narośl u podstawy wirguli regeneracyjnej, *d* linia dyskordancji systemów fuzellarnych teki pierwotnej i regeneracyjnej, *f* fałdy perydermy, *n*, *n* + 1 kolejne teki należące przypuszczalnie do teki pierwotnej, *1'* kompletnie utworzona teka regeneracyjna pseudokladium, *op* otwór powstały wskutek uszkodzenia teki, *rth* teka regeneracyjna, *rv* wirgula regeneracyjna (głaz narzutowy S. 181, Czarnogłowy, Pomorze Zach.); A_1-A_2, F_1-F_2 ca. $\times$ 22,5; *C*, C_1, *D*, E_1-E_2 ca. $\times$ 95.

Text-pl. XVI (p. 232)

Sukcesja astogenetyczna tek w normalnym rozwoju kolonii Monograptidae (*A*) oraz w przypadku uszkodzenia i regeneracji rabdozomu (*B-D*). Nożyce wskazują miejsce uszkodzenia pierwotnego rabdozomu, *B* — efekty regeneracji fragmentu

dystalnego gałązki pierwotnej przy jej przełamaniu w części dystalnej; C_1-C_2 efekty regeneracji fragmentu dystalnego głałązki pierwotnej przy jej przerwaniu w części proksymalnej; D_1-D_2 przypuszczalne efekty regeneracji przy założeniu, że regeneruję część sikularna gałązki pierwotnej. Dalsze objaśnienia — w tekście.

Text-pl. XVII (p. 238/239)

Stadia filogenetycznych modyfikacji astogenezy w obrębie monograptidowego typu rozwoju (stadia filastogenezy). Abiesgraptidowy typ pączkowania, zrekonstruowany hipotetycznie na podstawie jego przypuszczalnej analogii do wielokrotnego pączkowania kladiów sikularnych u *Linograptus*. Kolonia *Abiesgraptus* przerysowana z Jaegera (1959, fig 25). Dalsze objaśnienia — w tekście.

Pl. I
Linograptus posthumus (Reinh. Richter)
(Mielnik)

Fig. 1. Sikula z kompletną teką 1^1 i wirgellarium (głęb. 821,70 m); ca. $\times$ 46.

Fig. 2 *a*, *b*. Oderwane wirgellarium, widziane z dwóch stron (głęb. 820,10 m); ca. $\times$ 50.

Pl. II
Linograptus posthumus (Reinh. Richter)
(Mielnik)

Fig. 1. Późne stadium linograptidowe astogenezy, widoczny region sikularny wraz z wirgellarium, część aperturalna teki 2^1 uległa odłamaniu (głęb. 823,0 m); ca. $\times$ 30.

Fig. 2. Stadium diwersograptidowe w astogenezie, teki 2^1 i 2^2 silnie zdeformowane (głęb. 830,90 m); ca. $\times$ 30.

Pl. III
Linograptus posthumus (Reinh. Richter)

Fig. 1. Kolonia bipolarna bez sikuli w miejscu dywergencji dwóch serii tek, wykazująca kontrast w wielkości sąsiednich tek na gałązce pierwotnej i regeneracyjnej (okaz *A*, Chełm, głęb. 1553,50 m); ca. $\times$ 14.

Fig. 2. Podobna kolonia bez kontrastu w wielkości tek na obu gałązkacn (okaz *B*, Chełm, głęb. 1554,90 m); ca. $\times$ 14.

Fig. 3. Stadium diwersograptidowe w astogenezie, wykazujące słaby stopień dywergencji kladium sikularnego (Mielnik, głęb. 830, 90 m); *d* miejsce dywergencji, *p* oderwany fragment perydermy innego okazu, leżący obok okazu *B*; ca. $\times$ 30.

АДАМ УРБАНЭК

О РАЗВИТИИ И РЕГЕНЕРАЦИИ ВЕТОК В КОЛОНИЯХ ВЕРХНЕ-СИЛУРИЙСКИХ MONOGRAPTIDAE

Резюме

Настоящая работа содержит результаты изучения строения, развития колонии и стратиграфического распространения верхне-силурийских монограптид из

подсемейства Linograptinae. На основании обнаруженных фактов проведён ана-
лиз хода эволюции этих граптолитов. Материал, полученный из кернов глубокого
бурения проведенного Геологическим Институтом (Варшава) в Мельнике на Бугу
(восточная Польша) и из силурийских валунов, отпрепарирован химическим
методом. На основании обнаруженных фактов проведен анализ хода эволюции
выше упомянутых граптолитов.

В эволюции можно выделить несколько морфологических фаз. Самую при-
митивную из изученных фаз представляет *Neodiversograptus* n.gen., которого
представителями являются описанные тут *N. nilssoni* (Lapworth) sensu Urbanek
и *N. beklemishevi* n.sp.[1]. Как доказывается, первый вид, *N. nilssoni* — из одно-
именного горизонта — обладал способностью спорадического образования сику-
лярного кладия, которое появлялось в позднем периоде астогенеза, вследствие
чего возникала биполярная рабдосома с двумя ветками, почкующими незави-
симо друг от друга на сикуле в двух противоположных направлениях. Сикуляр-
ный кладий образовался упираясь на асимметрическом апертурном дорсальном
шипе сикулы. *N. beklemishevi* n.sp. из горизонтов *scanicus - leintwardinensis* пред-
ставляет более продвинутую фазу эволюции Linograptinae. Это выражается
потенциальной способностью к образованию большего числа сикулярных кла-
диев, некоторым ускорением их образования, равным образом как некоторой
дифференцировкой апертур в медиальных и дистальных теках. Сикулярный
кладий развивается упираясь на дорсальном апертурном шипе, который распо-
ложен тут уже симметрично. Еще более высокую фазу эволюции этой группы
представляет *Linograptus posthumus* (Reinh. Richter), который приобрел способ-
ность образования многоветочных колоний. На изученном материале можно было
установить способ развития первичной веточки и пяти сикулярных кладиев. Эти
последние почкуют независимо из апертуры сикулы, которая снабжена длинной
виргеллей; на ее конце находится особый орган, для которого предлагается на-
звание „виргелларий". Сохраненный виргелларий составлял повидимому только
скелетную часть более сложного образования, сложенного при жизни тоже
и мягкими тканками. Функционально являлся он прикрепительным или гидро-
статическим аппаратом.

В работе обсуждается вопрос происхождения Linograptinae и взаимное соот-
ношение родов *Linograptus* и *Abiesgraptus*.

Эволюция Linograptinae, прослеженная на изученном материале, позволяет
установить, что многоветвистого *Linograptus* предшествовали формы с немного-
численными ветками, представленные главным образом биполярными формами
с двумя ветками, как *Neodiversograptus nilssoni*.

Обследование процессов образования веток колонии в результате нормаль-
ного астогенеза (кладогенеза) позволило установить, что они подчиняются общей
закономерности, для обозначения которой предлагается название „правило

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[1] Названный в честь недавно умершего Профессора В. Н. Беклемишева,
знаменитого советского зоолога, которого чрезвычайно интересные исследования
по колониальным животным явились для автора стимулом к изучению органи-
зации колонии граптолитов.

Торштейнссона"[2]. Правило это определяет, что одновременно почкующие теки данной колонии монограптид обнаруживают такую-же величину, форму и строение, независимо от того, образуются ли они на первичной ветке или же на текальном либо сикулярном кладии.

Биполярно растущие *морфозы*, возникающие в результате регенерации (регуляции) колонии, следует противопоставить биполярным рабдосомам, являющимся результатом нормального астогенеза. Такие рабдосомы сложены двумя сериями тек растущих в противоположные стороны, причем на месте дивергенции обоих серий тек отсутствует сикула, которая очевидно оторвалась. В изученном материале такие регенерационные биполярные формы описано для *Lobograptus scanicus parascanicus* (Kühne) и *Linograptus posthumus* (Reinh. Richter). В первом случае удалось установить наличие образцов, представляющих отдельные стадии регенерации ветки, вплоть до создания полной регенерационной теки, растущей в противоположном направлении по сравнению с направлением роста тек на первичной ветке. В прошлом большинство исследователей не различало биполярных колоний, образующихся в результате нормального астогенеза, и биполярных регенерационных форм, которые описывали тоже как представителей рода *Diversograptus*.

Изученный материал не оправдывает такой таксономической практики, но говорит в пользу одной из гипотез, выдвинутых раньше Боучком и Пшибылем (Bouček & Přibyl, 1953), а именно в пользу гипотезы регенерационного происхождения некоторых биполярных форм. На основании обследованных фактов подвергнуто критике гипотезу Егера (Jaeger, 1959, 1960), который связывал выступание биполярно растущих рабдосом лишенных сикулы на месте дивергенции тек — с явлением смены поколений.

Возникающая в результате регенерации ветка, для которой автор предлагает название „псевдокладий", в своей начальной части значительно шире, чем первичная ветка в ее проксимальной части. Начальные теки псевдокладия напоминают формой теки, образующиеся в дистальной части первичной ветки. Эти факты хорошо понятны в свете гипотезы придающей колониям граптолитов полярную организацию, вызванную присутствием морфо-физиологических градиентов (Urbanek, 1960). В ходе нормального астогенеза дистальные теки образуются в результате приобретения соответствующей частью колонии относительной физиологической изолированности по отношению к сикулозоиду, который был повидимому доминирующим и индуцирующим центром в колониях монограптид. Теки же регенерирующейся ветки с самого начала имеют вид дистальных тек, так как возникают в условиях совершенной изолированности от влияния сикулозоида, который оторван вместе с сикулярной частью первичной ветки и отсутствует в таких колониях. В работе проводится попытка формулировки закономерностей более общего характера, управляющих так процессами асто-

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[2] Правило названо в честь выдающегося канадского геолога и палеонтолога Р. Торштейнссона (R. Thorsteinsson), который впервые обнаружил наличие общих зависимостей в развитии тек сложных колоний монограптид (1955).

генеза, как кладогенеза и регенерации веток (псевдокладогенеза). Закономерности эти следуют из полярной организации колоний граптолитов.

Изученный материал и прежние исследования других авторов дают некоторую картину модификаций процесса астогенеза, какие произошли в ходе эволюции Monograptidae. Послужили они для выделения 5 стадий монограптидового типа развития. Эти стадии отличаются количеством и способом образования кладиев, которых диференциация рядом с диференциацией тек грает повидимому выдающуюся роль в эволюции колоний Monograptidae.

Так как имеющаяся анатомическая терминология, относящаяся к монограптидам с многочисленными ветками в колонии, очень бедна, введено ряд новых названий и понятий, либо сделано попытку более точного определения понятий употребляемых до сих пор не всегда с нужной последовательностью.

PLATES

Linograptus posthumus (Reinh. Richter)
(Mielnik)

Fig. 1. Sicula with complete theca 1¹ and virgellarium (depth 821.70 m) ca. × 46.
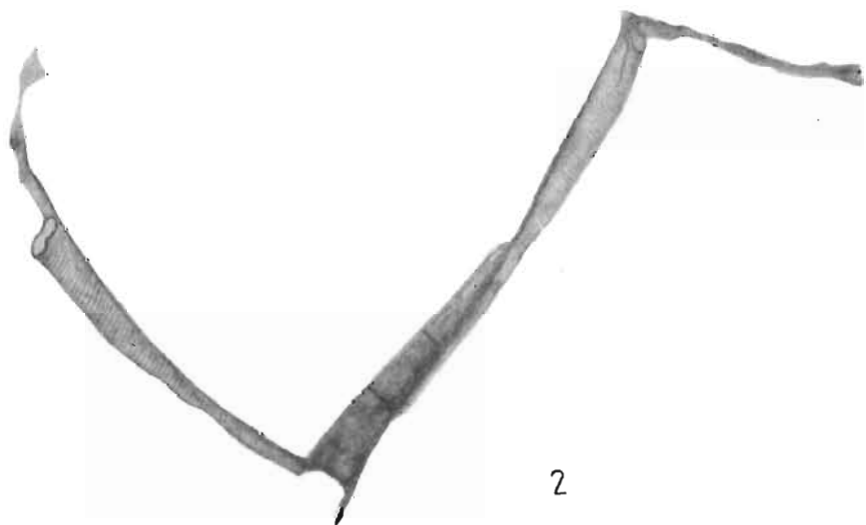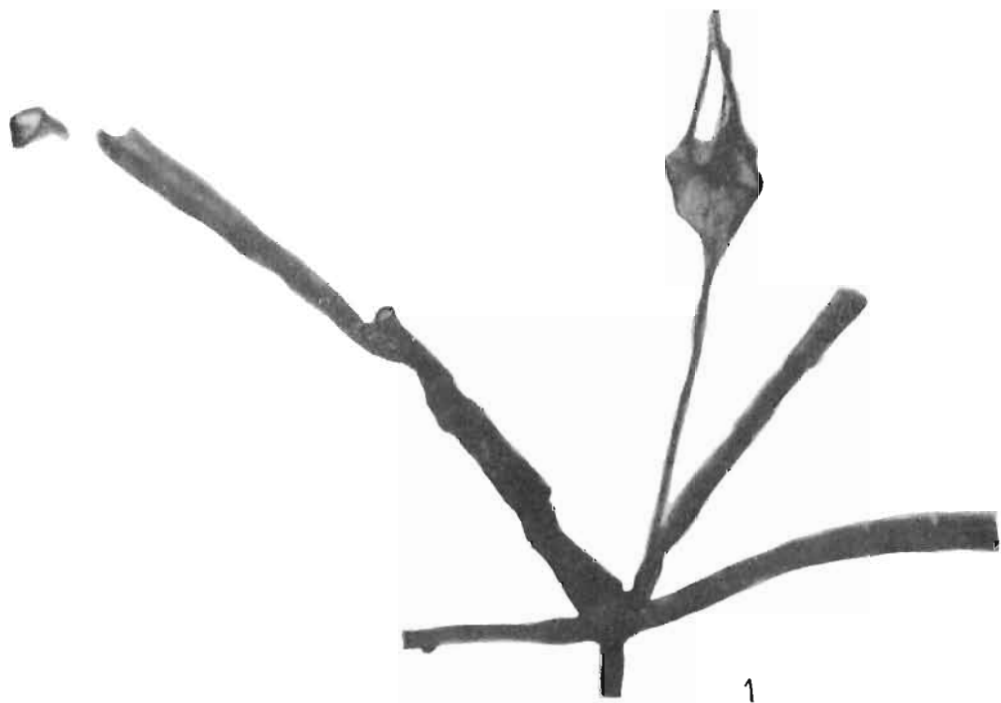Fig. 2 *a, b.* Isolated virgellarium visible from two sides (depth 820.10 m); ca. × 50.
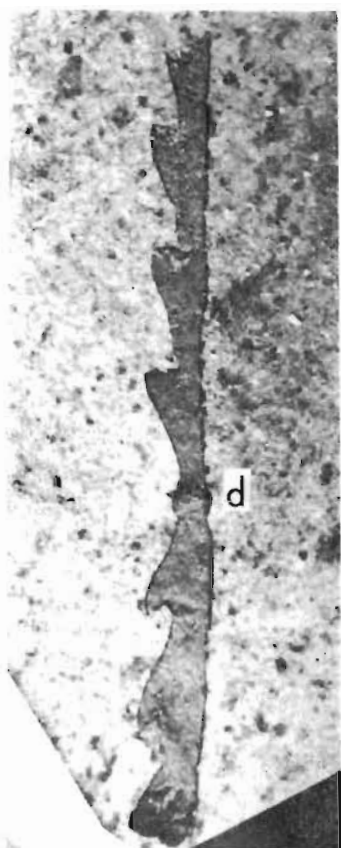
2a

2b

1

1

2

Linograptus posthumus (Reinh. Richter)
(Mielnik)

Fig. 1. Late linograptid stage in astogeny showing sicular region with virgel-
larium, apertural part of theca 2^1 has been broken off (depth 823.0 m);
ca. $\times$ 30.

Fig. 2. Diversograptid stage in astogeny, thecae 2^1 and 2^2 strongly deformed
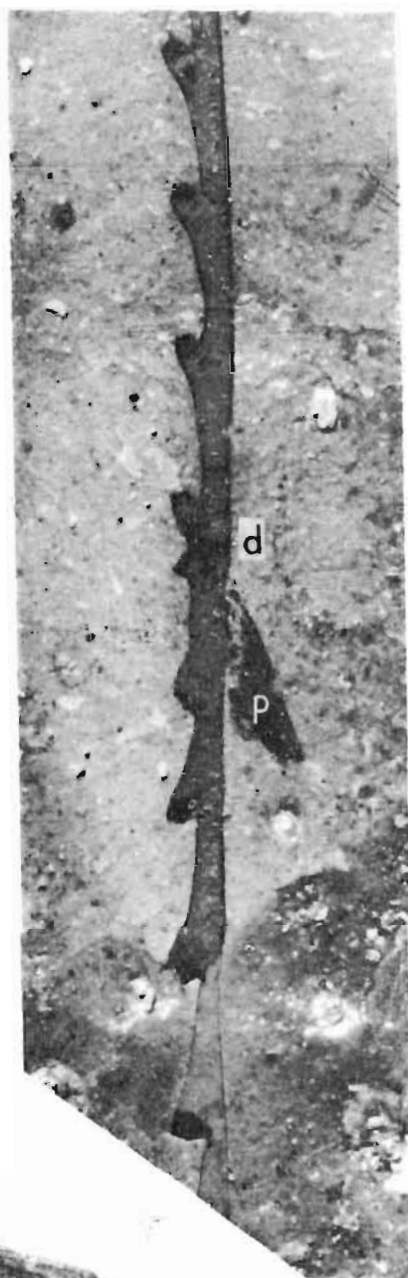(depth 830.90 m); ca. $\times$ 30.
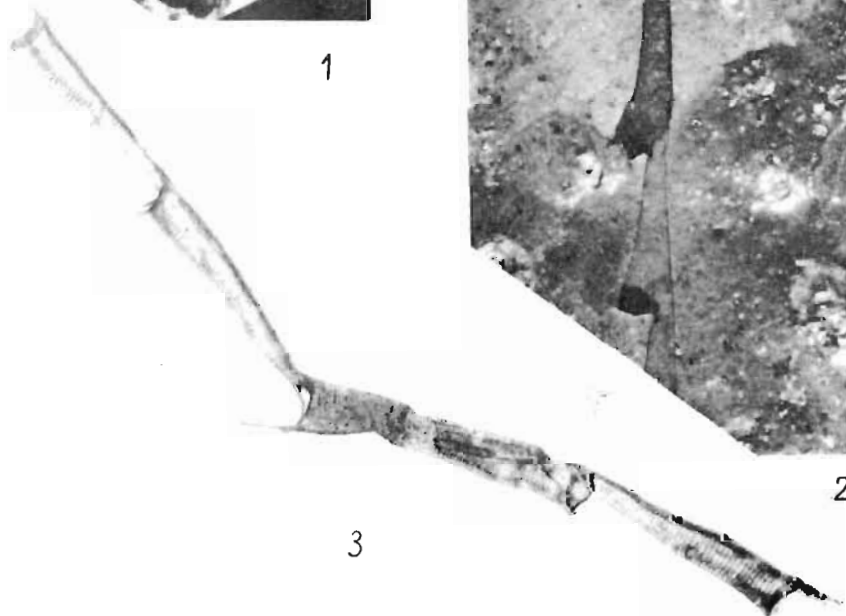
Pl. III

Linograptus posthumus (Reinh. Richter)

Fig. 1. Bipolar colony with sicula in region of divergence of two thecal series, showing contrast in size of thecae on primary and regenerating cladium (specimen *A*, Chełm, depth 1553.50 m); ca. × 14.

Fig. 2. Similar colony without contrast between thecae on both cladia (specimen *B*, Chełm, depth 1554.90 m); ca. × 14.

Fig. 3. Diversograptid stage in astogeny showing slight divergence of sicular cladium (Mielnik, depth 830,90 m); *d* point of divergence, *p* fragment of detached periderm of another specimen lying close to the specimen *B*; ca. × 30.