ACTA PALAEONTOLOGICA POLONICA
Vol. XV 1970 Nos. 2-3

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NEOCUCULLOGRAPTINAE N. SUBFAM. (GRAPTOLITHINA) — THEIR EVOLUTIONARY AND STRATIGRAPHIC BEARING

Contents

Page

Abstract. — A description of the morphology and evolution of a group of Upper Silurian monograptids, suggested to constitute Neocucullograptinae n. subfam., and including *Bohemograptus* Přib., *Neolobograptus* n. gen. and *Neocucullograptus* n. gen. is given. Studies were based on material etched from the core of Mielnik on the Bug (Eastern Poland) deep boring, and partly on erratic boulders of Baltic origin. In Lower Ludlovian Neocucullograptinae n. subfam. were represented by *Bohemograptus*, which on the boundary with Upper Ludlovian acquired the capability to produce microfusellar tissue. Further evolution of Neocucullograptinae n. subfam. marked by appearance of specialized representatives of Upper Ludlovian *Bohemograptus*, *Neolobograptus* n. gen. and *Neocucullograptus* n. gen., was closely connected with the utilisation of this peridermal fabric. Last named forms constitute characteristic elements of graptolite fauna in the Siedlce Beds of the Polish Platformian Silurian, which enable subdivision of their lower member into 5 new graptolite zones. Occurrence of this fauna on other areas of Eastern and Central Europe is indicated. Nature of changes in graptolite fauna on the boundary of Lower and Upper Ludlovian is discussed, and the probable role of biotic factors in extinction of Graptoloidea is emphasized. Origin and tentative phylogeny of Neocucullograptinae n. subfam. are discussed and probable biological interpretation of observed changes suggested. Quantitative analysis of long-lasted *Bohemograptus bohemicus* (Barr.) lineage has been given, and on the base of available evidence, a discrimination of two temporal subspecies is substantiated. Eight representatives (species and subspecies) of the Neocucullograptinae n. subfam. are described in systematic part. Three species and one subspecies are new. Moreover, appendix comprises description of two new aberrant species of "*Monograptus*".

INTRODUCTION

Since 1962, a gradually accumulated data on some Ludlovian monograptids have shown a close relationship between representatives of *Bohemograptus* Přib. and a highly specialized group of the Upper Ludlovian monograptids, mostly new or little known species. Studies on the material from a boring core at Mielnik on the Bug (comp. Urbanek, 1966), especially contributed to a better understanding of the phylogenetic relationships between the Lower Ludlovian *Bohemograptus bohemicus* (Barr.) and certain new or little known Upper Ludlovian species. The last-named group represents an entirely new faunal assemblage which strongly differs from the hitherto known Lower Ludlovian graptolite fauna, being nevertheless only a further development of *Bohemograptus*. The recognition of these relationships has induced the present writer to introduce a concept of Neocucullograptinae n. sufam. (for diagnosis see p. 265) so as to include the akin Lower and Upper Ludlovian monograptids mentioned above in a common taxonomic unit. Neocucullograptinae n. subfam., represented by the genera *Bohemograptus* Přib. (Lower and Upper Ludlovian), *Neolobograptus* n. gen. (Upper Ludlovian) and *Neocucullograptus* n. gen. (Upper Ludlovian), displays a remarkable similarity to the trends recognized earlier in Cucullograptinae Urb. The similar morphological characters are, however, based on entirely different structural foundation, namely on a special peridermal fabric called in the writer's previous studies a microfusellar tissue (Urbanek, 1966). The course of evolution of neocucullograptids in the Upper Ludlovian is closely connected with the utilisation of the microfusellar tissue and its derivatives.

The idea of the present monograph may be summarized as follows:

1) a detailed investigation of the structure of thecae and development of a colony in the whole group in question, based on the material etched by chemical treatment from the matrix;

2) a comparison of the structure of different representatives with the application of comparative-anatomical methods;

3) tracing particular evolutionary lineages on the basis of morphological and stratigraphic sequences of the taxa recognized;

4) a determination of certain regularities in morphological changes which took place in particular phyletic lineages and an attempt at their interpretation;

5) an investigation of stratigraphic ranges of the taxa described in order to determine the significance of neocucullograptids for the zonation and correlation;

6) a determination of the place occupied by the Upper Ludlovian graptolite fauna in a general sequence of the Silurian graptolite faunas, with closer analysis of faunal changes between the Lower and Upper Ludlovian.

In solving all these problems, the present writer based his studies mainly on the material from the boring at Mielnik on the Bug (Mielnik nad Bugiem, I. G. 1) in Eastern Poland, but the material, etched from a number of erratic boulders of the Baltic origin, also contributed to the knowledge of earlier (Lower Ludlovian) bohemograptids.

The results of the studies presented seem to be of a considerable significance for better understanding the Upper Silurian graptolite sequence found in the last decade by subsurface prospecting in the Polish Lowland.

The systematic part contains a detailed description of the following taxa:

Genus *Bohemograptus* Přibyl, 1967
B. bohemicus bohemicus (Barrande, 1850)
B. b. tenuis (Bouček, 1956)
B. praecornutus n. sp.
B. cornutus n. sp.

Genus *Neolobograptus* n. gen.
Neolob. auriculatus n. sp.

Genus *Neocucullograptus* n. gen.
Neocuc. inexspectatus inexspectatus (Bouček, 1932)[1]
Neocuc. inexspectatus supernus n. subsp.
Neocuc. kozlowskii n. sp.
Neocuc. kozlowskii var. *unicornus* n. var.

Moreover, appendix to systematic part contains description of two aberrant Ludlovian monograptids, unrelated to neocucullograptids but being of certain stratigraphic significance. They are:

"*Monograptus*" *proegregius* n. sp.
"*Monograptus*" *egregius* n. sp.

ACKNOWLEDGEMENTS

During a long period of preparing the present monograph, I availed myself of stimulating suggestions and of inspiring discussions with Professor Roman Kozłowski (Warszawa), to whom now I should like to express my warmest gratitude. This work is dedicated to Professor R. Kozłowski as the present writer's master in palaeontology.

My thanks are due to Docent R. Osika, Director of the Geological Institute in Warsaw, for his consent to supply valuable material from the Mielnik I. G. 1 borehole for my scientific elaboration and to Dr. H. Tomczyk and Dr. E. Tomczykowa from this Institute for their friendly cooperation and aid in sampling, and for subsequent most valuable explanations and opinions. I also used a friendly exchange of opinions with Dr. L. Teller (Institute of Geological Sciences of the Polish Academy of Sciences, Warszawa), to whom I express my sincerest thanks. My gratitude is also extended to Professor Zofia Kielan-Jaworowska, Director of the Palaeozoological Institute of the Polish Academy of Sciences (Warszawa) for a kind assent to the technical assistance given to the present writer by this Institute's scientific-technical staff.

I feel particularly indebted to Mrs. K. Budzyńska, Mrs. E. Gadomska and Mrs. D. Sławik for a careful inking of my pencil drawings, and to Miss

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[1] This is an emendation of original spelling "*inexpectatus*" used twice by Bouček (1932, 1936) and considered here as an inadvertent error, because its derivation from Lat. "*exspectare*" is obvious.

L. Łuszczewska for taking photographs. A warm gratitude is also due to all graptolitologists who, visiting Warsaw, looked through a part or a whole of the material and, discussing it with the present writer, offered their suggestions. Prof. O. M. B. Bulman (Cambridge, England), Dr. W. N. B. Berry (Berkeley, Calif., U. S. A.), Dr. S. Willefert (Rabat, Morocco), Dr. B. Rickards (Cambridge, England), Prof. B. Bouček (Prague, Czechoslovakia), Dr. A. Přibyl (Prague, Czechoslovakia), Dr. T. N. Koren (Leningrad, U. S. S. R.), Prof. D. E. Jackson (Alberta, Canada) were among them.

The present writer's gratitude is also due to Dr. V. Zázvorka (Prague, Czechoslovakia), Dr. R. Horný (Prague, Czechoslovakia), Prof. B. Bouček (Prague, Czechoslovakia) and Dr. J. Paškevičius (Vilnius, U. S. S. R) for their friendly cooperation and aid during the comparative studies of the type-specimens during his foreign journeys involved in the preparation of the work.

I feel deeply indepted to Mr. J. Dłutek for careful correcting my English in the systematic part of the work and for his translation of the general part of the manuscript. Furthermore, my gratitude is due to Dr. W. Jesionek-Szymańska for her friendly assistance in the preparation of the text for printing. Finally I thank my daughter Margaret who helped making certain calculations involved in the study.

GENERAL PART

INVESTIGATION METHODS

Etching the specimens from matrix by use of chemical treatment, the bleaching technique, preservation of specimens, and methods of drawing were much the same as those described in detail earlier (see Urbanek, 1966, pp. 302—304).

Measurements were taken with the "Lumipan" type microscope, making the appropriate drawings of the outline projected and measured them in a given scale. Measurements were taken in mm with an accuracy to the second decimal point. The scheme of measurements is presented on diagrams (Fig. 1). The numerical data quoted in the description of particular species are based on at least 3 measurements, less frequently on a greater number (to 7). In other cases, a number of the specimens measured (N) is indicated.

The specimens described and illustrated in the present work are preserved in the writer's collections at the Palaeontological Laboratory of the Faculty of Geology of the Warsaw University (Żwirki i Wigury 93, Warszawa, Poland), and marked with successive numbers of plates and figures in which they are shown. Several specimens, in particular brittle

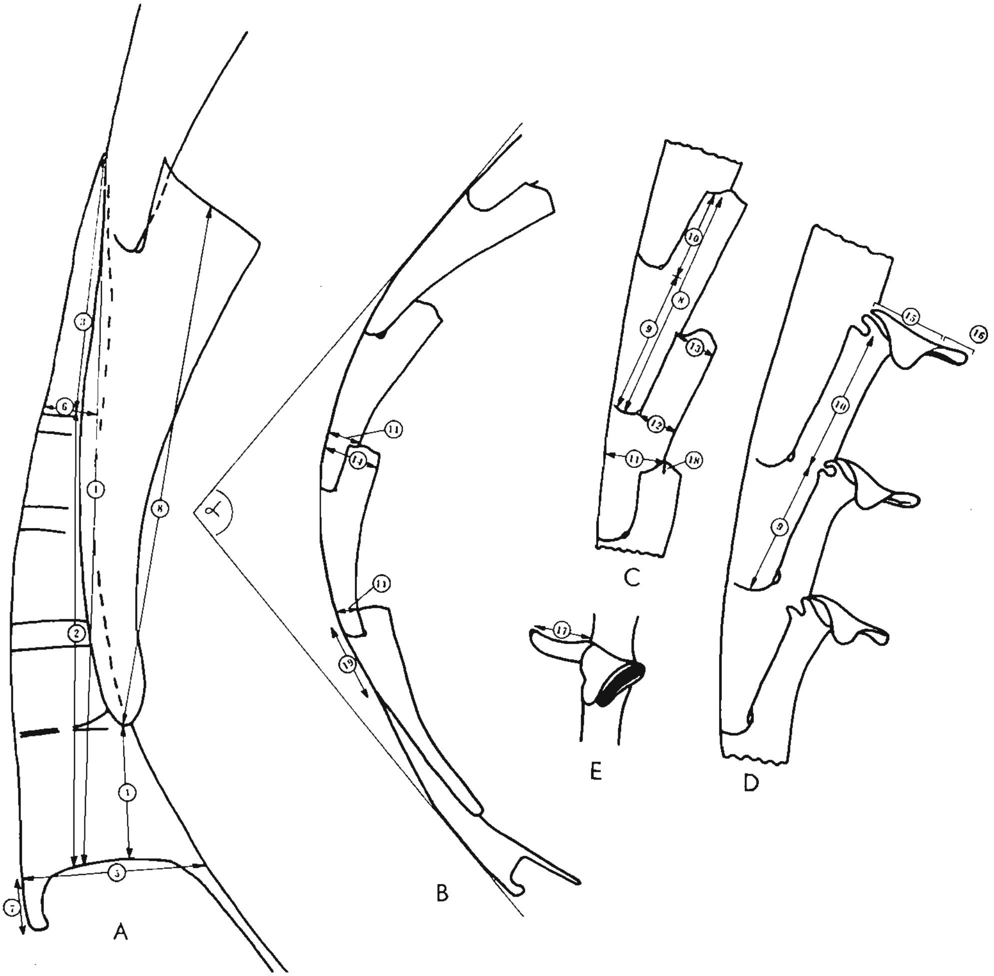


Fig. 1. — Scheme of measurements made on neocucullograptids. *1* length of sicula, *2* length of metasicula, *3* length of prosicula, *4* distance of initial bud from metasicular aperture, *5* diameter of metasicular aperture, *6* width of prosicular aperture, *7* length of dorsal process of metasicula, *8* length of theca, *9* length of protheca, *10* length of metatheca, *11* width of protheca at the level of aperture of preceding theca, *12* width at the base of metatheca, *13* width of metatheca at the aperture, *14* width of rhabdosome measured across the aperture, *15* length of left apertural lobe, *16* length of rostral process, *17* length of lateral process, *18* height of apertural elevation, *19* position of apertural level in th_1 (distance from prosicular apex). α angle indicating the degree of curvature.
A sicula and 1st theca, *B* proximal part of rhabdosome, *C* distal thecae, *D—E* thecae in *Neocucullograptus* n.gen. in lateral and ventral aspects.

and fragile ones, were damaged and, some of them, even destroyed when handled during or after drawing. The destroyed specimens have been replaced in the collection by other ones, taken from similar stratigraphic horizons, so that they might allow one to check the main structural features, mentioned in the text, or to observe details similar to those depicted in figures.

TERMINOLOGY

The terminology used in the present work, is mostly a standard terminology patterned after Bulman (1955), and to a certain extent, supplemented with some terms suggested earlier by the present writer (1960, 1963, 1966). The additional terminology refers to the notions and terms connected with the phylogenetic modifications of the astogeny and, to a lesser extent, with anatomical details of the thecal structure.

The investigations on Neocucullograptinae n. subfam. involved, however, a necessity to introduce a limited number of new terms, denoting certain special structures found in this group, and to use some others in a slightly different context. These terms are quoted below, together with a brief explanation.

New terms introduced or used in a special context

Dorso-lateral apertural incision — a notch formed on the dorsal slope of fusellar bilateral elevations of the apertural margin in *Neolobograptus auriculatus*, and in *Neocucullograptus* n. gen.

Evolutionary hysteresis — (after Greek *hysteresis*, delay, lag), a progressive delay in the adaptive response of organisms to changes in environment caused by certain properties of their genetic and epigenetic systems. Probably, this is an only general and repeatable factor involved in all cases of extinction (a term suggested to replace "lag" of Darlington, 1939).

Gular process — a term introduced by the present writer (Urbanek 1966) for an incurved portion of the left fusellar apertural lobe in *Cucullograptus aversus rostratus*; here used to describe a similar, tongue-like portion of the left microfusellar apertural lobe, situated below the rostral process and covering partly the apertural slit in some representatives of *Neocucullograptus* n. gen.

Lateral apertural process — a semitubular microfusellar outgrowth situated in the dorsolateral part of the right microfusellar apertural lobe, united through a dorsolateral incision with the internal cavity of the apertural apparatus.

Microfusellar addition — any structure composed of microfusellar tissue and, as a result of the delayed growth, superimposed on the fusellar part of the theca proper.

Microfusellar tissue — a previously defined by the present writer (Urbanek, 1966, p. 306) peridermal fabric consisting of very narrow, densely crowded strips (microfuselli), producing dark-pigmented, thick-walled periderm, that is, the microfusellar tissue proper, or consisting of wider, irregularly arranged strips making up a membranaceous, attenuated periderm, that is, the pseudomicrofusellar tissue.

Pelta — (after Lat. *pelta*, light shield), here used to denote a lobate membranaceous, microfusellar addition composed of pseudomicrofusellar tissue and attached to virgella in *B. b. tenuis* (Bouč.).

Rostral apertural process — a semitubular microfusellar outgrowth, which forms a ventral prolongation of the left apertural lobe in *Neocucullograptus* n. gen.

Velum — (after Lat. *velum*, a covering, a veil) an extreme form of microfusellar additions, found in *Bohemograptus* Přib. and forming broadly lobate, bilateral, or single platformlike (annular) structures, which surround the aperture and project outwards like a veil. A more thick-walled, basal part is composed of the microfusellar tissue proper, whereas the marginal, membranaceous part consists of the pseudomicrofusellar tissue.

Veliger morph — (after Lat. *velum*, a veil, and *gerere*, to bear), a morphological form capable to produce, in the course of the growth, microfusellar additions in a more or less advanced stage (including the velum). The presence of the veliger morph probably expresses the genetic polymorphism of *Bohemograptus* Přib. and *Neolobograptus* n. gen. in regard to a capability of secreting the microfusellar tissue. A term, first suggested by Urbanek (1968, *in press*).

Ventral apertural notch — an incision in the apertural margin, situated on the ventral zigzag suture and separating lateral apertural elevations.

Remarks. In certain cases, the abbreviations *tr.* and *long.* have been used to explain that a dimension has been measured across or along the longer axis of thecae or rhabdosome.

ORIGIN OF THE MATERIAL

The graptolite fauna under study in the present work comes from: 1) the core of a deep boring at Mielnik on the Bug, Eastern Poland, I. G. 1, made for the Laboratory of Iron-ore Deposits of the Geological Institute in Warsaw and 2) the Silurian erratic boulders of the Baltic origin, collected on Pomerania's sea beaches and from the Quaternary moraines in Central Poland (Fig. 2).

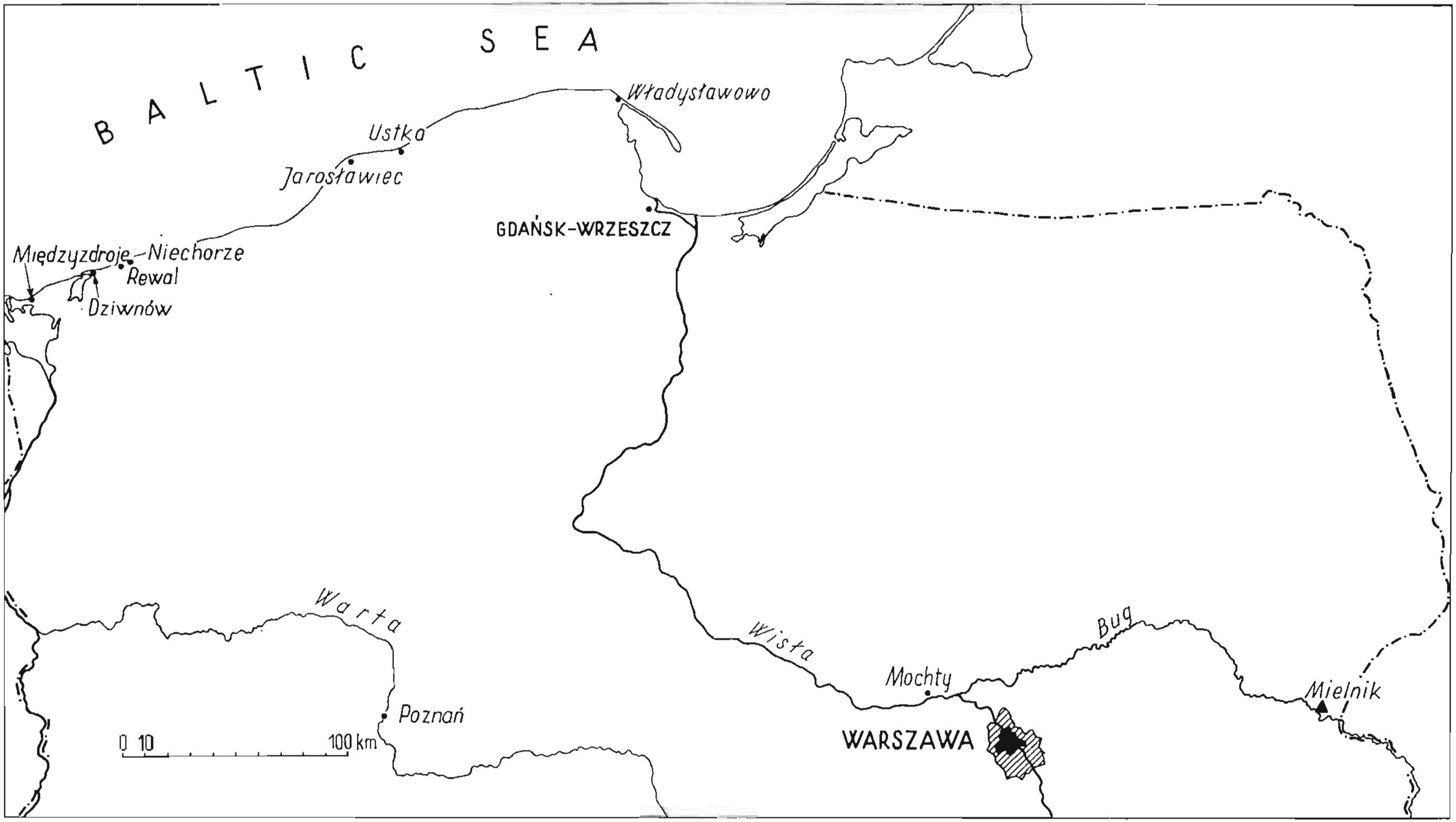
General lithological and stratigraphic characteristics, as well as the problem of the origin of Baltic erratic boulders, have been extensively dealt with in the present writer's previous work (Urbanek, 1966, pp. 299—302) and, therefore, there is no need to resume this subject. Likewise, general characteristics of Silurian deposits from the borehole at Mielnik on the Bug have been given before (Urbanek, 1966, pp. 296—299).

The occurrence of Neocucullograptinae n. subfam. at Mielnik is limited to two stratigraphic units within the platformian Silurian of Poland, distinguished by H. Tomczyk (1962, pp. 112—117, Engl. summary, 1964), that is: 1) Mielnik Beds and 2) Siedlce Beds.

Mielnik Beds, defined in the sequence of graptolite zones, comprise a series between the *Gothograptus nassa* and *Saetograptus leintwardinensis* zones inclusively (cf. Tomczyk, 1962, p. 119). Closer lithological and stratigraphic characteristics of Mielnik Beds have been given in a previous work (Urbanek, 1966, pp. 298—299 and 306—314). More noteworthy is, on the other hand, a series termed as Siedlce Beds. According to Tomczyk (1962, p. 119), they include, in the sequence of graptolitie fauna, series contained between the *Saetograptus leintwardinensis* (exclusively) and "*Monograptus*" *ultimus* (inclusively) horizons. Tomczyk (1960, 1962) deserves the credit for proving that the sediments of this age within the platformian Silurian of Poland contain a rich and diverse graptolite fauna in contrast to its poverty in contemporaneous sediments of neighbouring countries (Bohemia, Thuringia) or to its lack on the British Isles and in Scania. The sediments of Siedlce Beds, first recognized in the graptolite facies in the Żebrak borehole near Siedlce (Podlasie Syneclize), were subsequently found in many other bereholes in the area of South-eastern Poland and in the entire Polish peri-Baltic area (Tomczyk, 1962, 1964, 1968a, 1968b).

The stratigraphic terminology suggested by Tomczyk for the platformian Silurian of Poland has been accepted in the present work despite Teller's (1969, pp. 399—400 and partly p. 402) critical remarks, since it essentially fairly well corresponds to clearly marked stages in the development of the graptolite faunas.

The subdivision of the Polish platformian Silurian, suggested by Tomczyk (1962), was based on the distribution and changes of the graptolite fauna, and the members distinguished have been defined in orthostratigraphic terms. In the present writer's opinion, this subdivision has even a certain superiority over the internationally accepted and widely used British subdivision of the Upper Silurian, based mostly on lithostratigraphic premises. A recent confusion with the Wenlockian-Ludlovian boundary is a convincing example of conflicting palaeontological and lithological criteria of the determination of a demarcation line at the standard locality (Holland, Rickards & Warren, 1969). A suggested temporary solution of the problem, namely, the acceptance of the *nilssoni* zone as a base of the Ludlovian Series in the graptolite facies, is quite natural if we accept the view "that the Wenlockian Limestone must remain in the Wenlockian series" and if we take into consideration that the *Prist. ludensis* zone (= *P. vulgaris* = *P. gotlandicus*?), widely regarded as the base of the Ludlovian, "begins some 100 m below the base of the Wenlockian limestone in the Ludlovian District" (Holland *et al.*, *ibidem*). This solution


BALTIC SEA
Władysławowo
Ustka
Jarosławiec
GDAŃSK-WRZESZCZ
Międzyzdroje
Niechorze
Rewal
Dziwnów
Warta
Wisła
Bug
Mochty
Mielnik
Poznań
WARSZAWA
0 10 100 km

seems, however, less reasonable in regard to major changes in the graptolite fauna, because the boundary suggested coincides neither with the great crisis between Wenlockian and Ludlovian as previously defined, nor with the appearance of new elements that followed this event. The subdivision suggested by Tomczyk (1962) is, therefore, here considered as a more adequate from the viewpoint of the sequence of the graptolite faunas. The term "Lower Ludlovian", if used, is understood in a broader sense and includes a series between the *Gothograptus nassa* and *Saetograptus leintwardinensis* zones inclusively. In the present writer's opinion, Mielnik Beds include a stage contained between a great crisis, brought about by the extinction of Wenlockian faunas and related impoverishment in the taxonomic differentiation of graptolites, and before another, although perhaps less drastic episode, connected with the extinction of several lineages in the *leintwardinensis* horizon (the stage of the Lower Ludlovian). Siedlce Beds mark, therefore, a new development stage of the graptolite fauna, in which new trends were marked and new structural types were developed (Urbanek, 1968, *in press*). This is the stage of the Upper Ludlovian, which has now been more closely recognized only in the area of Polish Lowland and which constitutes a characteristic regional-stratigraphic member of the platformian Silurian justifying the application of a corresponding terminology. The analysis of the origin and main trends in the development of the graptolite fauna of Siedlce Beds is the main aim of the present work.

SIEDLCE BEDS IN THE BOREHOLE FROM MIELNIK ON THE BUG

A series defined by the name of Siedlce Beds, 242 m in thickness, is contained in the borehole of Mielnik on the Bug between a depth of 932.00 m and 690.00 m (Tomczykowa & Tomczyk, 1963, an unpublished archival report of the Geological Institute). Of the total thickness of these beds, the present work contains the results of studies on the graptolite fauna, found in their lower part between depths 932.00 and 823.00 m.

In its lithological development, the Silurian of Mielnik on the Bug is marked by a considerable variability, which, however, resolves itself into a mutual replacement of small layers and lenses, from a few to some scores of centimeters in thickness, alternately clayey (claystones in a light- and dark-tinted microfacies) and marly and carbonate rocks (Langier-Kuźniarowa, 1963, p. 200). This does not allow one to distinguish larger lithological complexes. A relatively smaller general thickness and that of particular stratigraphic members, a predominance of carbonate-marly

Fig. 2. — Sketch-map of Northern Poland showing: 1) localities where described erratic boulders were collected (black drops) and 2) situation of deep boring in Mielnik on the Bug River (black triangle).

sediments over relatively secondarily occurring clayey rocks, a frequent lenticular texture, a poorer diagenesis and a lack of distinct foliation are characteristic features of this section, while an increased content of carbonates, even in clayey rocks, is a characteristic feature of the rocks of all types (Langier-Kuźniarowa, 1963). Carbonate rocks occur in the form of many intercalations, lenses or intergrowths with marls. These are mostly pelitic and less frequently organodetritic rocks. Graptolite remains have been etched out mostly from carbonate-calcareous rocks whose petrographic characteristics are given by Langier-Kuźniarowa (1963, pp. 234—235).

The sedimentation of the Silurian deposits at Mielnik on the Bug maintains this monotonous, repeatable character within the range of both Mielnik and Siedlce beds. On the other hand, a frequently occurring lamination (micro- or macrolaminae consisting alternately of dark claystones, pelitic or organodetritic limestones and marls) represents a certain characteristic feature of Siedlce Beds. A similar lamination occurs only occasionally in older Silurian sediments of Mielnik, but is highly charateristic of Siedlce Beds (Tomczykowa and Tomczyk, 1963, an unpublished archival report; Langier-Kuźniarowa, 1963). Also characteristic are intercalations of the detrital material (quartz and mica), occurring in mudstones.

An intensification of volcanic phenomena, manifested by the presence of pyroclastic sediments in the form of relatively numerous bentonite intercalations also falls on Siedlce Beds in Mielnik on the Bug. Particularly frequent are bentonite intercalations in the *Neocuc. kozlowskii* — “*Monoclim.*” *ultimus* interzone and in the lower part of the latter zone in which they reach a thickness of 35 cm (Langier-Kuźniarowa, 1963, pp. 255—256).

In regard to biofacies, the Silurian deposits from Mielnik on the Bug may be assigned to what is known as a “mixed biofacies”, marked — in addition the occurrence of graptolites — by a more or less frequent presence of the shelly fauna. This fauna is particularly rich in the *ultimus-formosus* zone and hence Tomczykowa and Tomczyk (1963, an unpublished report of the Geological Institute) mention *Dayia* cf. *navicula* (Sow.), *Proetus conspersus* Ang., *Acaste* sp., *Leonaspis* sp., *Cardiola* sp., *Pterinea* sp., *Podolella* sp., “*Orthoceras*” sp., Eurypterida and beyrichiacean ostracods.

SEQUENCE OF GRAPTOLITE FAUNA RECOGNIZED WITHIN THE RANGE OF SIEDLCE BEDS IN THE MIELNIK ON THE BUG BOREHOLE

The aim of the present work is to trace the history of graptolites of the group Neocucullograptinae n. subfam. and not to study the graptolite fauna of a definite stratigraphic member. Hence the stratigraphic aspect of these studies is in fact of a secondary nature although they have resulted in erecting a few new graptolite zones determined by species of monograptids fairly unusual morphologically and although they significantly supplement the present state of knowledge of the sequence of the Upper Silurian graptolite faunas.

In the course of the Lower Ludlovian (Mielnik Beds — according to the terminology suggested by Tomczyk (1962) for the platformian Silurian of Poland and accepted in the present writer's previous work in 1966), Neocucullograptinae n. subfam. are represented by a persistent species of *Bohemograptus bohemicus* (Barr.), making up a group of a small stratigraphic significance. A more accurate knowledge of its history during the Lower Ludlovian does not contribute any significant elements to the stratigraphic division known so far (Urbanek, 1966). On the other hand, in the younger stratigraphic member, the Siedlce Beds, corresponding on the whole to the Upper Ludlovian (and perhaps the lower part of the post-Ludlovian, cf. pp. 187), Neocucullograptinae n. subfam. became a progressive group, producing several morphological forms conspicuously characteristic of individual horizons of this series of sediments. The occurrence of Neocucullograptinae n. subfam. is, however, limited to the lower part of these beds and hence, now this member of them are the best recognized stratigraphically, whereas the upper part of these beds, for which *Monoclim. ultimus*-"*M.*" *formosus* zone is here being used now as a working term describing them as a single graptolite zone, requires revision and probably will be subject to the writer's further studies.

Until recently, there was a common belief that between the *Saetograptus leintwardinensis* (or, *Saet. fritschi linearis*) and "*Monogr.*" *formosus* (with *Monoclim. ultimus* in the lower part) zone, the graptolite fauna is represented by a monotonous, little-differentiated assemblage of persistent species of no stratigraphic importance. Such views were expressed by Horný (1962, p. 893, "...eine ziemlich monotone Gemeinschaft: *Prist. bohemicus* (Barr.), *Prist.* ex. gr. *dubius* (Suess), *Monograptus* ex. gr. *scanicus* Tullberg") and Jaeger (1964, p. 41, "Die langlebigen Arten *dubius*, *bohemicus* und *haupti* sind die wichtigsten Vertreter, die das Interregnum zwischen *fritschi linearis*-Zone und dem Auftreten der *ultimus*- und *formosus*-Gruppe kennzeichnen").

Recent studies by borings in the areas of Polish Lowland have, however, led to a discovery of a rich graptolite fauna in the sediments of the age referred to above. Attention was attracted to this fact by Tomczyk (1960, 1962) who maintains that „the differentiation of graptolite fauna in the series from the *Prist. leintwardinensis* to the *Monograptus formosus* is also significant and by no means poorer than in the Lower Ludlovian" (Tomczyk, 1960, p. 138). In his further works, Tomczyk sought to determine accurately the composition of this assemblage, affirming that "abundant graptolite fauna comprises a large number of new species between *Saetogr. leintwardinensis* zone and *Prist. ultimus* zone" (Tomczyk, 1962,

p. 119, English summary). In this author's subsequent works, this assemblage is characterized as that containing new species of the group *Prist. bohemicus, Prist. tumescens*, new species of the group *Monogr. formosus*, as well as certain species known from a contemporaneous series of the Barrandian such as, *Prist. fragmentalis* and *Prist. longus*[2] H. Tomczyk also tried to show a considerable homeomorphy of this fauna to certain elements of the Lower Ludlovian fauna, a homeomorphy which may cause an erroneous identification.

In further publications, Tomczyk (1962) and Tomczykowa & Tomczyk (1962) put forward the view that in the upper part of Siedlce Beds in Polish Lowland, species of monograptids occur, which, in other areas, are characterictis of the Lochkovian. This view, subsequently upheld in a more or less resolute form (Tomczyk, 1963, 1964), became the subject of a heated dispute, summed up in Teller's (1969, pp. 461—463) work. Since the upper part of Siedlce Beds is not included in the considerations of the present work, the writer does not intend to resume this problem which seems to consist in inaccurate determinations and interpretative misapprehensions.

Despite Tomczyk's pioneer works, the graptolite assemblage of Siedlce Beds has not been accurately determined palaeontologically, as the terms of the open nomenclature applied (cf., ex. gr., n. sp., sp.) were obviously inadequate. The form identified specifically (*Prist. longus, Prist. fragmentalis*) belong to the category of doubtful taxons, or at any rate their stratigraphic significance has not been unqestionably demonstrated (Horný, 1962).

Thus, only the studies, exposed in the present work, have enabled an appropriate verification of earlier views, showing an actual degree of differentiation of the fauna of Siedlce Beds and stating precisely its relationship to the Lower Ludlovian fauna (cf. also Urbanek, 1968, *in press*). This picture departs by far from an "impoverished interregnum" accepted until recently.

On the whole, the lower part of Siedlce Beds may be characterized by means of the species belonging to *Bohemograptus* Přib. which here display a considerable quantitative increase (*B. b. tenuis, B. praecornutus* n. sp., *B. cornutus* n. sp.). Higher zones are marked by the occurrence of *Neolobograptus* n. gen. and *Neocucullograptus* n. gen., represented by more specialized forms.

The stratigraphic scheme, given below, is aimed at a division of Siedlce Beds on the basis of the occurrence of the graptolite fauna in definite borehole cores. For this reason, the units distinguished are described with

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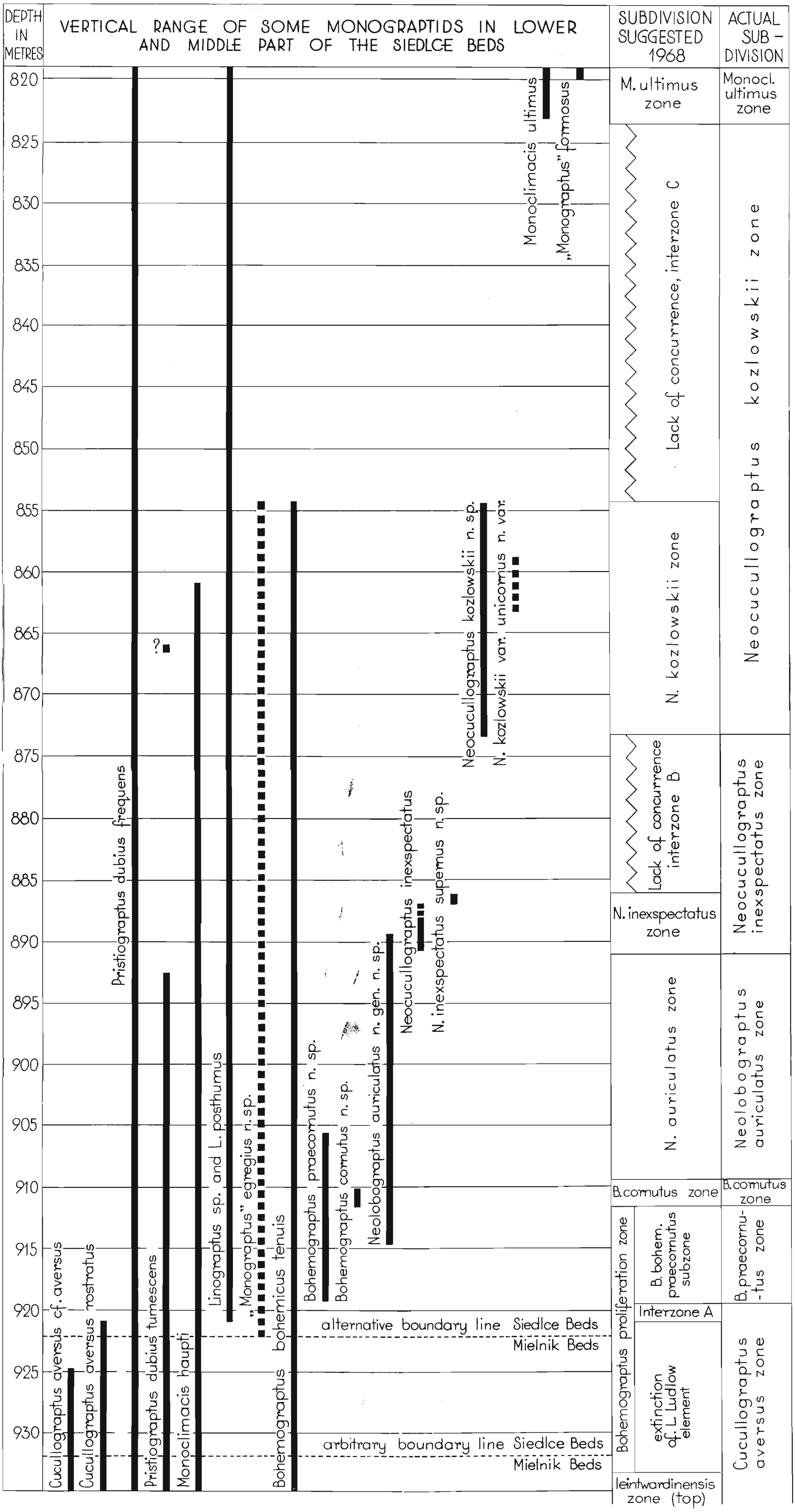
[2] *Retiolites* sp. is also mentioned by Tomczyk (1960, p. 138) from the lower part of this series. In the Mielnik on the Bug profile, the last Retiolitidae occur in the *leintwardinensis* zone (Urbanek, 1966, pp. 313—314). This unexpectedly high place of their occurrence allows one to expect that, in other borings, they may actually pass locally to the lower parts of Siedlce Beds.

PLATE I



Range chart showing vertical distribution of Neocucullograptinae n.subfam. and associated graptolite fauna in the Mielnik core, with suggested subdivision of the strata. Broken heavy black lines indicate that given form is very rare or absent in indicated horizons. Interrogative point indicate uncertain occurrence. Thin broken lines indicate alternative positions of lower boundary of the Siedlce Beds.

the use of the biostratic terminology. The comparison with adjacent areas indicates, however, that the scheme of the stratigraphic division suggested may be of a more general significance to the contemporaneous deposits of Central and Eastern Europe (Urbanek, 1968, *in press*).

In the light of the studies on the graptolite fauna, made in the present work, the series of Siedlce Beds in the Mielnik on the Bug borehole may be divided into the following range-zones (Pl. I, range chart):

6) *Monoclim. ultimus* (Perner) to *"Monogr." formosus* (Bouček) zone, depths 823.00—690.00 m;

5) *Neocuc. kozlowskii* n. sp. zone, depths 873.40—854.60 m and an interzone up to a depth of 823.00 m;

4) *Neocuc. inexspectatus* (Bouček) zone, depths 890.70—886.00 m and an interzone up to a depth of 873.40 m;

3) *Neolob. auriculatus* n. sp. zone, depths 910.10—890.70 m (from the top of zone 2 to the bottom of zone 4);

2) *Bohemogr. cornutus* n. sp. zone, depths 911.60—910.10 m;

1) *Bohemogr. praecornutus* n. sp. zone, depths 919.10—911.60 m (from the first appearance to the bottom of horizon 2).

As compared with an earlier suggestion of the stratigraphic division, put forward by the present writer (Urbanek, 1968, *in press*, preliminary report) and published after him by Teller (1969, p. 453), the scheme given above, differs in some essential respects. A more accurate recognition of the morphology, taxonomy and stratigraphic occurrence of the graptolite fauna in the lowermost part of Siedlce Beds makes the distinguishing of the "*Bohemogr.* proliferation zone" superfluous (Urbanek, 1968, *in press*). This zone, epibole in character ("peak-zone"), has been distinguished on the basis of a mass occurrence of *Bohemograptus* directly above the *Saet. leintwardinensis* zone. In the original conception, put forward by Urbanek (1968, *in press*), this zone was provisionally divided into a lower subzone, yet marked by the concurrence of the relics of the Lower Ludlovian fauna (Mielnik Beds), that is, *Cuc. aversus aversus* (Eisenack) and *Cuc. aversus rostratus* Urb., and an upper subzone. The latter would be marked by the occurrence of *B. praecornutus* n. sp. (Pl. I, range chart).

Recent studies allow one, however, for a somewhat different approach to the problem of the development of the graptolite fauna in this part of the section. Although *Bohemograptus* is frequent as early as the *aversus* zone, but its truly mass occurrence is observed only after the extinction of those Lower Ludlovian relics. The mass occurrence of *B. b. tenuis* (Bouček) coincides, however, in this place with the appearance of new species, unknown from Mielnik Beds. These are *"M." egregius* n. sp. and *B. praecornutus* n. sp. the first species which initiate a new phase in the development of the graptolite fauna, characteristic of Siedlce Beds. Establishing these facts enables the coordination of the subdivision of Siedlce Beds with formal requirements of the stratigraphic classification, in which more importance is attached to qualitative evolutionary changes (appearance of new taxons), rather than to events of a purely quantitative nature (quantitative increase in a given species). The development of the graptolite fauna of Siedlce Beds, considered in this aspect, begins, therefore, with an almost simultaneous appearance of "*M.*" *egregius* n. sp. (a depth of 922.10 m) and *B. praecornutus* n. sp. (a depth of 919.10 m).

A separation of the independent *praecornutus* zone (2) and *cornutus* zone (3) (Pl. I, range chart), in conformity with distinction of *B. praecornutus* n. sp. and *B. cornutus* n. sp., previously considered to be subspecies (Urbanek, 1968, *in press*), is another important difference.

Less significant corrections are introduced to the working scheme of the division of Siedlce Beds (in the form presented in Urbanek, 1968, *in press*, and Teller, 1969) by the redefinition of *B. b. bohemicus* (Barr.) and *B. b. tenuis* (Bouček) as "temporal subspecies" (cf. Table II). Previously, as a result of certain vagueness in their concept they have been provisionally distinguished according to purely morphological differences (Urbanek, 1968, *in press*). Finally, a morphological and taxonomic distinction of *B. praecornutus* n. sp. from extreme variants ("robust forms") of *B. b. tenuis* (Bouček) has been shown which changed the views on the range of the former species and allowed one to limit considerably this range as compared to earlier suggestions (Urbanek, 1968, *in press*, range chart).

For this reason, in the stratigraphic division of Siedlce Beds in the section of the Mielnik on the Bug borehole, now suggested, no concept of a zone of mass occurrence (epibole) of *B. bohemicus* is used. This does not preclude that the phenomena of 1) a great quantitative increase in this species, together with 2) accompanying considerable interpopulationary variability, 3) characteristic polymorphism (frequent occurrence of "veliger" morph., see terminolology) and 4) not less characteristic scarcity or lack of other graptolite association (caused by the impoverishment of the graptolite fauna above the *leintwardinensis* zone and lack of new elements beginning the development stage of this fauna within Siedlce Beds), may have a definite stratigraphic significance (Urbanek, 1968, *in press*, as well as Teller, 1969 after Urbanek, 1968 *in press* and personal communication). According to earlier views, this event in the history of *B. bohemicus* (Barr.) may locally provide a basis for the separation of such a peak-zone as a characteristic stratigraphic unit and besides, it seems to be of a certain correlative significance (Urbanek, 1968, *in press* and pp. 235 of the present work).

On the basis of Urbanek's yet unpublished studies (1968, *in press* and pers. comm.), Teller (1969, pp. 457—458) tried to give a classification of graptolite zones distinguished within Siedlce Beds and suggested a certain modification of this division as compared with the scheme given earlier by Urbanek (1968, *in press*). This modification consists in the distinction of the *B. cornutus* n. sp. zone only, determined jointly by the occurrence of *B. cornutus* n. sp. and of *B. praecornutus*. Urbanek (1968, pers. comm. given by Teller) has once been inclined to consider the latter as a subspecies of *B. cornutus*. Teller (1969, p. 457) has declared himself for combining both subzones to form one zone of *B. cornutus* n. sp. This view, obviously correct on the assumption that the differences between *B. praecornutus* n. sp. and *B. cornutus* n. sp. are subspecific in character (although the possibility of the division of thus understood unit into two subzones is not quite correctly denied by Teller), becomes out-of-date in the light of recent studies which do not leave the slightest doubt but that these are clearly two different species.

An attempt at a classification of Urbanek's (1968, *in press*) zones, presented in Teller's (1969) work, consists in a distinction of units of the nature of epibole (of the zone of mass occurrence of *B. bohemicus)* and an acrozone (the *B. cornutus, Neolob. auriculatus* and *Neocuc. inexspectatus* zones). The *Neocuc. kozlowskii* zone has not been referred by Teller to any of these categories. This classification, not quite accurate even in the light of the data previously quoted by Urbanek (1968, *in press*), requires — in view of the recent advance in studies — an additional commentary.

As a matter of fact, mutual overlaps of vertical ranges of *B. praecornutus* n. sp. and *B. cornutus* n. sp. on the one hand and of *B. praecornutus* n. sp. and *Neolob. auriculatus* n. sp. on the other, as well as of the latter and *Neocuc. inexspectatus* (Bouček), cause that the biostratic units, practically distinguished in the Mielnik on the Bug profile, mostly do not fully correspond to "acrozones" (range-zone, holozonite) [3].

The *B. praecornutus* n. sp. and *Neolobograptus* n. sp. zones should be assigned to the group of zones conspicuously deviating from the concept of a holozonite (or topo- or merozonite). In both cases, only part of the vertical range observed has been used for the characterization of a given biostratic unit. Thus, the *B. praecornutus* n. sp. zone in a here given sense (Pl. I, range chart) does not comprise the upper termination of the vertical range found in the profile on the Mielnik on the Bug and the *Neolob. auriculatus* n. sp. zone — of both the lower and upper end of its range (Pl. I, range chart). A considerable mutual overlap of the ranges would in fact allow one for the distinction of a certain number of "zones of concurrence" ("concurrent range-zones"), which, however, would contribute to a considerable complication of the stratigraphic division. Due to the working and provisionary character of the subdivision here suggested, the procedure accepted seems to be more appropriate, although the conception suggested is not fully satisfactory from the formal viewpoint.

As the first appearance of an index species is an event of greatest stratigraphic significance, further investigations may allow to lump

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[3] Due to a local character of determining the ranges (a single borehole core!), here we could rather consider topozonites.

certain zones into larger unit e. g. to "*Neolob. auriculatus* zone with *B. cornutus* in its lower part".

On the other hand, the zones of *Bohemograptus cornutus* n. sp. *Neocuc. inexspectatus* (Bouček), *Neocuc. kozlowskii* n. sp. correspond to the category of holozonites (or mero- or topozonites). The "*M.*" *formosus* (Bouček) zone is not sufficiently recognized but it probably also belongs to this category. The lack of mutual overlaps of vertical ranges is marked between the *Neocuc. inexspectatus* and *Neocuc. kozlowskii,* as well as between the last- named and the "*M.*" *formosus* zone. A close evolutionary relationship between the first and the second of the species mentioned above seems to be an evidence that these interzonal spaces are either accidental or local in character. A similar lack of the overlap of ranges between the two last--named forms is also in the Mielnik on the Bug section of the random or local nature, the evidence for which is a common occurrence of *Neocuc.* cf. *kozlowskii* n. sp. and *Monoclim. ultimus* (Perner), a species which is an associate of the "*ultimus-formosus*" coenozone in the boreholes of SW Lithuania (cf. pp. 186).

There may be a few causes of the lack of overlap of ranges of the two species. One of them is a decrease in the diameter of a core, which simultaneously decreases the probability of finding less numerous forms. Another may be an ingression of the linograptid fauna sometimes abundantly occurring in this place (in particular at a depth of 840.00—820.00 m). Most specimens of *Linograptus posthumus* (Reinh. Richter), described from Mielnik on the Bug (Urbanek, 1963) come from this series of sediments. This assemblage might temporarily displace other graptolites. Finally, relatively numerous intercalations of pyroclastic material (bentonites), in which no graptolite remains have been preserved, fall to this part of the core.

In the light of Tomczyk's data (1968, 1968c), such impoverishment of the graptolite fauna is, however, a stable and remarkable feature of the beds located between the last occurrence of *Bohemograptus* and the first appearance of "*M.*" *formosus.* He has recognized it in all boreholes from Podlasie syneclize (1968c, p. 264—265) and in the Peribaltic area (1968a, Fig. 2, pp. 28—29). This interzone may have, therefore, a wider regional character and its probable stratigraphic significance is discussed below.

According to formal principles of procedure, these interzonal spaces, understood not as barren layers, but as layers marked by the absence of index species, have been assigned, in the ultimate scheme of the division of Siedlce Beds, to a lower zone directly preceding them (cf. Pl. I, actual subdivision).

While in a scheme, suggested by the present writer, Siedlce Beds are divided into six graptolite zones, Tomczyk (1968a, 1968b, 1968c), suggested a more general division, distinguishing lower Siedlce Beds (mass development of *B. bohemicus* and *Pristiograptus* sp.), middle Siedlce Beds (marked by the occurrence of *Prist.* ex. gr. *dubius, Pristiogr.* sp. nov. in Tomczyk 1968a, or *Prist. dubius, Monoclim.* ex. gr. *ultimus* and *Prist. longus* in Tomczyk, 1968b) and upper Siedlce Beds(of which typical is the mass occurrence of "*M.*" ex. gr. *formosus,* in the top — also of *Dayia navicula* J. C. Sow., *Chonetes striatellus* De Koninck and in the uppermost part — of *Acastella spinosa* (Salter) and *Acastella prima* E. Tomczykowa).

In this general scheme of the subdivision of Siedlce Beds, the lower and upper parts are more or less satisfactorily defined by Tomczyk (the lower as controlled by the distribution of *Bohemograptus* and the upper part as *M. formosus* zone). The middle member of these Beds are, according to Tomczyk's concept (1968a, p. 29 and pers. comm.), defined rather as an interval, or "interregnum", characterized by the absence of both *Bohemograptus* and "*M.*" *formosus.* The graptolites cited are determined in terms of open nomenclature (cf. ex. gr., sp.). They belong to persistent species, or to dubious species without a recognized stratigraphic value.

The data quoted by Tomczyk indicate, however, that such a horizon marked by the impoverishment of the graptolite fauna is widely distributed in the Silurian of the Podlasie syneclize and in the Peribaltic area, its thickness being 7—180 m (in Mielnik approx. 30 m). According to Tomczyk (pers. comm.), it is a convenient marker bed for subsurface mapping, which, moreover, in all Polish platformian Silurian takes a very stable stratigraphic position.

The tripartite subdivision of Siedlce Beds is here retained as a convenient working scheme, although it should be borne in mind that its middle part can hardly be regarded as a biostratigraphic unit of a greater correlative value. Its lower boundary is controlled by the disappearance of *Bohemograptus*, an event which most probably occur heterochronically in adjacent areas. Moreover, in Lithuania, the vertical ranges of *Neocuc. kozlowskii* n. sp. and *Monoclim. ultimus* overlap each other, indicating that there is no interval between them comparable with an interzonal space in the Mielnik on the Bug boring (Pl. I, a subdivision suggested in 1968), or with the middle part of Siedlce Beds as defined by Tomczyk. The following interpretation is here suggested:

Siedlce Beds	upper part	— *Monoclim. ultimus*-"*M.*" *formosus* zone (6)
	middle part	— interzone between zones 5 and 6
	lower part	*Neocuc. kozlowskii* zone (5)
		Neocuc. inexspectatus zone (4)
		Neolob. auriculatus zone (3)
		Bohemogr. cornutus zone (2)
		B. praecornutus zone (1)

In the text below, the concepts of the lower, middle and upper Siedlce Beds are used precisely in this sense. The lower Siedlce Beds, which are the main subject under study in the present work, are at the same time the range-zone of "*M.*" *egregius* n. sp.

A certain additional commentary is required by the uppermost zone of Siedlce Beds, that is, the *Monoclim. ultimus* (Perner) — "*Monograptus*" *formosus* (Bouček) zone which begins at a depth of 823.00 m (the appearance of *Monoclim. ultimus*) or of 820.00 m (the appearance of "*M.*" *formosus*). A more precise definition of this zone will only be possible after conducting accurate studies. According to Tomczykowa & Tomczyk (1963, an unpublished archival report of the Geological Institute and Tomczyk, 1964, p. 516, Fig. 2), the top of the "*M.*" *formosus* zone in the Mielnik on the Bug borehole is situated at a depth of 690.00 m.

Due to the presence of an interzonal interval, occurring between the *Monoclim. ultimus* zone and the lower *Neocuc. kozlowskii* n. sp. zone, it is difficult to estimate the significance of a small difference in the occurrence of the former, accompanied subsequently by the "*M.*" *formosus* (3.00 m!). This difference may be purely accidental. Jaeger (1964) and Teller (1969) express the view that the two species appear simultaneously, similarly as it has been found in the Barrandian sections. Teller (1969) believes that they accompany each other throughout their existence period, but he determines the appropriate zone as an "*M.*" *formosus* horizon since the latter is a more characteristic form. In such a sense, this would be a coenozone of *formosus-ultimus*. A different approach is displayed by Tomczykowa & Tomczyk (1962) and Tomczyk (1962, 1964). The last-named author distinguishes a lower "*M.*" *formosus* (still assigned by him to Siedlce Beds) and an upper "*P.*" *ultimus* (already referred to Podlasie Beds or stage). Due to the prolonged concurrence of both species, the latter suggestion seems to be rather irrelevant but an appropriate determination of the two species will only be possible as a result of further studies. A contribution to better knowledge of graptolites from *formosus* zone was made by Teller (1966).

The problem of the lower boundary of Siedlce Beds

According to Tomczyk's (1962) definition of Siedlce Beds, their lower boundary is determined by the top of the *Saetograptus leintwardinensis* zone. Consequently, Tomczykowa & Tomczyk (1963, an unpublished archival report of the Geological Institute in Warsaw), suggest to draw a boundary between Mielnik and Siedlce beds in the Mielnik on the Bug borehole along the upper boundary of the range of *Saetograptus leintwardinensis* sensu lato (*Saetogr.* ex. gr. *leintwardinensis*), that is, along the upper boundary of the range of *Saetograptus*. A depth of 932.00 m has been adopted as a "rounded-off" limiting range between Mielnik and Siedlce beds (cf. also Tomczyk, 1964, p. 516, Fig. 2). As a matter of fact, a similar viewpoint was expressed by Teller (1969, p. 403, chart 1), who located this boundary in Poland between the Lower and Upper Ludlovian, on the boundary between the *Saetogr. leintwardinensis* and *B. bohemicus* zones. The two authors, mentioned above, emphasize a considerable correlative significance of the *leintwardinensis* zone which makes up a convenient "marker bed" easy to identify and widely distributed.

The fact that the graptolite fauna of the lowermost part of Siedlce Beds does not contain any new elements and only consists of taxons which are merely relics of the Lower Ludlovian fauna (*Cuc. aversus* cf. *aversus*, *Cuc. aversus rostratus*, *B. b. tenuis*, *Prist. dubius frequens*, *Prist. dubius tumescens*) is a disadvantage of thus defined boundary. This situation is not quite exceptional. It resembles conditions, found on the boundary of the Wenlockian and Ludlovian, on which, after the extinction of most Wenlockian elements, the occurrence of an impoverished graptolite fauna is recorded. The last-named fauna, at first devoid of new elements, is, however, marked by a mass occurrence of some of them (*Gothograptus nassa*, *Pristiograptus dubius*; "*dubius-nassa* Interregnum" according to Jaeger's terminology, 1959). The latter event provides an analogy to a mass occurrence of *B. bohemicus* directly after the extinction of many lineages on the boundary of Mielnik and Siedlce beds.

In regard to the problem of the Wenlockian-Ludlovian boundary, two standpoints have recently been marked. They also seem to be applicable to the problem of the boundary between the Lower and Upper Ludlovian which we are interested in. On the one hand, Jaeger (1959, 1964) and Horný (1962) are of the opinion that this boundary may be demarcated only by the appearance of new faunal elements that do not occur in the Wenlockian and, therefore, they still assign "*dubius-nassa* Interregnum" to the Wenlockian. On the other hand, many Polish stratigraphers have for a long time now attached much importance to such an event as the mass development of *Gothograptus nassa* above the *Cyrtograptus lundgreni* zone (Jaworowski, 1965).

The *Gothograptus nassa* zone, distinguished in the stratigraphic subdivision of the Silurian of Poland, is in a fact an epibole (Teller, 1969, p. 448) exceedingly characteristic of the Silurian of Central and Eastern Europe, including the Baltic area (Hede, 1942; of the Island of Gotland; erratic boulders). For these reasons, the *Gothograptus nassa* zone is considered as the first Ludlovian zone.

Being of the opinion that the extinction of *Saetograptus* and abundant occurrence of *Bohemograptus* combine to define the boundary between Mielnik and Siedlce beds, that is, at the same time, the boundary between the Lower and Upper Ludlovian, in the light of the viewpoint referred to above, analogous importance may be attributed to a mass occurrence of *Bohemograptus bohemicus* above the *leintwardinensis* zone. Another solution of the problem of the lower boundary of Siedlce Beds may consist in tracing such boundary in the zone of the first appearance of new faunal elements, that is, in this case, of *"M." egregius* n. sp. (at a depth of 922.10 m) or *Bohemograptus praecornutus* n. sp. (at a depth of 919.10 m). The appearance of these new elements is accompanied by an almost simultaneous extinction of the last Lower Ludlovian elements (*Cucullograptus aversus rostratus*, the last occurrence at a depth of 920.80 m). Thus, the boundary between Mielnik and Siedlce beds may be traced in the Mielnik on the Bug borehole at a depth of ca 920 m (cf. Pl. I, range chart).

The third viewpoint on the question the of the Wenlockian-Ludlovian boundary has recently been presented by Holland, Rickards and Warren (1969). It is based, however, on different criteria than the natural periodicity in the sequence of the graptolite fauna (comp. also p. 171 of the present work).

At the same time, the problem of the lower boundary of Siedlce Beds cannot be solved on the basis of the knowledge of one section only, for it requires a more many-sided knowledge of the stratigraphic distribution of the fauna. Studies aimed at obtaining such a knowledge will lead to the choice between the following two alternatives: 1) a boundary located in the top of the *Saetograptus leintwardinensis* holobiozone or in the bottom of the *Bohemograptus b. tenuis* hemera, analogously to the solution as to the boundary of the Wenlockian and Ludlovian, accepted by Polish geologists; 2) a boundary located in the bottom of a zone determined by the occurrence of the first new elements characteristic of Siedlce Beds, that is, *"M." egregius* n. sp. or *B. praecornutus* n. sp., or a boundary line "averaged" for practical purposes (cf. Pl. I, range chart, boundary lines).

COMPARISON WITH THE SEQUENCE OF GRAPTOLITE FAUNAS IN ADJACENT AREAS

Stratigraphic equivalents of Siedlce Beds may be sought in the areas, in which the change in facial conditions, marked on the boundary of the Lower and Upper Ludlovian, is not so radical in character as to break completely the continuity of the development of the graptolite biofacies. This is the reason why such areas as the British Isles and Scandinavia should be immediately excluded from further considerations. In regard to the character of the development of the Silurian and the state of recognition, the most promising areas are a) Barrandian in Central Bohemia; b) Lithuania; c) less so, but also with certain possibilities of comparing: the Baltic area, recognized on the basis of erratic boulders and d) the area of Thuringia.

a) *Barrandian.* — The sequence of the graptolite fauna in this area has recently been shown in detail and in a synthetic manner in Horný's (1962) work. On the whole, Siedlce Beds correspond here to the upper part of Kopanina Beds and to the lowermost part of the Přidoli Beds. The graptolite fauna of the former member is as yet little known and the forms of pristiograptids, used to characterize it, are inadequately defined morphologically, and doubtful as separate species, their stratigraphic significance not being confirmed[4]. This is the reason why Horný (1962, p. 883) includes these zones in a collective category of "nicht definierte Zonen" and rather thinks that, maybe for a certain sedimentary gap, the equivalents of Siedlce Beds do not occur in the area of Barrandian. Such a gap might result from the existence of a clear-cut boundary between Kopanina and Přidoli beds and from a different facial development of the latter, although Horný emphasizes that the nongraptolite fauna passes the boundary of these beds, many species being in common (1962, pp. 894, 905).

Some facts seem, however, to indicate that the graptolite sequence of Barrandian as high as the bottom of the *ultimus* zone (Horný, 1962, Fig. 7, preserved and insufficiently recognized. In this connection, considerable significance is acquired by the problem of forms, termed by Horný as "*M.* ex. gr. *scanicus* Tullb." (1962, p. 843). Thus termed forms reach in Barrandian as far as the bottom of the *ultimus* zone (Horný, 1962, Fig. 7, distribution table; explanations to Fig. 6, p. 881; Fig. 10, p. 987; Fig. 11, p. 887).

The "*M.* ex. gr. *scanicus*" group seems to include both typical Cucullograptinae and Neocullograptinae n. subfam. The presence of the last-named in Barrandian has been found in the Čertovy Schody near Koněprusy section and *Neocuc. kozlowskii* n. sp. was recognized directly underlying a layer of brecciated limestones, which in that place formed the bottom of Přidoli Beds, and *Neocuc.* cf. *inexspectatus* ca 15 m below this layer. Earlier recognition of *Neocuc. inexspectatus* (= *M. inexspectatus* Bouček, 1932) in the Pankrác near Prague section favours the supposition that at least the middle member of lower part of Siedlce Beds is well represented in the area of Barrandian. This precludes the possibility of the occurrence of the sedimentary gap below the *Monoclim. ultimus* zone, mentioned by Horný (1962, p. 883, Fig. 7 and p. 894).

The *Saetograptus fritschi linearis* zone, whose presence is connected with a locally longer persistence of saetograptids, and the *P.* ex. gr. *dubius*-*P. bohemicus* assemblage, occurring above, are the equivalents of the lower part of Siedlce Beds. It would be of interest to study whether or not this assemblage also includes the relics of *Cucullograptus* and whether or not the differentiation of *Bohemograptus*, which may be compared with such a process in the area of NE Poland, subsequently comes about in the area of Barrandian.

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[4] Nevertheless, these zones (of *P. longus*, *P. fragmentalis* and *P. fecundus*) continue to be distinguished by some authors (Přibyl & Vaněk, 1968).

b) *The area of Lithuania.* — In the area of Lithuania, Siedlce Beds correspond to Pagegiai Beds (probably excluding their lowermost part) and the lower part of Minija Beds (Paskevičius, 1968; Paskevičius-Karatajúté-Talimaa, 1968). Both series contain the graptolite fauna only locally and sporadically and the Pajavonys (SW Lithuania) borehole allows one to state that *Neocuc.* cf. *kozlowskii* n. sp. and *Monoclim. ultimus* (Perner) (Urbanek, 1968 *in press*, cf. also systematic part) occur on the boundary of Pagegiai and Minija beds. Finding common occurrence of *Neocuc.* cf. *kozlowskii* and *Monoclim. ultimus* is indicative not only of a wider geographical occurrence of the former, but also of a partial mutual overlap of the stratigraphic ranges of the two species mentioned above. In the Mielnik on the Bug borehole, they are separated from each other by a considerably thick interzone whose occurrence has been discussed above. The concurrence of *Neocuc.* cf. n. sp. and *Monoclim. ultimus* also allows one to correlate appropriately the boundary of the Pagegiai and Minija beds in Lithuania with the adjacent areas.

c) *The Baltic area.* — This area may be recognized on the basis of the graptolite fauna from erratic boulders. The uppermost zones of the Lower Ludlovian are represented by boulders containing *Cucullograptus hemiaversus*, as well as *C. aversus aversus* and *C. aversus rostratus* (Urbanek, 1960, 1966). Until recently, it has generally been assumed (Martinsson, 1962) that the Silurian erratic boulders with graptolites ("Graptolithengestein") do not reach above the *leintweardinensis* zone. The discovery of the fact that *C. aversus rostratus* survives above the *leintwardinensis* zone (Urbanek, 1960) gives, however, ample evidence that the range of this fauna includes yet younger zones, which already make up equivalents of the lowermost part of Siedlce Beds (Urbanek, 1966 & 1968, *in press*). This seems to be particularly true of the erratic boulders which either contain an association of *B. bohemicus* and *Prist.* ex. gr. *dubius* or are marked by an abundant monospecific occurrence of the former of these two species (association "O", cf. pp. 262). This assemblage, considered in the present work as a relic assemblage of the Lower Ludlovian fauna, is characteristic of the horizons directly overlying the *leintwardinensis* zone.

d) *The area of Thuringia.* — In this area, the *S. fritschi linearis* zone and an indeterminate part of the Ockerkalk series are equivalents of the lower part of Siedlce Beds. According to Jaeger (1964), this zone directly overlays the *S. leintwardinensis* zone and represents the first zone of the Upper Ludlovian of Thuringia. In Poland, the stratigraphic range of *S. fritschi linearis* is not unequivocally established. The E. and H. Tomczyk (1962) believe that the ranges of *S. leintwardinensis* and *S. fritschi linearis* display a considerable overlap but also that the last-named species passes somewhat higher up. On the basis of these facts, we may reject earlier suppositions admitting the possibility that the *S. fritschi linearis* zone includes even the entire Upper Ludlovian (Jaeger, 1964). In fact, it makes up a rather small part of this series and the Ludlovian-Downtonian boundary is situated much above this zone, probably on the boundary of the *Neocuc. kozlowskii-"M." formosus* zone [5].

The abundant occurrence of *B. bohemicus*, together with accompanying *S. fritschi linearis* and *P. dubius* (Jaeger, 1962, 1964) allows one to consider them as a relic assemblage of the Lower Ludlovian (comp. pp. 223).

COMPARATIVE-ANATOMICAL ANALYSIS OF NEOCUCULLOGRAPTINAE N. SUBFAM. AND REGULARITIES IN THEIR EVOLUTION

FUSELLAR STRUCTURES

Siculae, their size and shape. — As compared with the siculae of Cucullograptinae, those of Neocullograptinae n. subfam. are relatively robust. This type of a relatively long sicula (2.14—1.26 mm), provided with a strongly expanded aperture and a strongly developed dorsal process, persists in principle over the entire history of this group (Pls. II—IV).

A certain shortening of the sicula and subsequently a considerable reduction in the length of its dorsal process (*B. b. tenuis*) came about as a result of microevolutional changes within *B. bohemicus* (Barr.). These changes cannot be, however, compared with the phenomenon of a radical gracilization of siculae in some of the Cucullograptinae, in which a distinct arrest in the development of metasicula comes about and whose character is probably similar to that of foetilization (Urbanek, 1966, pp. 317—318).

Changes in the length of sicula in Neocucullograptinae n. subfam. were probably of the nature of a fluctuating evolution which may be shown by the comparison of variability ranges in two main lineages (cf. Table 1).

In regard to the variability range of this character, final evolutionary links represent a return to the state which is observed in early populations of *B. b. bohemicus*. Despite the fact that, as to the morphological evolution of the thecae, they represent divergent trends (gracilization in the *B. b. tenuis-Neocuc. kozlowskii* n. sp. lineage and preservation of original "robust" thecae in the *B. b. bohemicus-B. cornutus* n. sp. lineage), this phenomenon occurs conformably in both lineages.

Taking into consideration the structure of the sicula proper (prosicula plus metasicula, without microfusellar additions), the siculae of Neocucullograptinae n. subfam. may be best assigned to group 1 of "patterns of

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[5] Tomczyk and Tomczyk (1968) locate this boundary still higher up at the top of Siedlce Beds, as indicated by the occurrence of acastellid trilobites found also in the Upper Whitcliffian in the British Isles. Different views are represented by Obruchev, Karatajutė-Talimaa (1967), Paskevičius, Karatajutė-Talimaa (1968, *in press*) and Teller (1968).

PLATE II

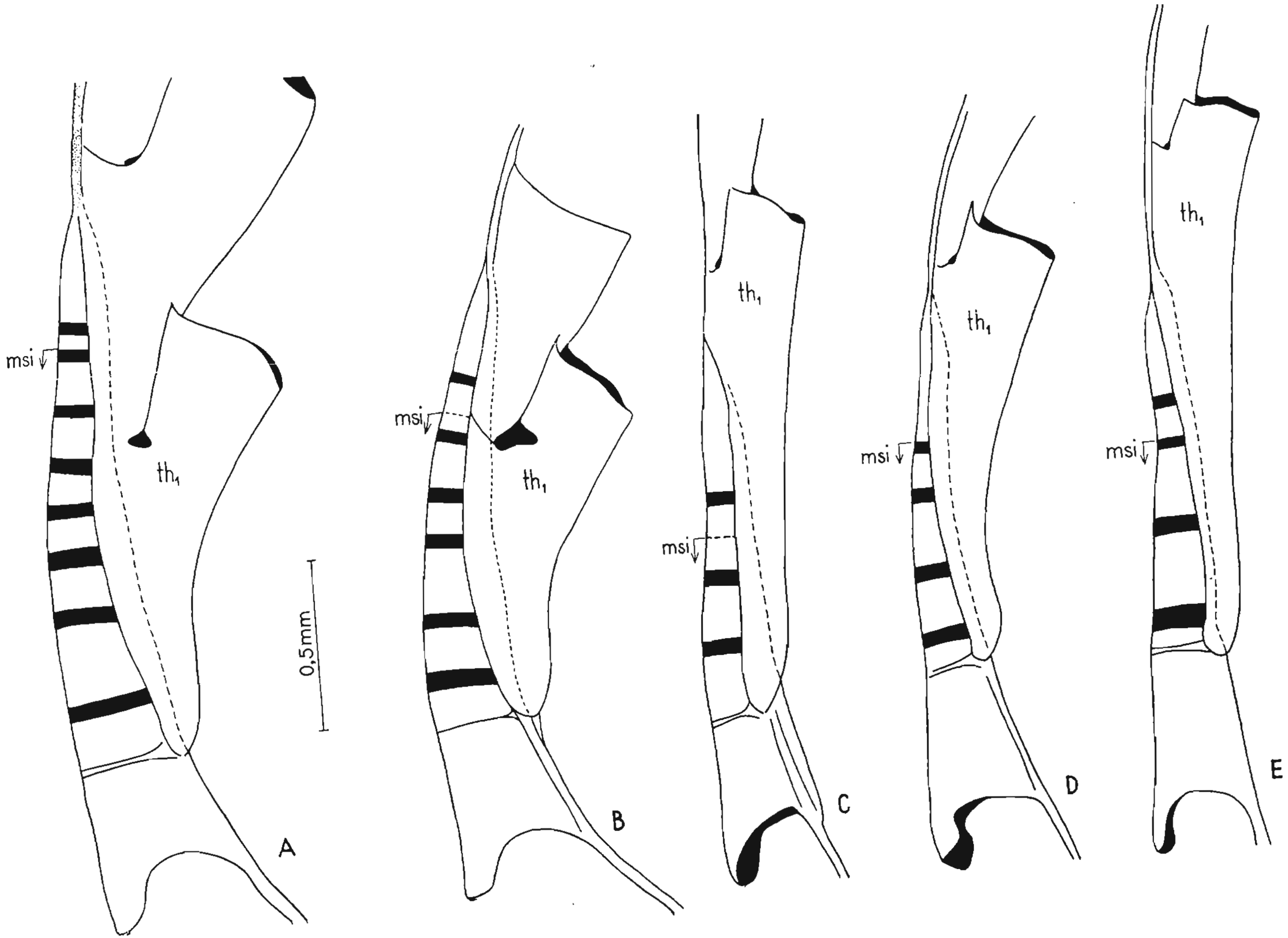
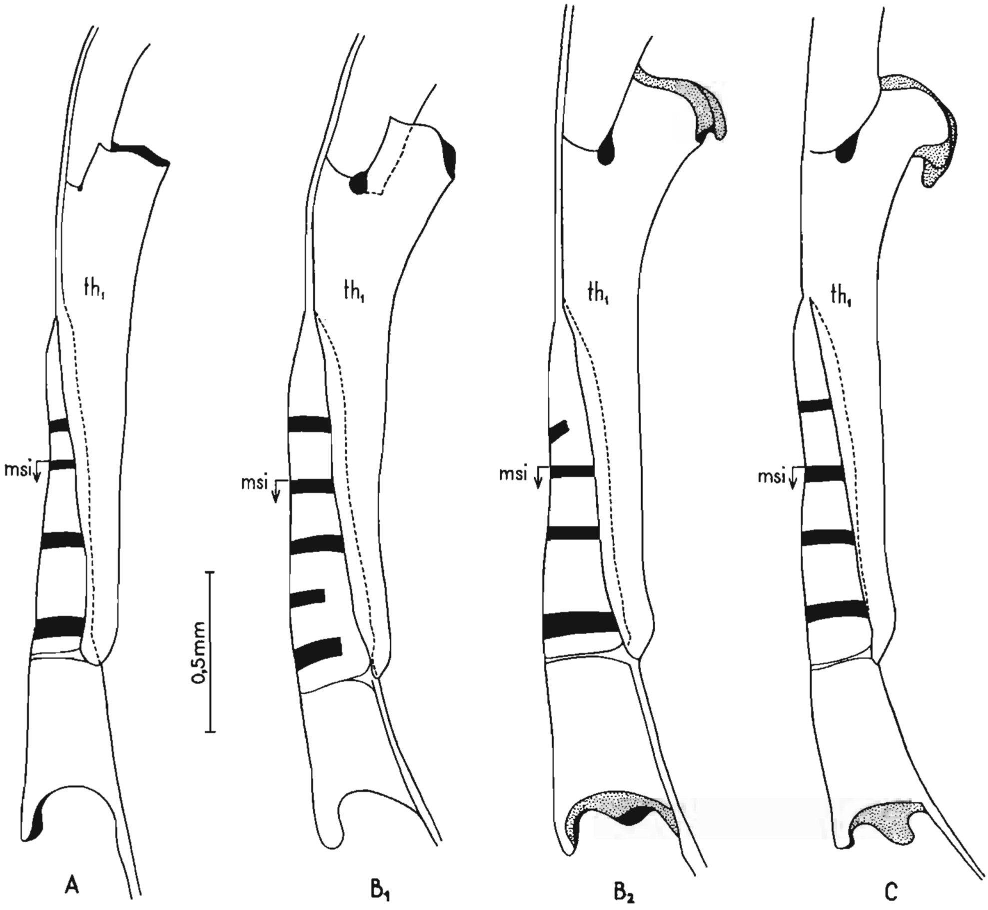


PLATE III



Changes in size and shape of siculae and first thecae in the line of *Neolobograptus* n.gen. — *Neocucullograptus* n.gen. (somewhat diagrammatically). *A* — *Neolob. auriculatus* n. sp. (*auriculatus* zone), B_1—B_2 young and adult *Neocuc. inexspectatus* (*inexspectatus* zone), *C* — *Neocuc. kozlowskii* n.sp. (*kozlowskii* zone). Microfusellar additions dropped.

Plate II

Changes in size and shape of siculae and first thecae in the line of *Bohemograptus* — *Neolobograptus* n. gen. (somewhat diagrammatically). *A* — *B. b. bohemicus* (*parascanicus* zone), *B* — *B.b. bohemicus* (*parascanicus* zone), *C* — *B.b. bohemicus* (*hemiaversus zone*), *D* — *B.b. tenuis* (*aversus* zone), *E* — *Neolob. auriculatus* n.sp. (*auriculatus* zone).

PLATE IV

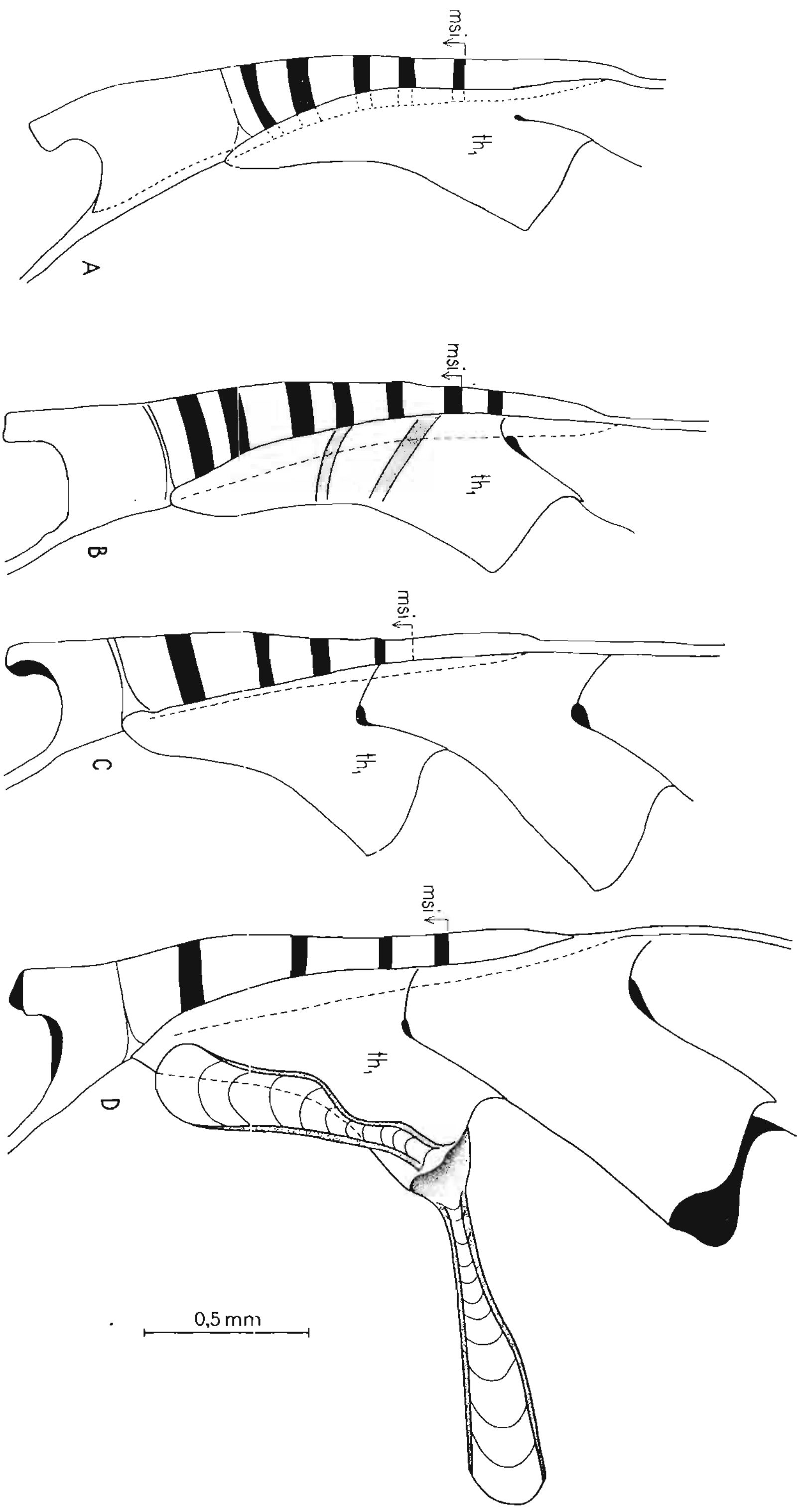


Table 1

Changes in length of sicula in two main lineages of Neocucullograptinae n. subfam. (length in mm)

B. bohemicus — *Neocuc. kozlowskii* lineage	*B. b. bohemicus*	*B. b. tenuis*	*Neolob. auriculatus*	*Neocuc. inexspectatus*	*Neocuc. kozlowskii*
	1,56-2.00	1.36-1.89	1.43-1.55	1.39-1.64	1.63-2.02
B. bohemicus — *B. cornutus* lineage	*B. b. bohemicus*	*B. praecornutus*	*B. cornutus*		
	1,56-2.00	1.40-1.71	1.61-2.14		

evolutionary behaviour of the sicula towards the remaining thecae of the rhabdosome", distinguished by Urbanek (1966, p. 320). This group is marked by a relatively considerable independence of sicula of the phylogenetic changes simultaneously taking place in the structure of thecae.

Quite different is the picture produced by microfusellar structures, simultaneously occurring on thecae and on a sicula (except for *B. cornutus* n. sp.) and which may be assigned to group 4 of these processes, distinguished by Urbanek (1966, p. 322).

Siculae of neocucullograptids are provided with many sicular rings. Attention has already earlier been attracted to a seemingly particular importance of the first sicular ring (r_1) in some of the monograptids (Urbanek, 1966, pp. 323—325). Like in "stem lobograptids", the position of r_1 in *B. b. bohemicus* is variable. It may be situated on the boundary of the pro- and metasicula or displaced to the area of either pro- or metasicula. In the process of further microevolutionary changes in *B. b. tenuis*, there comes to the stabilization of the position of r_1 which becomes settled on the boundary between the pro- and metasicula, that is, opposite to most Cucullograptinae (Urbanek, 1966, pp. 324—325). In *Neolobograptus* n. gen. and *Neocucullograptus* n. gen., on the other hand, a stabilization is observed in the position of r_1 which comes about by shifting this ring, in most cases, to the area of prosicula. This resembles a predominant trend found in the evolution of Cucullograptinae.

In the *B. praecornutus* n. sp.-*B. cornutus* n. sp. lineage, the position of

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Plate IV

Changes in size and shape of siculae and first thecae in the line *B.b. bohemicus* → *B. cornutus* n.sp. (somewhat diagrammatically). *A* — *B.b. bohemicus* (*hemiaversus* zone), *B* — *Bohemograptus* sp. (robust variety from *praecornutus* zone), *C* — *B. praecornutus* n.sp. (*praecornutus* zone), *D* — *B. cornutus* n.sp., young growth stage (*cornutus* zone).

r_1 at first remains unchanged (*B. praecornutus* n. sp.) to be fixed subsequently on the boundary of the pro- and metasicula (*B. cornutus* n. sp.), that is, much the same as in *B. b. tenuis* and differently than in *Neocucullograptus* n. gen.

Changes, observed in the position of r_1, may be interpreted in the light of a working hypotheses, adopted previously for the explanation of similar changes in the evolution of Cucullograptinae (Urbanek, 1966, pp. 324—325). This hypothesis assumes that the evolution consisted in this case in a segregation of the genetic variability occurring in ancestral populations of *Bohemograptus* and consequently descendant genetic systems contained only part of this variability which exerted an influence on a relative stabilization of phenotypic characters.

Changes in shape of thecae. — Much the same as in the present writer's earlier works, the following segments have been distinguished in the thecae of Graptoloidea: (1) a protheca and (2) a metatheca, the latter subdivided into (2a) a subapertural and (2b) an apertural part. Like in most other cases, the evolutionary changes in the thecae of Neocucullograptinae n. subfam. are mainly expressed in the modification of the metathecal segment, in particular in the development of its apertural part.

Regarding the prothecal segment, the only change found is a possible elongation, which with a relatively small width of protheca gives this process the nature of gracilization. This process is mostly marked in thecae of the proximal part of rhabdosome in a lineage represented by the following succession: *B. b. tenuis-Neolob. auriculatus* n. sp. *Neocuc. inexpectatus* n. sp.—*Neocuc. kozlowskii* n. sp., whereas the *B. b. bohemicus*—*B. praecornutus* n. sp.—*B. cornutus* n. sp. lineage behaves as a conservative one with respect to evolutionary chages of prothecae. In the last-named lineage, it remains relatively short and wide, which is ultimately decisive concerning the "robust" type of the theace of this group.

In primitive behomograptids (*B. bohemicus* tota species), the metathecal segment is in principle composed of the subapertural part only, which terminates in a straight-edged aperture. Sporadically, there however occur specimens with an aperture provided with slightly outlined bilateral apertural elevations, formed by one or a few wedgelike fuselli (Pl. I, Figs *A*, A_1). In *B. bohemicus*, the occurrence or lack of such elevations seem to depend of the population variability. They do not represent a settled specific character. Nevertheless, such poorly developed apertural elevations were probably a starting point for the formation of more advanced apertural apparatus in specialized neocucullograptids. Thus, the course of events strongly resembled the morphological evolution of thecal characters found earlier in Cucullograptinae, in which similar elevations were an incipient form of the apertural apparatus and its complex derivatives (Urbanek, 1966, p. 327).

PLATE V

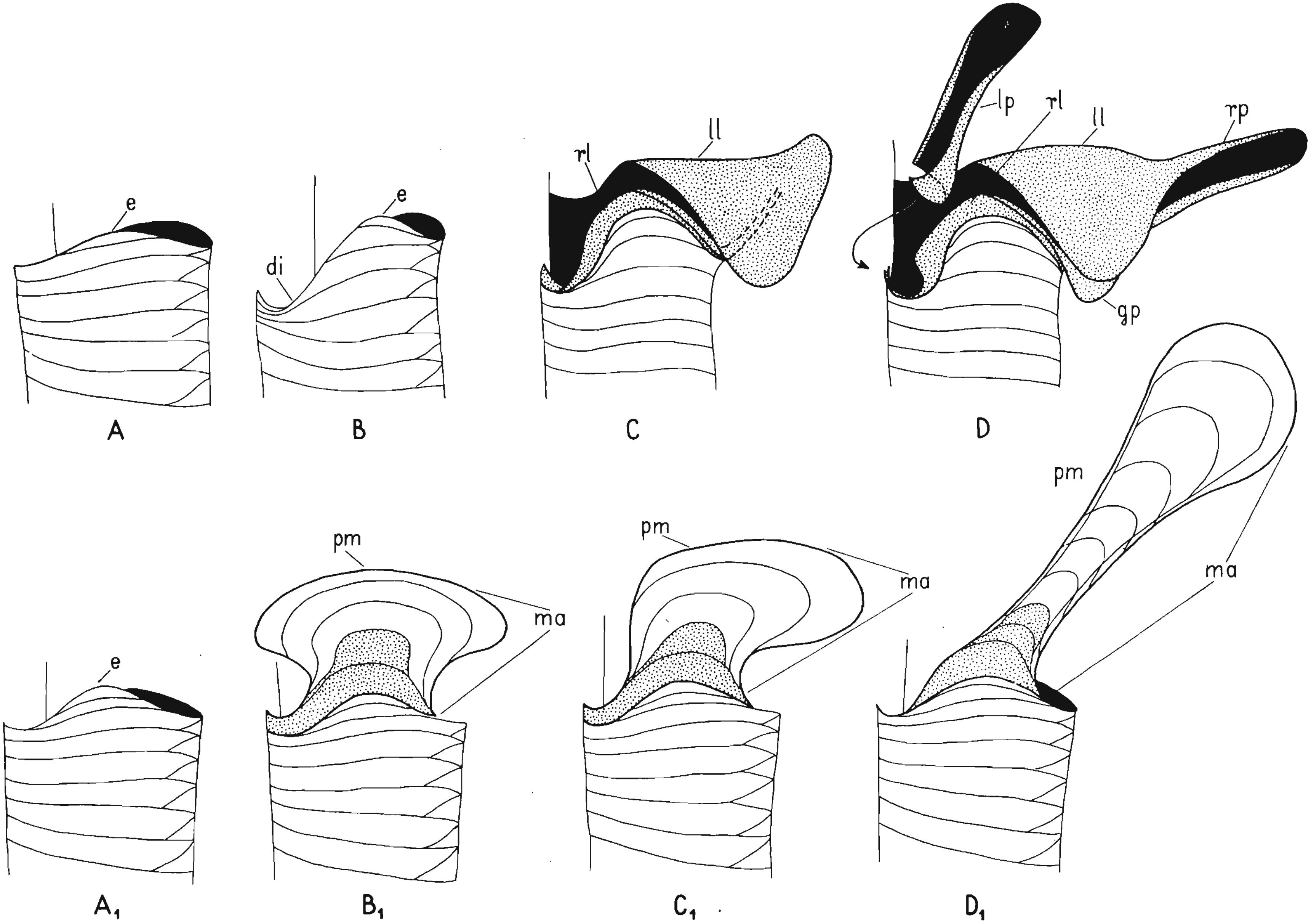


Diagram of changes in structure of metathecal segment in distal thecae of neocucullograptids. *A* — origin of apertural elevations in *B. bohemicus* (e), *B* — advanced elevations and origin of dorsolateral incision (*di*) in *Neolob. auriculatus* n.sp., *C* — origin of apertural apparatus in *Neocuc. inexspectatus*, composed of left (*ll*) and right (*rl*) lobes, *D* — formation of superstructures in *Neocuc. kozlowskii* n.sp., (*rp* rostral process, *lp* lateral process, *gp* gular plate). In order to show its relation to internal cavity of aperture lateral process figured as dissected (arrow indicate its primary position). A_1 — origin of apertural elevations (*e*) in *B. praecornutus* n.sp., B_1—C_1 — shape of microfusellar additions (*ma*) in *B. praecornutus* n.sp. made of microfusellar tissue (dropped) and pseudomicrofusellar tissue (*pm*), D_1 — form of microfusellar additions in proximal and distal thecae of *B. cornutus* n.sp.

Particularly progressive was the development of the fusellar part of apertural segment in the *Neolob. auriculatus* n. sp.—*Neocuc. kozlowskii* n. sp. lineage. The formation of strongly expressed apertural elevations, whose presence is a permanent specific character of *Neolob. auriculatus* n. sp., comes about in *Neolobograptus* n. gen. The modification of simple, arcuate apertural elevations, resulting from a peculiar dorsolateral incision (Pl. V, Fig. *B*) takes place in medial and distal thecae. Such a structure of the fusellar apertural part of the matathecal segment was also a foundation on which its microfusellar part was based in *Neocucullograptus* n. gen. In early growth stages, the apertural apparatus was represented in medial and distal thecae of the representatives of the last--named genus by structures strongly resembling lateral elevations in *Neolobograptus* n. gen. It was only later that a microfusellar addition was developed on the basis of these structures. We may suppose that this process was, also in phylogeny, an additive process which led through 1) the formation of the elevations, 2) complication in their structure by forming the dorsolateral incision and 3) formation of microfusellar additions. A regular morphological and stratigraphic sequence of individual species, represented by the *B. b. tenuis* — *Neolob. auriculatus* n. sp.- *Neocuc. inexspectatus* — *Neocuc. kozlowskii* lineage, corresponds to this sequence of growth and astogenetic events (Pl. V, Figs. *C*-*D*).

The astogenetic development of thecal characters in *Neolob. auriculatus* n. sp. is indicative of two simultaneously operating trends in the introduction of phylogenetic novelties. One of them, responsible for the formation of dorsolateral incision, indicates a distal introduction of this novelty, the other, connected with the elongation of thecae — a proximal introduction. The entire picture of changes is consistent with previous ideas concerning the phylogenetic modifications in astogeny (Urbanek, 1960, 1963, 1966).

In the *B. praecornutus* n. sp.—*B. cornutus* n. sp. lineage, there also comes to the stabilization of apertural elevations as a permanent specific character (Pl. V, Fig. B_1). They, however, preserve the original character of an arcuate structure, over which a microfusellar superstructure is formed sporadically (*B. praecornutus* n. sp., veliger morph.) or permanently (*B. cornutus* n. sp.; Pl. V, Figs. B_1, D_1).

The thecae of Neocucullograptinae n. subfam. preserve their character of straight tubes. Their ventral wall does not, therefore, form a distinct geniculation or a sigmoidal bend on the boundary of the pro- and metatheca, characteristic of many cucullograptids (Urbanek, 1966, pp. 326—327). A certain tendency to a slight sigmoidal bend of the ventral wall is observed only in *Neolob. auriculatus* n. sp.

Shape of rhabdosome. — While in the evolution of Cucullograptinae far-reaching changes occurred in the shape of rhabdosome (as, a change in the character of curvature in the proximal part), the rhabdosomes of Neocucullograptinae n. subfam. behaved in this respect in a conservative manner. In all cases, rhabdosomes display a distinct, more or less strong ventral curvature in the proximal and a similar, but much slighter curvature in the distal part. Pls. VI—VII present an attempt at a reconstruction of the rhabdosomes of Neocucullograptinae n. subfam., based on the fragments preserved and without taking into account their actual lengths. A considerable similarity in a general shape of rhabdosomes is self-evident.

In the *B. b. bohemicus—B. b. tenuis* lineage, the degree of curvature of the rhabdosome increases in the proximal part (Pl. VI, Figs. *A-B*). The rhabdosome, strongly bent ventrally in its proximal part, is preserved in *Neolobograptus* n. gen. and *Neocucullograptus* n. gen. (Pl. VII, Figs. *A-C*).

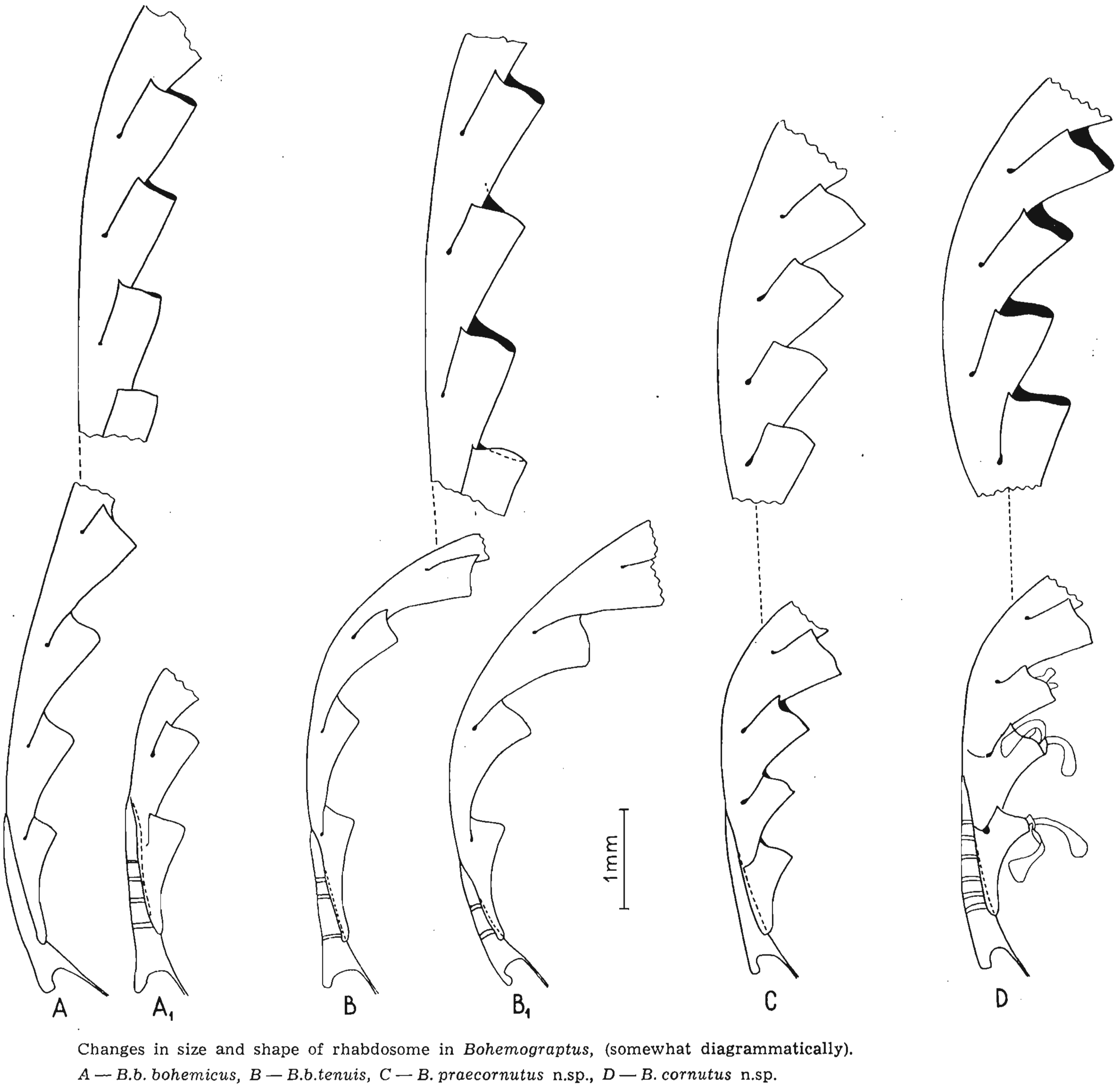
On the other hand, in the *B. praecornutus* n. sp.-*B cornutus* n. sp. lineage, primitive conditions inherited from *B. b. bohemicus* (a slighter ventral bend of the proximal part of rhabdosome) persist without any changes or be even a certain secondary decrease in the degree of this curvature may come about (Pl. VI, Figs. *C-D*).

MICROFUSELLAR STRUCTURES

A microfusellar tissue as a separate peridermal material of the Graptoloidea. — A microfusellar tissue, which in some Graptoloidea, particularly in certain monograptids, participates in the formation of peridermal structures, consists of many, very narrow growth strips (ca 0.01 mm in width), sometimes relatively long and sometimes markedly shorter than normal fuselli. Thus, the width of strips in the microfusellar tissue is ca five times smaller than that of a normal fusellus of the distal metatheca and the arrangement of such strips may be fairly regular. In some other cases, distinct inconsistencies are observed between bundles of separate strips allowing one to distinguish, in the microfusellar tissue, two structural units: 1) microfuselli (bands) and 2) bundles (bunches) of microfuselli. Due to the form and size of elementary units of this tissue (microfuselli), it strongly contrasts in all cases with the adjoining fusellar tissue (Pl. XLIV, Figs. *A-C*; Pl. XLV, Figs. *A-C*).

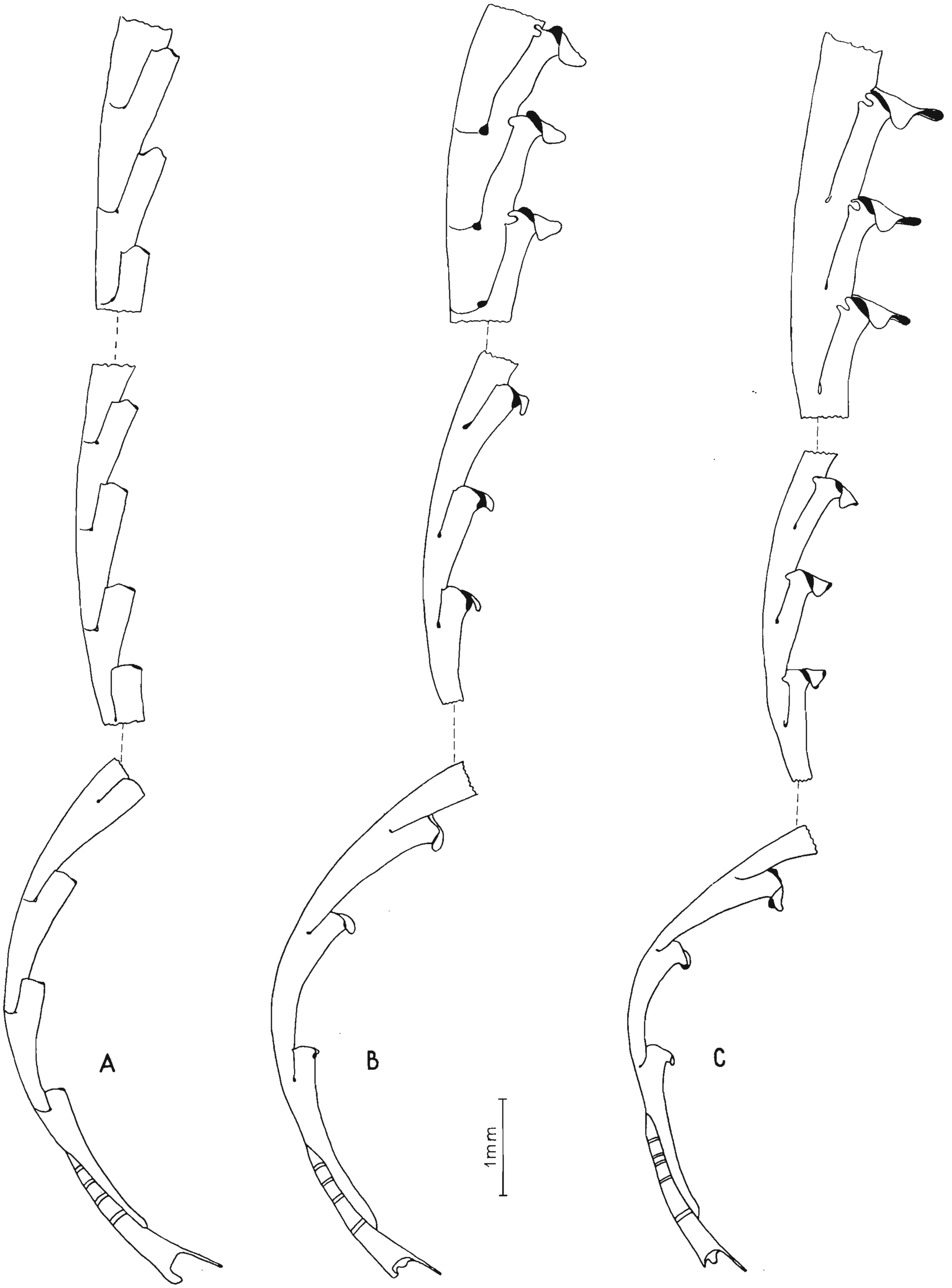
A typical microfusellar tissue displays a strong pigmentation, is resistant to bleaching and, even after strong bleaching usually remains tan-coloured or dark-brown. In the last-named preparations, the fusellar tissue is orange- or straw-coloured and strongly transparent (Pl. XLIV, Figs. *A-C*). This may be caused by a chaotic, multi-layered deposition of microfuselli resulting in aposition and swelling of the peridermal wall, or else by a slightly different ultrastructure of the microfusellar material.

PLATE VI



Changes in size and shape of rhabdosome in *Bohemograptus*, (somewhat diagrammatically).
A — B.b. bohemicus, B — B.b.tenuis, C — B. praecornutus n.sp., *D — B. cornutus* n.sp.

PLATE VII



Changes in size and shape of rhabdosome in *Neologobraptus* n.gen. and *Neocucullograptus* n.gen. (somewhat diagrammatically).
A — Neolob. auriculatus n.sp., *B — Neocuc. inexspectatus* n.sp., *C — Neocuc. kozlowskii* n.sp.

In typical cases, the microfusellar tissue displays a sharp contrast as compared with the adjoining fusellar tissue. Such a contrast is expressed in the lack of a gradual transition from one to the other tissue. This allows one to distinguish the microfusellar from fusellar tissue, the latter formed in initial (juvenile) parts of the sicula and the first theca, or in certain special structures such as, e. g., a "gorget" in *Cucullograptus aversus rostratus,* in which a gradual transition is, however, observed from normal to narrowed fuselli.

The microfusellar tissue has first been described for *Monoclimacis micropoma* Jaekel (Urbanek, 1958, pp. 23 and 93, Fig. 68) and initially no appropriate technical term was applied to it. The term itself has formally been introduced by Urbanek (1966, pp. 306 and 322), who, however, even earlier used it in frequent discussions which contributed to its dissemination.

The discovery that the apertural lobes of *Monoclim. micropoma* are composed of the microfusellar tissue, helped demonstrate that "*M.*" *micropoma* Jaekel and *M. uncinatus* Tullberg, homeomorphic morphologically, are not only separate species but also belonging to different lineages. In both cases, the apertural apparatus is non-homologous, was formed on a quite different structural basis and, as shown by Urbanek (1958, p. 93). displays quite a different mode of growth [6], viz., the microstructural lobes are formed in *Monoclim. micropoma* with a considerable delay and a distinct interval is marked between the completion of the growth of fusellar and microfusellar parts of theca.

The microfusellar tissue occurs sporadically in various Graptoloidea (angular fuselli at the apertural margin in *Gymnograptus linnarsoni* Urbanek, 1959, p. 293; apertural hoods and dorsal spines in *Glossograptus holmi,* Whittington & Rickards, 1969, pp. 805—806), but *Monoclim. micropoma* Jaekel and *Neocucullograptus* n. gen. now represents, among the monograptids, the only known two cases of an extensive use made of this material for constructing thecae. The evolution of the neocucullograptids is to a considerable extent related precisely to the utilization of the microfusellar tissue (Urbanek, 1968 *in press*). It is not unlikely that in future other instances of the use of this tissue will be discovered, the more so as even the present data indicate that it might appear in different lineages independent of each other. The present writer's (Urbanek, 1960, pp. 205—206) earlier suggestion that monograptids of the *hercynicus* group may have apertural lobes composed of the microfusellar tissue has not been, however, confirmed (Jaeger, 1966, p. 406).

Among the representatives of Neocucullograptinae n. subfam., the

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[6] Jaeger (1959, pp. 120—121), who at first was inclined to consider differences, shown by Urbanek (1958, pp. 23 and 93) for *M. uncinatus* and *Monoclim. micropoma,* as relative, has recently adopted the viewpoint that the apertural lobes of the last-named species "are not homologous with the hoods of all the other uncinate *Monograptus* species" (Jaeger, 1966, p. 410).

microfusellar tissue occurs in two principal varieties. The first is the microfusellar tissue proper in the form in which it also occurs in *Monoclim. micropoma*. Even after a strong decolourization, it remains strongly pigmented and slightly transparent, probably as a result of a multi-layered arrangement of microfuselli. Such a tissue, displaying the presence or lack of the discordance between bundles of microfuselli, forms basal parts of microfusellar additions in *Bohemograptus* and entire microfusellar additions in *Neolobograptus* n. gen. and *Neocucullograptus* n. gen. (comp. Pl. XXIX, Figs. *C*-*E*; Pl. XXXIV; Pl. XXXIX, Pl. XLIV).

This is probably a principal form of the microfusellar tissue, that is, the microfusellar tissue proper.

On the other hand, the presence of a different variety of the microfusellar tissue is observed in peripheral and terminal parts of microfusellar additions in *Bohemograptus*. (Pl. XLV, Fig. A-D, m) It is composed of considerably wider bands than those discussed above. Their width, amounting to 0.03—0.05 mm, more than once reaches and even exceeds a half of the width of a normal fusellus in a given metatheca. The bands are arranged irregularly, frequently wedged-out and sometimes allowing one to discover the presence of bundles or bunches of such bands, separated from each other by discontinuities or more strongly pigmented (thickkened?) microfuselli (Pl. XXI, Figs. A_2—A_3; B_1—B_2, *Pl.* XXII, Figs. A_2—A_3, Pl. XLIV, Fig. D, p). I suggest to call this variety of the microfusellar tissue a pseudomicrofusellar tissue. The wall of periderm, composed of the pseudomicrofusellar tissue, is, in all cases, thinned, membranaceous and, without decolourization, semi-transparent. Gradual transitions, existing between the microfusellar and pseudomicrofusellar tissue, prevent them from being sharply contrasted with each other. In the case in which both varieties of the microfusellar tissue occur within one and the same structure, the pseudomicrofusellar tissue, preceded by the microfusellar tissue proper, is formed in the final stage of growth. In many cases, the pseudomicrofusellar tissue does not occur at all.

Structures, composed of the microfusellar tissue, were always formed in the final stage of growth of theca and consequently, constituted an addition of the growth of the apertural thecal segment which was, however, separated by a considerable stretch of time from the completion of the growth of the fusellar part of theca. In this sense, a term "microfusellar addition" has been introduced to the present work to denote the entire structure formed by the microfusellar tissue as a result of an additional and delayed growth. Morphological forms of microfusellar additions in Neocucullograptinae n. subfam. were fairly variable. In the present work, the following principal morphological forms of such structures have been distinguished: 1) "velum" — a microfusellar addition in the form of wide lobes or apertural platforms, composed of both the microfusellar proper and pseudomicrofusellar tissue, occurring in *B. bohemicus* (Barr.)

(tota species) and *B. praecornutus* n. sp. (comp. Pl. XLV); 2) a slightly modified form of "velum", composed only of the microfusellar tissue, occurring in *Neolobograptus* n. gen. 3) asymmetrical apertural lobes, forming, together with appropriate superstructures (rostral and lateral processes, gular plate), a complex apertural apparatus, in many respects homeomorphic with the apertural apparatus of *Cucullograptus* Urb. They are composed only of the microfusellar tissue proper (comp. Pl. XLIV); 4) tapelike and terminally fanlike, expanded apertural processes of *B. cornutus* n. sp., composed of both varieties of the microfusellar tissue.

Morphological and stratigraphic facts seem to indicate that velum was an original form of microfusellar additions, from which all the remaining ones were later developed. A great variability of velum, irregular astogenetically, may be one of the proofs for the primitive character of this structure and, moreover, velum is probably a morphological expression of a genetic polymorphism and not a permanent specific feature.

In the lineage which led from the *Neolobograptus* n. gen. to *Neocucullograptus* n. gen., morphological changes undergone by the microfusellar additions consisted in: 1) an elimination of the pseudomicrofusellar tissue, maybe caused by the omission of the final growth stage; 2) a rise of asymmetry of microfusellar apertural lobes; 3) a formation of superstructures on microfusellar apertural lobes, that is, a lateral process, gular plate and rostral process. Morphological stage 1 was reached within *Neolobograptus* n. gen. and stages 2—3, gradually, within *Neocucullograptus* n. gen. (comp. Pl. V, Figs. *B*—*D*). The available data seem to indicate that the changes here occurring were not only gradual, additive, but maybe also mosaic in character. This implies that appropriate incipient structures were not developed uniformly but probably displayed varying rate of development. In the light of these data, there was probably the following order of development: 1) lateral process, 2) incipient rostral process, followed maybe by 3) gular plate and 4) elongation of the rostral process. Lateral process might gradually increase together with development stages 2—4 (comp. Systematic Part).

In the *B. praecornutus* n. sp. — *B. cornutus* n. sp., the character of changes was different. As the pseudomicrofusellar tissue remains unchanged (1), changes take place in the morphological form of the microfusellar addition, whose base narrows (2), at whose end a fanlike widening is formed (3) and thickened lists are developed on the edges of the structure (4) (Pl. V, Figs. B_1—D_1).

The mechanism of the formation of the microfusellar tissue cannot be of course explained accurately. A delayed growth of the microfusellar addition, compared with the same growth of the fusellar derivatives of the apertural metathecal part, suggests that it was related with a late growth stage of the zooid. A distinct interval between the formation of the fusellar and microfusellar part implies that the latter might be formed as late as after the zooid has reached a definite physiological stage. This was an additional growth, which, however, took place not as a result of a simple prolongation of the growth, but after a period of its temporary inhibition and which was subsequently resumed according to new structural principles. A "matural" or "postmatural growth" are the names here suggested to designate this type of growth.

A peculiar form of microfuselli, occurring as narrow bands and the occurrence of many discontinuities in growth might probably be explained by a decrease, in each, separate phase of secretion, in a secretive efficiency of epithelial glands responsible for the production of peridermal substances. A frequent occurrence of two secretionary units, that is, microfuselli and bundles of such microfuselli separated from each other by more or less distinct discontinuities, gives evidence for a spasmatic, irregular rhythm of secretive processes. The decrease in secretive efficiency is probably connected with a late life period of a zooid and with a decrease in its physiological efficiency. A relatively large width of growth bands of the pseudomicrofusellar tissue may be elucidated by a certain "compensation" or economization of the material, effected by the thinning of the periderm itself.

The manner of introducing microfusellar additions as "phylogenetic novelties" to the process of phylogenetic modifications of astogeny is difficult to determine. In *B. bohemicus,* the microfusellar additions are connected with a considerable number of proximal thecae. They also occur on sicula, but there is no definite evidence that they also were formed on thecae in the distal part of rhabdosome (comp. Systematic part). In *B. praecornutus* n. sp., it seems that additions also occurred on thecae in the medial and distal parts, as well as on sicula (comp. Systematic part). Maybe, in *B. bohemicus,* all thecae of rhabdosome in "veliger morph" were already capable of producting microfusellar additions. The latter were, however, formed with a considerable delay in a late growth stage. This was precisely the reason why proximal thecae, formed earliest of all, most frequently reached an appropriate growth stage, whereas the rest of the colony might usually die before the distal thecae had reached a growth stage enabling the development of such additions. The latter would be presumably formed only in the gerontic stage of rhabdosome. Thus, the phylogenetic novelty, connected with the postmatural growth of thecae, behaves as a feature with a "quasi-proximal" mode of introduction both in the case in which it appears "simultaneously in all individuals of the colony" (Urbanek, 1960, p. 172; 1966, pp. 347—348) and in the case in which it at first appears by a polar introduction. For the postmatural character of the growth of structures conceals an actual type of introduction, causing — as a result of a delayed growth of microfusellar additions — the occurrence of a growth gradient (e. g., a decrease in the size of microfusellar apertural lobes progressing distally, which was described for *Monocli-*

macis micropoma by Urbanek (1958, pp. 93—94, Pl. V, Fig. 4) and which produces an apparent (or actual) effect of the proximal introduction.

Thus, the manner of introducing microfusellar additions in *Bohemograptus* in the form of phylogenetic novelties cannot be at present accurately determined. On the other hand, many other morphological characters connected with a continued evolution of these additions behave as typical characters of a distal introduction, that is, the degree of their expressivity increases distally. These characters include: a degree of asymmetry of apertural lobes (symmetric apertural lobes on sicula, a low degree of their asymmetry in the first proximal thecae, a strong asymmetry and a strong overlap of apertural lobes in distal thecae of *Neocuculograptus* n. gen.) and of their superstructures (a distal increase in the dimensions of lateral and rostral processes and gular plates in *Neocucullograptus* n. gen.).

Particularly noteworthy is involving the sicula in thecae which display a capability of producing microfusellar additions. In this phenomenon also lies a rare parallelism in the morphological evolution of siculae and thecae, to which attention has already been attracted earlier (Urbanek, 1966, pp. 322—323). In *B. bohemicus*, the sicula sometimes displays a capability of forming strongly developed microfusellar additions ("pelta", comp. Pl. XXI, Fig. A_4; Pl. XXII, Fig. A_4) which are equal to those on proximal thecae.

Significant deviations are, however, recorded in other cases — additions on siculae are much less developed than those on adjoining proximal thecae although a siculozooid has been formed earlier and should earlier reach an appropriate growth stage (comp. Pl. XXI, Fig. A_1, Pl. XXII, Fig. A_1). conditions are also displayed by the "veliger morph" specimen of *B. b. bohemicus*, the oldest geologically and which has been recognized from the *hemiaversus* zone where, admittedly, siculae are distinct but (much slighter than those on proximal thecae (Fig. 11, *A*).

Thus, the sicula is an exception from the principle of the "quasi-proximal" introduction. Likewise, it is not included in later phylogenetic modifications, concerning microfusellar structures of the remaining thecae (it remains poorly developed and always symmetric, not forming superstructures). This fairly peculiar behaviour of microfusellar additions on the sicula cannot be interpreted otherwise but as a new symptom which is indicative of its fundamental morphogenetic separateness and independence of the remaining individuals of the colony (particularly strongly postulated in Urbanek, 1960, pp. 151, 1963, pp. 233; 1966, pp. 320—323). A generally slighter development of microfusellar additions on the sicula may be an evidence that it was included in them with a certain "reluctance", to a smaller extent and, maybe, somewhat later, which might be indicative of a previously postulated smaller degree of reactivity of the tissue of siculozooid to morphological factors which determine evolutionary changes in blastozooids and their thecae (Urbanek, 1960, pp. 150—154 and 165).

The less strongly fixed mechanism of the formation of microfusellar additions on the sicula, which in *B. bohemicus* is expressed in a considerable variability of these structures, possibly facilitated a relatively easy and probably secondary change in *B. cornutus* n. sp. In this case, much the same as in a vast majority of known evolutionary changes in graptolite colonies, the sicula is omitted from the sequence of morphological modifications undergone by the individuals of a colony (Urbanek, 1966, pp. 320—321). In *B. cornutus* n. sp. microfusellar additions are not formed on the sicula, although they are strongly developed in proximal thecae.

Despite displaying certain peculiarities (e. g., "quasiproximal" introduction) the astogenetic development of microfusellar additions seems to be subordinated to more general rules, which control phylogenetic modifications in the astogeny of Graptoloidea (Urbanek, 1960, 1963, 1966). Although the mode of introduction of these additions (proximal, distal, simultaneous) cannot be at present unequivocally determined and although initially they show irregular astogenetic variability, their further changes are subordinated to the polar organization of the colony. For instance, *Neocuc. inexspectatus* (Bouček) and *Neocuc. kozlowskii* n. sp. are biform in relation to the structure of their microfusellar apparatus, the latter species representing a higher degree of biformism as indicated by a greater difference, between proximal and distal thecae, in degree of asymmetry and length of apertural processes (Pl. VII, Figs. *B*-*C*).

ABNORMALITIES OF ASTOGENY

The relatively rich material of *Bohemograptus*, elaborated in the present work, also includes forms representing the symptoms of certain developmental anomalies (a double or additional nema) or regenerative morphoses (a regeneration of the periderm of thecae, presumable cases of the regeneration of rhabdosome, marked by strong differences in size and shape of thecae; comp. Pl. XI, Fig. *H*, *rdp*; Pl. XVIII, Fig. *A*, *reg*).

Particularly noteworthy are, however, the anomalies in the manner of budding and direction of growth of the first theca.

In the former case, the anomaly may be assigned to *B. b. tenuis* (Bouč.), the specimen having been etched out from the core of the Mielnik on the Bug borehole (at a depth of 888.20 m, *inexspectatus* zone). This specimen is represented by a sicula with broken-off prosicular part and by a long, tubular th_1 growing downwards (Fig. 3, A_1-A_2). Metasicula, provided with sicular rings (*r*), also displays the presence of a normally developed region of the "primary notch", formed in a manner normal in monograptids, that is, by an arcuate bend of fuselli on the "reverse" side in relation to virgella (*ac*). Metasicular aperture displays the presence of a lingulate dorsal process (*dp*) and an immensely elongated virgella (*vi*).

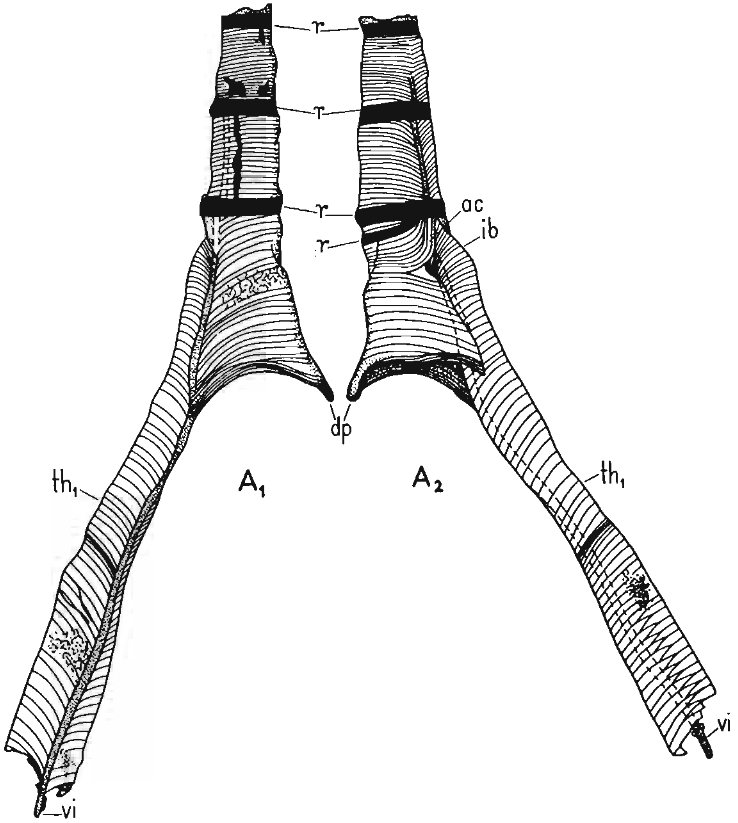


Fig. 3. — *Bohemograptus bohemicus bohemicus* (Barr.). Malformation expressed in change of the growth direction in the first theca. A_1, A_2 specimen seen from obverse and reverse sides. (Mielnik, depth 888.20 m, *inexspectatus* zone); ×50.

ac archlike arrangement of fuselli on the side of the primary notch, *dp* dorsal process of metasicular aperture, *ib* initial bud showing a downward direction of growth, *r* sicular black rings, th_1 first theca with abnormal direction of growth, *vi* virgella strongly elongated and playing the role of a pseudovirgula.

The budding of th_1 is clearly visible on the reverse side (Fig. 3, A_2), where it has been found that the initial bud (*ib*) is, admittedly, formed by apertural budding, but displays certain characteristic deviations from a normal monograptid development. As far as it can be determined, the first fuselli of th_1 are formed in an adapical and not lateral corner of the primary notch and the initial bud grows directly downwards (Fig. 3, A_2, *ib*). The resulting thecal tube initially grows on the ventral wall of metasicula, slightly shifting to the reverse side and subsequently projects freely outside the reach of the metasicular aperture (th_1). The free part of th_1 forms a relatively narrow and long tube consisting of fuselli, which on the ventral side form a zigzag suture and on the dorsal side fuse with virgella (*vi*). The latter turns, therefore, into a sort of pseudovirgula (Urbanek, 1963). The apertural part of th_1 has not been preserved.

As a result, the direction of growth of th_1 resembles that of a sicular cladium in Linograptinae on the condition that budding is subapertural in character and the thecal tube, placed ventrally to sicula, uses virgella as a sort of a "pseudovirgula".

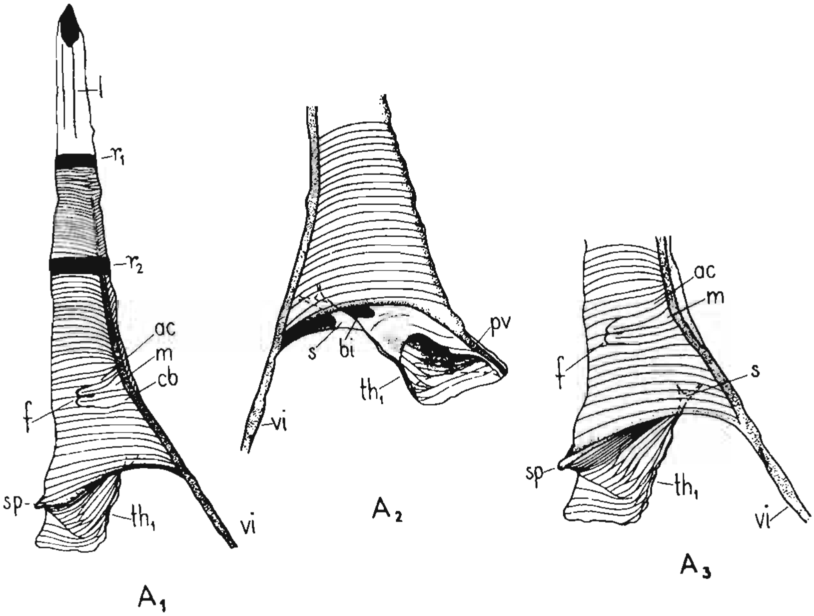


Fig. 4. — *Bohemograptus bohemicus tenuis* (Bouček). Malformation of proximal end of rhabdosome, due to change of the mode of budding of the first theca. A_1 general appearance of the specimen seen from reverse side; A_2, A_3 details of structure of the first theca seen from obverse and reverse sides. Broken lines indicate translucent structure or denote restored parts (A_2) (S. 224, Reval); A_1 ×50, remaining ×63.

ac arch-like arrangement of fuselli on the side of the primary notch, *bi* basal incision of the first theca, *cb* fusellar bands closing the primary notch, *f* thickened fibers lying on periderm, *l* longitudinal threads on prosicula, *m* membrane sealing up the primary notch, *pv* pseudovirgula, r_1—r_2 successive sicular black rings, *s* peridermal septation penetrating inside the aperture, *sp* spine-like process situated on the dorsal process, th_1 first theca, *vi* virgella

A somewhat different abnormality in the manner of budding of th_1 is represented by a specimen shown in Fig. 4, A_1-A_3, coming from an erratic boulder (S. 224, Rewal) and probably belonging to a form, termed as *B. b.* cf. *tenuis* (Bouč.) (comp. pp. 263—4). It consists of a complete sicula and an initial part of th_1 (Fig. 4, A_1). The region of the primary notch is developed abnormally, which is expressed in a small number of arcuate fuselli (Fig. 4, A_1, A_3, *ac*), after the formation of which a band of fuselli (*cb*) was soon formed. This band closes a slightly marked primary notch.

Porus is completely sealed by a triangular peridermal membrane (Fig. 4, A_1, A_3, *m*). A thickened band of periderm, shaped like a double horseshoe, (Fig. 4, A_1, A_3, *f*) has been formed in the region of the lateral corner of the closed porus. This is a trace of certain disorders in the production of the peridermal material.

It is likely that the incompletely developed porus has never been functional, that is, it did not serve the bud of th_1 for getting outwards. A consideration of existing conditions leads to the conclusion that this bud, having no sufficient space inside the sicula, got outwards through a definitive sicular aperture. An incipient thecal tube (th_1), situated on the dorsal side of the aperture may serve as an evidence for the correctness of this conclusion. On the reverse side (Fig. 4, A_3, th_1), we may find that the thecal tube originates on the edge of the metasicular aperture in the form of many, narrow fuselli, which subsequently turn into normal fuselli forming a zigzag suture on the lateral surface. The ventral wall of the tube forms, on the reverse side, a short inner wall which adheres to the inner wall of metasicula (Fig. 4, A_2, A_3 *s*, partly marked, by dotted lines, as structure, seen through the transparent metasicular wall). On the obverse side, the wall of the tube has a poorly visible fusellar structure and its upper margin seems to be damaged. It may be ascertained, however, that in this place, th_1 grew along a thickened apertural bar forming a sort of pseudovirgula (Fig. 4, *pv*). The latter was situated asymmetrically, that is, slightly shifted to the obverse side, while the apertural margin itself, in the form of a short spine (Fig. 4, A_1, A_3, *sp*), was situated in the plane of symmetry. Fig. 4, A_2 demonstrates that a basal incision (*bi*) similar to that occurring at the base of the first thecae in sicular cladium of *Linograptus* (Urbanek, 1963, pp. 147 and 183) was situated at the base of the thecal tube.

The results of this abnormality resemble to a considerable extent the manner of budding of the sicular cladium in Linograptinae. In both cases, budding took place from a definitive metasicular aperture. The bud is shifted dorsally and has a basal incision. Part of the metasicular aperture remains free and the bud of th_1 grows supported by a structure which resembles the apertural spine extending to form pseudovirgula. The fundamental difference consists, on the other hand, in the absence of a normal series of thecae growing upwards from metasicula and started with subapertural budding (procladium, Urbanek, 1963, p. 147), since its growth was directed, through the metasicular aperture, downwards while this series of thecae itself was transformed into a sort of a "sicular cladium".

The two abnormal cases in the process of budding and growth of th_1, described above, give evidence of the regulative nature of astogenetic processes (a considerable lability and adaptability to changed conditions of growth).

PHYLOGENY AND HISTORY OF NEOCUCULLOGRAPTINAE N. SUBFAM.

The concept of Neocucullograptinae n. subfam. is connected with proving close phylogenetic relationships between nonspecialized representatives of *Bohemograptus* Přib. from the Lower Ludlovian and specialized monograptids from the Upper Ludlovian such as, on the one hand, *Neolobograptus* n. gen. and *Neocucullograptus* n. gen. and, on the other, *B. cornutus* n. sp. This is, therefore, a group of species probably closely related to each other and forming a stock, which develops parallel to Cucullograptinae Urb. and is represented at first by a slowly evolving stem lineage (Lower Ludlovian) and subsequently differentiated into three lineages, two of which are markedly progressive (Upper Ludlovian). First represented only by forms with a simple structure of thecae (Lower Ludlovian), later this group is represented, besides conservative forms, by species with a considerably advanced apeertural apparatus. In this sense, the succession of events gives, within the limits of this group, a far reaching analogy to the pattern of evolution in Cucullograptinae Urb.

In the history of Neocucullograptinae n. subfam., the following phases may be distinguished which allow one for analysing it: 1) the origin of *Bohemograptus* which in itself is a problem of the origin of Neocucullograptinae n. subfam.; 2) the microevolutionary development of *B. b. bohemicus*; 3) the splitting of the *B. bohemicus* lineage; 4) the development of the *auriculatus-kozlowskii* lineage and 5) the development of the *praecornutus-cornutus* lineage (Pl. VIII).

The origin of Bohemograptus. — Until recently, *Bohemograptus* Přib. constituted an only group of species within limits of the genus *Pristiograptus* Jaekel. However, attention has recently been attracted to a considerable morphological separateness of this group of "pristiograptids", as well as to the differences in the trends in their further evolution (Urbanek, 1963, p. 206; 1966, pp. 383—384). Greatly on the basis of these views, Přibyl (1967) has ected a separate genus of *Bohemograptus* with a type species of *Graptolithus bohemicus* Barr.

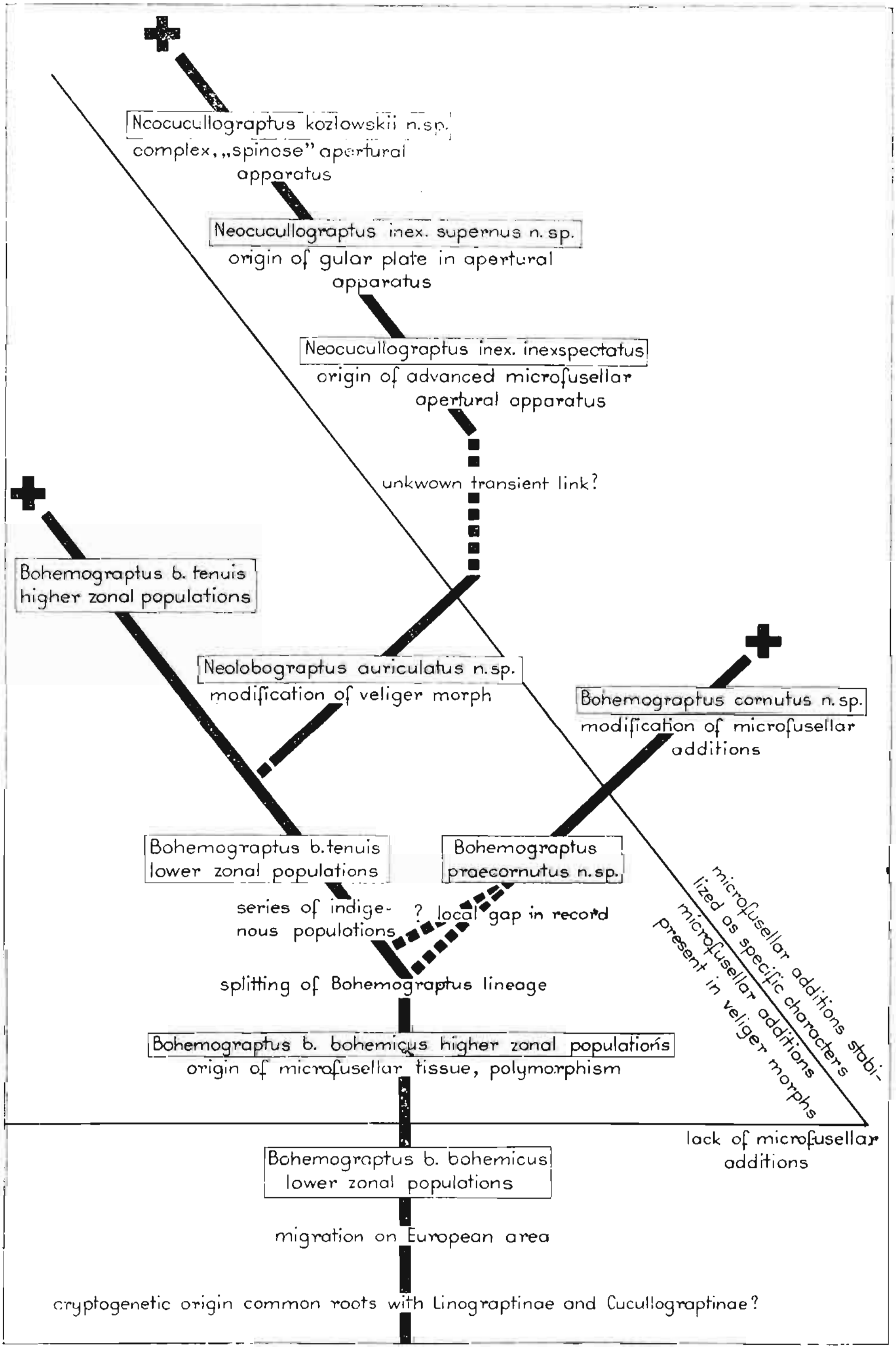
Urbanek (1966) also pointed out a considerable morphological similarities in the structure of the proximal part of rhabdosome in the early representatives of Cucullograptinae and Linograptinae, as well as in Neocucullograptinae n. subfam. (*L. progenitor* Urb., *Neodiv. nilssoni* Lapw., *B. bohemicus* Barr.). This indicates that the differences between these, after all quite divergent, lineages were at first insignificant and that the divergence progressively increased with further evolution. This might suggest possible phylogenetic relationships between the three stocks mentioned above. Such a working conclusion has for the present been formulated by Urbanek as a pure hypothesis (1966, p. 384 and Pl. VIII on p. 365). According to a previously suggested view (Urbanek, 1963, pp. 195—196), the Lower Ludlovian fauna was formed, after the great extinction, on the Wenlockian-Ludlovian boundary on the basis of the following three elements: 1) very few indigenous survivors of the Wenlockian fauna; 2) new elements developed by speciation from indigenous relic elements; 3) immigrants, which represented an element strange geographically and making up a) a continuation of lineages which occurred as early as the Wenlockian and b) new lineages derived from little known pre-Ludlovian ancestors.

The importance of the last-named element to the formation of the Lower Ludlovian fauna was emphasized by Urbanek (1963). It seems that Linograptinae, Cucullograptinae and Neocucullograptinae n. subfam. (specifically *Bohemograptus*) should be assigned to category 3*b*. In the Ludlovian fauna, they are in fact a cryptogenic element.

Considering that the three groups referred to above are perhaps mutually related more closely, one may suppose that they are descendants of a common ancestral group, an unknown or not yet recognized Wenlockian graptolites. Likewise, one may guess that the early divergence of these groups took place still prior to the ingression on European areas and this seems to be the reason why the early representatives of all the three stocks, although displaying considerable morphological similarities, do not reveal the presence of transitional forms. The ingression of this cryptogenic element was not, however, simultaneous. The available data indicate that *Bohemograptus* and *Neodiversograptus* appeared earlier and, maybe, simultaneously, while *Lobograptus* appeared somewhat later. Some data (see below) give evidence that *Bohemograptus* was, however, the earliest immigrant, while *Neodiversograptus* and *Lobograptus* successively appeared later. The early *Bohemograptus* is in many respects the least specialized genus but it is not certain whether or not it can be considered because of it is a primitive form most closely related to the ancestors of all the three lineages. Likewise, it is not certain whether or not the order of ingression is an evidence of the order of separation of particular stocks from the common ancestral group. If all the three tribes descend from a common ancestral group, the problem of their origin is closely connected with that of the origin of Linograptinae, which has recently been discussed widely (Urbanek, 1963, pp. 193—206; 1966, pp. 378—384), but continues to be still debatable.

Morphological similarities in shape of sicula and proximal part of rhabdosome in early representatives (Urbanek, 1966, pp. 378—384, Pl. X) (including similar tendency to the situation of the first sicular ring on the prosicula in some of Neocucullograptinae n. subfam. and Cucullograptinae, as well as Linograptinae) may be an evidence of a possible, but quite hypothetical, relationship of Neocucullograptinae n. subfam., Linograptinae and Cucullograptinae. The same may be testified to by further evolutionary events such as, an independent and heterochronic gracilization of the-

PLATE VIII


Neocucullograptus kozlowskii n.sp.
complex, „spinose" apertural apparatus
Neocucullograptus inex. supernus n. sp.
origin of gular plate in apertural apparatus
Neocucullograptus inex. inexspectatus
origin of advanced microfusellar apertural apparatus
unkwown transient link?
Bohemograptus b. tenuis higher zonal populations
Neolobograptus auriculatus n.sp.
modification of veliger morph
Bohemograptus cornutus n.sp.
modification of microfusellar additions
Bohemograptus b.tenuis lower zonal populations
Bohemograptus praecornutus n.sp.
series of indigenous populations
? local gap in record
microfusellar additions stabilized as specific characters
microfusellar additions present in veliger morphs
splitting of Bohemograptus lineage
Bohemograptus b. bohemicus higher zonal populations
origin of microfusellar tissue, polymorphism
lack of microfusellar additions
Bohemograptus b. bohemicus lower zonal populations
migration on European area
cryptogenetic origin common roots with Linograptinae and Cucullograptinae?

cae and sicula, the formation of similar apertural elevations in all the three stocks, etc. Although general trends in the evolution of these three stocks are strongly divergent, there occur certain striking morphological similarities, which might be ascribed to the heterochronic parallelism. Some other similarities as, the development of asymmetry by the hypertrophy of the left side of the body in *Cucullograptus* and *Neocucullograptus* n. gen., are too general in character so as a definite phylogenetic significance might be ascribed to them. They are on the boundary of the phenomena caused by parallelism and by convergence and are evoked rather by the similarity of adaptive types, not precluding a certain similarities in genetic potential and morphogenetic system.

Microevolution of B. b. bohemicus. — In the Mielnik on the Bug borehole, *B. b. bohemicus* appears as late as in the *progenitor* zone. There is the certainty, however, that, on the whole, it appears in the European area as early as in the *nilssoni* zone (comp. pp. 273). There are data which might indicate even an earlier appearance of *B. bohemicus* (Jaeger, 1959, p. 35; Horný, 1962, p. 883, Fig. 7; Přibyl & Vaněk, 1968, p. 416) in the *Pristiograptus vulgaris* (= *M. ludensis* Murch.?) zone. These important observations still require confirmation, for they are of a great importance to the ascertainment of a possible origin of *Bohemograptus*, as well as presumable genetic relationships between the Lower Ludlovian graptolites.

The material available recommends the hypothesis that the lineages of *B. b. bohemicus*, on the whole conservative throughout the entire Lower Ludlovian, display a zonal microevolution (comp. chapter on analysis of variaton). In the *nilssoni-progenitor* zones, *B. b. bohemicus* is represented by forms belonging to extremely "robust" types, which are marked by a large and strongly expanded sicula with a strong dorsal process, wide thecae and a considerable width of rhabdosome in its proximal part. It is as early as the *parascanicus* zone that the extreme "robust" types disappear or become rarer. Advanced "gracile" types appear as late as the *hemiaversus* zone. They are represented by forms with thin and usually much shorter siculae, with thinner and higher thecae (the aperture of th_1 being usually situated at the level of the prosicular apex or higher up) and with the rhabdosome which is thinner in the proximal part. This allows one to distinguish in principle two separate "morphotypes", a robust and a gracile one, but the boundaries between them are arbitrary because of the occurrence of many transitional forms. The change in the range of variability, that is, the disappearance of the extreme

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Plate VIII

Tentative phylogeny of Neocucullograptinae n. subfam. Broken heavy black lines indicate discontinuities of the record whose nature is discussed in text. Thin black lines mark the morphological boundaries, crosses mean — extinction.

"robust" morphotypes and the appearance of the "gracile" morphotypes, is certainly an evidence of microevolutionary processes that take place in them. The variability remains, however, continuous and not polymorphic in character.

The appearance of a new morphotype, capable of producing characteristic apertural structures on the sicula and thecae composed of a special peridermal tissue, here called a microfusellar tissue (or what is known as microfusellar additions) is a characteristic feature of late populations of *B. bohemicus*. The definition of this tissue, which is a phylogenetic novelty in the *Bohemograptus* lineage but occurring sporadically in various Graptoloidea, has already been given before (comp. terminology). The specificity of *B. bohemicus* and descendant lineages, derived from it, consists in the fact that microfusellar structures reach in them a high degree of development and seemingly are of a great prospective significance. The morphological form of microfusellar additions in *Bohemograptus*, their astogenetic variability and a manner of phylogenetic introduction are discussed separately.

The occurrence, in one and the same population, of the representatives of *Bohemograptus* which are capable of producing microfusellar additions and those devoid of such a capability, is in this case a symptom of a discontinuous variability. Different possibilities are suggested by a biological interpretation of such a variability (comp. e. g., an elementary discussion of such possibilities presented by Mayr, Linsley & Usinger, 1953, pp. 78-104). In the present work, the interpretation is adopted, according to which the occurrence of this variability in *B. bohemicus* is based genetically as an effect of a genetic polymorphism (comp. the definition and discussion of this phenomenon in Mayr, 1963 and Ford, 1964). This is indicated by the following facts: 1) a discontinuous character of variability; 2) a relatively small frequency of the representatives of morphotype capable of producing microfusellar additions (a morphotype here called a "veliger morph", comp. terminology), combined with a considerable persistency of this morphotype; 3) a consistency in a general morphological structure (a foundation of thecae, shape of sicula and rhabdosome, size) displayed by "normal" forms and "veliger morph", associated in one and the same population; 4) an occurrence of analogous morphotypes in *B. b. bohemicus*, *B. b. tenuis*, as well as in *B. praecornutus* n. sp. and, in a somewhat changed form, in *Neolob. auriculatus*, n. sp.

The last-named (4) feature of this phenomenon clearly favours polymorphism as an adequate explanation, for another alternative of interpreting such variability (distinction of separate taxons) would require appropriate number of "sister" species or subspecies in each of these cases (comp. pp. 299). Such conditions should be considered extremely unlikely, while the occurrence of similar morphs in the case of polymorphism in a certain group of species is very likely (heterostyly in *Pri-*

mula, Ford, 1964; also Mayr, 1963). We may assume that the microfusellar polymorphism in *Bohemograptus* was at first of the nature of a balanced polymorphism. Such a state characterizes genetic systems in *B. b. bohemicus* (at the end of its occurrence), *B. b. tenuis*, *B. praecornutus* n. sp. and *Neolob. auriculatus* n. sp. (during the entire period of their occurrence). The occurrence of polymorphism of this type was surely conditioned adaptatively due to e. g., adaptive superiority of heterozygotes as compared with both homozygotes (Ford, 1964). The microfusellar polymorphism in *Bohemograptus* was undoubtedly a factor favourable to its survival during the period of great faunal changes on the boundary of the Lower and Upper Ludlovian and afterwards turned out to be a factor favourable to a further differentiation of descendant evolutionary lineages. An appropriate polymorphism, increasing the range of phenotypic variability, facilitates the transition to a new environment or adaptation to changing conditions (Schmalhausen, 1968, pp. 183—185) and is one of the factors which increase the eurybiotism of the species as a whole and the possibility of reaching a constitutional access to a new environment. As shown by facts, the balanced polymorphism was probably a starting point to the development of complex microfusellar structures in *B. cornutus* n. sp. and *Neocucullograptus* n. gen. Under changed environmental conditions, first, here probably took place a reorganization of genetic systems, which consisted in a change of the balanced into transitional polymorphism, and finally — a displacement of the normal by the mutational form. At the same time, a transformation takes place in the phenotypic expression of the mutational morph (a morphological evolution of "veliger" morph). Both processes are known from the studies on the transitional polymorphism of recent organisms (e. g., industrial melanism; Ford, 1964).

The conception of the genetic polymorphism, as applied to Graptoloidea, has for the first time been formulated by Skevington (1967) on the basis of a one- and two-stiped form in *Nicholsonograptus fasciculatus* (Nicholson). The same interpretation has even earlier been applied by Urbanek (1963) to a form capable of forming the sicular cladium or devoid of such a capability in *Neodiversograptus nilssoni*. Urbanek (comp. Urbanek, 1963, pp. 161, 198, 202) did not, however, use the term "polymorphism" and reach any unquestionable conclusions. Polymorphism is surely a very general biological phenomenon (Mayr, 1963) and hence its occurrence also in Graptoloidea is not any surprise. In a fossil material, it is particularly easy to discover its occurrence in the case of characters in outer morphology which appear according to the rule of "all-or-none" and, therefore, produce sharply separated morphological forms (presence or absence of additional stipes of rhabdosome, capability or incapability of producing microfusellar tissue), that is, characters which may be easily discovered in a fossil.

In the present work, it has been assumed that polymorphism, caused by the presence of a "normal" and "veliger" morphs, occurred secondarily in the evolution of *B. b. bohemicus* and was an original polymorphism in the decendant species, that is, *B. b. tenuis*, *B. praecornutus* n. sp. and *Neolob. auriculatus* n. sp. In all these cases, it seems more likely that the polymorphism of the species mentioned above was conveyed from the genetic pool of an ancestral species rather, than was formed anew as a result of an independent mutation. This is the more likely as the morphological form of the veliger morph in the representatives of *Bohemograptus* referred to above is marked by a considerable similarity, while in the case of *Neolobograptus* n. gen. it is subject to only limited modifications.

Splitting the B. bohemicus lineage. — In the *hemiaversus* zone, the populations of *B. bohemicus* display a considerable morphological variability. In addition to forms of the "robust" type, there occur those of the "gracile" type, as well as those provided with microfusellar structures. It should be assumed that this considerable degree of intraspecific variability was a starting point for a later differentiation of the *B. bohemicus* lineage into two different evolutionary trends represented by *B. bohemicus tenuis* (Bouč.) and *B. praecornutus* n. sp.

This event may be classified as a splitting of the lineage without a simultaneous development of new morphological characters. The last-named are rather subject to segregation only; the "robust" morphotype begins to characterize only one, definite lineage (the *praecornutus-cornutus* lineage). Such characters as a long sicula, low position of th_1, relatively wide and low thecae become permanent specific characters of *B. praecornutus* n. sp., while a relatively shorter sicula, high situation of th_1, presence of long and thinner thecae, that is, features of the "gracile" morphotype become characteristic of *B. bohemicus tenuis*. This is the manner in which a permanent morphological difference is marked between the two species. Prior to the occurrence of these differences, that is, prior to the appearance of the splitting of the *Bohemograptus* lineage, both morphotypes probably concurred within the range of the intraspecific variability.

An average morphological type of *B. praecornutus* n. sp. approaches a primitive form of *B. bohemicus* from the lowermost horizons of the Lower Ludlovian. For this reason, we may consider, after Henning (1966), that it is a plesiomorphic form, which to a greater extent preserves the morphological characters of the ancestral species rather, than the sister form *B. b. tenuis*, representing, in a given case, a more apomorphic form. This criterion, on the whole of a relative importance, is in this definite case probably especially deceptive due to the course of evolutionary processes consisting in the segregation of morphotypes, which during a certain period are equally characteristic of *B. bohemicus*. The discrimination between which one is more and which less typical may here consist only in determining which of the morphotypes was more primitive against the background of the entire microevolution of the parent species.

In the Mielnik on the Bug borehole, a continuous series of transitional populations occurs between *B. b. bohemicus* (Barr.) and *B. b. tenuis* (Bouč.). This series poses a hard problem in determining morphological and time boundaries between the two subspecies. This problem is discussed in chapter on analysis of variation. It is beyond any doubt that the changes which here took place were continuous in character and occurred sympatrically and that both subspecies were successional. Less clear is the way in which *B. praecornutus* n. sp. was formed. In the occurrence of the bohemograptids with a relatively "robust" habitus, a certain discontinuity is noted in the Mielnik on the Bug core. It is expressed in their temporary disappearance (in the lower part of the *aversus* zone, *C. aversus aversus* subzone). Although this disappearance may be accidental and caused by extremely spotty sampling, it is not unlikely that the ancestors of *B. praecornutus* n. sp. should be looked for among the representatives of *B. b. bohemicus* from the *hemiaversus* zone and not among those extreme representatives of *B. b. tenuis* which are less gracile and more robust and which from the purely morphological viewpoint could also be a starting point for the formation of *B. praecornutus* n. sp. Such forms appear in the upper part of the *aversus* zone but they are not marked by a particularly appropriate assemblage of characters (large, 1.73—1.99 mm long siculae, but a high, +0.05 — +0.10 mm, situation of thecae). Forms with relatively large siculae and comparatively low position of th_1, which sporadically occur later, are very rare and already accompanied by *B. praecornutus* n. sp. proper. They cannot be taken into account as ancestors of the last-named species and are only extreme variants within the range of variability of *B. b. tenuis* or *B. praecornutus* n. sp.

The appearance of *B. praecornutus* n. sp. as a form clearly separate morphologically and determined by a characteristic assemblage of features, with a simultaneous lack of the variants which, within the variability range of *B. b. tenuis*, would completely meet the requirements of ancestral forms for the former species, allows one to look for its ancestors among the populations of *B. b. bohemicus*. The separation of the latter as an indepedent lineage probably did not take place earlier than in the upper part of the *hemiaversus zone*, for the microfusellar additions of *B. praecornutus* n. sp. so strongly resemble analogus structures in *B. b. tenuis* that it seems logical to suppose that they were inherited from one and the same ancestral genetic pool rather, than that they were formed as a result of independent mutations. The separation of both lineages could not, therefore, take place earlier than the appearance of the "veliger morph" in the populations of the ancestral species and the genetic factors responsible for the origin of this polymorphic form were conveyed to the descendant genetic pool. Since in the material from Mielnik on the Bug no transitions were found between *B. b. bohemicus* and *B. praecornutus* n. sp. which would be so continuous as those in the case of *B. b. tenuis*, one could presume that this speciation took place outside the area under study, that is, in this particular sense, allopatrically. The latter suggestion does not necessarily mean that we assume an orthodox mechanism of the geographical speciation by the formation of an isolate and appropriate isolating barriers. Certain elements of this process seem, however, to appear in the process of the formation of *B. praecornutus* n. sp. The latter is marked not only by the stabilization of an increase in frequency of occurrence of features characteristic of the "robust" morphotype (a relatively strong sicula and wide, rather short thecae), but also by the correlation, with these features, of such one as a permanent presence of apertural elevations on thecae (which in the "robust" morphotype of *B. b. bohemicus* occurs only sporadically) and a permanently low situation of the initial bud of th_1, which in this form never occurs in *B. b. bohemicus*. The last-named two features might indicate that, in addition to the process of variability segregation whose mechanism surely consisted in a division of the variability pool by a certain isolation (or, at least, decrease in the gene flow), a certain differentiation also took place within the descendant population, which became an incipience of *B. praecornutus* n. sp. The lack of a continuous series of populations linking *B. b. bohemicus* with *B. praecornutus* n. sp. in the material from Mielnik on the Bug might provide evidence that this process of division and early differentiation took place outside this area and maybe also included some marginal populations of *B. b. bohemicus*. The lack of more definite data on the geographical occurrence of the last-named species makes drawing final conclusions difficult. A certain gap between the occurrence of *B. b. bohemicus* with morphotypes, which might be considered as a starting point for *B. praecornutus* n. sp., and the appearance of the latter (a gap in the *aversus* zone) might suggest that the process of speciation, referred to above, took place in an indeterminate area precisely during that period. The significance of this fact must not, however, be overestimated because of an exceedingly spotty character of sampling. Besides, it is not unlikely that the speciation of *B. praecornutus* n. sp. took place without the participation of a geographical isolation and a later ingression of an already formed species of the area under study, but through the medium of some other mechanism. Since the ancestral subspecies is present in the area of Mielnik on the Bug, during the analysis of changes in fauna *B. praecornutus* n. sp. has not been assigned to the category of "immigrants" but to the category of "indigenous speciation", although in fact its formation took place on the boundary of the two processes.

According to Brundin's (1968) views, the plesiomorphic species are formed as a rule in the central area of occurrence of the parent species, while the apomorphic species are evolved from its marginal populations. From a certain point of view, the example of division of the *Bohemograptus* lineage might be considered as opposite, since it is not unlikely that of the two descendant forms *B. praecornutus* n. sp. should be regarded as plesiomorphic and, at the same time, certain facts indicate that it was likely to arise from the differentiation of the marginal forms of the parent species. This suggests a rather questionable importance of such views.

Brundin (1968) maintains that the division of a lineage, connected with the separation from an ancestral species of two independent lineages determines by itself that the first representatives of these new lineages make up taxons of the specific rank or what is known as "sister species". Brundin considers this conclusion to be a logical postulate which does not require a separate justification. Thus, the separation of the *B. praecornutus* n. sp. lineage from *B. b. bohemicus* would at the same time be tantamount to the fact that the continuing *B. bohemicus* lineage is also represented by an already new species (in this case, *B. tenuis*). This view, forcing a character of a full symmetry upon the process of splitting evolutionary lineages, although indispensable to keep the conception of "sister species" as a general model of evolution, arouses serious doubts and is difficult to apply to the taxonomic practice ("splitting", a character not easy to be proved, also introduces the element of phylogenetic speculation to the conception of the species). In the case under study, the present writer's opinion is founded on the taxonomic asymmetry, that is, on the view that one of the lineages is represented by a new species (*B. praecornutus*) and the other by a subspecies of a parent species (*B. b. tenuis*) only. In this view, the starting point is the analysis of morphological variability, the presence or absence of relatively permanent morphological features, or possibly the character of evolutionary changes (occurrence or lack of sympatric transitional series). These features seem to be more significant than Brundin's logical postulates.

The *B. b. tenuis* lineage subsequently initiated the development of the *auriculatus-kozlowskii* lineage, but its independence is manifested by its certain own morphological trends. As shown by morphological and stratigraphic data, the *auriculatus-kozlowskii* lineage, descending from early populations of *B. b. tenuis* (*aversus-auriculatus* zone), was probably separated in the *praecornutus* zone. In this zone, the last-named species still represents a generalized morphological type (among other characters, the sicula is provided with a strong dorsal process), which might give rise to *Neol. auriculatus* n. sp. A "secondary trend" towards a certain morphological specialization (atrophy of the dorsal sicular process, *inexspectatus-kozlowskii* zone, comp. pp. 254) is subsequently marked in the evolution of *B. b. tenuis*. These changes are here estimated as microevolutionary processes, whose taxonomic significance is infrasubspecific in character.

The auriculatus-kozlowskii lineage. — This lineage represents the morphological and stratigraphic sequence of 1) *Neolob. auriculatus*, 2) *Neocuc. inexspectatus* (Bouč.) and *3) Neocuc. kozlowskii* n. sp., allowing one to distinguish the following two separate morphological stages of evolution: a) *Neolobograptus* n. gen. and b) *Neocucullograptus* n. gen. Some, so far unknown transitional, link might also occur to fill a certain gap between these two stages of evolution (Pl. VIII).

The *Neolobograptus* n. gen. stage is represented by one species — *Neolob. auriculatus* n. sp. As compared with *B. b. tenuis*, the following changes are recorded in the fusellar structures of thecae: 1) elongation and gracilization of thecae, in particular proximal ones, 2) stable position of the aperture of th_1 above the apex of prosicula, 3) presence of apertural elevations with dorsolateral incisions as a permanent specific character. The former two characters appeared, as a phylogenetic novelty, by proximal introduction and the latter, especially the dorsolateral inicisions, by distal introduction. Two characters: 1) size and shape of sicula and 2) a strong ventral curvature of the proximal part of rhabdosome have been inherited by *Neolob. auriculatus* n. sp. from *B. b. tenuis* in principle without changes. Virtually the same type of genetic polymorphism as that in *B. b. tenuis* is kept by *Neolob. auriculatus* n. sp. The occurrence of this type is caused by the presence of "veliger" morph, that is, forms capable of producing microfusellar structures. A fundamental change is, however, observed in the morphological form of "veliger" morph which, in all cases, is composed only of the microfusellar tissue proper, without the pseudofusellar part. These conditions, much the same as the presence of microfusellar additions on the metasicular aperture, persist subsequently without any changes in the entire *auriculatus-kozlowskii* lineage. Precisely these characters manifest a distinct divergence as concerns the trend in the development of microfusellar structures in the *auriculatus-kozlowskii* and *praecornutus-cornutus* lineages.

The results of the morphological and astogenetic analyses suggest that between *Neolob. auriculatus* n. sp. and *Neocuc. inexspectatus* there probably existed some transitional link, which probably filled a certain morphological discontinuity between *Neolobograptus* n. gen. and *Neocucullogratus* n. gen.

Within this so far hypothetical link the following changes should have taken place: 1) as a result of the transformation of a "balanced polymorphism" of *Neolob. auriculatus* n. sp. into a "transient polymorphism" which led to the uniformity of the genetic system, the presence of microfusellar additions became a permanent specific character, developed in all individuals in appropriate growth stages; 2) microfusellar additions took the morphological form of apertural lobes with a certain degree of asymmetry, in particular in the distal part of rhabdosome. The entire microfusellar structure of thecae would rest on typical apertural elevations, provided with a dorsolateral incision, inherited from *Neolob. auriculatus* n. sp. The morphological foundation of this type causes the occurrence, in *Neocucullograptus* n. gen., of a recapitulatory growth stage, called an "*auriculatus* stage", which emphasizes a close relationship of this genus to the species *Neolob. auriculatus* n. sp. (comp. pp. 341).

A further course of events is illustrated by *Neocuc. inex. inexspectatus* (Bouč.), which displays a continued increase in asymmetry of the apertural apparatus (a strong hypertrophy of the left lobe, particularly marked in distal thecae) and the formation of superstructures resting on microfusellar lobes, the same as an incipient rostral process on the left lobe and a somewhat more strongly expressed lateral process on the right lobe.

The tentacular apparatus surely displayed a considerable asymmetry; the left arm of the lophophore rested on an incipient rostral process and the right arm on a corresponding dorsolateral incision, around which a relatively long microfusellar process was developed. Only the sicula continues to be marked by the presence of symmetric microfusellar additions in the form of lobes. (see also Systematic part).

Neocuc. inex. supernus n. subsp. takes a stratigraphic position transitional between *Neocuc. inex. inexspectatus* (Bouč.) and *Neocuc. kozlowskii* n. sp. Despite some characters of specialization, this form may be considered transitional also in the morphological sense (comp. Systematic part). It provides evidence that a further evolution of thecal characters consisted, in this lineage, in a complication of the structure of apertural apparatus by a gradual addition of new structures such as (in this case), what is known as a gular plate which accompanies the incipient rostral and lateral processes.

The last link of the series, *Neocuc. kozlowskii* n. sp., is marked by a further progressive development of microfusellar structures of the apertural apparatus. In addition to a strongly developed gular plate, this leads to the formation of a strongly elongated rostral process on the left lobe and of a long lateral process on the right lobe. One of the most complex apertural apparatus of the Monograptina is developed as a result. A form, here described as *Neocuc. kozlowskii* var. *unicornus* n. var. and which represents a group of extreme variants rather, than a separate taxon, might indicate that the development of the apertural apparatus in *Neocucullograptus* n. gen. was additive and mosaic. In the stage represented by *Neocuc. inexspectatus inexspectatus* (Bouč.), this apparatus in distal thecae consisted only of: 1) lobes, 2) an incipient rostral process, 3) a more strongly developed lateral process. In the stage of *Neocuc. inex. supernus* n. subsp., besides unchanged elements 1—3, an additional superstructure appears, that is 4) a gular plate and in the stage of *Neocuc. kozlowskii* n. sp. the rostral (2) and lateral (3) processes stretch out yet more strongly. The analysis of *Neocuc. kozlowskii* var. *unicornus* n. var. might be an evidence that, in the last-named stage (*Neocuc. kozlowskii*), first a strong elongation of the lateral process took place and then, after a certain delay, the same happened to the rostral process. In *Neocuc. inex. inexspectatus* (Bouč.), the lateral process is also already longer than the rostral one and conditions become almost equal as late as in the *Neocuc. kozlowskii* stage.

The apertural apparatus of *Neocucullograptus* n. gen. resembled morphologically and adaptively that in *Cucullograptus* Urb., although in each of them the structural foundation (microfusellar and fusellar tissue) and the mechanism of growth (prematural and postmatural growth) are quite different. Striking is the homeomorphy of the apertural apparatus in *Neocuc. inex. inexspectatus* (Bouč.) and *Cucullograptus aversus aversus* Eisen., as well as — to a smaller extent — of *Neocuc. kozlowskii* n. sp. and *C. aversus rostratus* Urb. (comp. Urbanek, 1966). In the evolution of both *Cucullograptus* and *Neocucullograptus* n. gen., the development of the asymmetry of apertural apparatus is expressed by the hypertrophy of the left apertural lobe. *Neocucullograptus* n. gen. is marked by the type of asymmetry similar to that in L-cucullograptids in which evolutionary changes are concentrated only on the apertural apparatus, that is, probably on the tentacular apparatus of zooids (Urbanek, 1966, p. 338). The last-named apparatus also in this case played, therefore, the role of "key organs".

As compared with the apertural apparatus of the group *C. aversus*, in *Neocucullograptus* n. gen. this structure was subject to a slighter modification. While in the former case, the right arm of the lophophore was probably considerably or almost completely atrophied, which was compensated by the hypertrophy of the left branch (Urbanek, 1966, pp. 340—342), these conditions in *Neocucullograptus* n. gen. were quite different. The lateral process, occurring on the right lobe, may be interpreted as an equivalent of the rostral process rather, than as a sort of an anal tube. The former was probably a sort of a support and protection for the left branch of lophophore. The lateral process would fulfill the same functions to the advantage of the right branch of lophophore. Judging from the size of this process, its earlier appearance in astogeny and dimensions larger than those of the rostral process, reached by it as early as in *Neocuc. inexspectatus* (Bouč.), the conclusion may be drawn that the right branch of lophophore was not subject to any reduction. The asymmetry of the soft parts was probably expressed by a curvature of the body axis, or at least of the lophophore, so that its left arm was turned ventrally and the right branch dorsolaterally. These conditions resemble, to a certain extent, *Lobograptus cirrifer* Urb., in which the asymmetry of the apertural apparatus (related, however, with the hypertrophy of the right lobe as in all R-cucullograptids) did not result in a reduction of either of the two branches of lophophore (Urbanek, 1966, p. 340). The external similarity of the apertural apparatus in *Neocucullograptus* n. gen. to that in *Cucullograptus* Urb.

which, as we know, was a cause of considerable misconceptions, cannot slur the fact that in both cases, the peridermal tissue, manner of forming and relations of soft parts were quite different. On the other hand, the adaptive significance of these structures seems to be very similar in both genera.

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The praecornutus-cornutus lineage. — *B. praecornutus* n. sp., whose origin has already been discussed earlier, represents a form, in which fusellar thecal structures are closely approaching the state observed in *B. cornutus* n. sp. and which turn appeared by the modernization of microfusellar additions on the foundation of *praecornutus*.

On the other hand, the microfusellar structures of *B. praecornutus* n. sp. only slightly differ from those in "veliger " morph of the species *B. bohemicus*. This species continues to be polymorphic in its capability of forming microfusellar structures and its sicula also displays the presence of corresponding microfusellar additions. It is of interest that forms which represent "veliger" morph in *B. praecornutus* n. sp., unknown in earlier populations *(praecornutus* zone), were found only upwards (*auriculatus* zone). Its earlier lack is considered as accidental, since these additions are so similar to microfusellar structures of "veliger" morph in *B. b. bohemicus* that they were probably inherited from the latter. It should be assumed, therefore, that early populations of *B. praecornutus* n. sp. also included "veliger" morph and that the microfusellar structures of *B. cornutus* n. sp. were developed on their foundation.

A general morphology and stratigraphic occurrence of *B. cornutus*. n. sp. dispel all doubts concerning the descent of this species from *B. praecornutus*. n. sp. In the morphology of thecae and siculae, the previously observed trend is maintained, which started with the process of the emergence of *B. praecornutus* n. sp. and in which some of the characters were secondarily intensified (a secondary trend towards increasing the length of sicula).

The occurrence of the "*praecornutus*" growth stage in astogeny, in which the aperture of thecae is provided with only ear-like elevations, seems to be here of a clearly recapitulative significance.

Fundamental changes, which in fact mark a distinct morphological discontinuity between the two species, occur in the domain of microfusellar structures. The presence of the latter becomes a permanent specific character, this fact causing the disappearance of the polymorphism typical of *B. b. bohemicus* (Barr.) and *B. praecornutus* n. sp. At the same time, the morphological form of microfusellar additions is subject to fundamental transformation. Apart from these changes, whose hypothetical course has been analysed elsewhere (comp. Systematic part), a principal homology with the microfusellar additions, occurring in "veliger" morph of *B. b. bohemicus* and *B. praecornutus* n. sp., may be proved. This homology consists in, among other things, a concurrence of both the microfusellar and pseudomicrofusellar tissue, produced in the same order on apertural additions. On the other hand, a lack of microfusellar additions on the sicula is a specific character of microfusellar structures in *B. cornutus* n. sp. In this respect, astogenetic characteristics of these additions differ from those in "veliger" morph of *B. b. bohemicus*, as well as of *B. praecornutus* n. sp., in which these additions are also present on the sicula. Likewise, a strong divergence is marked in relation to *Neolobograptus* n. gen. and *Neocucullograptus* n. gen., in which the sicula also is provided with microfusellar additions.

The functional role of the apertural apparatus in *B. cornutus* n. sp. probably did not differ fundamentally from the microfusellar structures present in "veliger" morph and which have been described elsewhere. These structures probably supported the tentacular apparatus, or maybe also played a protective role. Due to an increase in the carrying surface which resulted from the presence of relatively extensive and thin-walled membranes, these structures might also play a certain role as floats. Also noteworthy is a certain general similarity of apertural additions in *B. cornutus* n. sp. to "proximal end structures", recently described by Müller & Schauer (1969, pp. 8—12, Figs 21 and 22) in *Diplograptus* cf. *magnus* Lapw. Admittedly, they seem to be non-paired but, at first threadlike and thin, subsequently they expand to form an elliptic structure. Müller and Schauer maintain, however, that these are branchings of the virgula.

Examination of the tentative family-tree of Neocucullograptinae n. subfam. (Pl. VIII) is indicative for sequential evolution (each species or subspecies being successive in single line of descent, as in *B. bohemicus* lineage and in *Neocucullograptus* n. gen.) and for divergence (splitting) of lineages as well. Splitting in each case was connected with appearance of clearly separated new species, initiating certain new line. Appearance of *B. praecornutus* n. sp. and *Neolob. auriculatus* n. sp. are such cases. Lack of transient populations and certain resulting morphological discontinuity may indicate that splitting was not sympatric (sympatry being here understood in special narrow sense, owing to spotty sampling in localized boring), but owed its origin to spatial separation and subsequent migration from elsewhere. Probable spatial parameter in processes of splitting, may suggest rather allopatric speciation, for instance from peripheral populations of the ancestral species. This do not indicate, lowever, necessarily the orthodox mechanism of geographic speciation suggested for terrestrial organisms. Origin of *B. cornutus* n. sp. showing time overlap with its ancestral species and appearing as rather clear-cut morphological entity, may also indicate certain splitting of generally same nature as discussed above, but being of short duration (this splitting is not indicated therefore on Pl. VIII). Origin of *Neocucullograptus* n. gen. from *Neolob. auriculatus* n. sp. is marked by distinct discontinuity clearly indicating for presence of certain unknown transient link. There was a clear shift in direction of changes, but it is difficult to say whether processes involved were entirely sequential, or connected with splitting. Short coexistence of *Neolob. auriculatus* n. sp. with earliest representatives of *Neocuc. inexspectatus* (Pl. I, range chart) may suggest rather splitting as mechanism of origin of this last line.

Species which appear in result of allopatric splitting are nevertheless included into category of "indigenous speciation" in our further considerations on formation of Upper Ludlovian fauna, because their parental species or subspecies were present on investigated area, and in this respect they do not represent a strange element.

CHARACTER OF CHANGES IN THE GRAPTOLITE FAUNA ON THE BOUNDARY BETWEEN THE LOWER AND UPPER LUDLOVIAN

A far-reaching change in the graptolite fauna is recorded in Europe on the boundary between the Lower and Upper Ludlovian. On the British Isles and in Scania, it causes an irreversible disappearance of the graptolite biofacies, in other areas (Central and Eastern Europe) — a temporary crisis and decrease in taxonomic differentiation of the graptolite fauna.

The following elementary events make up the change in the graptolite fauna on the boundary between the Lower and Upper Ludlovian:

a) extinction of numerous lineages;
b) survival of some others;
c) appearance of new evolutionary lines.

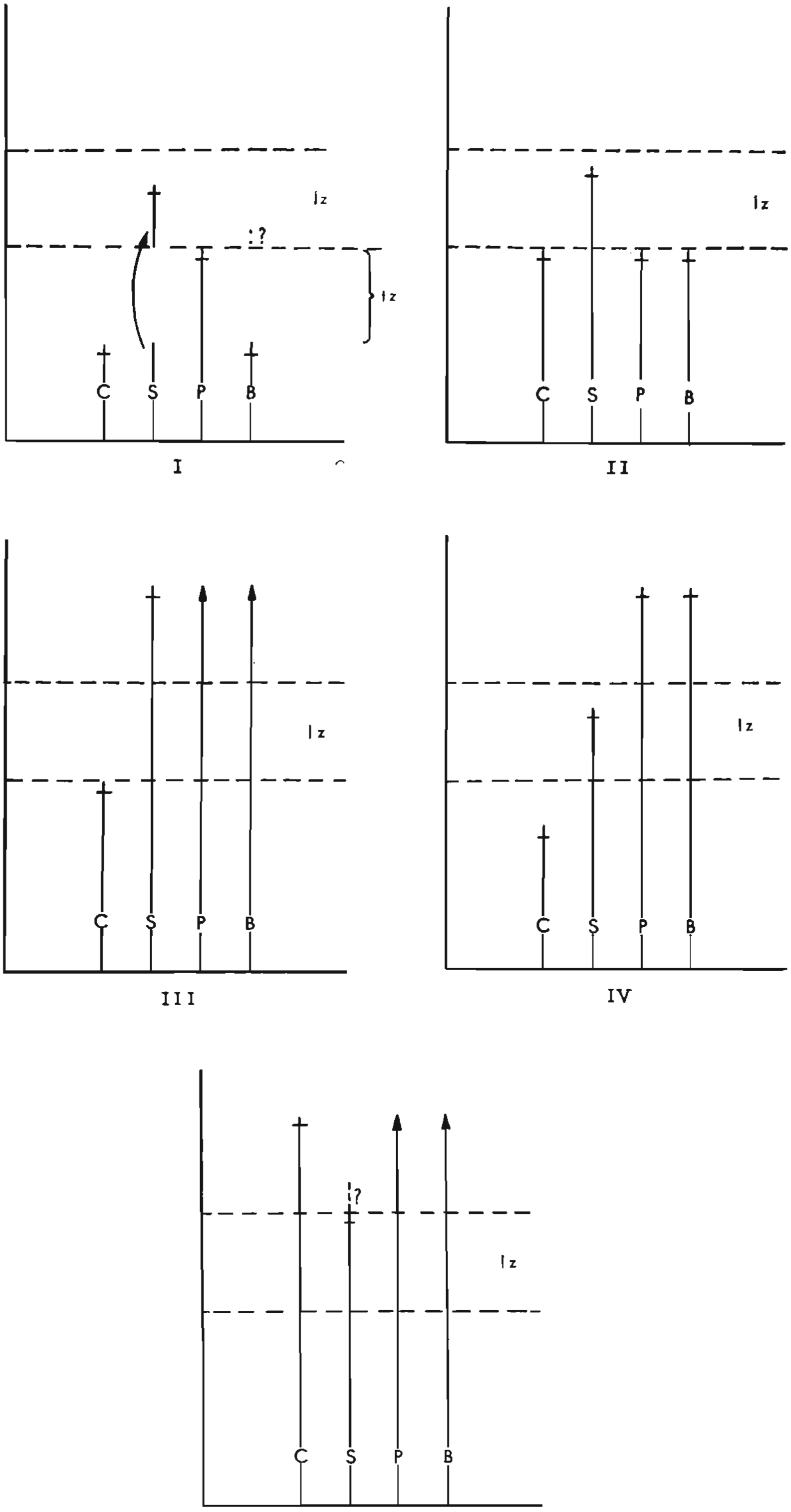
To make the analysis of this process as complete as possible, these events are considered below separately.

a) *Extinction of the lineages of the Graptoloidea.* — The lineages representing the genera *Lobograptus* and *Saetograptus* (the latter probably continued somewhat above the *leintwardineisis* zone, comp. Pl. IX) become extinct in the *leintwardinensis* (the lower part of the *aversus* zone) zone or directly below or above it. No descendants were also left by *Holoretiolites,* together with which the last Retiolitidae become extinct (Urbanek, 1966, comp. also remark on p. 176). Slightly above the *leintwardinensis* zone, the extinction is recorded of the last representatives of *Cucullograptus,* together with the entire group of Cucullograptinae, which make up an unusually characteristic element of the Lower Ludlovian fauna (Urbanek, 1960, 1966).

On the other hand, the extinction of *Neodiversograptus* is only apparent, for this genus transforms into *Linograptus* which appears above the *leintwardinensis* zone (Urbanek, 1963) or halfway its thickness (Jaeger, 1959).

The extinction of particular lineages of the Graptoloidea was not simultaneous in various geographical regions, on the contrary, it took

PLATE IX



I

II

III

IV

V

place heterochronously. Thus, in the area of Poland, there is no distinct evidence of the longer survival of *Saetograptus* above the *leintwardinensis* zone, whereas in Bohemia and Thuringia, many instances were recorded of the occurrence of *Saet. fritschi linearis* above this zone where it forms a separate zone (Jaeger, 1959, 1964; Horný, 1962). Particularly instructive are the studies of British palaeontologists conducted in Ludlovian type area (Ludlow-District; Earp, 1944; Elles, 1945; Earp, 1945; Holland, 1959), compiled by Holland (1962) and interpreted from the viewpoint we are interested in by Jaeger (1962). In the shallower shelf facies, a discontinuity is marked in the occurrence of saetograptids which, frequent in the *scanicus* (sensu lato) zone and represented by *Saet. chimaera*, give way to a monospecific occurrence of *Pristiograptus dubius tumescens* (known as a *tumescens* zone). After the reappearance of favourable conditions, the phenomenon is observed of the reappearance of saetograptids represented by *Saet. leintwardinensis*. In this area, the disappearance of saetograptids was a reversible process depending on fluctuations in ecological conditions. On the other hand, in a deeper basin facies, a continuity is maintained in the occurrence of saetograptids which, after an earlier extinction of cucullograptids, become the main component of fauna. For these reasons, the *tumescens* zone has not been distinguished here (Pl. IX; I-II).

A survival of saetograptids longer than that of the representatives of *Pristiograptus* and *Bohemograptus*, on the whole more persistent in other areas, is a common feature of the extinction of the graptolite fauna on the boundary between the Lower and Upper Ludlovian in the British Isles, in both the shelf and basin facies. These conditions stand in contrast with, for instance, the data for the area of the Polish Lowland, where saetograptids disappear earlier than cucullograptids (Urbanek, 1960, 1966) and where the most persistent are pristiograptids and *Bohemograptus*. Discussing the causes of the heterochronus extinction of graptolites in various regions of Europe, Jaeger (1962, p. 112), expressed the correct opinion that they lie in local changes in ecological situation. According to his earlier views (Jaeger, 1959), he relates, however, these changes primarily with

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Plate IX

Simplified diagram showing heterochronic disappearance of certain monograptid lineages on the boundary of Lower and Upper Ludlovian in particular regions of Europe

I — shelf area of Welsh Borderland, British Isles, II — basin area of Welsh Borderland, British Isles, III — Barrandian, Central Bohemia, IV — Holy Cross Mountains, Poland, V — Platformian Silurian, Poland. Note that I-II shows longest persistance of saetograptids, discontinuous (I) or continuous (II); III—IV the same for pristiograptids and bohemograptids, differing however in longer persistence of saetograptids over cucullograptids (III—IV) or showing just opposite conditions (V).

B — Bohemograptus, C — Cucullograptus, P — Pristiograptus, S — Saetograptus, lz leintwardinensis zone (broken thin lines delimits its upper and lower boundary), *tz tumescens* zone, arrows indicate continuation, crossed line disappearance, arched arrow in I indicate reappearance of *Saetograptus*.

those in the abiotic environment. Changes in lithofacies are indicative of the last-named ones.

In view of the heterogenity of changes involved in the abiotic environment and their regional, local or, sometimes, contrary character the picture of the extinction of the Graptoloidea, observed on the boundary between the Lower and Upper Ludlovian, seems to indicate that the physico-geographical changes could not be an only and sufficient cause of these animals' extinction. Biotic conditions, if only those which were created in particular regions as a result of the heterochronous extinction (for instance, the *Saetograptus-Pristiograptus-Bohemograptus* association in Bohemia and Thuringia, the *Cucullograptus-Pristiograptus-Bohemograptus* association in Polish Lowland, a monospecific occurrence of *Saetograptus* in the British Isles in the final stages of the extinction of the Lower Ludlovian fauna) should be considered as a significant component of local ecological conditions. A varying taxonomic composition of such relic assemblages surely exerted its inescapable influence on biocoenotic conditions in individual areas (comp. diagram Pl. IX, I—V).

Particular relic assemblages differ from each other in its taxonomic composition, in some cases these differences being extremely significant. There are, however, certain characteristic features common to all relic assemblages, namely: 1) a decrease in the degree of differentiation caused by the predominance of extinction over speciation and immigration, if the last-named two factors are operative at all; 2) a strong quantitative increase in some elements of a relic assemblage (one or few species), being of the nature of a population explosion.

It should be supposed that the population explosion of some elements of an assemblage is caused by a decrease in competition on the part of other adaptative zones, emptied as a result of extinction. To sum up, a survival of definite elements of a relic assemblage and an exuberant quantitative increase in some of them gives ample evidence that the changes in an abiotic environment were not sufficiently radical so as to preclude to an equal extent the existence of all lineages.

It seems that the relic assemblages may be divided into: 1) monospecific, represented by one species only and 2) multispecific, on the whole composed of more than one but rather few species. The difference between the two categories being conventional, it is not certain whether or not the completely monospecific relic assemblages existed at all. In sober fact, they represent assemblages marked by a great predominance of one species over a very scant sporadic occurrence of others.

The local zone of *Pristiograptus dubius*, distinguished in the Lower Ludlovian of the Holy Cross Mts. above the *nassa* zone (Tomczyk, 1962), the local zone of *Prist. tumescens*, distinguished within the range of the shelf facies in the Welsh Borderland (comp. Pl. IX, I), the zone of *Saetograptus leintwardinensis* in the area of the Welsh Borderland and Central Wales, where it occurs monospecifically or almost monospecifically (there are certain clues of a sporadic concurrence of vary rare *Bohemograptus bohemicus* and *Monoclim. haupti* = *M.* cf. *ultimus* Perner sensu Elles) may serve as examples of monospecific relic assemblages. Finally, such examples of monospecific relic assemblages may also be supplied by a local abundant occurrence of *Saetograptus fritschi linearis*, almost devoid of associations of other forms (calcareous concretions from the Mušlovka quarry near Reporyje, Barrandian, Czechoslovakia, Bouček, 1936; Jaeger, 1964; "orthoceratoid" limestones from Lindener Mark near Giesen, Germany, Jaeger, 1962, 1964).

The formation of monospecific relic assemblages indicates that the species which formed them were completely withdrawn from the intragroup competition, that is, the intragroup competition ended by the elimination of other graptoloids, displaying adaptive inferiority.

Examples of multispecific relic assemblages: *Prist. dubius*+*Gothograptus nassa* assemblage, frequent within the range of the epibole (zone) *nassa*, an assemblage of the upper part of the *Cucullograptus aversus* zone (the *rostratus* subzone in the area of the Polish Lowland, consisting of *Cucull. aversus rostratus*, *Pristiograptus dubius* and *Bohemograptus bohemicus tenuis* (Urbanek, 1966)) and a similar assemblage of the *Saet. fritschi linearis* zone in Thuringia, consisting, besides this species, of *Prist. dubius* and *Bohemograptus bohemicus*. In the last-named assemblage, the index form is not an only frequent species, *Bohemograptus bohemicus* also occurring abundantly (Jaeger, 1962, 1964).

It is beyond any doubt that relic assemblages similar to those composed of the graptolite fauna, may be recognized in many other cases, e.g., where a differentiating extinction of fauna (e. g., the Pontian basin in the Tertiary) takes place as a result of changes in the hydrological regime (e. g., changes in salinity). If similar relic assemblages persist for a longer time in one and the same definite area, we can consider it as an occurrence of asylums or refugees (e. g., the Permian fauna of the Island of Timor, where the survival of many Pelmatozoa and Trilobita makes up an interesting episore of the great Permian-Triassic extinction). Usually, however, after some time, either a final extinction takes place, or a new radiation deprives the assemblage of its relic character.

Relic assemblages indicate that a relative decrease in competition in new biocoenotic systems compensated for unfavourable changes in the abiotic environment and facilitated an exuberant quantitative increase in some of their elements. Within the range of graptolites, competition was decreased by the extinction of several lineages and decrease in a mutual adaptive overlap. Unfavourable effects of the abiotic environment are revealed even by forms, displaying a population explosion, in the form of their "dwarf habitus", which may be a phenotypic response to local environmental conditions. Examples of this effect are: dwarf forms of

Prist. dubius frequens in various regions after the extinction of the Wenlockian fauna and small dimensions of *Prist. tumescens* and *Saet. leintwardinensis* under the extreme conditions of the British Isles as compared with the dimensions they reach in the Polish Lowland. The factors responsible did not, however, retard the quantitative increase in these species.

These facts seems to be an evidence of the differences between a physiological optimum, determined by favourable conditions of growth and development of particular colonies and a population optimum, determined by such conditions for an increase in the numbers of individual colonies. The significance of these differences has recently been emphasized in particular by Zavadskii (1968). In the aspect of extinction, we are interested in, such phenomena seem to be an evidence that this process has its biocoenotic aspect and cannot be unequivocally explained by a study on the organism-abiotic environment relationships.

b) *Survival of some lineages of the Graptoloidea.* — The differentiating survival of some lineages has been discussed above together with the process of the heterochronous extinction (comp. Pl. IX). In the long run, however, only the most persistent lines survive, such as primarily the pristiograptids of the *dubius* group (*Pristiograptus dubius frequens*, *P. dubius tumescens*), the out-of-the-way *Monoclimacis haupti* (its relationship to the Lower Silurian *Monoclimacis* is not quite certain but possible, comp. Urbanek, 1958) and *Bohemograptus bohemicus tenuis*.

From the formally morphological viewpoint, most taxons referred to above may be considered as nonspecialized[7] ones (lacking a differentiated apertural apparatus). The appearance of the microfusellar tissue in *Bohemograptus* should, however, be considered as a symptom of the morphological specialization which did not lead to the elimitation of the prospective evolutionary possibilities.

In the case of the *dubius* group, we have to do with an exceptionally persistent stock with a very slow rate of evolution (morphological and taxonomic rate). With a considerable degree of probability, we my consider this group of monograptids as an exceptionally eurybiotic one. Its survival is, therefore, a survival of a nonspecialized group. The survival of *Bohemograptus* is a boundary phenomenon, since it cannot be assigned

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[7] The present writer is of the opinion that a certain formalization is necessary for a consistent understanding of the specialization. It should be accepted, after Abel (1929) and Simpson (1950), that a specialization is tantamount to a state opposite to the primitive state and is measured by a degree of deviation from the conditions typical of the ancestors and primitive representatives of the stock. It has, therefore, a relative meaning. Thus defined specialization may be considered in morphological, ecological, adaptive and any other aspect. Understanding specialization as a limitation of prospective evolutionary possibilities, limitation of the range of adaptibility or as an outright "abortive" adaptation introduces to this concept subjective elements or makes certain aspects of the process absolute. The specialization in the sense accepted in the present work may, for instance, lead to a decrease in prospective possibilities or the state of a relative stenobioticity, but these are not necessary consequences of this process (comp. also Urbanek, in Kuźnicki, Urbanek, 1970).

to the category of the survival of specialized or nonspecialized ones. Microfusellar structures represent a symptom of specialization but, in the case of *B. bohem. tenuis,* they do not form a permanent specific character; they only contribute to the polymorphism of the intraspecific variability. This polymorphism probably formed a basis for a considerable source of population variability and consequently was decisive in regard to the evolutionary plasticity, opening a wide range of prospective possibilities in the adaptive and morphogenetic sense.

At any rate, concluding only from the fact of the survival, on the lack of specialization in the surviving forms (e. g., Jaeger, 1959, p. 66, in reference to the survival of *Retiolites nassa*), seems to be an evident misunderstanding, for we know frequent instances of the survival of more specialized forms (Simpson, 1950). A survival of retiolitids more specialized than diplograptids with a continuous periderm, a survival of the Monograptina more specialized than the Diplograptina and a replacement of the primitive *Neodiversograptus* by the more specialized *Linograptus* may be quoted as examples of this phenomenon in the history of graptolites.

Desired seems also to be avoiding such subjective notions as "harmoniously built" and concluding from it on the adaptive perfection (e. g., Jaeger, 1959, p. 66: "sehr harmonisch gebaut" in reference to *Prist. dubius*; "ganz normal und harmonisch gebaut" in reference to *"M." hercyniens, ibidem,* p. 174). Microfusellar structures, clearly "inharmonious", that is, strongly variable and irregular were also clearly advantageous to the survival of *Bohemograptus* (comp. pp. 209).

c) *Appearance of new evolutionary lines.* — The processes of extinction of some lineages and survival without changes of some others were accompanied by the survival with changes of still other lineages. Linograptinae, in whose evolution *Neodiversograptus* was transformed into *Linograptus,* and which on the whole are synchronous with the boundary of the Lower and Upper Ludlovian (Urbanek, 1963), belong to the last-named. Likewise, the survival of *Bohemograptus,* discussed above, belongs in part to the category of survival related to the evolutionary transformation, provided that it remains at the level of a subspecific transformation (origin of *B. b. tenuis* directly below the *leintwardinensis* zone. The process of the splitting of the *B. bohemicus* lineage, occurring in the last-named zone, initiates another, later process of its differentiation which leads to the separation of the main elements of the Upper Ludlovian graptolite fauna, connected with the use of the microfusellar tissue as a new material for forming peridermal structures (the *B. praecornutus—B.* cornutus and *Neolobograptus* n. gen. — *Neocucullograptus* n. gen. lineages).

The formation of new taxonomic groups, characteristic of the Upper Silurian fauna, clearly took place on the basis of autochthonous relics of the Lower Ludlovian fauna (local relics). In this place, no intensive immigration is recorded of strange elements from other geographical areas or elements of a cryptogenic origin (except for "*M.*" *egregius* n. sp.), which probably took place during the formation of the Lower Ludlovian fauna in the area of Europe after a great crisis in the Upper Wenlockian (comp. Urbanek, 1963, p. 196) and with the change in fauna on the boundary of the Upper Ludlovian and post-Ludlovian (ingression of the fauna of "*M.*" *formosus* and reappearance of cryptogenic monograptids with thecae of the "triangulate" and „hooked" type).

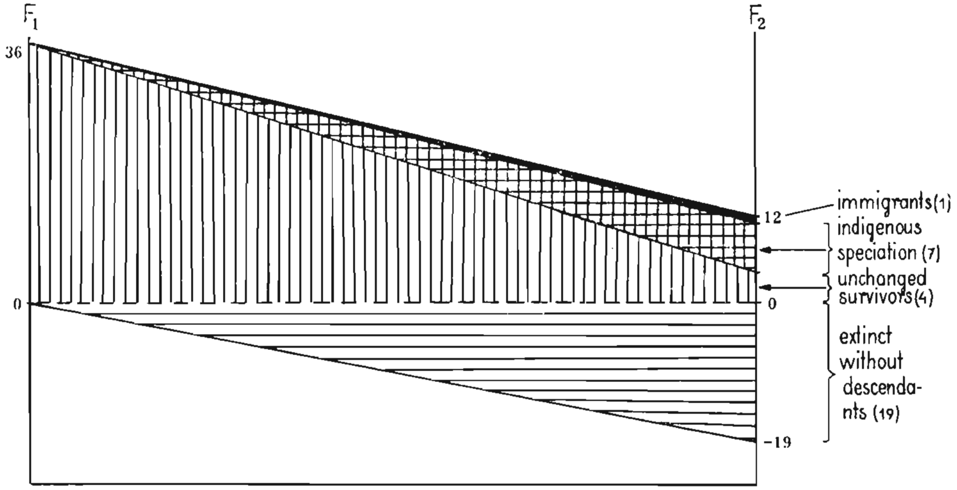

Fig. 5. — Diagram of faunal changes on the boudary of Mielnik Beds and Siedlce Beds and encountered in the Mielnik on the Bug River borehole. F_1 graptolite fauna of the Mielnik Beds, F_2 graptolite fauna of the Siedlce Beds. Numbers indicate total of species, or number of species in particular analytical class (explanation in text).

The data concerning changes in the graptolite fauna on the boundary of the Lower and Upper Ludlovian are synthetically presented in a diagram patterned after the model of changes in fauna, suggested by Fischer (1960). This diagram (Fig. 5) presents a comparison of the specific differentiation of the Lower Ludlovian graptolite fauna (Mielnik Beds) in the Mielnik on the Bug borehole (F_1) with that for the lower part of Siedlce Beds (F_2). While the faunal assemblage of Mielnik Beds (F_1), treated as a whole, consists of 36 species, the analogous assemblage from the lower part of Siedlce Beds (F_2) has only 12 species and, therefore, is nominally poorer by 24 species. Actually, however, only 19 species of F_1 die out without leaving descendants, four species survive without changes, seven new species are developed from indigenous relics as a result of speciation and only one species, which appeared by way of immigration ("*M.*" *egregius* n. sp.), is of the cryptogenic origin.

The arrangement of changes, discussed above, generalizes certain problems and contains some conventional elements. The boundary between faunas F_1 and F_2 is traced in the top of the *leintwardinensis* zone, owing to which *Cucullograptus aversus* passing slightly above has already been assigned to the category of "unchanged survivors". Likewise, *Bohemograptus bohemicus tenuis*, appearing somewhat below this boundary had to have been assigned to the same category although its evolutionary changes (of the subspecific rank) are almost synchronous with the boundary of both faunas and might have also been assigned to the category of "transformed survivors".

The taxonomic analysis of both faunal assemblages is given in the following table (figures denoting the number of species):

Genera	F_1	F_2
Holoretiolites	6	0
Spinograptus	2	0
Plectograptus	1	0
Gothograptus	1	0
"Retiolites"	1	0
"Barrandeograptus"	1	0
Monograptus	1	0
Colonograptus	1	0
Saetograptus	2	0
Neodiversograptus	2	0
Lobograptus	8	0
Cucullograptus	3	1
"Monograptus"	1	1
Monoclimacis	2	1
Pristiograptus	3	1
Bohemograptus	1	3
Neolobograptus	0	1
Neocucullograptus	0	2
Linograptus	0	2
Total	36	12

On the whole, the faunal assemblage of the lower part of Siedlce Beds (F_2) contains only 1/3 of the number of species which make up the fauna of Mielnik Beds (F_1). These proportions are probably distorted by the fact that the Lower Ludlovian is likely to correspond to a longer period than the Upper Ludlovian. Judging by the thickness of corresponding series at Mielnik on the Bug, expressed in a similar facies, which might indicate a fairly similar rate of sedimentation, the ratio of the time of persistence amounted, in round numbers, to 1.5 : 1 (148 m of the thickness of Mielnik Beds as against 109 m of the thickness of the lower member of Siedlce Beds).

The extinction, in the late Lower Ludlovian, of the Retiolitidae, which in regard to their numbers were almost 1/3 of a total number of the species in F_1, was the most dramatic moment which differed both faunal assemblages. On the other hand, one third of the fauna of the lower part of Siedlce Beds (F_2) consists of the relicts of F_1 and about two thirds — the species formed as a result of indigenous speciation. Although the species formed decisively predominate over relicts, they do not compensate even by half for the losses caused by extinction.

The aberrant monograptid "*M.*" *egregius* n. sp. is an only species in the fauna of the lower and middle part of Siedlce Beds which undoubtedly appeared by immigration and which, in addition, is of the cryptogenic origin. A limitary case is, on the other hand, represented by *B. praecornutus* n. sp., whose mechanism of speciation might resemble certain elements of an allopatric speciation (a speciation which takes place outside the area under study, from marginal populations of *B. b. bohemicus*). It has, however, been assigned conventionally to the category of "indigenous speciation", for its parent subspecies (*B. b. bohemicus*) did occur in the area under study.

CHANGES IN THE ABIOTIC AND BIOTIC ENVIRONMENT ON THE BOUNDARY BETWEEN THE LOWER AND UPPER LUDLOVIAN

In Europe, the changes in the graptolite fauna on the boundary between the Lower and Upper Ludlovian, discussed above took place against the background of lithofacial changes and were accompanied by clearly marked changes in the non-graptolite fauna (shelly fauna).

The lithofacial changes have been more accurately recognized in a few regions only, but it should be expected that they were more or less marked in the entire area of Europe. We shall examine them primarily in regard to the area of Poland (a) and also to a few selected regions of Europe (b). Changes in the composition of the non-graptolite fauna, mostly benthos, will be examined separately. This analysis seems to evidence the participation of abiotic and biotic factors in the arisal of crises in the development of the graptolite fauna.

a) *The area of Poland.* — At the end of the Lower Ludlovian or perhaps on the boundary between the Lower and Upper Ludlovian, a distinct change in facial conditions is marked in the areas of the Holy Cross Mountains and Southern Poland (Carpathian Foredeep).

In the Holy Cross Mountains, the clayey sedimentation of the graptolite facies becomes gradually replaced (locally in the *Lobograptus scanicus parascanicus* or *Saet. leintwardinensis* zones) by the sedimentation of a thick greywacke-clayey or conglomeratic series (Wydryszów Beds). They contain only an impoverished and poorly preserved graptolite assemblage (*Pristiograptus, Bohemograptus*). The continuity of sedimentation is maintained only in the northern area of the Holy Cross Mts., whereas in the southern area the sedimentation becomes subject to an early disruption and the area itself — to an emergence (Czarnocki, 1957; Tomczyk, 1956 with a review of earlier literature, 1962, 1968 a, b).

Similar conditions to those of the southern part of the Holy Cross Mts. have been found in the area of the Carpathian Foredeep (Łydka, Siedlecki & Tomczyk, 1963; Tomczyk, 1968 b). A thick greywacke-conglomeratic series, closing the Silurian sedimentary cycle, was deposited at the end of the Lower Ludlovian. According to Tomczyk, these far-reaching changes in the facial regime are a synorogenic symptom of one of the events in the Caledonian orogeny (which is called Cracow phase), whose consequences are particularly strongly marked in the are of Southern Poland (Carpathian Foredeep, S part of the Holy Cross Mts.).

Tomczyk (1964, 1968a) also sees certain analogies between the sedimentation of the greywacke Wydryszów Beds in the Holy Cross Mts. and the sedimentation of Siedlce Beds, in particular in the peri-Baltic area. The inclusions of a coarser sandy material with muscovite in the lower part of Siedlce Beds are interpreted by this author as an analogy to the deposits of the Wydryszów Beds (Lębork and Bytów boreholes) and considered as synorogenic deposits of the Cracow phase, connected with an uplift of continental areas in the neighbourhood.

On the other hand, in the area of the Podlasie Syneclize (a depression of the crystalline substratum of the East-European Platform), the lithofacial changes on the boundary between the Lower and Upper Ludlovian are marked to a limited extent only or even are not manifested at all (Mielnik on the Bug). Nevertheless, a far-reaching change in the composition of the graptolite fauna does take place on the boundary referred to above. Judging by palaeogeographical maps reproducing facial conditions of the Silurian in the area of the western margin of the pre-Cambrian platform (Tomczyk, 1963, Figs. 5 and 6), only small changes in the range of the basin and distribution of facies take place on the boundary between Mielnik and Siedlce beds. Teller (1969, Figs. 3 and 4), who is of the opinion that on the boundary of the Lower and Upper Ludlovian the Caledonian folding (Ardennian phase) took place locally in the marginal area of the platform, ascertains that resulting palaeogeographical and facial changes were of a limited character.

b) *Other European areas.* — Similar lithofacial changes have been recorded in many other areas occupied by the Upper Silurian basin. In many cases, the problem involved is the replacement of the clayey by carbonate-calcareous sedimentation, sometimes represented by deposits of a considerable thickness. In the area of Barrandian, an increase in carbonate sedimentation (beginning with the upper part of the *Lobograptus scanicus parascanicus* zone) is observed against a background of a generally considerable differentiation in lithofacial conditions on the boundary of the Upper and

Lower Ludlovian. Trilobite-brachiopod limestones, frequently containing many corals and orthoconic nautiloids (in earlier literature called "Orthoceras limestones"; Horný, 1958, 1962) are formed in this area. An ingression of a new benthonic fauna (comp. p. 232) is connected with the beginning of the sedimentation of these limestones.

In the area of Thuringia, the boundary of the Lower and Upper Ludlovian is marked by the sedimentation of a thick series of ochre limestones ("Ockerkalk"), whose beginning probably falls within the *parascanicus* zone and termination within or below the *Prist. transgrediens* zone. In this area, the lithofacies mentioned above in principle interrupts the development of graptolites (Jaeger, 1959, 1962, 1964) and its beginning falls in the upper part of the Lower Ludlovian. Local changes in lithofacies, expressed by patches of shales, cause transitory recurrences of the graptolite fauna.

In Scania, the Lower Ludlovian is represented regionally by what is known as "*Colonus* shale", a traditional but rather not very accurate term designating a series in which the *nilssoni* and *scanicus* (probably *L. scanicus parascanicus*) zones were recognized. Above the last-named zone, a thick series of Öved-Ramsåsa is deposited, composed of limestones, variegated shales and sandstones (Regnéll, Hede, 1960). According to Martinsson (1967), the lower member of this series, whose sedimentation is marked by a distinct change in lithofacies, corresponds to an upper part of Leintwardine Beds in Great Britain. Thus, this facial change also displays a distinct coincidence with the boundary between the Lower and Upper Ludlovian.

Distinct facial changes (Holland & Lawson, 1963; Holland, Lawson & Walmsley, 1963) have also been found in the typically Ludlovian area of the British Isles (Welsh Borderland, Central Wales). A graptolite facies at first predominant in both the shelf and basin facies, during the period of the Eltonian stage (the *vulgaris* through *scanicus* zones in a previous, broad sense), is gradually replaced by other lithofacies. In the shelf area, there begins the predomination of turbidite and laminated siltstone facies, in the shelf area, *tumescens* siltstone facies are temporarily deposited to be replaced by strophomenid siltstone facies and finally, by the sedimentation of massive limestones, frequently with beds of *Conchidium* (Aymestrey Limestone). The Upper Ludlovian (Whitcliffian) is marked by an equalization of facial conditions in both areas, the sediments being expressed by calcareous siltstone facies.

Analyzing the character of lithofacial changes which take place on the boundary of the Lower and Upper Ludlovian in Poland and in a few other European areas, we find that 1) these changes are not completely synchronous and 2) they are of the fairly variable nature. The beginning of the changes, which cause the disappearance of the graptolite facies in a given area, is somewhat diachronous and is manifested at the earliest in the area of the British Isles. Local differences occur even within a given area, but on the whole the changes begin to manifest themselves within or above the *L. scanicus parascanicus* zone. Most frequently, the sedimentation of clayey graptolite shales is replaced by a carbonate-calcareous sedimentation, but sometimes it may be replaced by the deposition of clastic rocks (greywackes in Poland or claystones in the basin area of Welsh Borderland, Central Wales). The carbonate-calcareous sedimentation may also occur as an episode which leads to a sandy sedimentation (Scania).

If we cling to the correct opinion that the lithofacial changes remain in a definite, although sometimes indistinguishable, relationship to physico-geographical conditions, then a relative variability of these changes in particular areas seems to be an evidence of the heterogenity of causes involved in the changes. Even the carbonate-calcareous sedimentation does not constitute a uniform change in facial conditions, but itself is a complex analytical category. It is beyond any doubt that the conditions of forming ochre limestones (Ockerkalk, Thuringia) were different than those of, for instance, the formation of limestones with *Conchidium* (e. g., Aymestrery Limestone, Ludlow District).

Thus, although it is unquestionable that a general coincidence of lithofacial changes with those in the graptolite fauna on the boundary of the Lower and Upper Ludlovian is not accidental, 1) it is difficult to establish definite physical elements of a concrete configuration of the environmental conditions, responsible for particular changes and 2) the configurations of these factors seem to be in particular cases so varying that it is impossible to distinguish any universal, repeatable element of these configurations which would have occurred in each case studied.

If, therefore, we consider the lithofacial changes as reflecting definite changes in the environment (primarily of an abiotic environment; changes in the hydrological regime and physico-geographical conditions), the acceptance of the last-named conclusion (2) leads to the rejection of the thesis on the possibility of existence of one, definite ("universal") abiotic factor responsible for the occurrence, in the entire area under study, of the changes in the graptolite fauna here discussed. In geology, there is a tradition of referring to diastrophism (in this case, Caledonian movements) as an ultimate factor which controls the environmental conditions. This view, in principle quite sound, cannot justify the opinion that diastrophism represents, therefore, a "universal" factor of faunal crises. The Caledonian movements could not be a direct cause of the extinction of individual lineages of graptolites, to say nothing of the fact that they make up a complex process, manifested in various forms of diastrophism. In particular areas, these movements created various environmental conditions, which not always were comparable and repeatable. Using a somewhat paradoxical phrase, we may say that the factor of change itself was here an only repeatable element, while the nature of these changes was in each case slightly different. Thus, the element of change in the abiotic environment was a common element of various configurations in this environment, although the last-named change is manifested by a complex of factors and conditions, varying in each case.

The analysis of changes in the abiotic environment, whose certain index is represented by lithofacial changes, leads, therefore, to the development of the thesis on a relative heterogenity of these changes. This heterogenity reduces the share of diastrophism primarily to the introduction of an element of change in the abiotic environment, expressed regionally in various configurations of environmental factors and ecosystems, transmitted in the chain of dependencies to particular local populations. The existence of the ecological transmission of such type is confirmed by the fact that even in the areas in which the changes in lithofacies are not marked at all, or marked very slightly, on the boundary between the Lower and Upper Ludovian (Polish Lowland), a profound transformation takes place in biotic conditions (comp. pp. 226). It is not unlikely that changes in the abiotic environment generated by diastrophic movements, were primarily reflected in benthos and only later exerted their influence on planktonic-pelagic assemblages.

c) *Changes in the nongraptolite fauna on the boundary of the Lower and Upper Ludlovian.* — It is beyond any doubt that changes in the abiotic environment had to be accompanied by changes in the biotic conditions. Proofs for such a state of matters concern primarily the benthonic fauna.

In the mid-Bohemian Silurian, an "invasion of the fauna of *Encrinurus*" (Horný, 1962, pp. 903—904) is one of the turning points, marking the beginning of a new stage in the development of fauna. The late invasion of the trilobites of the genus *Encrinurus* of the Barrandian area (*scanicus* zone sensu lato; probably the middle part of the "Cucullograptid band" sensu Urbanek, 1966, while *Encrinurus* has already been known from the Wenlockian of Scandinavia and the British Isles) is accompanied by a many-sided change in the assemblages of benthonic fauna, primarily by an explosive development of some genera of trilobites and an extinction of some others.

The mechanism of ingression of the *Encrinurus* fauna is not accurately known. Horný (1962, p. 904) suggests changes in climate and currents or in biological competition as causes of this phenomenon. Judging from Jaeger's (1962, p. 116) reasoning, he assumes that this mechanism was in fact similar to an ecological invasion, connected with the disappearance of appropriate isolating barriers.

Not less striking phenomenon which, during an approximately the same period, occurred in the area of Polish Lowland, was the appearance and abundant occurrence of trilobites of the genus *Spathacalymene* (Tomczykowa & Tomczyk, 1962; Tomczykowa, 1970). The development of these triolobites marks a distinct episode in the development of the vagile benthos (*Cucullograptus hemiaversus* zone — the lower part of *Cucullogr. aversus* zone = *Saet. leintwardinensis* zone). Their occurrence is related to the marly-calcareous facies in the area of NE Poland. According to Tomczykowa (1970), *Spathacalymene*, a specialized representative of Calymenidae known from the Middle Silurian of North America and England and which appears in the area of Poland at the end of the Lower Ludlovian, occurs abundantly and differentiates into at least three species.

In the shelf area of the British Ludlovian, there occur changes in the benthonic fauna, which confirm its gradual impoverishment (Lawson, 1960). Three faunal assemblages may be distinguished which indicate a gradual, local extinction of the benthonic fauna (or, more generally, of the shelly fauna) and a "new" fauna of Whitcliffe Beds (Lawson, 1960; Holland & Lawson, 1963). In view of the extinction of species which is quicker than the appearance of new ones, the last-named fauna is in fact characterized by a pronounced poverty, especially in brachiopods, while molluscs and ostracods play a more important role. It is also in the basin area that the disappearance of fauna predominates.

Discussing the causes of the phenomena of the disappearance of fauna, Lawson (1960) states: "The conclusion seems irresistible that this successive disappearance of faunas was related to the main phase of the Caledonian orogeny. Even the graptolites, the fossils of the Silurian least dependent on environment, made an early escape from the British area and the abundant spinose monograptids may reflect a final desperate attempt at adaptation to conditions which were growing increasingly uncongenial. What such conditions were which could trouble even the graptolites is not easy to decide. In Central Europe, by contrast, there was a vigorous new radiation of the graptolites ranging through the Upper Ludlovian and perhaps into Geddinian; here the spinose forms are comparatively unimportant (p. 123)."

Although the material, concerning changes in the nongraptolite fauna on the boundary between the Lower and Upper Ludlovian, is rather fragmentary, it strikes by the variety of the picture it presents. In the British Isles, changes in fauna lead to its steady impoverishment and disappearance, the extinction being predominant over differentiation and immigration. In Central Europe, there takes place a profound exchange of the assemblages and the extinction is compensated or prevailed by immigration and differentiation. The last-named is based in various regions on various faunal elements, producing local radiation. It is beyond any doubt that a variable composition of these assemblages makes up an evidence of different biocoenotic conditions in particular regions.

In all cases, changes in the graptolite fauna are preceded or accompanied by far-reaching changes in the assemblages of benthonic fauna.

The changes in benthos seem to be fairly closely related to the changes in a physico-geographical environment, whose general geological background has been discussed above. In the chain of ecological dependencies, these changes also seem to exert an influence on a pelagic and planktonic fauna, including graptolites.

The present state of knowledge of the Upper Silurian microflora does not allow one for a clear and precise statement concerning the changes which took place in microplankton and which were related to other changes in the organic world. Richardson's and Lister's work (1969) on changes in the Upper Silurian and Lower Devonian assemblages of sporomorphs from classical areas of England and Wales contains a rather scant observations material. These authors do not find, however, any major transformations in the composition of the Ludlovian sporomorphs. Those, which appear in the Lower Ludlovian, survive the boundary of the Lower and Upper member and a more significant change is recorded only on the boundary with the Downtonian.

The phenomenon itself of the differentiating extinction of graptolites also belongs, however, to changes in the planktonic and drifted fauna which could exert their influence on changes in the fauna of graptolites. This phenomenon has traditionally been examined only as extinction of some lines and survival of some others and discussed from the viewpoint of the survival of more eurybiotic (or, less specialized) and extinction of more stenobiotic (or, more specialized) stocks. This aspect of the problem does not, however, explain the entire complexity of the phenomenon of the heterochronous and differentiating extinction. The previously presented analysis of changes in the graptolite faunas on the boundary between the Lower and Upper Ludlovian indicates that the extinction of some species is accompanied not only by the survival but also even by a mass development of some others. A complex change in the conditions of an environment (abiotic and biotic one) was not ,therefore, to an equal extent disadvantageous to individual species and represented a background of the biological competition within the range of the graptolites themselves. The extinction of definite species of graptolites did not, therefore, take place without a competition on the part of other species which, under new environmental conditions gained an adaptative superiority and displayed a quantitative expansion.

The phenomenon of a quantitative proliferation of surviving species, which takes place only after the extinction of other elements in a given assemblage and which is frequently recorded in stratigraphy, is mostly interpreted as filling up of emptied ecological niches, whereas it may be an apparent phenomenon, connected with certain regularities determining the properties of a fossil record. As a result of a significant incompleteness of this record, caused by taphonomic (biostratonomic) regularities, such as, for instance, a "rule of small numbers", local character of observations (studies on some, definite sections only), as well as a biased selection of observation data, the changes in the dynamics of the frequency of fossil species acquire the nature of apparently abrupt changes, markedly separated in time from each other. In the concrete instance of Mielnik on the Bug, the extinction of particular elements of the Lower Ludlovian fauna, is finally compensated by an exuberant development of the *Bohemograptus* populations. It is as early as the upper part of the *Cucullograptus aversus* zone that *Bohemograptus* is more frequent than in lower zones, but its truly mass occurrence is recorded only after the extinction of the last elements characteristic of the Lower Ludlovian (*Cucullograptus*). Such is the picture observed in a single borehole ("nondimensionally") whereas actually, this was probably a gradual, although relatively rapid shift of a quantitative equilibrium.

Judging from the fauna, contained in erratic boulders, different conditions occurred in the Baltic area. This fauna lacks the most specialized terminal form, that is, *Cucullograptus aversus rostratus* (Urbanek, 1966, pp. 517—518). It should be expected that this species disappears in this area earlier than in the Polish Lowland. At the same time, erratic boulders frequently contain abundant *Bohemograptus bohemicus tenuis* which occurs almost monospecifically. On the other hand, no *Bohemograptus praecornutus* n. sp., which together with *B. bohemicus tenuis* participates in the proliferation of *Bohemograptus* after the extinction of *Cucullograptus* in the Polish Lowland, is known from erratic boulders. It seems, therefore, that the proliferation of *Bohemograptus* in these two areas was also somewhat heterochronous which had to be related with an identically heterochronous disappearance of *Cucullograptus* which controlled this process. In the Baltic area, this took place earlier, that is, prior to the appearance of *B. praecornutus* n. sp. and in the area of the Polish Lowland — later, that is, after the appearance of this species. This phenomenon is an evidence of biocoenotic and competitive conditions determining the process.

These considerations lead, therefore, to the conclusion that the changes in an abiotic environment, although an important element of a general, complex cause of the change in the graptolite fauna on the boundary between the Lower and Upper Ludlovian, cannot be understood as a sufficient factor or as an outright "mechanical" cause of the extinction of some part of this fauna. The changes in an abiotic environment were only a general background and represented the conditions determining a more complex ecological situation within a biotic environment, which probably was a final factor directly determining the extinction. The process of a differentiating extinction of a given group was probably inseparably connected with a competition between its individual taxons, which was due to their varying capabilities of adaptation to the changing environmental conditions. A good deal of thought should be given to the question to what a degree these conclusions may be generalized and applied to a complex problem of the factors which caused the extinction of the Graptoloidea.

THE PROBLEM OF THE EXTINCTION OF THE GRAPTOLOIDEA

The credit for suggesting a certain general, working hypothesis on the extinction of the Graptoloidea has been deserved by Jaeger (1959). Its main suggestions are as follows:

1) Changes in the environment were direct causes of faunal crises and the extinction of the Graptoloidea. The environment is understood by Jaeger as an abiotic environment determined by, e. g., temperature and climate, conditions of currents, salinity, water oxidation, physico-geographical changes such as, situation of bariers, extent of connection between particular basins, relief of the bottom, bathymetric conditions, etc. Jaeger (1959, p. 175) states: "Umweltveränderungen, und zwar höchstwarscheinlich allein ihre anorganischen Faktoren, sind die primären, zweifellos sehr komplexen Ursachen des Rückganges und schliesslich des Aussterbens der Graptolithen anzusehen."

2) The changes in abiotic environment referred to above were ultimately evoked by geological, namely, tectogenic factors, which in this case were the Caledonian movements: "man kann folgerichtig behaupten, die kaledonische Faltung führte zum Aussterben der Graptolithen, und zum weiteren Verbreitung und Blüte der Tentaculiten" (Jaeger, 1959, p. 174).

3) Judging from Jaeger's reasoning, the role of biotic factors was insignificant. Planktonic tentaculids, which seem to replace the Graptoloidea, in fact only fill a previously emptied ecological niche. "Das heisst, die ökoligische Ablösung der Graptolithen von der Tentaculiten erfolgte warscheinlich mehr passiv, die Graptolithen wurden durch anorganische Kräfte aus der Erdgeschichte gedrängt" (Jaeger, 1959, p. 174).

4) The process of the extinction of graptolites, which were probably a stenobiotic group, was gradual and connected with a slow decrease in area, resulting from unfavourable climatic conditions (Jaeger, 1959, pp. 175—176).

Regarding the last-named postulate, Jaeger's standpoint was not, however, completely consistent. He was of the opinion that the last Graptoloidea were represented by the fauna of the "*M.*" *hercynicus* zone. He maintained this view both when this species was believed to have a rather limited geographical distribution (Jaeger, 1959) and later, when it has already been found that it makes up a widely distributed faunal element (Jaeger, 1962, 1964). In the latter case, the extinction of the last Graptoloidea would have taken place "right along a ruler," as it was correctly termed in other contexts by Ruzhencev and Sarytscheva (1965) — that is, rather abruptly.

In fact, very similar views on the causes of the extinction of the Graptoloidea (and all graptolites) were expressed by Obut (1964, p. 298), who attributes them to tectonic movements. According to this author, the resulting changes in physicogeographical conditions exerted their influence on changes in facial conditions and caused a gradual decrease in areas suitable for the life of graptolites.

The present writer does not intend either to classify Jaeger's and Obut's views on the extinction of the Graptoloidea as one of the categories that may be distinguished (Davitashvili, 1969, assigns them to the group of what is called "tectonic hypotheses"), or to evaluate them from the viewpoint of a definite evolutionary causality, postulated by them. Of interest is, however, the comparison of these hypotheses with a picture of actual changes in the faunas and extinction of this group.

The dependence of the Graptoloidea on the conditions of an abiotic environment is indubitable, although their relationship to the lithofacies of dark clayey sediments is not as close as frequently accepted (Bulman, 1955; Berry, 1962). The lithofacies as an index of primarily bottom conditions of a basin cannot unequivocally determine an environment of the planktonic and probably pelagic Graptoloidea (Urbanek, 1960; Berry, 1962; Bulman, 1964). They might inhabit the upper parts of basins with various bottom conditions and various sedimentation, to say nothing of the fact that frequently graptolites were probably drifted by storms in their lifetime or post mortem (as a necroplankton) and deposited in sediments which served as a taphotop only (Urbanek, 1960; Berry, 1962). In this case, fossil sediments are of a yet smaller significance as an index of physical conditions of the graptoloidean biotope. Sometimes, however, an amazing dependence of the occurrence of planktonic graptolites on lithofacies is recorded in point of fact as, for instance, in the case of intercalations of black shales in thick series of carbonate rocks, accompanied by a recurrence of the graptolite lithofacies (e. g., patches of black shales with graptolites in the Ockerkalk series, Jaeger, 1962; the same phenomenon in a series of Branik limestones of the Upper Pragian, Bouček, 1966). A similar phenomenon has also been recorded with the transformation of light or variegated Żdanów shales in the Sudeten Mts. into dark, graptolite shales (Teller, 1960).

Perhaps, such recurrences of the lithofacies of dark claystones, closely correlated with the recurrences of the graptolite biofacies should be interpreted as a restoration of conditions favourable to the preservation of graptolite remains in a reductive environment of fine-grained bottom sediments rather, than as a restoration of life conditions particularly favourable to the Graptoloidea in the upper layers of a basin.

The Graptoloidea display a definite relation to geological-structural conditions, the fullest sequences of the graptolite faunas being known from miogeosynclinal areas or from areas transitional between mio- and eugenosynclinal ones. The chances are, however, that these areas were usually marked by broad connections with oceanic areas (Berry, 1962) and that the graptolites were in fact an oceanic plankton (Bulman, 1964). The evolution of facial conditions in particular geosynclines, although — as a result of definite tectonic cycles — summing up to represent events with a very wide extent, is not sufficient in itself to explain changes in the graptolite fauna on the world scale. It requires an adoption of a mechanism of transmission of these regional changes and, therefore, we have previously sought to show that biotic conditions might to a considerable extent be such a mechanism. This is the reason why faunal changes (e. g., extinction) take place also in the areas in which facial changes are not marked (comp. pp. 229). To be sure, we may indicate the factors of an abiotic environment whose activity is spread out over considerable distances due to the physical nature of the factor itself. Temperature, "possibly the most important of all physical factors connected with the geographical distribution of pelagic organisms" is assigned by Bulman (1964) to such factors. On the other hand, certain facts are indicative of a relationship between graptolites and a warm moderate and tropical climate. No concrete data are, however, available which might be an evidence of a climatic evolution on the boundary of the Silurian and Devonian with a world-wide range and consisting in the cooling-down of the climate. According to Schwarzbach (1963), the entire Europe was, during the Silurian and Devonian, within the range of a hot or warm climate. On the Silurian-Devonian boundary, the Caledonian orogeny might cause local changes in the distribution of thermal gradients. There is also evidence of a certain aridization, which, however, could not greatly affect the marine plankton.

Many authors (Newell, 1952, 1956; Ruzhencev & Sarytscheva 1965; Ginsburg, 1964, comp. also Rhodes, 1967) have recently concluded that extensive regressions were the most common and repeatable abiotic factor of a mass extinction of marine faunas. The occurrence of this factor, as rightly pointed out by Ruzhencev and Sarytscheva (*ibidem*), may, however, be hardly considered as the only and immediate cause of extinction, being probably only a background for especially severe competition and strong selection pressures.

Regarding the whole group of graptoloids, the withdrawal of the epicontinental seas, as a result of young-Caledonian movements, had hardly a very drastic direct effect on their fate, if we accept that they were ocean dwellers, with enough space, which remained essentially stable, for their further exuberant development. More probable seems to be an indirect influence due to changes in ecosystems started first on continental shelves involved in diastrophic changes, and then transformed into chains of modified biotic relations (plankton productivity ?; competition from new adaptive zones formed in shallow-shelf seas ?). There is, however, ample evidence to support the view that the rise and fall of organic phyla were neither determined entirely by factors of external environment, nor shaped by internal factors of the organism itself, but that their main determinant consisted in an interaction between the organism and its biotic and abiotic environment (Simpson, 1953; Mayer, 1963).

On this basis the present writer does not share Jaeger's (1959) view on a monopoly or an absolute predominance of abiotic factors in the changes which occurred in the graptolite faunas and in the extinction of the Graptoloidea. These causes should be understood in a complex manner, as a set of abiotic and biotic conditions of the environment. Probably, these or other changes in the abiotic environment always or almost always accompanied changes in the graptolite faunas, but the appearance of new elements of ecosystems and biocoenoses, or an evolutionary progress of already existing ones, introduce an equally significant factor to the changes in the environment. The mass appearance of planktonic tentaculites in the "*M.*" *hercynicus* zone in various regions of the world was such an element of a biotic environment which probably strongly affected the final stage of the history of the Graptoloidea. The opinion that the thin-shelled Dacryoconarida lived a planktonic or nectopelagic life seems to be sufficiently founded (Bouček, 1964, pp. 8 and 37, 156—157; Fischer, 1962, pp. 50—51; also Lyashenko, 1959). The occurrence of graptolite-tentaculite associations is indicative of a possibility of a rather "immediate replacement", and a similarity in the adaptive type (microphagy, planktonic mode of life) and character of occurrence in time (the more abundant tentaculites, the less numerous were graptolites) seem to be an evidence of a process of ecological substitution of both groups and, altogether, of an "active" replacement — by way of competition — of the Graptoloidea by planktonic tentaculites. Modern views on the ecological mechanisms of the "replacement" (Sloan & Van Valen, 1968) require a considerably smaller similarity in adaptive types for the arisal of the conditions of competition than the earlier ones (Simpson, 1953).

Planktonic tentaculites appear, however, too late to be responsible for earlier crises in graptolite faunas. The last-named might be connected with their earlier groups, which represented mobile benthonic or nectobenthonic forms whose range of adaptability partly overlapped that in the Graptoloidea. The decline of the Graptoloidea in shallow miogeosynclinal areas might, therefore, be partly connected with disadvantageous changes in abiotic environment and partly with the competition from the adaptive zone which was represented by necto-benthonic tentaculites.

As a matter of fact, a similar competition might take place on the part of Eurypterida, Pisces (in particular Acanthodii and perhaps also Actinopterygii). In the adjoining Baltic area, Acanthodii appear for the first time in the upper part of the Kaugatuma formation which corresponds approximately to the upper part of Siedlce Beds (Obruchev, Karatayuté-Talimaa, 1967), while Teleostomi (probably Actinoperygii) occur in this area in the Ohesaare formation (Gross, 1969), which corresponds approximately to the upper part of the post-Ludlovian (Podlasian or marine Downtonian).

Finally, soft-bodied organisms which, like some of the Recent *Solenogastres* (= *Aplacophora*) feed on the coelenterates, might also feed on colonies of the Graptoloidea destroying tissues of zooids and playing the role of a competitive factor.

Likevise, the soft-bodied plankton, particularly planktonic larvae, including the larvae of benthonic animals, might play this role in relation to graptolites. Soft-bodied organisms always make up parts of biocoenoses and so, such "palaeontological ghost-groups" might also contribute to the extinction of the Graptoloidea.

As a matter of fact, an identical view has already earlier been expressed by the present writer (Urbanek, 1960, pp. 198—201) in reference to the causes of evolutionary changes in graptolites and with emphasis put on the following two facts: 1) These changes take place intensely, over periods which are long geologically and when the lithofacial conditions give testimony to relatively very stable abiotic conditions, equalized over extensive areas (e. g., in the Wenlockian). 2) Palaeontological data indicate on the whole that in many cases, evolutionary changes might make up a direct response to the changes in an abiotic environment, while in some other cases, they took place under stable conditions of this environment and might make up mostly an expression of changes in biotic conditions. This view does not, therefore, contradict the important and sometimes maybe even decisive influence of changes in abiotic conditions, but it calles in question other views according to which these changes participate in each of the individual cases (Urbanek, 1960, p. 199). Since the factors responsible for the extinction of organic stocks do not differ specifically from those which also determine their development, the remarks presented above also concern the extinction of the graptolites. They seem to be the more strongly justified as recently the cases have also been recognized of profound and relatively rapid changes in entire graptolite faunas and not only of evolutionary changes in particular phylogenetic lineages, taking place under comparatively stable abiotic conditions (at least within the range which is evidenced by lithofacial conditions).

The acceptance of a complex cause of the extinction as a whole of environmental conditions (abiotic and biotic) does not, however, constitute a satisfactory theory of extinction. First of all, thus formulated theory does not differ at all from the theory of evolutionary factors, as rightly observed by Simpson (1953), and consequently does not explain why in each of these cases the results are so different (development or extinction). For, each non-catastrophic change in environment is accompanied by a potential possibility of adaptation to new conditions and of survival through these changes. Significant to the theory of extinction would, therefore, be the determination of the causes which specifically preclude an adaptive response of a given evolutionary lineage or taxonomic group. At present, the formulation of such a theory of extinction of the Graptoloidea is in fact impossible. On the whole, thus understood factors of the extinction of the Graptoloidea do not seem to differ fundamentally from the factors postulated for other organisms. Darlington (1939) maintains that the extinction is caused by a lag in the adaptive response of organisms to changes in the environment. The mechanisms of this process may consist in both genetic (lack of appropriate mutations, difficulties of an appropriately rapid mobilization of variability) and partly phenogenetic or morphogenetic (lack of appropriate modifications and of the polymorphism, organization of an epigenotype which makes difficult an appropriate phenotypical manifestation of the mutation) factors. It is clear from these considerations that the causes of extinction do not lie in the environment itself, even if it is understood as a complex, but they result from the conditions which arise between the organism and its complex environment[8] (Simpson, 1953).

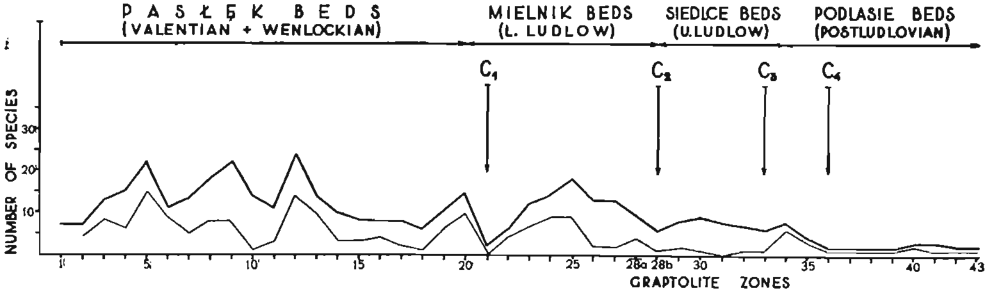

Fig. 6. — Time-frequency curve for Silurian graptoloids on the area of Poland. Thick line = total frequency, thin line = first appearances, C_1—C_4 indicates successive crises in development of graptolite fauna, 28*a*—28*b* lower and upper part of *aversus* zone distinguished to show decrease of differentiation in its upper part (quantitative data based largely on Teller, 1969, partly revised, stratigraphic scheme based on subdivision of Polish Platformian Silurian according to Tomczyk, 1962).

Obviously, it is impossible to discover these mechanisms in the Graptoloidea, but the picture of their evolution may be accurately interpreted from this point of view. Diagram on Fig. 6, presents the dynamics of the

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[8] We do not examine the third alternative, that is, that the extinction depends on the organism itself (autogenic theories of extinction), since we do not consider it to be justified by the history of the graptolites. The Lower Devonian Graptoloidea still represented morphologically a number of types among which did not include particularly specialized ones.

phylogenetic development of the Graptoloidea during the Silurian on the area of Poland by means of a frequency distribution curve. The trace of curves representing a total number of species living in a given zone and a number of newly formed species, allows one to distinguish the following two main stages: 1) Valentian-Wenlockian, 2) Ludlovian-Lower Devonian. In the first stage, the extinction is compensated by differentiation and the development takes place without faunal crises. The adaptive response of the Graptoloidea may be considered to remain adequate to changes in the environment. In the Upper Silurian, the occurrence is observed of several crises, after which there takes place a next radiation or immigration (or else, both take part in the differentiation). On the whole, after a successive crisis, the differentiation does not reach the previous degree, which may be caused by the fact that the periods between particular crises become progressively shorter and shorter. The Silurian Graptoloidea (mostly Monograptina) behave, therefore, as a regressive group as understood in a sense, introduced by Müller (1961). This picture of evolution differs just enough from the earlier stage to suggest the occurrence of organism-environment relations varying qualitatively. The adaptive response of the Graptoloidea becomes less and less adequate to changes in the environment and as we may suppose, slower and slower, thus producing a characteristic "lag". The progressively increasing evolutionary lag causes a gradual biological regress of a group, that is, a decrease in its taxonomic differentiation and in general area.

This picture of the decline of Graptoloidea in the Upper Silurian, and especially in the Lower Devonian, agrees rather well with the views of A. N. Severtzoff (1949) and S. A. Severtzoff (1951), who considered extinction as a gradual process of biological regress caused by evolutionary failure, and as a process directly opposite to biological progress connected with an evolutionary success of the group.

It is only the acceptance of the theory on the arisal of conditions making impossible an adaptive response of the Graptoloidea which allows one to understand to a certain extent why the tectonic movements of the Taconian phase did not exert a delaying influence on their development, while the young-Caledonian movements did result in faunal crises.

These factors are so unspecific that it is difficult to consider them as a hypothesis of the extinction of the Graptoloidea. A mechanism involved in this process is, on the other hand, so general that the present writer suggests to replace Darlington's term "lag" by a more general term of "an evolutionary hysteresis" (Greek *hysteresis* = delay, lag), suggesting appropriate analogies to physical phenomena. The last-named term, more international in character, is the more justified as now, more than in the past, we tend to attach a greater importance to epigenetic and morphogenetic factors as agents of the lagged adaptive response (Mayr, 1963, pp. 612—615).

PROBLEM OF DISCRIMINATING TEMPORAL SUBSPECIES IN THE *BOHEMOGRAPTUS BOHEMICUS* LINEAGE

Classification of persistent lineages, displaying only limited sequential differences, and still more limited (or not at all) spatial differentiation is a rather difficult task faced by a palaeontologist. In general terms it may be described as a subdivision of a single lineage changing into a temporal species or subspecies. The division of lineages into successional taxa is based mainly on a criterion of range overlap and on a subsequent estimation of differences between intergrading populations, observed from the standpoint of certain conventional "rules", accepted for taxonomic interpretation (Simpson, 1961, pp. 163—176). Graptolitologists face such situations, although rather infrequently. *Pristiograptus dubius* (Suess) and *Bohemograptus bohemicus* (Barr.) are concrete examples of the Upper Silurian graptolite fauna.

The former species is extremely long-ranged (uppermost Valentian-lowermost Přidolian (= Postludlovian)) and displays very limited morphological changes throughout its range of occurrence. Nevertheless, in particular horizons or localities, *Prist. dubius* seems to reveal certain peculiarities, which were used as a basis for the distinction of a number of subspecies. Some of them were recognized rather as temporal subspecies (chronosubspecies, palaeosubspecies, segmental subspecies): *Pristograptus dubius dubius* (Suess, 1851); *Prist. dubius frequens* Jaekel, 1889 (= *Prist. dubius ludlovensis* (Bouček, 1936)); *Prist. dubius tumescens* (Wood, 1900), perhaps also *Prist. jaegeri* (Holland, Rickards & Warren, 1969). Some others were recognized as contemporaneous morphological subspecies, based on a certain differentiation of a lineage (branching, offshoots of main line?): *Prist. dubius latus* (Bouček, 1932), or on both certain spatial and temporal influences as, e. g. *Prist. dubius thuringicus* (Jaeger, 1959). Most probably, certain other Upper Silurian pristiograptids from *dubius*-group, recognized by some author (mainly in Bohemia) as separate species, present at most only subspecies of *Prist. dubius*. Most likely, however, the majority of them are only subjectively selected groups of intra-populationary variants, or preservational forms.

The long history of *Prist. dubius*, connected with a number of abundance-peaks (acme, episodes of populationary explosions, in particular regions most probably heterochronic; comp. Bouček, 1953; Tomczyk, 1960, 1962; Jaeger, 1964), doubtlessly resulted in definite microevolutionary changes of a certain taxonomic significance. Morphological differences in *Prist. dubius* populations from particular horizons (chronodemes) are, however, small and quantitative in character. It seems doubtless, therefore, that the erection of such taxa should be adequately supported by a certain amount of quantitative data and their elementary analysis. Nevertheless, in the majority of cases, the taxa were recognized without a satisfactory analysis of quantitative characters and there is little hope that they could be proved by critical examination. The taxonomical procedure, in regard to persistent lineages described above, seems therefore to be unacceptable for the purposes of future application.

Although not so extreme as in the case of *Prist. dubius*-lineage, the taxonomy of *Bohemograptus bohemicus* group is also unsatisfactory.

The forms in question belong to a stem of *Bohemograptus* (occurrence: *Neodiv. nilssoni* — *Neocuc. kozlowskii* zone, probably to the bottom of "*Monograptus*" *ultimus* zone; the earlier occurrences requiring more evidence) geographically widely distributed, persistent and conservative. In the area of the Central and Eastern Europe, the following taxa, bellonging to *B. bohemicus* group, were recognized so far: [9] *B. b. bohemicus* (Barrande, 1850), *B. b. tenuis* (Bouček, 1936), *Monograptus rarus* Perner, 1899, *M. zarizelliensis* Haberfelner, 1936.

The last two species were already recognized as junior synonyms of *B. b. bohemicus* (Bouček, 1936, p. 2; Přibyl, 1948, p. 68; for *M. rarus* Perner; and Přibyl, 1948, p. 68, for *M. zarizelliensis* Haberfelner). Both were erected on the basis of only few specimens and it is little doubt that they represent a merely arbitrarily selected group of variants not very significant morphologically and stratigraphically. Views of Bouček (1936) and Přibyl (1948) on the status of the two forms are, therefore, here confirmed.

The subdivision of *B. bohemicus* into two subspecies deserves, however, more attention. From Bouček's (1936, pp. 1—2) brief considerations it seems that this distinction has been based both on morphological and stratigraphical reasons tabulated below:

I. *B. b. bohemicus*
1. morphological characteristics:
   a) greater width of rhabdosome in distal part (0.8—1.6 mm),
   b) more inclined thecae (degree of inclination not indicated),
2. stratigraphic characteristics:
   a) occurrence in lower part of the Ludlovian (*nilssoni* and *scanicus* zones).

II. *B. b. tenuis*
1. morphological characteristics:
   a) smaller width of rhabdosome in distal part (0.5—0.8 mm),
   b) less inclined thecae (at 25—30° to the axis of rhabdosome);
2. stratigraphic characteristics:
   a) occurring in higher horizons (the upper part of the Ludlovian, *Saet. fritschi linearis* zone).

No morphological details have been added to these rather scanty remarks by further investigations, but judging from Přibyl's (1948, p. 68; 1967, p. 136) and Přibyl's and Vaněk's (1968, p. 416) notes, stratigraphic

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[9] "*M.*" *butovicensis* Bouč., tentatively referred by Přibyl (1967) to *Bohemograptus*, distinctly differs from other representatives that it has here been excluded from considerations.

distributions of both forms is believed to exclude each other. It has not, however, been clearly stated whether there is a certain overlap in vertical ranges of both subspecies and whether *B. bohemicus* is represented in the upper part of Kopanina Beds in Barrandian by its variety *tenuis* alone or associated with an earlier typical form.

The examination, by the present author, of original materials of Barrande (1850), Perner (1899), Bouček (1936), recently refigured by Přibyl (1967) and housed in Narodní Muzeum (Prague), also little contributed to a better understanding of the morphological concept of both subspecies. Measurements quoted by Bouček (1936) were generally confirmed, but both speciments of *B. b. tenuis,* figured by Bouček (1936, Pl. 1, Figs. 4—5; N. M. Akc. Nr 25.676, 25.677), were found rather incomplete (without sicula), with no association at all, or associated with indeterminable graptolites.

Although this has not clearly been stated by previous authors, the concept of *B. bohemicus* subspecies seems to be essentially temporal, both subspecies being exclusive in time. This conclusion is consistent with the material collected from the Mielnik core. In the light of these data, populations of *B. bohemicus* from lower horizons display a predominance of rather robust forms which may be roughly identified with *B. b. bohemicus* (Barr.) (as defined by Bouček, 1936). The prevalence of more gracile form, probably *B. b. tenuis* (Bouč.) has been found in higher horizons. In the present writer's opinion, the morphological differences between these two groups of populations, expressed in their quantitative characteristics and frequence of particular variants in populations, may serve as a basis for a redefinition of both subspecies. Previously, the present writer tried to distinguish both subspecies on purely morphological ground, being of the opinion that they could partly coexist synchronically, say due to the mosaic pattern of environment, or their coexistence was merely secondary, which was caused by an allochtonous deposition of fossil remains (Urbanek, 1968, *in press*).

To obtain a number of quantitative data, measurements of specimens of *B. bohemicus* from successive horizons have been taken, with special reference to sicula and proximal thecae. Proximal fragments of rhabdosome with the sicula preserved are preferable for biometric studies, for, in this case, an exact position of each theca may be determined. This enables a proper evaluation of data and discriminates between the astogenetic and intrapopulationary variation of thecae. In the study on the variation in graptoloids this seems to be so important that even long fragments of rhabdosome without preserved sicula may be considered as useless for appropriate numerical observations.

Attention has been focused on such characters as length of sicula (1), position of aperture of the first theca (2) and width of rhabdosome in proximal part (3). Other characters seem to have a lesser significance to the distrimination of subspecific taxa in *B. bohemicus* (3) and were used to a limited extent for their redefinition (for measurements consult Fig. 1).

ANALYSIS OF SOME QUANTITATIVE CHARACTERS IN *BOHEMOGRAPTUS BOHEMICUS*

1. *Analysis of variation in the length of sicula.* — One of the characters in which populations of *B. bohemicus*, taken from particular horizons, differ rather distinctly, is the length of sicula (*lsic*). A preliminary morphological analysis shows that this quantitative character may have certain significance to subspecific discrimination among populations of *B. bohemicus* from particular horizons.

A joint histogram (Fig. 7) produced primarily for all measurements lumped together shows, in spite of distinct morphological differences between extreme populations measured, a unimodal curve, with variation range 1,30—2.00 mm, and mode placed between 1.50—1.60 mm.

The material was then analyzed by taking appropriate measurement and drawing separate scatter-diagrams for samples collected in particular zones. A small number of observations, especially for lower horizons (*progenitor-hemiaversus* zones, where in an extreme case N was 1, and never exceeded 11), has been responsible for rather contradictory picture of variability. It is supposed that differences between population from particular zones ("chronodemes", according to Sylvester-Bradley) were in this case produced largely by chances of sampling. Nevertheless, even this preliminary analysis indicated a more pronounced change in variability between *hemiaversus* and *aversus* zones, connected with a distinct change in frequency of siculae of definite size. In contrast to samples from *hemiaversus* and lower zones it reveals a predominance of specimens with a rather short sicula ($lsic < 1.70$ mm), while specimens with larger siculae ($lsic \geqslant 1.70$ mm) represent only a minority ($\sim 20\%$).

In further investigations, samples from particular horizons were lumped together to form two larger samples, probably more representative and more reliable statistically in reflectin greal changes in variation. It was considered convenient to place the dividing line between both samples on the boundary of *hemiaversus/aversus* zones. Thus produced sample A contained specimens derived from *L. scanicus parascanicus-Cuc. hemiaversus* zones, and sample B comprised series of specimens collected from *Cuc. aversus -Neocuc. kozlowskii* zones.

The results obtained are presented as histograms on Fig. 7. The ranges of variability for *lsic* are in sample A 1.56—1.96 mm (N = 21) and in sample B 1.36—1.89 mm (N = 50). Variability of *lsic*, observed in both samples, was subsequently analyzed, and established differences were estimated by the use of elementary statistical methods [see below at a) and b)]. Data from *progenitor* zone (only observation) are not involved in the following considerations and are discussed below.

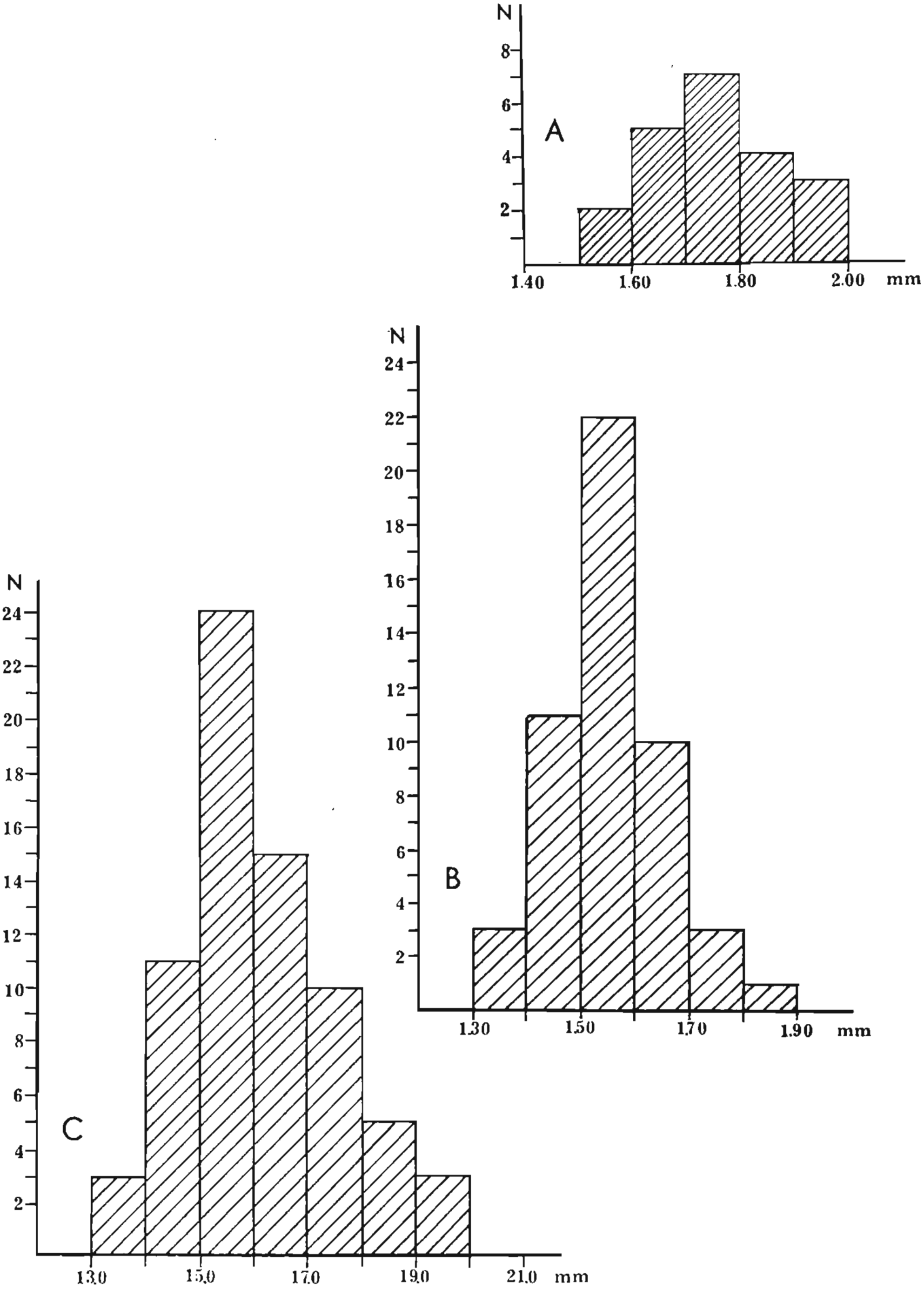

Fig. 7. — Histograms showing length of sicula of *Bohemograptus bohemicus* (Barr.) in populations from sample A and B (*A*, *B*) and jointly for both samples lumped together (*C*). Ordinates = length of sicula in mm, abscissae = number of specimens.

a) Samples from particular horizons, lumped together to form larger samples A and B, were analysed into morphotypes ("typological analysis" as suggested by Sylvester-Bradley, 1958). Each morphotype is here arbitrarily defined as a group of specimens displaying specified quantitative peculiarity and for the reasons indicated above two such morphotype groups were selected according to the following key:

1) morphotype group α . . . . . length of sicula $\geqslant 1.70$ mm
2) morphotype group β . . . . . length of sicula < 1.70 mm

In sample A (lower horizons) morphotype group α prevails quantitatively (66,66% of N), while in sample B (higher horizons) morphotypes of group β are predominating (92.0% of N). Proportions of the morphotypes distinguished in both samples are therefore quite different. To test whether this difference is statistically significant, the following contingency table was used to calculate the value of χ^2:

Samples	Morphotypes α	 β	Totals
1	14 a	7 b	21 r
2	4 c	46 d	50 s
Totals	18 p	53 q	

$$\chi^2 = \frac{(p+q)(ad-bc)^2}{pqrs} = \frac{71(644-28)^2}{(18)(53)(21)(50)} = \frac{26941376}{1001700} = 26.89$$

The value of χ^2 (= 26.89) for 1 degree of freedom is large enough to be assumed without further calculations as highly significant. χ^2 test indicates therefore that the difference in frequencies of both morphotype groups in the samples investigated is not due to chance (e. g., the samples belong to populations different statistically).

b) Instead of employing a "typological analysis", both samples were compared by standard quantitative methods. To test a difference in length of sicula between samples A and B, means (M) of both samples and standard deviations (S) were used. Arithmetic means (M) and standard deviations (S), calculated by a simplified method of data grouped in classes (cf. Fig. 7), are as follows:

Sample A: $M_A = 1.749$ mm; $S_A = 0.103$
Sample B: $B_B = 1.549$ mm; $S_B = 0.104$

Standard deviation values were calculated according to the following formula:

$$S = \sqrt{\frac{\sum f-d^2}{N-1}}$$

Standard errors (m) calculated according to the formula

$$\frac{S}{\sqrt{N}}$$

are for sample A; $m_A = 0.022$ and for sample B; $m_B = 0.014$. According to the requirement:

$$M_A - M_B \geqslant 3(m_A + m_B)$$

we form the opinion that the difference in size of sicula is highly reliable statistically, since in this case $M_A — M_B = 0.200$, and $m_A + m_B = 0.036$. The same is indicated by a standard error of difference (md) given by

$$md = \sqrt{(S_A)^2 + (S_B)^2} = \sqrt{(0.022)^2 + (0.014)^2} = 0.026$$

which is roughly 10 times smaller than $M_A — M_B$.

Even a cursory examination of the histogrames (cf. Fig. 7) suggests a rather great degree of overlap in variation range. Only 13.8% of the population from sample A do not overlap the variation range of the sample B and 28% of the population from the latter sample are outside the range of the former.

An attempt was thus made to estimate for taxonomic discrimination the degree of overlap in variation range observed in both samples. According to a routine method suggested by Mayr, Linslay and Usinger (1933, pp. 142—147), a coefficient of difference (*Cd*) was calculated as follows:

$$Cd = \frac{M_A - M_B}{S_A + S_B} = \frac{1.749 - 1.549}{0.103 + 0.104} = 0.936$$

According to data tabulated in Mayr *et al.* (*l. c.*, p. 146, Table 12). this value of difference coefficient corresponds approximately to 83.27% of joint nonoverlap of variation ranges, being well below the level of conventional subspecific distinctness (1.28 for *Cd*, and 90% of joint nonoverlap according to a "75% rule", in the sense adopted by Mayr *et al.*, 1953). For these reasons, populations represented by samples A and B are not considered worthy of separation as subspecies (cf. further discussion below).

c) Decisive significance for taxonomic evaluation of morphological differences attained in *B. bohemicus* lineage seems to have comparison of range overlap in its terminal populations. For this purpose populations from *parascanicus-invertus* zones, and from *inexspectatus* — *kozlowskii* zones were thus compared. χ^2 value calculated by using "typological analysis" for length of sicula is in this case 20,16 that is highly significant statistically, mean values being for each population indicated 1.755 mm, and 1.538 mm, standard deviations 0.1195, 0.0955 correspondingly. Coefficient of difference (C. d.) is therefore 1.01, that is still below the level of conventional subspecific distinctness (1.28).

2. *Analysis of variation in position of apertural level in* th_1. — Even preliminary morphological observations indicate that the position of aperture of the first theca measured in relation to apex of prosicula, displays a considerable variation range and remarkable differences in proportions of plus and minus variants in samples A and B as defined above.

The significance of this character to the discrimination between *B. b. bohemicus* and *B. b. tenuis,* has already been noted by Ulst and Koren (*in* Gailite, Rybnikova & Ulst, 1967, p. 254) as they said that in the former "apex of the sicula reaches basis of th_2" and in the latter "apex is situated

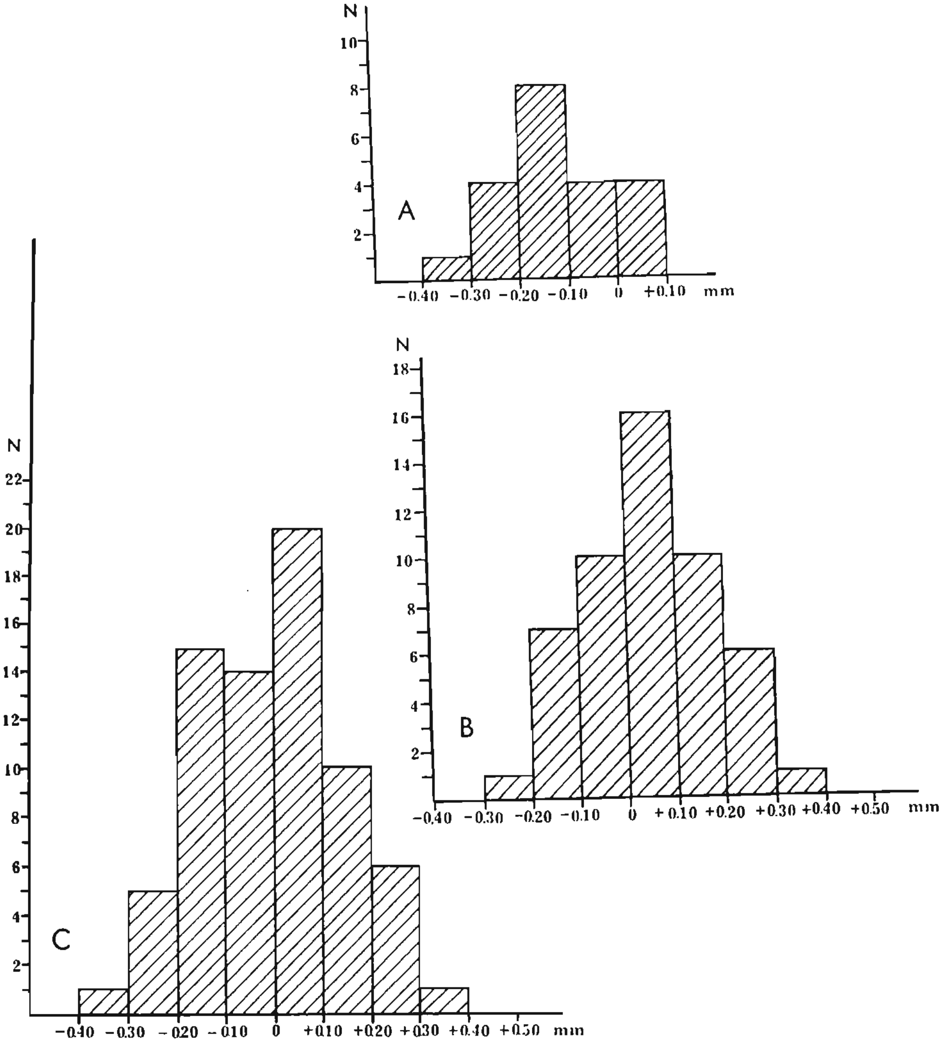

Fig. 3. — Histograms showing position of apertural level in th_1 of *Bohemograptus bohemicus* (Barr.) in populations from sample A and B (*A*, *B*) and jointly for both samples lumped together (*C*). Ordinates = distance of apertural level in th_1 below (−), or above (+) the apex prosiculae in mm, abscissae = number of specimens.

at the level of th_1". Although not quite precisely stated, the observation is essentially the same.

For a more accurate description, a series of specimens from both samples were measured (N = 21 from sample A; N = 51 from sample B) and the position of apertural level of the first theca defined as a distance from it to the apex of prosicula. Plus (+) and minus (−) variants were distinguished, depending on the position of aperture above or below the prosicular apex. Histograms based on these data are presented in Fig. 8.

The population represented in sample A (from lower horizons) shows a variation range of −0.35—+0.05 mm, and its mean value of $M_A = -0.126$ mm. Specimens with the aperture of the first theca situated below the prosicular apex (minus variants) greatly predominate (80.96%).

In contrast to sample A, the population represented by specimens from sample B (higher horizons) displays a variation range of −0.25—+0.29 mm and the mean value $M_B = +0.021$ mm. Plus variants (+) having the apertural level at a distance of 0.00 mm and more above the apex of prosicula. predominate (64.70%). There is therefore a remarkable shift in proportions of minus and plus variants in both populations towards the latter group. An average value of this change may be expressed by the shift in position of mean values being 0.147 mm.

Taking plus and minus variants defined above, as distinct morphotypes and using "typological analysis" to test binomial proportions in both samples, χ^2 value was calculated as being $\chi^2 = 12.413$, that means highly significant statistically.

In order to compare differences in position of apertural level in th_1 by standard quantitative methods, plus and minus values were transformed into ordinary values indicating distance from arbitrarily defined point, in this case lowermost limit of observed class of variation (−0.40 mm), taken here as being 0.00. Plus values were calculated according to formula (0.40+n), and minus values according to formula (0.40−n). This gives for mean values redefined in this way: $M_A = 0.274$ mm, $M_B = 0.421$ mm. Standard deviations were calculated as being $S_A = 0.114$, $S_B = 0.135$, and coefficient of difference Cd correspondingly as 0.590. This value of Cd is much below the level of conventional subspecific distinctness as accepted above.

Comparison of extreme populations in *B. bohemicus* lineage, selected as in the case of the length of sicula (*parascanicus* — *invertus* zones on one, and *inexspectatus*—*kozlowskii* zones on the other hand) gives following results: χ^2 value calculated by using "typological analysis" is in this case 6.454, which would be considered significant mean values redefined as indicated above are for each population 0.234 mm, and 0.421 mm, standard deviations being 0.114 and 0.149. Coefficient of difference is therefore C. d. 0.71, that is well below the level of conventional subspecific distinctness.

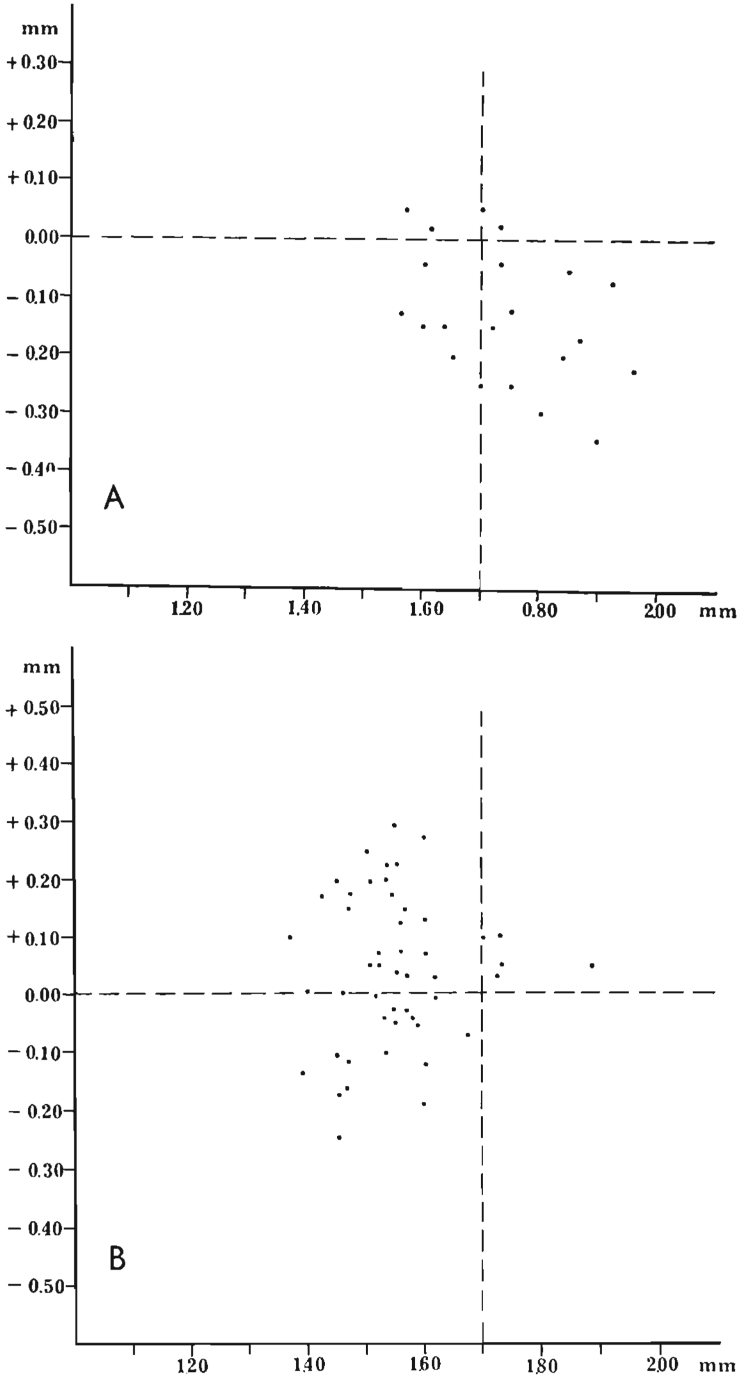

Fig. 9. — Analysis of correlation of length of the sicula (ordinates, in mm) and position of apertural level in th_1 (abscissae in mm, below –, or above + the apex prosiculae) for population from sample A (*A*) and sample B (*B*),

In the case of *B. bohemicus* the change in position of the aperture of the first theca has been accompanied by a simultaneous, progressive shortening of the sicula. To evaluate the relationship of these two characters (length of sicula, position of aperture in th_1), appropriate scatter-diagrams were plotted (Fig. 9) to enable a bivariate analysis. The distribution of Y-values in relation to X-values on both diagrams clearly indicate for a very small, or even no correlation between characters considered. Both may be considered as largely independent. This conclusion is also supported by the following simple calculation, which reveals a small degree of dependence of the position of aperture in th_1 on the length of sicula. The results, showing percentage ocurrence of + and — variations of th_1, associated with particular morphotypes of the sicula (as here understood) and their distribution in both samples, are tabulated below:

Samples	Sicula			
	morphotype α		morphotype β	
	—	+	—	+
A	85.71%	14.29%	71.42%	28.58%
B	0.00%	100%	39.2%	60.8%

Especially indicative in this respect is that all (100%) representatives of morphotype α (large sicula) in the population from sample B are associated with th_1 belonging to plus variants (+), and that most representatives of morphotype β (small sicula) in the population from sample A fall into category of minus variants as concerns their th_1 (71.42%). In contrast, only 60.8% of the representatives of latter morphotype in the population from sample B belong to + variants.

In contradistinction certain "zonal influence", that is the dependence of a geologic horizon (time) seems to be clearly demonstrated, as shown in the following table

Horizons	Aperture of th_1	
	below apex prosiculae — (minus)	above apex prosiculae + (plus)
Lower (sample A)	80.96%	19.04%
Higher (sample B)	35.30%	64.70%

An increase in relative frequency of + variants in higher horizons is distinct, although it does not reach the level of frequency of — variants in lower horizons.

The changes in size of sicula and position of aperture th_1, analyzed in the populations of *B. bohemicus*, seem to be largely independent (uncorrelated or very imperfectly correlated). In general, it seems safe to generalize from the data presented above, that the predominance of β — morphotypes (small-sized siculae) and + variants (great relative frequency of th_1 with aperture placed above the prosicular apex) is characteristic of the populations of *B. bohemicus* in higher horizons.

3. *Other quantitative characters used for discrimination.* — Other characters which may be used for discrimination of temporal subspecies in *B. bohemicus* are: 1) diameter of the metasicular aperture, 2) length (*long*) of the dorsal apertural process (*dp*), 3) diameter of the aperture in the first theca (th_1), 4) width (*trans.*) of the rhabdosome measured at the level and just above the aperture of th_1 and index of the widening of rhabdosome in the proximal part, 5) angle of inclination of thecae.

3.1. Differences between both samples in diameter of metasicula are very small but indicate a certain trend toward widening this aperture. The following values have been found for sample A: range 0.26—0.46 mm, ($N = 17$), $M_A = 0.385$ mm; for sample B: range 0.28—0.50 mm, ($N = 38$), $M_B = 0.406$ mm. Although the population from sample B displays a certain increase in values, the significance of this character to the discrimination of temporal taxa in question, seems to be rather small.

3.2. Differences in length (*long.*) of the dorsal apertural process in metasicula (*dp*) are more promising. The following values were found for sample A: range 0.10—0.17 mm, ($N = 17$), $M_A = 0.144$ mm and for sample B: range 0.04—0.19 mm ($N = 42$), $M_B = 0.121$. There is a remarkable increase in the variation range of the population from sample B, but the central (dominating) tendency, as indicated by the mean value, is toward a certain decrease in the dorsal process. Moreover, there is a distinct difference in this respect between the populations collected from lower and higher horizons lumped together into sample B. These values calculated separately for lower horizons (*aversus-auriculatus* zones) are the range of 0.10—0.19 mm ($N = 21$) $M_{BL} = 0.143$ mm; and for higher horizons (*inexspectatus-kozlowskii* zones) the range of 0.04—0.14 mm; ($N = 21$); $M_{BH} = 0.099$ mm. This seems to indicate rather clearly a certain secondary trend toward reduction of *dp* in *B. b. tenuis*, starting first to operate in *Neocuc. inexspectatus* zone. Its significance is discussed elsewhere (see p. 300).

3.3. Differences in diameter of aperture in th_1 seem rather negligible. The following values have been found for sample A ($N = 15$): range 0.23—0.40 mm, $M_A = 0.352$ mm and for sample B: range 0.23—0.40 mm, (N = 44) M_B = 0.332 mm. There is no remarkable difference between both populations in variation ranges and mean values.

3.4. Even a morphological observation indicates certain differences in width of the rhabdosome measured at the level of aperture of th_1 (3—4a) and just above this level across the base of th_2 (3—4*b*).

Concerning the first character (3—4*a*), the following values were obtained for sample A: range 0.30—0.40 mm, (N = 17); M_A = 0.598 mm and for sample B: range 0.23—0.40 mm (N = 42), M_B = 0.478 mm. The width of rhabdosome, measured at the level of aperture of th_1 in the population from sample B, is somewhat narrower, and the same seems to be true of the rest of rhabdosome.

In the representatives of the same population particularly remarkable is the narrowing of the rhabdosome at the base of th_2. In contrast to the conditions observed in the specimens from sample A, just above the aperture of th_1, rhabdosomes have only a narrow neck (comp. Pl. VI, Fig. A, B and Pl. XIII, Figs. A, B). The width (*trans.*) of rhabdosome, measured across it from dorsal to ventral wall, gives the following values: for sample A range 0.25—0.40 mm, (N = 17), M_A = 0.328 mm and for sample B range 0.12—0.25 mm, (N = 11), M_B = 0.199 mm. There is almost no overlap in variation ranges and the mean values differ considerably. The strong decrease in the width of rhabdosome above the level of aperture in th_1 seems to be a character rather peculiar of the population from sample B ("narrow neck").

The ratio of width of the rhabdosome above aperture of th_1 to that above th_2:

$$\frac{\text{width of rhabdosome above aperture } th_1}{\text{width of rhabdosome above aperture } th_2}$$

may serve as a certain measure of the relative narrowing of the rhabdosome above the apertural level of th_1. This index caculated for a rather limited number of specimens is:

sample A = 0.840 — 0.869 (N = 3)
sample B = 0.568 — 0.666 (N = 3)

This indicates a greater narrowing at the point considered in relation to the width of succeeding theca in the population from sample B. These indices may be a certain measure of the degree of widening of the rhabdosome in the proximal part. In spite of a decrease in absolute width of rhabdosome at the base of th_3 (sample A 0.44—0.55 mm, sample B 0.25—0.44 mm) judging from the data quoted, the representatives of the latter population, display a relatively more rapid widening, connected with the presence of a "narrow neck" above the aperture of th_1.

The increase in width of the proximal part of rhabdosome is to some extent indicated by the ranges observed in specimens from both samples, as given below. Based on a very different number of observations (N drops to 3 for th_3, sample A) this table has an only tentative significance.

Thecal number	1	2	3
Sample A	0.30—0.40	0.58—0.70 0.37—0.40	0.77—0.86 0.44—0.55
Sample B	0.30—0.40	0.55—0.70 0.12—0.25	0.65—0.70 0.25—0.44

Remarks. — Upper values — width of rhabdosome (mm) measured across the aperture of a given theca, lower values — that measured above the aperture of a preceding theca.

Although the width of rhabdosome in proximal part is smaller in specimens from sample B, there is however no indication of the same in a more distal one. The most distal fragments reach approximately the same maximal width of rhabdosome (in sample A 1.00 mm, measured across the base of theca and 1.40 mm at the aperture, 0.94 mm, 1.33 mm being the same measurements in sample B). The latter values are much larger than a maximal value quoted by Bouček (1936) for *B. b. tenuis* (0.8 mm) and fit well into the range of variability in width of rhabdosome observed by him in *B. b. bohemicus* (0.8—1.6 mm). In the light of the data presented in the populations from both samples there is no distinct difference in width of rhabdosome in distal part.

3.5. Bouček (1936, p. 2) mentioned as distinctive for both subspecies of *B. bohemicus* lesser inclination angle of thecae toward the axis of rhabdosome (comp. p. 244). The values observed show however no greater difference in representatives of *B. bohemicus* from both samples in this respect. (Sample A, proximal thecae 30°—35°, medial 32°—38°, distal 40°; sample B proximal thecae 30°—38°, medial 40°, distal (40°—42°). Differences mentioned by Bouček seems to be rather apparent.

Summarizing our previous analysis of certain quantitative characters in order to evaluate its significance for subspecific discrimination in *B. bohemicus*, it must be remembered that "the degree of morphological difference necessary to warrant the distinction of a population as a subspecies is a matter of arbitrary and personal decision" (Sylvester-Bradley, 1958, p. 222), above considerations of the differences in quantitative characters between the populations from the two samples as previously defined, although supplied a certain amount of quantitative data necessary for a more accurate description of variation, their cursory examination is not conclusive for a clear discrimination of temporal subspecies. This is especially true in regard to the length of sicula (*lsic*) and position of apertural level in th_1 which have been analysed on the basis of the greatest number of observations. Although reliable statistically the differences in both characters examined does not warrant, according to the accepted standard criterion of nonoverlap, the distinction of the population from sample B as a separate subspecies. This criterion, however, was established mainly for discrimination of contemporaneous populations and does not necessarily indicate that precisely the same morphological scale should be applied to evaluate the differences in vertical sequence.

Moreover considerable overlap in ranges of variation may theoretically be expected in case of nearly continuous sequence of populations, as result of previously chosen analitical method, based on lumping together variation from a great number of chronodemes. By the nature of facts such vertical sample should include nearly complete series of all morphological transients, what results in great range overlap with underlying "segmental unit" of same lineage.

It seems reasonably therefore in our case, to base the discrimination criteria and to place the demarcation line between temporal subspecies on the ground of whole evidence, including biological and stratigraphical criteria.

Following arguments may be quoted to substantiate the distinction of *B. bohemicus* from sample B as a separate subspecies: 1. existence of distinct morphological characters, as demonstrated by terminal populations (comp. Fig. 10 and Pl. XVIII), which are doubtlessly great enough to distinguish even two separate species, according to traditional, "subjective" procedure of species recognition; 2. populations from sample B made in fact a natural segment of *B. bohemicus* lineage, which started with a distinct event, namely a shift in the direction of changes, being then persistent trend of evolutionary significance. Its lower limit is marked therefore by node of branching (splitting) of this lineage. This "nodal" argument should not be overemphasised (comp. pp. 213) but can not be entirely oversight as far as we accept that the base of an evolving species is in "its separate and unitary evolutionary role and tendencies" (Simpson, 1961); 3. and last not least, also some qualitative and stratigraphic characteristics of both populations seems to require a greater taxonomic evalution than that indicated by an analysis of purely quantitative features. They are discussed below.

SIGNIFICANCE OF QUALITATIVE MORPHOLOGICAL CHARACTERS AND STRATIGRAPHIC CRITERIA OF DISCRIMINATION

Characters of the qualitative nature, which in this connection should be mentioned first are the appearance and distribution of the microfusellar additions in the populations from sample B. Although the first appearance of the microfusellar additions was noted in *hemiaversus* zone, it is represented by a single specimen only. It seems safe, therefore, to generalize that in the populations from sample A microfusellar additions were absent, or extremely rare. They make their first appearance only in the uppermost horizons comprised by this sample.

In contrast to the former population, the population from sample B displays a rather abundant occurrence of microfusellar additions, present in each larger single population (chronodeme), obtained from particular segments of the core.

The appearence of microfusellar tissue and its derivatives roughly coincides with the suggested boundary between temporal subspecies of *B. bohemicus*. The development of microfusellar tissue which undoubtedly changed the evolutionary role and tendencies in populations of this species, younger geologically, is consistent with their separation into subspecies. The appearance of rhabdosomes having thecae provided with microfusellar additions, especially in the extreme form of "velum", considerably changed the character of intrapopulationary variation and produced a polimorphism (appearance of the "veliger" morph) peculiar only of this group of populations.

The stratigraphical evidence also seems to indicate a greater significance of the suggested limit between populations from both samples. The lower boundary of *aversus* zone lies somewhat below the *leintwardinensis* zone, which roughly coincides with the extinction of the Lower Ludlovian graptolite lineages. It seems logical to expect that this, rather profound, change in environment (especially biotic) opened new possibilities to *B. bohemicus,* which resulted in a certain reorganization of variability and subsequently in the origin of a new temporal subspecies. The redefinition of the stratigraphic range of this subspecies here suggested only slightly affects its lower limit. *B. b. tenuis* was mentioned by Bouček (1936) and Přibyl (1948, 1967) from the zone of *Saetograptus leintwardinensis primus* (= *B. fritschi linearis*). The last named zone is considered by Jaeger (1964) as immediately overlying the *leintwardinensis* zone, although it is not unlikely that the two forms display a considerable range overlap (cf. p. 221). In any case, this roughly corresponds to *aversus* zone, especially so to its upper part distinguished as *rostratus* subzone (Urbanek, 1966). The shift of this limit to the lower boundary of *aversus*-zone is based on a continuous occurrence in the core of *B. bohemicus* which, although not very common, also occurs in the lower *aversus* subzone, where it morphologically approaches the representatives of the younger rather than the older horizons.

Placing the boundary between subspecies in question still lower, in the lower part of the *hemiaversus* zone, where microfusellar tissue makes its first appearance, seems less convenient from practical reasons. Certain coincidence of suggested boundary between both temporal subspecies, and already accepted stratigraphic subdivision, seems desirable.

The upper limit of the stratigraphic range of *B. b. tenuis* extends to the top of *kozlowskii* zone, marking the upper boundary of the lower

Table 2

Characters of subspecies in *Bohemograptus bohemicus* (Barr.)

B. bohemicus bohemicus	*B. bohemicus tenuis*
1. Sicula mainly large-sized (66,66% of specimens with 1 sic $\geqslant$ 1.70 mm), range 1.56—1.96 mm, M = 1.749 mm*)	1. Sicula mainly small-sized (92,0% of specimens with 1 sic $<$ 1.70 mm) range 1.36—1.89 mm, M = 1.549 mm
2. Smaller apertural diameter of metasicula; range 0.26—0.46 mm; M = 0.385 mm	2. Larger apertural diameter of metasicula; range 0.28—0.50 mm, M = 0.406 mm
3. Dorsal process of metasicula rather longer; range 0.10—0.17 mm, M = 0.144 mm	3. Dorsal process of metasicula rather shorter; range 0.04—0.19 mm, M = 0.121 mm
4. Aperture of th$_1$ placed mainly low (-variants being 80.96% of specimens), range -0.35—$+0.05$ mm, M = 0.126 mm	4. Aperture of th$_1$ placed mainly high (+ variants being 64.70% of specimens), range -0.25—$+0.29$ mm, M = $+0.021$ mm
5. Greater width of rhabdosome in proximal part base of th$_2$ rather wide (0.25—0.40 mm)	5. Smaller width of rhabdosome in proximal part base of th$_2$ rather narrow (0.12—0.25 mm)
6. Microfusellar additions — absent or extremely rare	6. Microfusellar additions — frequent, persistent throughout the range
7. Occurrence: *vulgaris* zone?, *nilssoni* — *hemiaversus* zones	7. Occurrence: *aversus* — *kozlowski* zones

*) Specimens from *progenitor* zone in the Mielnik-core, and from Baltic drift indicate tha this range should be extended to be 1.56 — 2.00 mm.

part of the Siedlce Beds. The stratigraphic significance of extinction of *B. b. tenuis*, being the last representative of *Bohemograptus*, at the boundary of Kopanina and Prídoli Beds in Barrandian, has been stressed already by Přibyl and Vaněk (1968).

Summing up, then, we may say that certain morphological qualitative characters enable, and quantitative data support, the discrimination, according to a key tabulated below (Table 2), between two temporal subspecies of *B. bohemicus*.

As indicated above, the redefinition of temporal supspecies in *B. bohemicus* is only partly based on quantitative data, and to a great extent on a certain evaluation of characters by distinguishing the category of "qualitative" features. This approach is of course in controversy to modern phenetic classification, and reminds rather older views, which while adopting quantitative methods appeal nevertheless to an art of classification.

DISCRIMINATION BETWEEN TEMPORAL SUBSPECIES IN *BOHEMOGRAPTUS BOHEMICUS* FROM DRIFT MATERIAL

B. bohemicus is also common in fauna etched from erratic boulders of Baltic origin[10]. In a collection of Silurian graptolitebearing boulders analyzed by the writer (236 boulders in total), *B. bohemicus* has been found as a frequent associate in 28 boulders. The stratigraphic position of some boulders has been determined on the basis of associated graptolites which contained associations indicating definite zones. Most boulders with *B. bohemicus* (19 boulders) belong, however, to a category without any association or are associated with a long-ranged stratigrhaphically nonindicative species (*P.* ex gr. *dubius* (Suess), *Monocl. haupti* (Kühne)). It seems reasonable to distinguish this group of boulders as a group of an "O"-association. The remaining boulders contain an association indicative of *nilssoni* zone (1 boulder), or are associated with *S. chimaera* (Barr.) and different Cucullograptinae (8 boulders in all, in 4 of them more frequent). Since both *S. chim.* cf. *chimaera* and *S. chim. cervicornis* have been found (zone of *S. chimaera* as suggested by Jaeger, 1964) they indicate *progenitor-invertus* zones. For the sake of convenience, the latter two groups of boulders were lumped as a group of "N"-association (*Neodiv. nilssoni*) and "Ch"-association (*S. chimaera*). Table 3 shows particular boulders which contain more frequently occurring *B. bohemicus*, grouped in the classes mentioned above with associated forms indicated.

If the stratigraphic position of groups "N" and "Ch" of the boulders is rather clear, group "O" requires a certain consideration. The lack of associated graptolites may be entirely random. This seems especially probable in the case of small boulders (the majority of the boulders consi-

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[10] For origin of these boulders and collecting localities see Urbanek (1966, pp. 299—302).

Table 3
Graptolite association at *Bohemograptus bohemicus* in erratic boulders

Analitical class	„N"	„Ch"				„O"																		
Boulder number / Species associated	S. 20	S. 32	S. 111	S. 174	S. 185	S. 61	S. 68	S. 102	S. 112*	S. 113	S. 122	S. 124	S. 136	S. 147	S. 154	S. 176	S. 179	S. 187*	S. 202	S. 209	S. 212	S. 224*	S. 233	S. 234
Neodiversograptus nilssoni	+																							
Monograptus uncinatus	+																							
Colonograptus colonus	+																							
Saet. chimaera cervicornis		+																						
Saet. chimaera cf. *chimaera*				+	+																			
Saet. chimaera subsp.			+																					
Cucullograptus pazdroi		+		+																				
Lobogr. scanicus parascanicus		+		+	+																			
Neodiversograptus beklemishevi		+																						
Holoretiolites erraticus					+																			
Monoclimacis micropoma																								
Monocl. haupti										+			+						+					
Prist. dubius frequens	+	+																						
Prist. ex gr. *dubius*											+	+								+	+		+	

*) Denoted boulders in which *B. bohemicus* has been analyzed morphologically and taxonomically.

dered were rather small, of palmsize), in which the absence of other forms may be due to unrepresentative sampling. On the other hand, this may be also primarily due to local differences in the differentiation of fauna. In both cases, the lack of association is hardly indicative stratigraphically.

Although heterogenous stratigraphically, the "O"-group of boulders seems, however, to derive mostly from one geological horizon, as suggested earlier by Urbanek (1966, p. 301, and especially 1968, *in press*). It seems reasonable to suggest that the prevailing majority of these boulders derive from a horizon immediately overlying *S. leintwardinensis* zone, and marked by a great proliferation (mass occurrence) of *B. bohemicus*. Urbanek (1968, *in press*) even suggested the distinction of this horizon of acme in development of *Bohemograptus* as en epibole of *B. bohemicus* (comp. also discussion, pp. 177). The impoverishment in the associated fauna may be explained by a great extinction of graptolite lineages in underlying *leintwardinensis* zone. The rare association of *P.* ex gr. *dubius* and *Monocl. haupti* (Table 3), concerns the survivors of this extinction.

The derivation of "O" boulders suggested by the writer would require that *B. bohemicus* belonged in these boulders to the subspecies *tenuis*, as redefined previously. The analysis of assemblages from certain boulders pertaining to group "O" reveals that morphological characters of the associated *B. bohemicus* are strongly indicative of *tenuis* (S. 224, S. 187, and also S. 234). On the other hand, *B. bohemicus* found in some other boulders of the same group, more closely approches true *bohemicus* (S. 112), which may indicate rather lower horizons and a random absence of a richer graptolite association.

In general, morphological characteristics of *B. bohemicus* from boulders of "N", "Ch" and "O" groups are not only consistent with the previous definition of its temporal subspecies, but also in certain cases help clarify the stratigraphic origin of drift material (1—3).

1. *Morphological characteristics of B. bohemicus from the boulders of "N" group.* — Range in *lsic* — 1.73—1.95 mm (N = 3), diameter of metasicular aperture 0.40 mm; *ldp* 0.15—0.20 mm; position of apertural level in th_1 0.15—0.23 mm; width of rhabdosome at apertural level in th_1 0.58—0.65 mm, width of the base of th_2 0.31—0.35 mm. The form of dorsal apertural process of metasicula which in most specimens is pointed rather than shovel-like, may indicate a certain specialization of the population analyzed. No microfusellar additions noted. All features indicative of *B. b. bohemicus.*

2. *Morphological characteristics of B. bohemicus from boulders of "Ch" group.* — Range in *lsic* — 1.65—2.00 mm, 1 specimen 1.65 mm, mostly 1.75—2.00 mm (N = 7); diameter of metasicular aperture 0.37—0.44 mm; *ldp* 0.16—0.18 mm; position of apertural level in th_1 0.12—0.30 mm; width of the rhabdosome at apertural level of th_1 0.60—0.68 mm; width of the base of th_2 0.25—0.38 mm.

Dorsal apertural process, in all forms examined, shovel-like. No microfusellar additions noted. All features indicative of *B. b. bohemicus.*

3. *Morphological characteristics of B. bohemicus from boulders of "O" group.* — Only 4 boulders of this group were selected for quantitative characteristics (S. 112, S. 187, S. 224, S. 234). These were boulders from which richer and better preserved fauna was isolated by chemical treatment. Due to a relative scarcity of material, no attempt was made to characterize quantitatively *B. bohemicus* from the remaining boulders of group "O".

Boulder S. 112. — Range in *lsic* 1.70—1.80 mm (N = 3); diameter of metasicular aperture 0.36—0.40 mm; l *dp* 0.15—0.16 mm; position of apertural level of th_1 0.15—0.20 mm; width of the rhabdosome at the apertural level of th_1 0.60—0.65 mm; width of the base of th_2 0.30 mm.

Dorsal apertural process, in all forms examined, shovel-like. No microfusellar additions noted. The following characters seem to indicate the assignment to *B. b. bohemicus* — length of sicula, low position of apertural level in th_1 (all strong — variants), great width in the proximal part of rhabdosome (width at the apertural level of th_1 exceeds even the range established for *B. b. bohemicus* in the Mielnik core).

Boulder S. 187. — Range in *lsic* 1.35—1.50 mm (N = 3); diameter of metasicular aperture 0.30—0.41 mm; *ldp* 0.10—0.15 mm; position of apertural level of th_1 0.00—0.10 (mean — 0.056 mm); width of the rhabdosome at the apertural level of th_1 0.45—0.50 mm; width at the base of th_2 0.19—0.20 mm.

Dorsal apertural process of metasicula, in all forms examined, shovel-like. No microfusellar additions noted. Most characters indicate *B. b. tenuis* (*lsic, ldp,* width at the base of th_2). In contradistinction to characters mentioned above are: rather low (but on the average moderately low) position of the aperture in th_1, and rather wide rhabdosome at the level of aperture in th_1.

Boulder S. 224. — Range in *lsic* 1.30—1.50 mm (N = 6); diameter of metasicular aperture 0.32—0.40 mm; *ldp* 0.10—0.15 (mean 0.12 mm): position of apertural level in th_1 0.12—+0.18 mm mostly + variants): width of rhabdosome at the apertural level of th_1 0.42—0.52 mm; width at the base of th_2 0.12—0.25 mm.

Dorsal apertural process of metasicula, in all forms examined, shovel-like. No microfusellar additions noted. The following characters are indicative of *B. b. tenuis: lsic, ldp,* prevailing + variants in position of aperture in th_1, width at the base of th_2. Only in width of rhabdosome measured at the level of th_1 these forms deviate from *tenuis* and rather approach *bohemicus.* Morphological characters of the specimens examined are shown in Pl. XI.

Boulder S. 234. — Range in *lsic* 1.50—1.95 mm (mean 1.72 mm)

(N = 7); diameter of metasicular aperture 0.45—0.70 mm; *ldp* 0.12—0.20 mm; positions of apertural level of th_1 0.30—+0.16 mm (50% + variants), width of rhabdosome at the apertural level of th_1 0.53—0.55 mm; width at the base of th_2 0.20—0.25 mm.

Dorsal apertural process of metasicula strongly variable (Pl. XIX, Figs. A-E), in some cases, strong, shovel-like or conspicuously bifid, in others smaller or almost atrophied. Numerous fragments of rhabdosome, proximal and distal as well, provided with microfusellar additions (Pl. XIX, Fig. F).

Morphological characters of the specimens from boulder S. 234 present themselves as a mixture of features indicative of *bohemicus* (*lsic*, particularly high mean length; rhabdosome very wide at the level of th_1), and, on the other hand, of *tenuis* (diameter of metasicular aperture, small *ldp*, small width at the base of th_2). The evaluation of these contradictory features is very difficult since some quantitative characters as a very long sicula may indicate rather primitive conditions, while some others (as strongly expanded aperture of sicula and a strong variation in size and shape of the dorsal process) — more advanced conditions, or even a certain specialization (deviation from the main direction of evolution). The strongly expanded aperture is, however, not unlike that in some specimens of *B. b. tenuis* found in the Mielnik core (depth 896.20 m; Pl. XV, Figs. B. F), if more extreme one.

The presence of microfusellar additions, indicating the assignment to *B. b. tenuis* seems to be decisive in defining the systematic position. In view of certain peculiarities the form from boulder S. 234 is here referred to as *B. b.* aff. *tenuis*.

Summing up these considerations, we may say that the samples obtained from the boulders of "N" and "Ch" group fit well into the suggested range of *B. b. bohemicus*, extending only ranges of certain characters into greater values (*lsic*, width of rhabdosome in proximal part). This more even strongly stresses their pertinence to the subspecies mentioned above.

The material of *B. bohemicus* obtained from the boulders of "O" group is more heterogenous. Boulder S. 112 may be rather safely assigned to *B. b. bohemicus*, boulders S. 187, S. 224 rather distinctly approach *B. b. tenuis* and the form from boulder S. 234 has features of its own and seems to represent in decisive features a rather specialized local population (chronodeme) which is however, markedly advanced (microfusellar additions, expanded aperture, small *dp* on sicula) and here assigned to *B. b.* aff *tenuis*.

As compared with the material analyzed from the Mielnik core, a greater width in proximal part of rhabdosome is a common feature of *B. bohemicus* from drift material.

SYSTEMATIC PART

Order **Graptoloidea** Lapworth, 1875
Suborder **Monograptina** Lapworth, 1880
Family **Monograptidae** Lapworth, 1873
Subfamily **Neocucullograptinae** n. subfam.

Diagnosis.— Bohemograptids with thecae of simple fusellar structure, or monograptids with microfusellar additions on the apertural margins, based on bohemograptid foundation, but provided with an apertural apparatus in the form of lobate, annular and tapelike structures, or with a complex asymmetric apertural apparatus. Rhabdosomes markedly or strongly curved ventrally in the proximal part.

Genera assigned.— *Bohemograptus* Přibyl, 1967, *Neolobograptus* n. gen., *Neocucullograptus* n. gen.

Stratigraphic distribution.—Prist. vulgaris zone?, *Neocuc. nilssoni* — *Neocuc. kozlowskii* zones (Ludlovian).

Remarks.— Neocucullograptids being, like cucullograptids, a very progressive group of the Upper Silurian monograptids, comprise both the representatives with simple thecal structures and much more specialized forms with a a highly differentiated apertural apparatus. The entire group, embracing forms rather different structurally, is very difficult to determine as a morphological concept. It is more convenient to speak of Neocucullograptinae n. subfam. as a group displaying certain trends than of definite characters, peculiar of this entire assemblage.

These trends are: 1) a persistence of the bohemograptid foundation in the shape of rhabdosome and in thecal structures, resulting in an essentially bohemograptid appearance of all representatives; 2) a tendency to develop microfusellar additions in later stages of phylogeny; 3) a lack of the tendency towards the gracilization of the sicula and its robust appearance throughout the group.

A prefix *neo* is used to stress the similarity to cucullograptids, expressed in the shape of apertural apparatus in *Neocucullograptus* n. gen., combined with its independent and geologically later appearance.

Genus *Bohemograptus* Přibyl, 1967

Type species: Graptolithus bohemicus Barrande, 1850

Emended diagnosis: Monograptids with a distinct or strong ventral curvature of the rhabdosome. Thecae broad and subtriangular, with straight or gently elevated apertural margins, either devoid of or provided with microfusellar additions forming broadly lobate, annular or tapelike apertural structures. Sicula rather robust.

Species assigned: B. bohemicus (Barr., 1850), *B. praecornutus* n. sp., *B. cornutus* n. sp., *B.? butovicensis* (Bouček, 1936).

Stratigraphic distribution: Prist. vulgaris zone? *Neodiv.nilssoni—Neocuc. kozlowskii* zones.

Remarks on the present concept of Bohemograptus. — When erected by Přibyl (1967), *Bohemograptus* was considered as essentially monotypic genus, very uniform morphologically. The discovery of a number of new structural differentiations and new Upper Ludlovian species, described in the present work, contributed to a much wider comprehension of the genus in question. The relationships between known representatives of *Bohemograptus*, and their relationships to other neocucullograptids are briefly discussed below.

An earlier representative, that is *B. b. bohemicus* seems to represent an ancestral species and a common stem of later *Bohemograptus* lineages. It is indicated by its stratigraphic occurrence and morphological characters. Initially represented by robust forms (*nilssoni-progenitor* zones), it displays a certain gracilization as early as in the *parascanicus* zone, and especially in *hemiaversus* horizon, where more advanced gracile forms appear. The variation range in *B. b. bohemicus* seems to comprise both robust and gracile "morphotypes" with numerous transient between them and with the predominance of former "type". Only later these "morphotypes" became segregated to be associated constantly with separated contemporaneous lineages. A further development of the robust type of *B. b. bohemicus* resulted in the appearance of an extremer form, here ranked as a separate species — *B. praecornutus* n. sp. (in *praecornutus* zone). The evolution of the gracile type gave rise to *B. b. tenuis*. In the case of *B. praecornutus* n. sp., this process resulted in the appearance of a rather clear-cut form with distinct specific characters, although doubtlessly being only a further development of *B. b. bohemicus*. Unlike this, the line of evolution leading to *B. b. tenuis* runs through a continuous series of populations and its discrimination consists in the evaluation of certain quantitative and qualitative differences combined with stratigraphical factors (comp. chapter on quantitative analysis). Further speculations on possible mechanisms involved in these changes are given elsewhere (comp. chapter on phylogeny).

Later representatives — *B. praecornutus* n. sp. and *B. b. tenuis* which were appeared as a result of certain divergence (splitting) from *B. b. bohemicus*, are probably themselves ancestral forms of separated lineages. One line extends from *B. praecornutus* n. sp. to *B. cornutus* n. sp., each form of this lineage differing from their ancestor in: 1) stabilized, low position of th_1, placed distinctly below apex prosiculae, 2) presence of lateral elevations on thecal apertures, 3) large-sized sicula. All the three features are only an extremer development of certain characters which do occur in the variation range displayed already by *B. b. bohemicus,* here being only segregated and stabilized.

The other line of evolution, perhaps more important, is that from *B. b. tenuis,* through *Neolobograptus auriculatus* n. gen., n. sp. to *Neocucullograptus* n. gen. It displays great differences between the ancestor and its final descendant, but the starting point in relation to the thecal structure was in 1) a certain gracilization of th_1, 2) its elongation and 3) placing of the thecal aperture in a stabilized position above apex prosiculae. Early populations of *B. b. tenuis* (*aversus-praecornutus* zones) were apparently ancestral to *Neolobograptus* n. gen., but in its later evolution the former subspecies displays a certain specialization (reduction of the dorsal process in sicula.

The divergence of trends in the two lineages with common ancestry is also expressed in a different fate of microfusellar additions. In *B. b. bohemicus,* the microfusellar tissue appears for the first time in *hemiaversus* zone and the primitive pattern of its derivatives are broad lobes or annular platforms composed of a micro- and pseudo-microfusellar tissue. Essentially the same pattern of these derivatives was inherited by *B. praecornutus* n. sp. and *B. b. tenuis.* A later development of these derivatives, produced in the final stage of the first lineage represented by *B. cornutus* n. sp., microfusellar additions composed of both micro- and pseudomicrofusellar tissue (preservation of pseudomicrofusellar fabric) and taking the shape of tape-like lappets. Sicula is omitted and displays no microfusellar additions.

In the second line, the pseudomicrofusellar fabric has already been eliminated in the stage represented by *Neolob. auriculatus* n. sp., the whole additional structure being formed only of the microfusellar tissue. A further development of microfusellar additions resulted in a characteristic and complex apertural apparatus with marked asymmetry and composed of the microfusellar tissue. Sicula, involved into these changes, displays microfusellar additions.

Bohemograptus bohemicus bohemicus (Barrande, 1850)

(Pl. X; Pl. XIII, Fig. *C;* Pl. XX, Fig. *A;* Figs. 10, 11)

1850. *Graptolithus bohemicus* Barrande; J. Barrande, Graptolites..., p. 40, Pl. 1, Figs. 15-18 (Lectotype, Barrande, 1850, Pl. 1, Fig. 15).

1851. *Graptolithus bohemicus* Barr.; E. Suess, Über böhmische..., pp. 110-111, Pl. 8, Fig. 6 *a-e*.

1899. *Monograptus bohemicus* Barr.; J. Perner, Studie..., IIIB, pp. 25-26, Pl. 14, Figs. 15-16; Pl. 17, Figs. 3, 8, 9, 11; Figs. 17-18.

1899. *Monograptus rarus* Perner; J. Perner, *Ibid.,* p. 26, Pl. 17, Fig. 10.

1911. *Monograptus bohemicus* Barr.; G. Elles & E. Wood, Monograph...., pp. 367—368, Pl. 36, Fig. 4 a-d; Fig. 239 a-c.

1936. *Monograptus bohemicus* (Barr.); B. Bouček, Graptolitová fauna..., pp. 3-4, Pl. 1, Figs. 1-3.

1936. *Monograptus zarizelliensis* Haberfelner; E. Haberfelner, Neue Graptolithen..., pp. 87-88, Fig. 1 a-b.

1955. *Monograptus bohemicus* Barr.; W. G. Kühne, Unterludlow-Graptolithen..., pp. 382-384, Fig. 9 (partim, especially Fig. 9 A-D).

1958. *Pristiograptus bohemicus* (Barr.); A. Urbanek, Monograptidae..., pp. 77-80, Figs. 46, 47, 49.

1965. *Pristiograptus bohemicus* (Barr.); A. M. Obut & R. F. Sobolevskaya (*in* Obut, Sobolevskaya & Bondariev), Graptolity silura..., pp. 62-63, Pl. 9, Figs. 5-11; Pl. 10, Figs. 1-2 (Fig. 3 = *B. b. tenuis*?).

1966. "*Pristiograptus*" *bohemicus* (Barr.); A. Urbanek, On the morphology..., pp. 379-380, Pl. 10, Fig. D.

1967. *Pristiograptus bohemicus* (Barr.); T. Koren & R. Ulst (in Gailite, Rybnikova & Ulst), Stratigrafija, fauna..., pp. 253-254, Pl. 29. Fig. 6 a-b; Fig. 68.

1967. *Bohemograptus bohemicus* (Barr.); A. Přibyl, O rodu Bohemograptus..., p. 136, Pl. 1, Figs. 1-6.

Material. — Numerous siculae and rhabdosome fragments including both proximal and distal parts. Most specimens well preserved, unflattened or flattened. Material obtained by chemical treatment from the Mielnik core and erratic boulders of Baltic origin (particularly boulders S. 20, S. 32, S. 111, S. 112). The material obtained enables the analysis of sicula and thecal structure.

Description. — Sicula robust, 1.56—2.00 mm long, gently curved ventrally, rather strongly expanded at the aperture and provided with a distinct dorsal apertural process (Fig. 10; Pl. X; Pl. XIII, Fig. *C*). Certain other quantitative characters of sicula have been analyzed previously (comp. chapter on quantitative analysis). Prosicula 0.40—0.55 mm long, with apex situated, in most specimens, above the apertural level of th_1 Prosicular aperture some 0.11—0.15 mm in diameter, may be situated at the level of the lower margin of the interthecal septum in th_1 (Fig. 10 *B;* Pl. X, Fig. *C*), well above (Fig. 10 *A*), or markedly below it (Pl. X, Figs. *A*, *B*). In certain cases, prosicula provided with the first sicular ring (r_1), situated approximately in the middle or slightly shifted toward aperture (Fig. 10 *A*, *B*). The second sicular black ring (r_2) may be, in these cases, placed right on the boundary of the pro- and metasicula (Fig. 10 *A*) or on the metasicula proper at a certain distance from this boundary (Fig. 10 B). In other cases, prosicula is lacking black rings, the first black ring being situated just on the boundary of pro- and metasicula (Pl. X, Figs. *A*-*C*). Neither longitudinal threads, nor a helical line were discernible, doubtlessly due to unsatisfactory state of preservation.

Metasicula 0.85—1.60 mm long, only slightly curved ventrally, with the strongest bend at the level of the initial bud. Metasicula has 4—6 sicular black rings. The number of these rings varies over the entire sicula from 8 (Fig. 10 *A*) to 3 (Pl. XIII, Fig. *C*), amounting mostly to 5—7. Metasicula gradually widens toward the aperture, being, at the level of the primary notch, 0.25—0.30 mm wide and reaching, at the aperture, a width of 0.26—0.46 mm. Aperture of metasicula displays the presence of a usual-

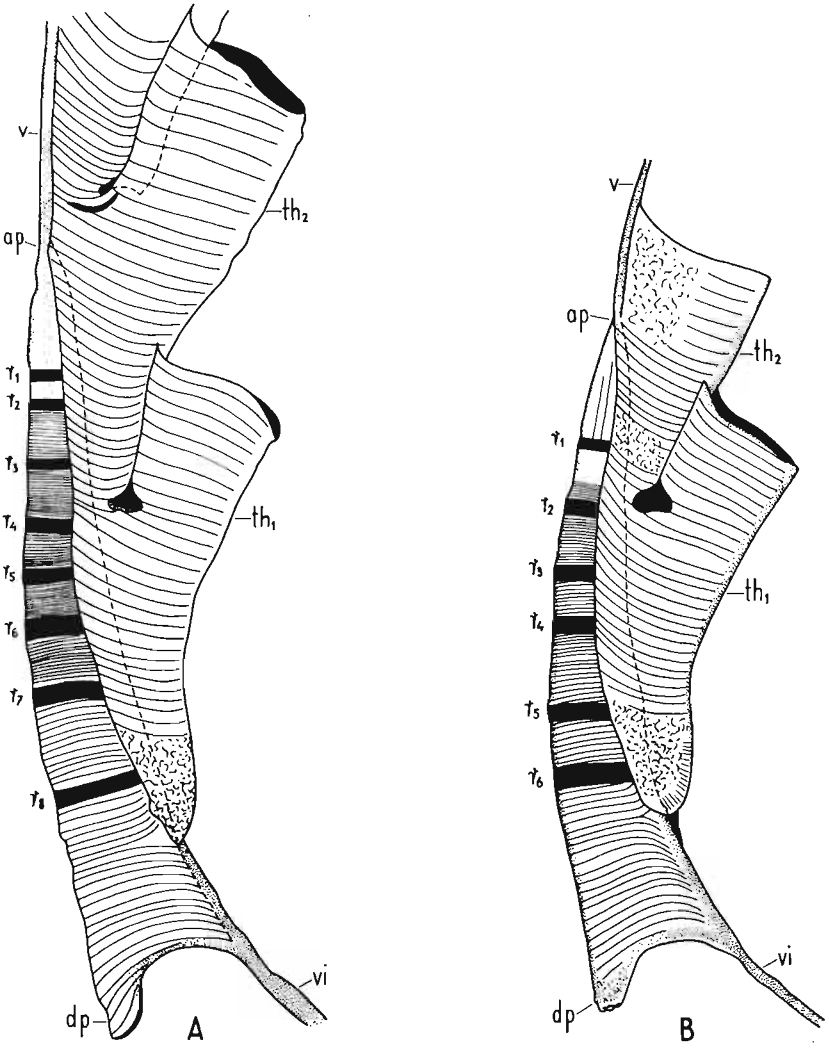


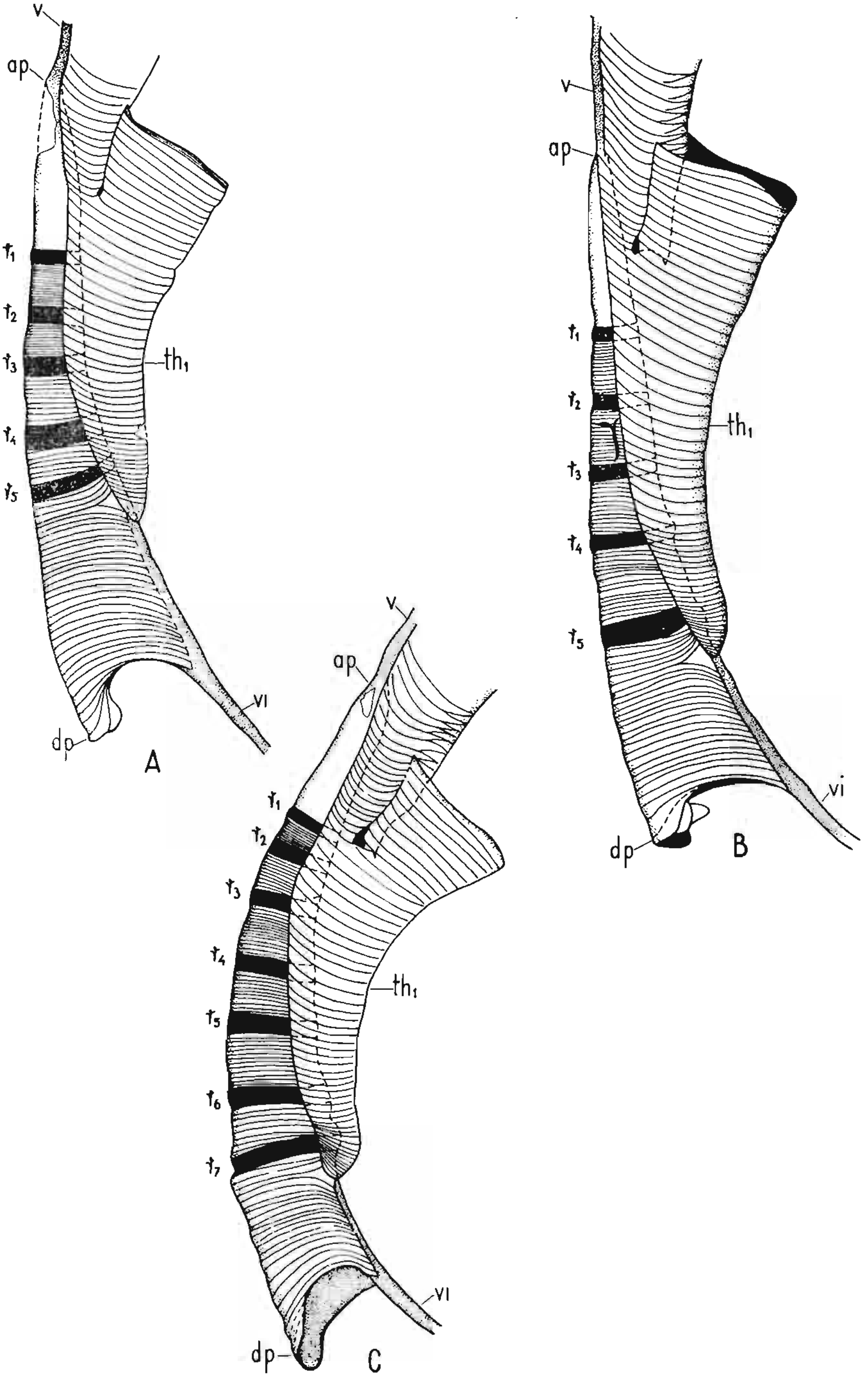
Fig. 10. — *Bohemograptus bohemicus bohemicus* (Barr.). Proximal parts of rhabdosome, *A* fragment of a proximal part, *B* growing proximal part. (Mielnik depth *A* — 1,009.90 m, *B* — 1,005.90 m (*parascanicus* zone); ×50

ap apex of prosicula, *dp* dorsal process of metasicular aperture, r_1—r_8 successive sicular black rings, th_1, th_2 successive thecae, *v* virgula, *vi* virgella.

ly strong virgella and a distinct, mostly shovel-like dorsal process (Fig. 10 *A-B;* Pl. X, Figs. *A, C, dp*) which only rarely is slightly bifid and with two wing-like outgrowths (Pl. X, Fig. *B, dp*). For the development of the dorsal process — see also analysis of quantitative characters.

The structure of the primary notch region indicates a normal monograptid pattern of development. Initial bud is situated 0.75—1.15 mm from the aperture of prosicula and 0.28—0.32 mm from the aperture of

PLATE X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metasicula (for details of the budding of th_1 in *B. bohemicus* see the description of *B. b. tenuis*.

The first theca (th_1) may be rather wide, roughly broadly obtriangular (Figs. 10 *A-B*) to fairly narrow or tubular (Pl. XIII, Fig. *C*) through a certain number of intermediate types (Pl. X, Figs. *A-C*). The first theca is 1.02—1.45 mm and its metathecal par 0.25—0.45 mm long, the prothecal part taking therefore about 60—63% of the total thecal length. In the specimens from Mielnik core, the width at the lower margin of the interthecal septum is 0.23—0.40 mm and at the aperture 0.23—0.40 mm and in the specimens from erratic boulders up to 0.47 mm. In connection with a different shape of th_1, its ventral is more or less gently sloping.

Aperture of th_1 is more or less oblique, in some specimens quite simple (Fig. 10 *P*; Pl. X, Fig. *A*), in others provided with very slight lateral elevations of the border (Fig. 10 *A;* Pl. X, Figs. *B-C;* Pl. XIII, Fig. *C*). For more details on the position of aperture of th_1 in relation to the apex prosiculae see quantitative analysis.

Proximal thecae reach 1.50—1.52 mm in length, their metathecae being 0.49—0.50 mm and prothecae 1.00—1.03 mm long. They are to 0.33—0.35 mm wide at the base of protheca, 0.42 mm at the base of metatheca and 0.49—0.50 mm at the aperture. Prothecal segment takes about 67—70% of a total length. For other dimensions in proximal thecae see also chapter on quantitative analysis.

Distal thecae are 1.73—2.05 mm and their metathecal segments 0.55—0.85 mm long. Prothecal parts occupy about 59—69% of a total thecal length. The width of distal thecae, measured at the apertural level, increases to some 0.53—0.57 mm, amounting to 0.40—0.42 mm at the base of metatheca.

Microfusellar additions were noted only in a specimen from Mielnik core (depth 957.90 m, *hemiaversus* zone; Fig. 11). Microfusellar additions seem, therefore, to occur in *B. b. bohemicus* very rarely, to appear late and only in the uppermost part of its distribution range. This conclusion is confirmed by the observation of specimens from erratic boulders. In boulders of groups "N" and "Ch", as defined previously, no traces of microfusellar tissue were found (comp. chapter on *B. bohemicus* from drift material).

Microfusellar additions, found in a specimen with clear characteristics of true *B. b. bohemicus* (*lsic* — 1.97 mm, *ldp* — 0.15 mm, diameter of aper-

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Plate X

Bohemograptus bohemicus bohemicus (Barr.). Proximal parts of rhabdosome. *A—C* siculae with first thecae showing variation of certain characters (Mielnik, depth 957.90 m *hemiaversus* zone); ×50.

ap apex of prosicula, *dp* dorsal process of metasicular aperture, r_1—r_7 successive sicular black rings, th_1 first theca, *v* virgula, *vi* virgella.

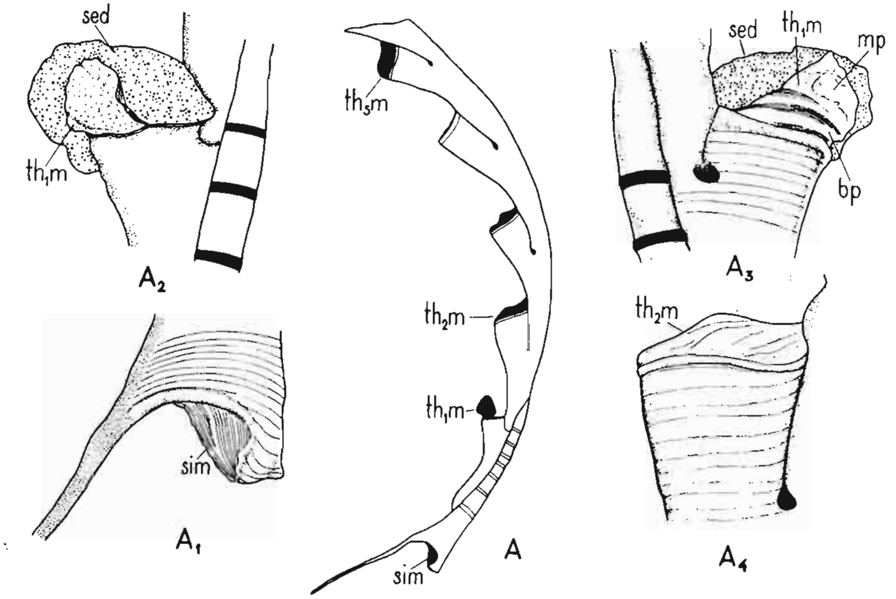


Fig. 11. — *Bohemograptus bohemicus bohemicus* (Barr.), Proximal part of rhabdosome with microfusellar additions, *A* general appearance of specimen from obverse side (microfusellar additions shown in solid black), A_1 details of microfusellar additions of metasicular aperture, A_2—A_3 same in th_1 seen from obverse and reverse sides, A_4 details of microfusellar addition on th_2 (Mielnik, depth 957.90 m, *hemiaversus* zone); ×12, A_1—A_4×47.

bp basal part of microfusellar addition, *mp* membranaceous part of microfusellar addition, *sed* grains of sediment attached to periderm, *sim* microfusellar addition on metasicular aperture, th_1m-th_5m microfusellar additions in corresponding thecae.

ture in *msi* — 0.40 mm, position of aperture in th_1 — 0.23 mm), consist of minute additional, microfusellar membranes laid down in corners of the dorsal apertural process of metasicula (Fig. 11 — *sim*) and of additions built of microfusellar tissue and superimposed on thecal apertures. Especially remarkable are microfusellar additions in th_1 (Fig. 11, $th_1\,m$), which consist of a basal part, forming an elevation composed of densely crowded fuselli (*bp*) and of a broad, membranaceous prolongation (*mp*). The latter produces, on both sides of apertural margin, a kind of a wing-like, thin-walled lobe, each of these lobes being probably separated on the ventral side of the aperture by a narrow fissure. This structure, which does not differ principally from typical velum, described further in *B. b. tenuis*, has therefore been paired.

The fact that microfusellar additions in *B. b. bohemicus* may attain more extreme form of membranaceous, widely spread, lobate structures is indicated by the findings of isolated, probably broken-off thecal apertures, fragments of such structures displaying a characteristic microstructure (depth 950.90 m, *hemiaversus* zone). Microfusellar additions found in other thecae are simple, paired, lateral elevations (as in the case of th_2

(Fig. 11, th_2m), or a rather high, continuous walls ("collars") laid down on the apertural border of the theca proper (Fig. 11, th_5m). As in *B. b. tenuis*, microfusellar additions here display, in one and the same rhabdosome, a remarkable, irregular variation in morphological form. The significance of the appearance of a capability to produce microfusellar tissue and its derivatives to the intrapopulationary variation is discussed below.

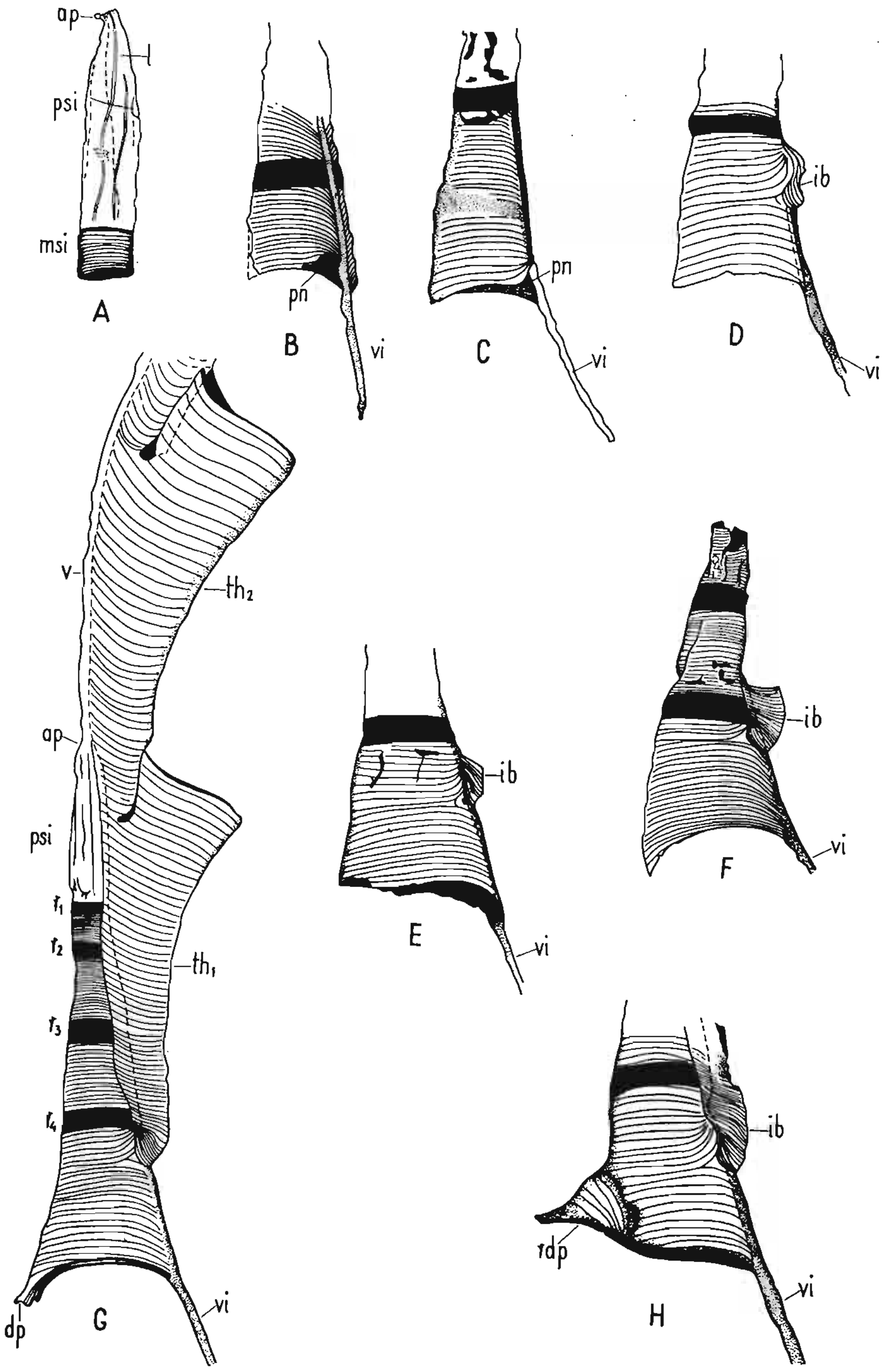
The lack of more complete rhabdosomes does not enable determining its shape. The degree of curvature in proximal part of rhabdosome seems, however, to be smaller than in *B. b. tenuis*, this part being almost straight or only gently curved. The curvature, measured as an angle between lines tangential to the dorsal wall of sicula and to the fourth theca (Fig. 1) may be estimated at 140°. Due to the lack of suitable, sufficiently long fragments, the number of thecae in 10 mm has not been determined.

Stratigraphic range. — In the Mielnik core, *B. b. bohemicus* makes its first appearance at a depth of about 1.020 m in the *progenitor* zone of the Mielnik Beds (Urbanek, 1966, Pl. 1, range chart). Fauna, etched from the Baltic erratic boulders, clearly indicates, however, its earlier appearance and occurrence in the underlying *nilssoni* zone (comp. pp. 207). A later appearance of *B. b. bohemicus* in Mielnik seems to have only local significance. It may be safely generalized that *B. bohemicus* is already present in the *nilssoni* zone. Reports on its still earlier occurrencies in the *vulgaris* zone (Jaeger, 1959, p. 35; Horný, 1962, p. 883, range chart; Přibyl & Vaněk, 1968, p. 416), are probably reliable but need more evidence. The upper limit of the distribution range of *B. b. bohemicus* coincides, as here defined, with the boundary of *hemiaversus* and *aversus* zones, which in the Mielnik core corresponds to a depth of 940.5 m and may be roughly correlated as lying somewhat below the bottom of the *leintwardinensis* zone (see Urbanek, 1966, p. 314, Table 1).

Throughout its range, *B. b. bohemicus* is a rather rare form, never predominating in graptolite associations obtained from particular samples. The same is indicated by fauna from Baltic drift, where *B. b. bohemicus*, found in boulders of "N" and "Ch" groups is by no means rare but nevertheless represents rather an admixture to much a richer association of other species.

The variation of *B. b. bohemicus* in particular horizons seems to be indicative of a certain zonal evolution in its morphological characters. The only well preserved sicula from *progenitor* zone is large-sized (*lsic* 2.00 mm) and associated thecae are robust. About the same has been noted in *B. bohemicus* from the lower part of the *parascanicus* zone, in which robust forms of *B. bohemicus* (Fig. 10) still predominate. Characteristics of *B. b. bohemicus* from boulder S. 20 (*nilssoni* zone) are consistent with the above generalization. The boulders with association indicative of the *parascanicus* zone contain also in most cases rather robust forms.

PLATE XI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We may tentatively distinguish: 1) a group of lower zonal populations of *B. b. bohemicus*, characterized by the predominance of specimens with large-sized sicula (1.75—2.00 mm), a low position of aperture in th_1 (— variants), and a greater width of rhabdosome in proximal parts (*nilssoni-parascanicus* zones); 2) a group of higher zonal populations (*invertus-hemiaversus* zones) marked by a certain gracilization (comp. Pls. X, XI, Fig. C), less frequent occurrence of robust forms with large-sized siculae and wide proximal part of rhabdosome. In the highest horizons, microfusellar additions appear for the first time.

Bohemograptus bohemicus tenuis (Bouček, 1936)

(Pls. XI, XII; Pl. XIII, Figs. *A-B;* Pls. XIV-XIX; Pl. XX, Fig. *B;* Pls. XXI-XXII; Figs. 12-15)

1936. *Monograptus bohemicus tenuis* Bouček; B. Bouček, Graptolitová fauna..., p. 4, Pl. 1, Figs. 4-5.
1955. *Monograptus bohemicus* (Barr.); W. G. Kühne, Unterludlow-Graptolithen..., pp. 382-384, Fig. 9 (partim, especially Fig. 9 G).
1958. *Pristiograptus bohemicus* (Barr.); A. Urbanek, Monograptidae..., pp. 77-80, Figs. 48, 50, 51; Pl. 4, Figs. 1-3.
1965. *?Pristiograptus bohemicus aff. tenuis* (Bouč.); A. M. Obut & R. F. Sobolevskaya (*in* Obut, Sobolevskaya & Bondariev), Graptolity silura..., Pl. 10, Fig. 4.
1967. *Pristiograptus bohemicus tenuis* (Bouč.); T. Koren & R. Ulst (in Gailite, Rybnikova & Ulst), Stratigrafija, fauna..., pp. 254-255, Pl. 29, Fig. 7.

Material. — Numerous siculae and fragmentary rhabdosomes (the longest, 40 mm), including both proximal and distal parts. Most specimens well preserved, unflattened, or flattened. Material obtained by chemical treatment from Mielnik core and from erratic boulders of Baltic origin (especially boulders S. 187, S. 224, S. 234). Young siculae and early stages of astogeny best preserved in drift material.

Description. — Adult sicula 1.36—1.89 mm in length, almost straight or gently curved ventrally with the strongest bend at the level of initial bud (Pl. XI, Fig. *G;* Pl. XIII, Figs. *A-B;* Pl. XIV, Figs. *A-B;* Pl. VI, Fig. *A;* Pl. XVI, Figs. *A-B;* Pl. XVII, Figs. *A-C;* Pl. XVIII, Fig. *A*).

Prosicula 0.39—0.58 mm, rarely to 0.60 mm and usually to 0.40—0.45 mm in length. Prosicula 0.10—0.12 mm wide at aperture, in adult siculae, invariably provided with the first black ring (r_1). Stabilization

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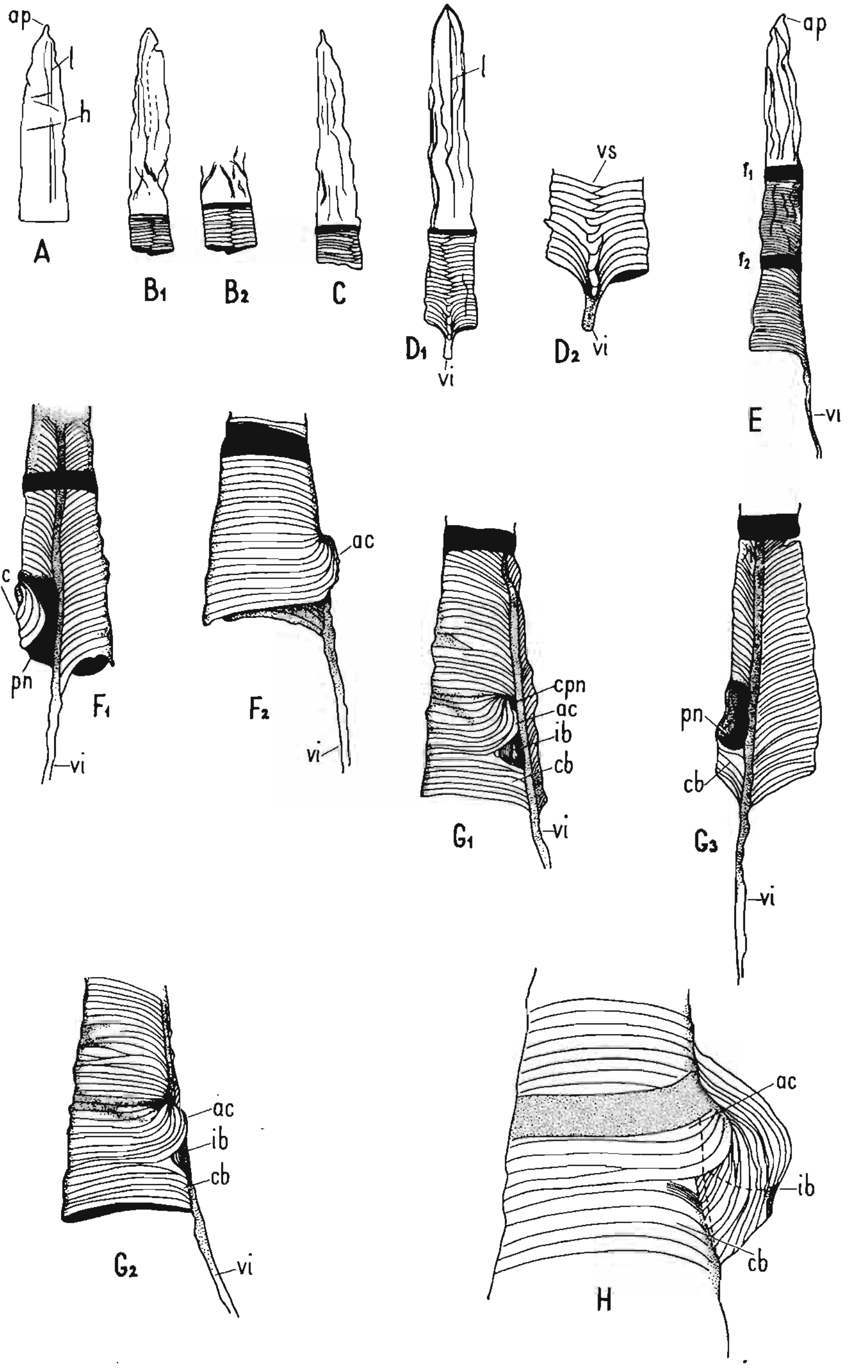
Plate XI

Bohemograptus bohemicus tenuis (Bouč.). Early growth-stages and the proximal part of rhabdosome. A prosicula and early growth-stage of metasicula, *B—C* primary notch seen ventro-laterally and laterally, *D—F* successive growth-stages of of initial bud, *G* proximal part of rhabdosome, *H* regeneration of damaged dorsal process of metasicula (erratic boulder S. 224, Rewal); *F—G*×63 all remaining×50

ap apex of prosicula, *dp* dorsal process of metasicular aperture, *ib* initial bud, *l* longitudinal threads on prosicula, *msi* metasicula, *pn* primary notch, *psi* prosicula, r_1—r_4 successive sicular black rings, *rdp* regenerated dorsal apertural process in metasicula, th_1, th_2 first and second theca, *v* virgula, *vi* virgella.

PLATE XII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of r_1 right on the boundary with metasicula contrasts rather sharply with its changing position in *B. b. bohemicus.*

Prosiculae analyzed in young, growing siculae (Pl. XII, Figs. *A*-D_1; Pl. XI, Fig. *A*), display the presence of a number of longitudinal threads (*l*) and rather indistinct, faint traces of a helical line (*h*). Apical parts of prosicula (*ap*) somewhat pointed, but not forming a distinct nema.

The growth of metasicula begins with deposition of first fuselli, as illustrated in Pl. XII, Figs. *B-C* and Pl. XI, Fig. *A, msi.* At a certain distance, through change in arrangement of fuselli on ventral zigzag suture, a short outgrowth is formed, which is the beginning of a virgella (Pl. XI, Fig. D_1-D_2, *vi*). In the meantime, incipient thickening discernible at the prosicular aperture (Pl. XII, Fig. B_2) is gradually transformed into the first sicular black ring (r_1), and successive black rings appear as the metasicula grows (r_2, Pl. XII, Fig. *E*). Virgella is prolonged into a strong spine, projecting beyond the aperture (*vi*).

Primary notch begins as an incision in the margin of metasicula close to virgella (Pl. XI, Figs. *B, C, pn*), being formed by a peculiar, well known arrangement of fuselli, typical of the monograptid type of development. By further deposition of arcuately curved fuselli the primary notch is completed (Pl. XII, Figs. F_1, F_2 *pn, ac*) to form a deep foramen for the th_1 bud ("sinus" stage). A number of fuselli growing to meet once again the virgella, enclose the primary notch (Pl. XII, Figs. G_1-G_3, *cb, pn*). This results in a closed primary notch stage of development ("lacuna" stage).

Meanwhile, when metasicula continues to grow, initial bud appears, with first narrow, fusellar strips laid along the corner of the primary notch on the reverse side opposite the virgella (Pl. XII, Figs. G_1-G_3; Pl. XI, Figs. *D-E, ib*). The first strips are very short and single, filling only the incision formed between arcuately curved fuselli (*ac*) and fuselli which enclose the primary notch in the form of a closing bar (*cb*). Later, fuselli gradually extend along the margins of the primary notch and consist of two strips joining their oblique sutures to form initially irregular zigzag suture (Pl. XI, Fig. *E*; Pl. XII, Fig. *H, ib*). By later addition of fuselli, the initial bud takes the form of a short, widely open tubule, gently turning

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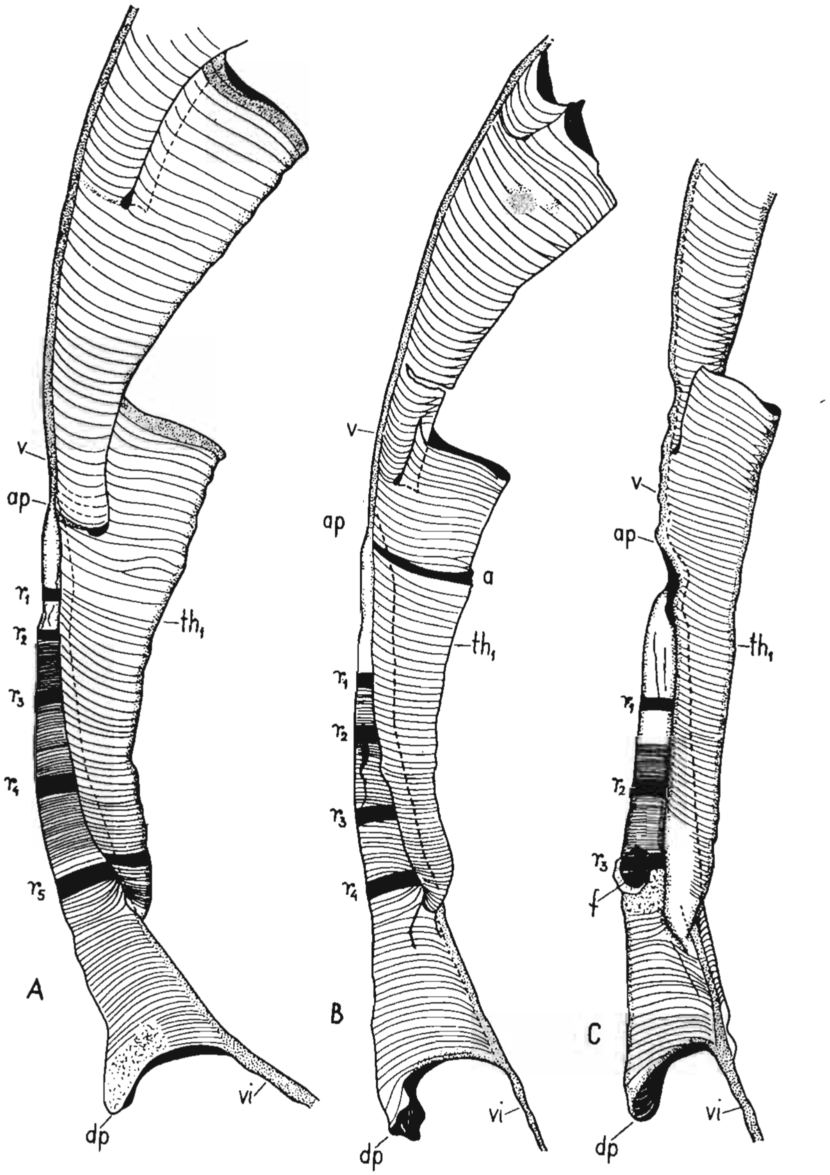
Plate XII

Bohemograptus bohemicus aff. *tenuis*. Growth-stages of sicula and formation of initial bud. *A* prosicula, B_1—B_2—*C* early growth-stages of metasicula, D_1—D_2 early stage of formation of virgella, *E* young metasicula seen in reverse aspect, F_1—F_2 open primary notch ("sinus stage") in ventral and lateral aspects, G_1—G_3 closed primary notch ("lacuna stage") in ventrolateral, reverse and ventral aspects, *H* early stage in formation of initial bud (erratic boulder S. 234, Mochty); B_2,D_2, *F*—*G*×63, *H*×120 all remaining×50.

ac series of fuselli on side of the primary notch showing an archline arrangement, *ap* apex of prosicula, *cb* fusellar bands closing the primary notch, *cpn* cloced primary notch („lacuna"), *h* traces of helical line. ib initial bud, *l* longitudinal threads on prosicula, *pn* open primary notch („sinus"), r_1—r_2 successive sicular black rings, *v* virgula, *vi* virgella, *vs* ventral zigzag suture.

PLATE XIII



Bohemograptus bohemicus tenuis (Bouč.). (*A,B*) and advanced gracile morphotype in *B.b. bohemicus* (Barr.) (*C*). Proximal parts of rhabdosome in reverse aspect. (Mielnik, depth *A*, 934.50 m, *B* 932.70 m, *aversus* zone, *rostratus* subzone; c 955.90 m, *hemiaversus* zone); ×50.

a thickening marking interrupted growth and earlier level of aperture, *ap* apex of prosicula, *dp* dorsal apertural process of metasicula, *f* foramen formed probably due to damage of the periderm, r_1—r_5 sucsessive sicular black rings, th_1 first theca, *v* virgula, *vi* virgella.

the direction of its growth from the reverse side, to the plane of symmetry (Pl. XI, Fig. *H*; Pl. XII, Fig. *H*, *ib*). The first theca continues to grow upwards by further addition of fuselli to the edges of the thecal tubule.

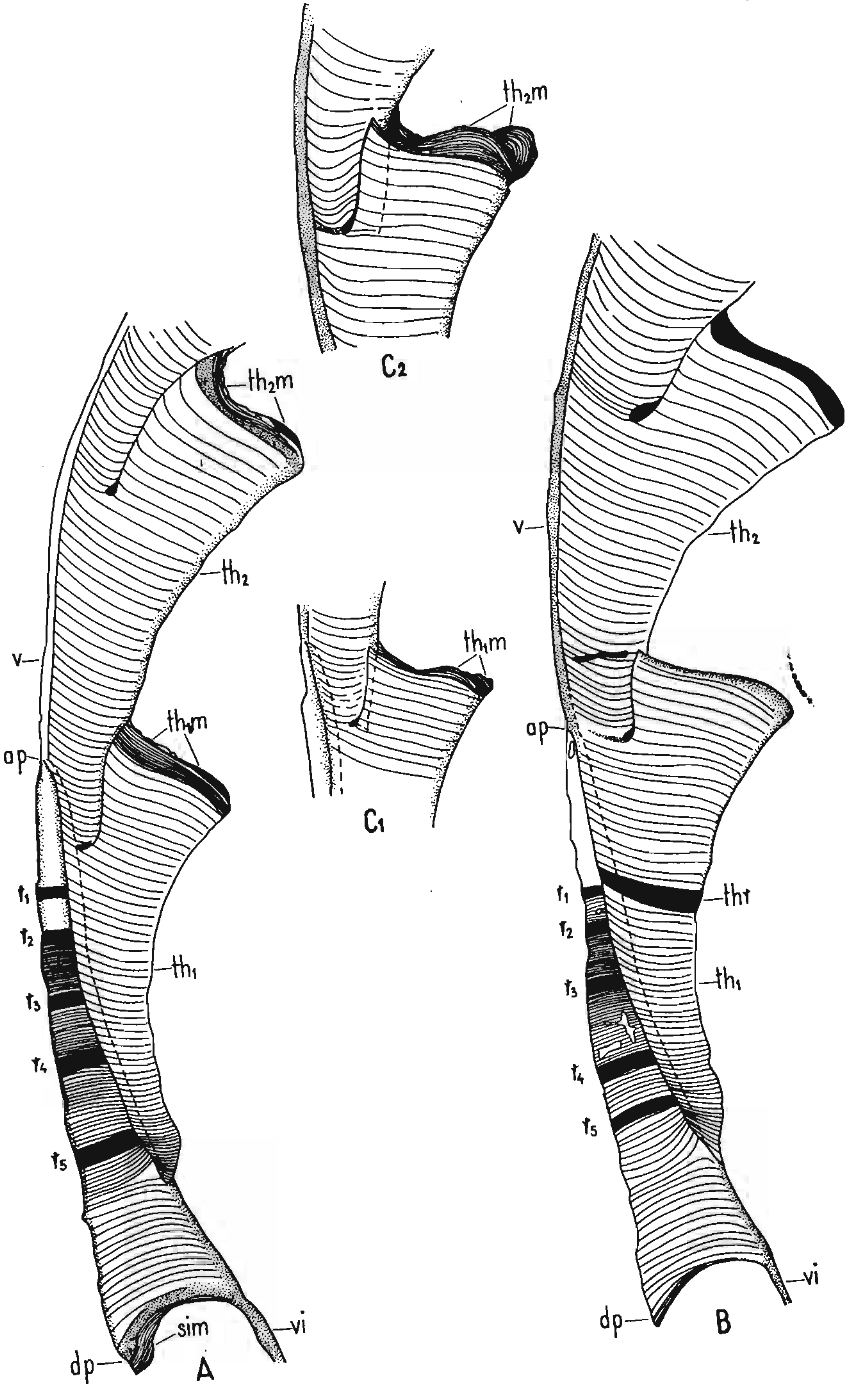
Adult metasicula 0.93—1.23 mm long, 0.21—0.27 mm wide at the level of the primary notch, and 0.28—0.50 mm at the aperture. Aperture of metasicula is provided with virgella and the dorsal process. In populations from lower horizons (*praecornutus-auriculatus zones*), this process is more prominent, although on the average rather smaller than that in *B. b. bohemicus* (Pl. XI, Fig. G; Pl. XIII, Figs. *A-B*; Pl. XIV, Figs. *A-B*; Pl. XV, Fig. *A*; Pl. Figs. *A-B*, *dp*).

In the representatives of higher horizons (*inexspectatus-kozlowskii* zones), the length of the dorsal process markedly decreases (Pl. XVII, Figs. *A-C*; Pl. XVIII, Figs. *A-D*, *dp*), which seems to indicate a progressive tendency toward reduction of the process (for numerical data see quantitative analysis). In metasicula, there is a considerable range in variation of the character of aperture, even in single sample (Pl. XV, Figs. *B-F*, *dp*). A number of extreme variants with strongly expanded aperture, giving the sicula a peculiar, trumpet-like shape, have been noted (Pl. XV, Figs. *E*,*F*). Especially remarkable is the shape of the metasicular aperture in specimens of *B. b.* aff. *tenuis* from boulder S. 234. This population displays a predominance of specimens with extremely expanded apertures (0.65—0.75 mm) provided with a normal dorsal process (Pl. XIX, Fig. *C*, *dp*), or an abnormal one, which forms paired elevations on the margin (Pl. XIX, Fig. *B*, *adp*), separated by a shallow notch. It may also display an only rudimentary dorsal process (Pl. XIX, Fig. *A*). Specimens provided with a normal dorsal process also show a rather great morphological variation, this process being entire and shovel-like (Pl. XIX, Fig. *D*, *dp*), or bifid, with two lateral wings separated by a median notch (Pl. XIX, Fig. *E*, *w*, *n*). This great variation is not significant evolutionary as indicated by rich populations from *kozlowskii* zone showing again rather normal aperture and rudimentary dorsal process which is only a slight, tongue-like elevation on the margin (Pl. XVIII, Figs, *A-D*, *dp*). The variation may be related with process of rudimentation of the structure in point.

In *B. b. tenuis*, sicula displays 3—7 (mostly 4) black rings. The first sicular black ring (r_1) is invariably placed on the boundary of pro- and metasicula. Its stabilization and a certain limitation of the number of black rings as compared with *B. b. bohemicus*, seems to be characteristic of the subspecies under study.

In most specimens the first theca (th_1) is more gracile than in *B. b. bohemicus* (Pl. XI, Fig. *G*; Pl. XIII, Figs *A-B*; Pl. XIV, Fig. *A*; Pl. XV, Fig. *A*; Pl. XVI, Figs. *A-B*; Pl. XVII, Fig. *A*), although specimens with rather short and wide th_1 also occur in lower (Pl. IV, Fig. *B*, from *praecornutus* zone) and higher horizons (Pl. XVIII, Figs. *B-C*, from *kozlowskii*

PLATE XIV



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zone). It is 1.05—1.47 mm and its metathecal part 0.12—0.30 mm long, the prothecal part taking about 73—80% of the total thecal length. The width of the th_1 is 0.22—0.35 mm at the base of its metatheca and 0.23—0.40 mm at the aperture. Aperture of th_1 more or less oblique, in most specimens above or at the level of the apex prosiculae (for numerical data see quantitative analysis). But even in higher horizons, considerable differences occur in a relative position of th_1, as in the specimens from *kozlowskii* zone, in which it varies from markedly low (Pl. XVII, Fig. *C*, *h*), through that almost at the level of prosicular apex (Pl. XVII, Fig. *B*, *h*), to the aperture of th_1 occurring clearly above the latter (Pl. XVII, Fig. *A*, *h*). Frequently, this high position of aperature in th_1 has been reached secondarily as a result of the interrupted growth (Pl. XVI, Fig. *C*). Primarily, the aperture was situated at the level of prosicular apex (a_1) and even produce a characteristic thickening of the margin. Later, the next segments corresponding to lower and upper parts of metatheca were built on, separated by a discordance marking the next temporary apertural level (Pl. XVI, Fig. *C*, a_2). Consequently, a definite aperture of th_1 occurs well above the apex of prosicula (a_3). These periods of arrested growth in th_1 were reflected in similar periods of less rapid growth in a simultaneously growing th_2 and marked by condensations of very fine strips (Pl. XVI, Fig. *C*, p_1, p_2). This slightly abnormal mode of growth in th_1 contrasts with specimens displaying continuous upward extension of th_1 (Pl. XVI, Figs. *A*, *B*, th_1).

In certain specimens, th_1 displays thecal black rings, which are internal thickenings of the thecal tube, probably homological with sicular black rings. Their number varies from 1 to 4, in the last-named cases some of them are rather faintly marked (Pl. XVII, Fig. *B;* Pl. XVIII, Fig. *B;* Pl. IV, Fig. *B*, *thr*).

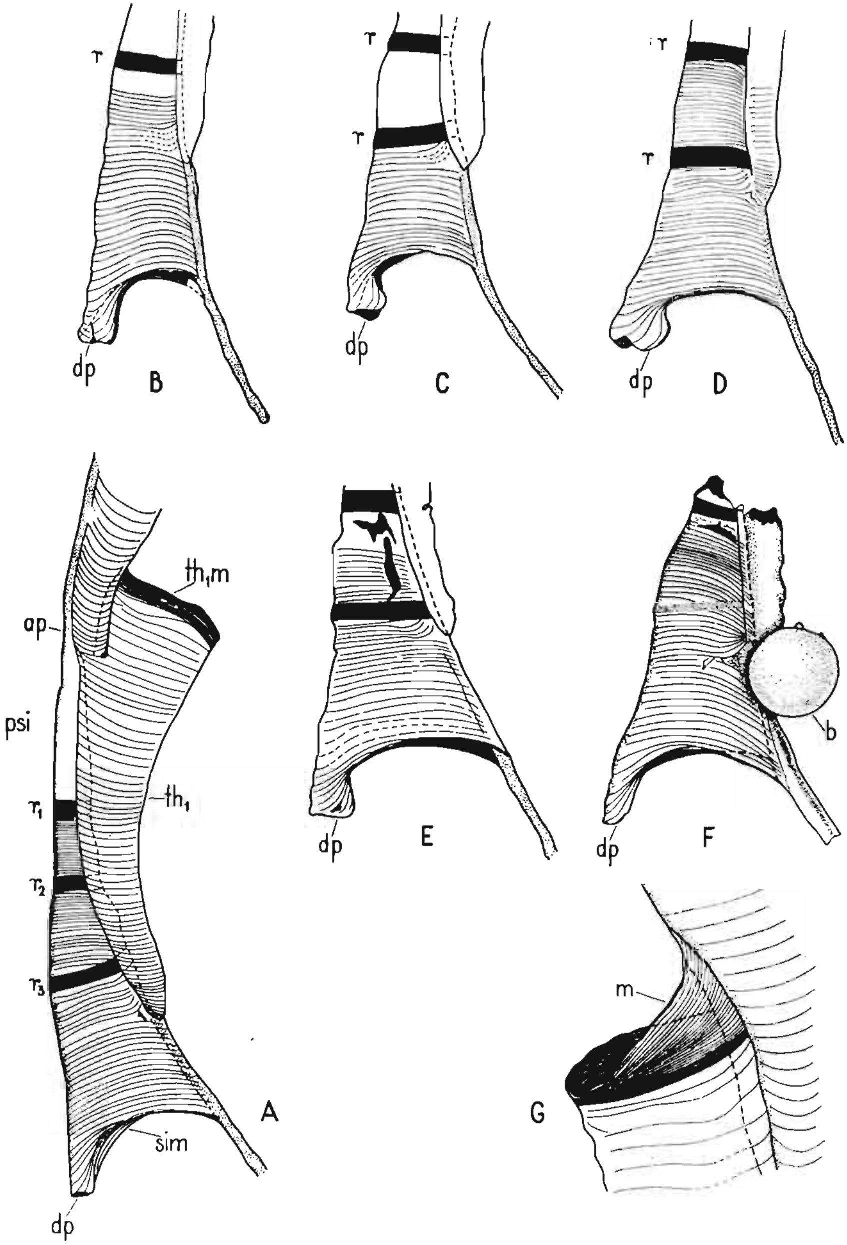
Apertural margins of th_1 are almost straight (as in Pl. XVI, Figs. *A*-*B*; Pl. XVII, Fig. *A*), or somewhat elaborated and forming gentle elevations (Pl. XVIII, Figs. *A*-*D*; Pl. XVII, Fig. *C*; Pl. XIV, Fig. *B*).

Proximal thecae (Pl. XVI, Figs. D_1-D_2) 1.35—1.60 mm in length, their metathecae being 0.35—0.50 mm and prothecae about 1.00—1.12 mm long.

Plate XIV

Bohemograptus bohemicus tenuis (Bouč.). Proximal parts of rhabdosome showing thecae lacking and provided with microfusallar additions. *A* sicular part of rhabdosome showing sicula and thecae provided with microfusellar addition, *B* proximal part of rhabdosome showing sicula and thecae lacking the microfusellar structures, C_1—C_2 apertural part of the first and second theca of another rhabdosome provided with microfusellar additions (Mielnik, depth *A* 922.10 m, *aversus* zone; *B*—*C* 856.80 m, *kozlowskii* zone).

ap apex of prosicula, *dp* dorsal process of metasicular aperture, r_1—r_5 successive sicular black rings, *sim* microfusellar addition on aperture of sicula, th_1, th_2 first and second theca, th_1m, th_2m microfusellar addition on aperture of first and second theca, *thr* thecal rings, *v* virgula, *vi* virgella.



Bohemograptus bohemicus tenuis (Bouč.). Proximal part of rhabdosome (*A*), variation of metasicular aperture (*B—F*), and form of the microfusellar additions (*G*). (Mielnik, depth 896.20 m, *auriculatus* zone).

ap apex of prosicula, *b* foreign body attached to sicula, probably a *Tasmanites*, *dp* dorsal process of metasicular aperture, *m* asymmetric microfusallar addition laid down on aperture of third theca, *psi* prosicula, r_1—r_3 successive sicular black rings, *sim* incipient microfusellar addition on aperture of metasicula, th_1m incipient microfusellar addition on aperture of the first theca.

They are 0.27—0.48 mm wide at the base of metatheca and 0.32—0.50 mm at the aperture. The length of a prothecal segment is about 70% of the total thecal length. For other dimensions in proximal thecae see analysis of variation.

Distal thecae (Pl. XX, Fig. *B*) are 1.55—1.86 mm and their metathecal segments 0.55—0.84 mm long. Prothecal parts occupy about 54—64% of the total thecal length. The width of distal thecae, measured at the base of metatheca, is 0.53—0.65 mm and 0.60—0.72 mm at the aperture. Frequently, the aperture in distal thecae is slightly elaborated, displaying the presence of gently marked lateral elevations. Certain elaboration of thecal apertures seems to be especially characteristic of higher zonal forms, where it prevails in distal and proximal thecae as well (comp. Pls. XVII, XVIII).

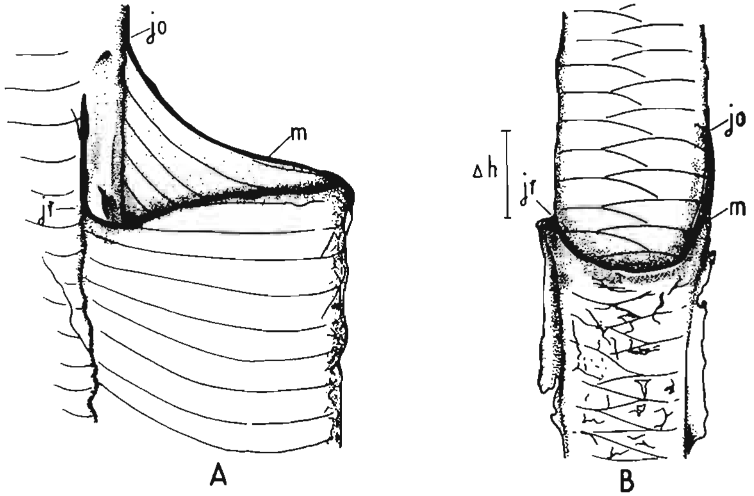
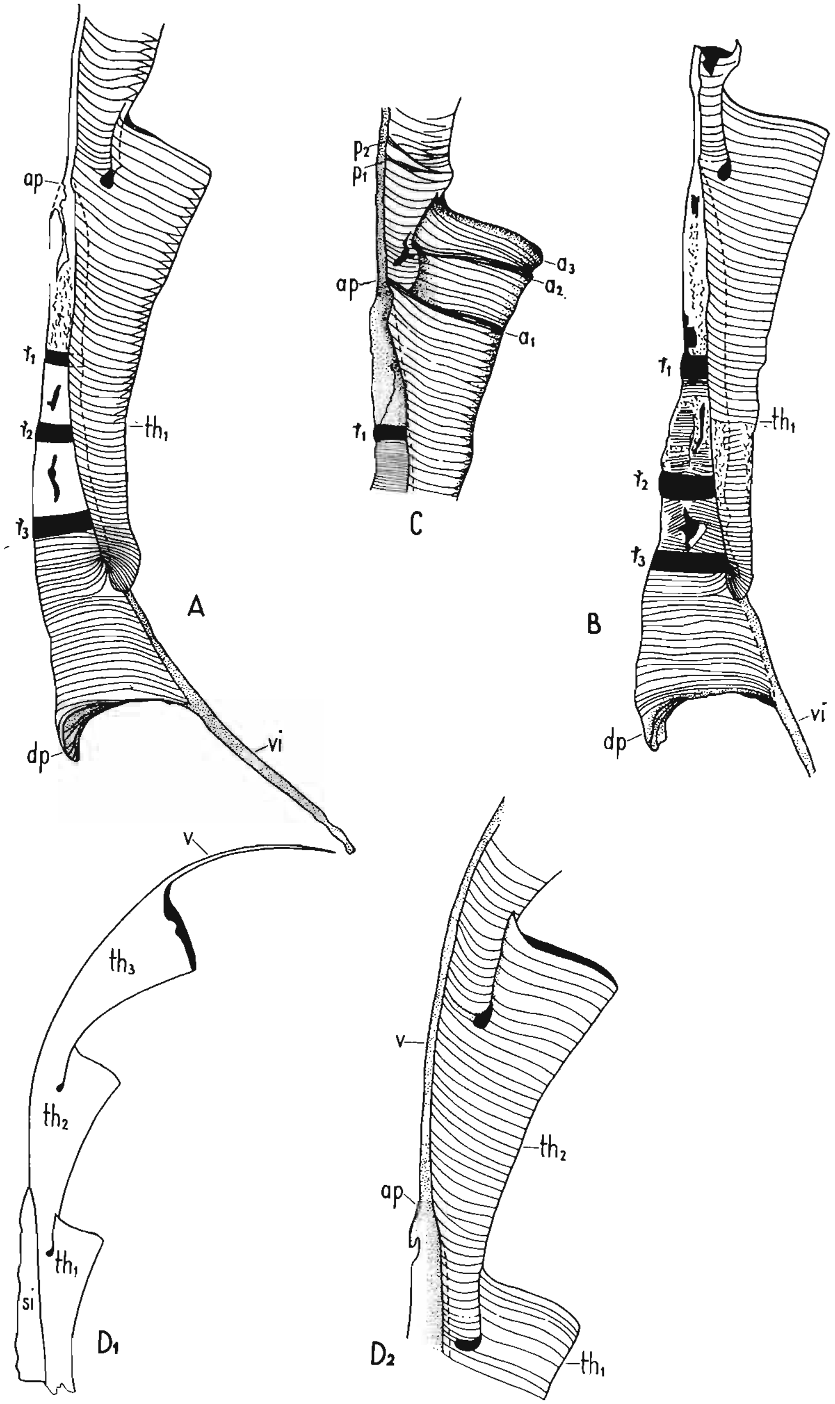


Fig. 12. — *Bohemograptus bohemicus* cf. *tenuis* (Bouček). Asymmetric apertural margin in a theca *A* seen from reverse side, *B* from ventral side (erratic boulder S. 61, Dziwnów);×50.

Dh difference between levels of junction of apertural margin on reverse and obverse side, *jo*, *jr* point of junction of apertural margin to wall of adjacent theca on obverse and reverse sides, *m* thickened margin of aperture.

In certain cases (erratic boulder S. 61 and a sample from the Mielnik core, depth 872.40 m, *kozlowskii* zone), specimens were found whose medial and distal thecae displayed a certain asymmetry (Figs. 12, *A*-*B*). This is due to the difference between the levels of fusion of apertural margins with the ventral wall on the obverse and reverse side of the adjacent theca (*jo*, *jr*). Apertural margin is thus suspended conspicuously higher on its left, obverse side. Associated proximal thecae reveal no or only very slight asymmetry. The significance of this asymmetry being not clear, its rather abrupt manifestation may indicate a certain latent asymmetry of *B. b. tenuis* (asymmetry of soft parts only rarely reflected in peridermal structures?).

PLATE XVI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The picture of thecal structure presented above may be complicated by the appearance of microfusellar additions.

In the proximal part of *B. b. tenuis* rhabdosome is rather strongly curved ventrally. The degree of this curvature displays a considerable variability, which is probably partly due to preservational factors and partly corresponds to primary variability. There is, however, no indication of tectonic deformations of the fossils and the secondary changes connected with lithogenesis, although difficult to estimate quantitatively, seem to be rather limited. The curvature in the proximal part of rhabdosome, measured as an angle between lines tangential to dorsal walls of sicula and th_4 (comp. Fig. 1) varies between 105° and 135°. A strong bend observed on some specimens at the level of th_2 or th_3 (up to 80°) seems to be a secondary deformation, due rather to extreme narrowness of rhabdosome at the points indicated. *B. b. tenuis* seems to be generally more strongly curved than *B. b. bohemicus.*

Seven thecae occur in 10 mm of the distal part of rhabdosome, 8 in medial part, and an estimated number of thecae in proximal part is about 10 in 10 mm.

Microfusellar additions and the "veliger" morph concept. — In *B. b. tenuis*, microfusellar additions have been noted almost throughout its range of distribution from the upper part of the *aversus* zone (*rostratus* subzone, the first occurrence noted at a depth of 925.90 m in the Mielnik core), to the upper part of the *kozlowskii* zone (depth 854.60 m in the Mielnik core, in population marking last appearance of *B. b. tenuis* in this core). Also in the drift material (erratic boulder S. 234), the microfusellar tissue is associated with the thecae determined above as *B. b.* aff. *tenuis.*

Although never frequent, microfusellar structures on sicula and thecae seem to be a steady and characteristic element in populations of *B. b. tenuis* from all horizons. Each larger sample from the Mielnik core contains a number of specimens with microfuselar additions. These display a considerable, usually capricious pattern of variation, representing a number of morphological structures, whose significance and mutual relations are not easy to determine (Pl. XIV, Figs. *A*, C_1-C_2; Pl. XXI; Pl. XXII).

In most cases, rhabdosomes which display a capability of forming microfussellar tissue are provided with siculae also displaying some

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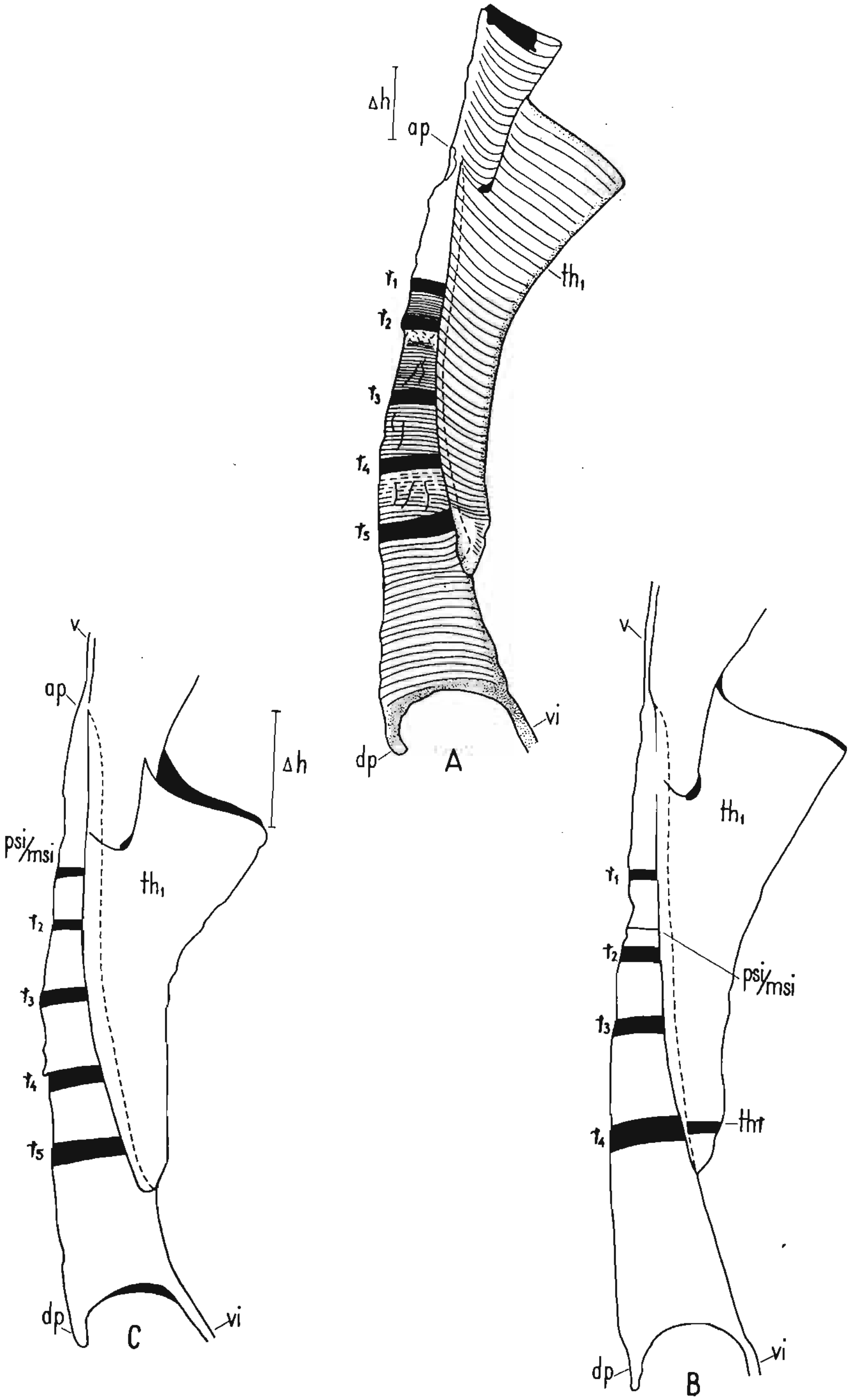
Plate XVI

Bohemograptus bohemicus tenuis (Bouč.). Sicula and proximal part of rhabdosome. *A—B* sicula with first theca, *C* interruptions of growth in first theca, *D* thecae of proximal part of rhabdosome (D_1) with enlarged second theca (D_2). (Mielnik, depth 893.70, *auriculatus* zone); D_1×25, all remaining×50.

a_1—a_3 successive apertural levels of the first theca, *ap* apex of prosicula, *dp* dorsal process of sicular aperture, p_1—p_2 traces of arrested growth in the second theca, r_1—r_3 successive sicular black rings, *si* sicula, th_1—th_3 successive proximal thecae, *v* virgula, *vi* virgella.

PLATE XVII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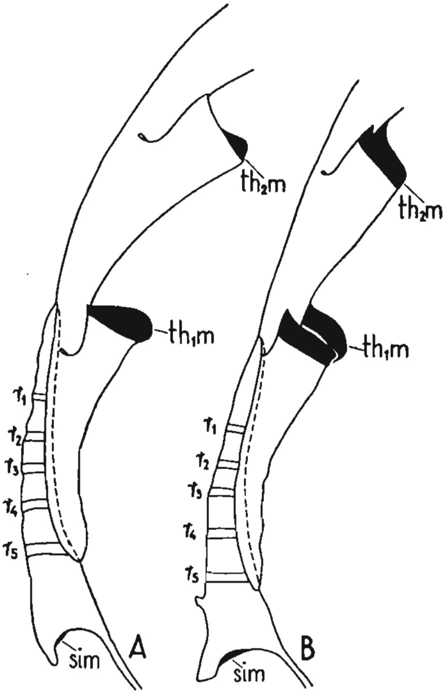

Fig. 13. — *Bohemograptus bohemicus tenuis* (Bouček). Mode of introduction of microfusellar novelties (heavy black) in *Bohemograptus bohemicus* (Barr.) as shown by its less (*A*) and slightly more advanced stage (*B*). Compare with Pl. XV, Fig. *A*. (Mielnik, depth *A* — 886.00 m, *inexspectatus* zone, *B* — 925.10 m, *aversus* zone); ×25.

r_1—r_5 successive black rings of metasicula *sim* incipient microfusellar addition on apertural margin of metasicula, th_1m, th_2m microfusellar addition on first and second theca.

microfusellar additions. The simplest form of this addition on a sicula are few microfusellar strips laid down secondarily on the border of a normal metasicular aperture (Fig. 13 *A-B*, *sim*), usually in the corner of the dorsal apertural process. A further deposition of microfusellar material probably results in the formation of a broader belt around the dorsal process of metasicula and, to a lesser extent, on the remaining part of the apertural margin (Pl. XIV, Fig. *A*, *sim*). This belt is made of densely crowded, minute microfusellar strips, dark pigmented and contrasting with neighbouring fusellar tissue of metasicula proper. In more extreme cases, microfusellar additions of metasicular margin are transformed into

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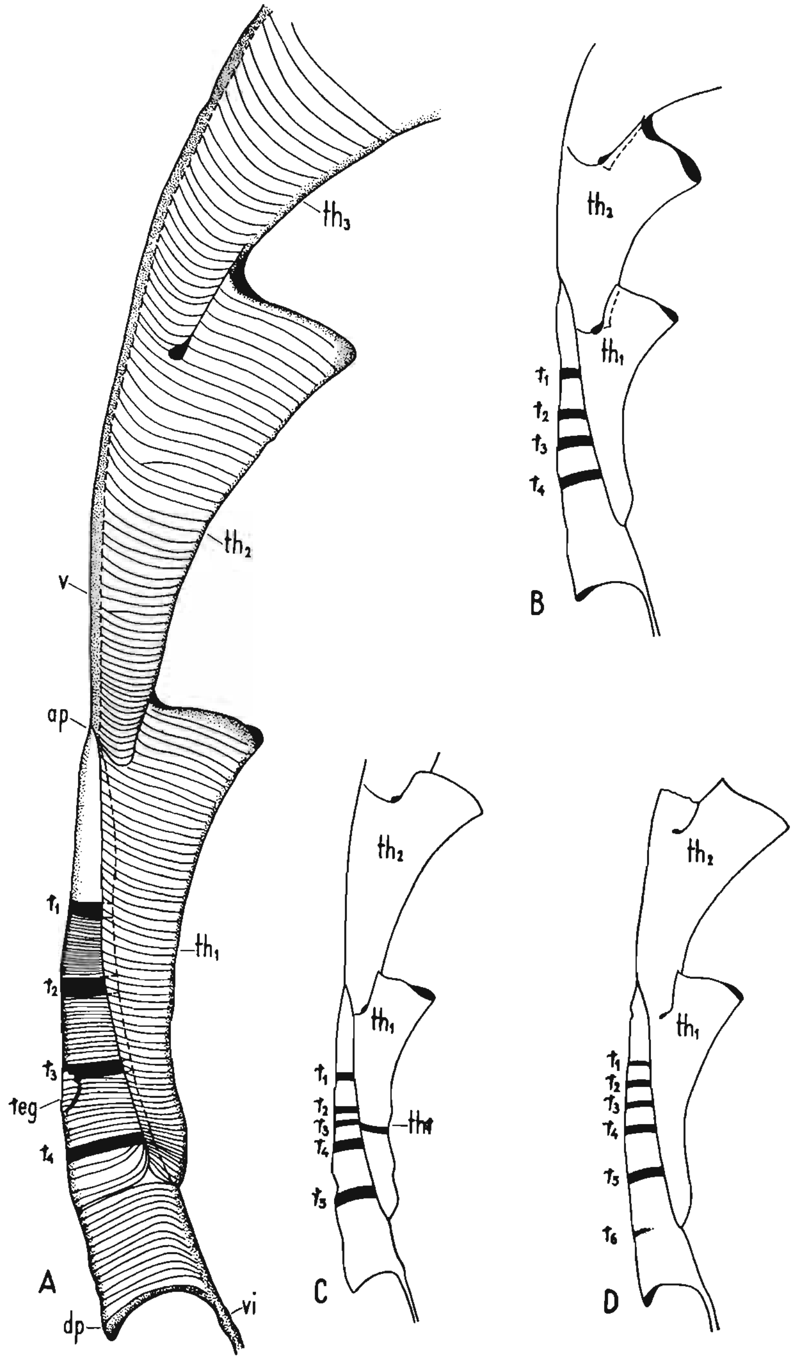
Plate XVII

Bohemograptus bohemicus tenuis (Bouč.). Proximal parts of rhabdosome, *A* structural details of sicula and the first theca with aperture placed at the level of apex prosiculae, *B* diagrammatical sketch showing sicula and first theca with intermediate position of its aperture, *C* similar to *B* but with lower position of the apertural level (Mielnik, depth 873.40 m, *kozlowskii* zone); ×50.

ap apex of prosicula, *dp* dorsal process of metasicular aperture, Δh difference between the level of ventral margin of the first theca and that of apex, prosiculae. *psi/msi* boundary between prosicula and metasicula, r_1—r_5 successive sicular black rings, th_1 first theca, *thr* thecal black ring, *v* virgula, *vi* virgella.

PLATE XVIII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a rather high wall around the aperture (Pl. XXI, Figs. A_1, A_4, *sim*; Pl. XXII, Figs. A_1, A_4, *sim*) with an additional membrane produced by microfusellar tissue displaying irregularly arranged strips on virgella (*vim*). A microfusellar addition on the virgella of the specimens examined is actually an unpaired membrane attached to one side of virgella. It seems, however, probable that primarily this structure has in fact been double and formed two membranaceous, lobate or wing-like, thin-walled platforms, each of them attached to the basis of a free end on one side of virgella. If the reconstruction of this microfusellar additions here suggested is true, it clearly differs from such terminal virgellar structures as "virgellarium", described in *Linograptus posthumus* (Urbanek, 1963, pp. 175—179), but it displays a certain remote resemblance to bilateral web structures associated with virgella, basal spines and proximal end of rhabdosome (as in climacograptids of *Climacograptus bicornis* group, especially in *Cl. papilio* and, to a lesser degree, in "*Monograptus*" *pala*, an only monograptid recognized so far having the web structure in proximal end of rhabdosome. The structural nature of such proximal end structures is obscure. The suggestions were made that they were primarily vesicular ("saccoid") and only secondarily flattened during preservation. They may be also primarily simple, unilamellar membranes and, if such would be the case, their morphological resemblance to structures recognized in *B. b. tenuis* would be much closer. The discussion of the proximal end structures in graptolites mentioned above has been more recently given by Hsiü (1959), Mu (1963), Bulman (1964) and Sobolevskaya (1969).

For the sake of convenience, virgellar web in *B. b. tenuis* (probably bilaterally connected with virgella) will here be termed "pelta" (from Lat. *pelta*, light shield) as this term has already acquired a certain tradition and has been used to describe a roughly similar proximal end structure in climacograptids (*Cl. peltifer* Lapworth).

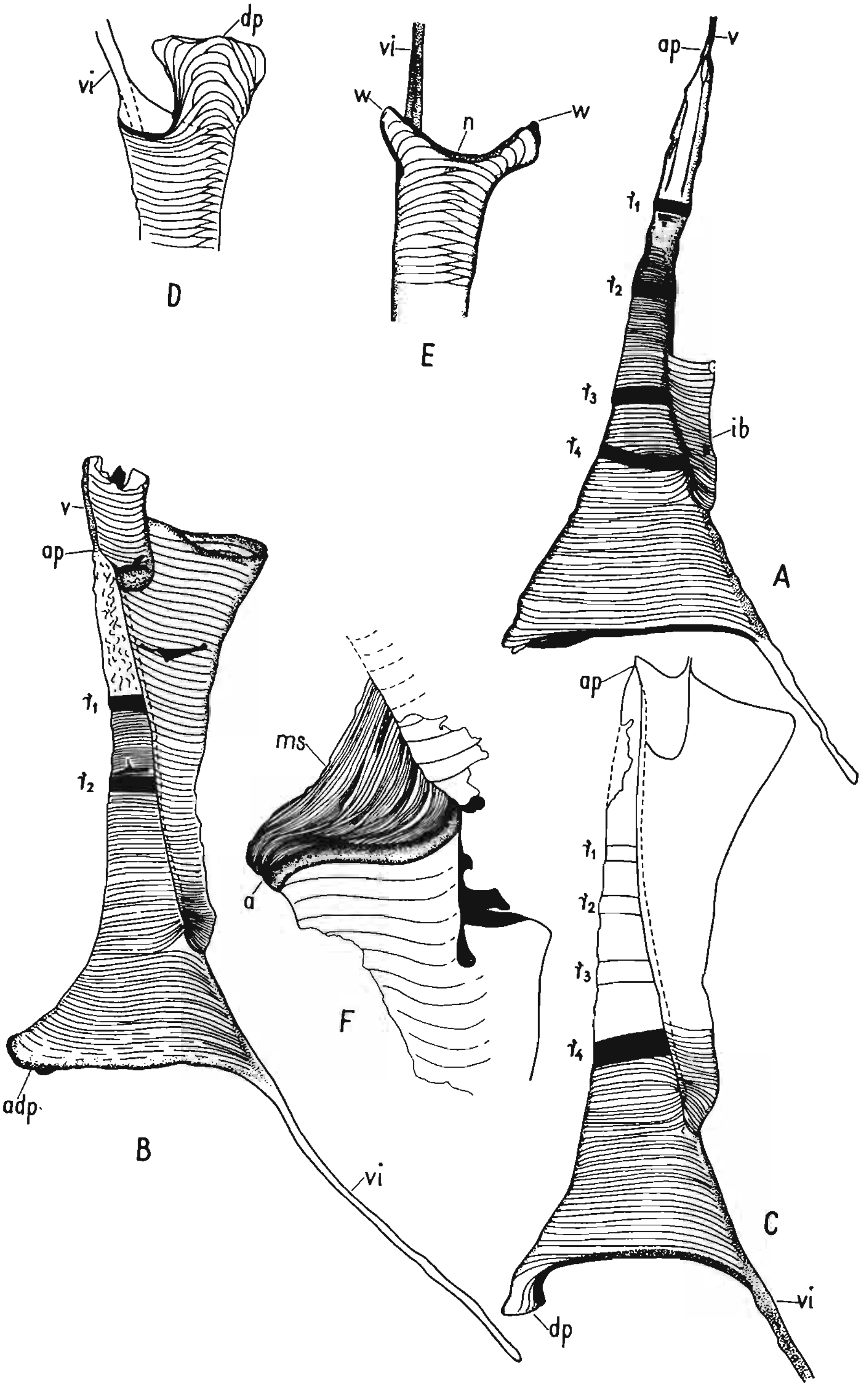
In the remaining thecae, microfusellar additions are also surprisingly diverse. Lateral elevations or walls, placed on both sides of apertural margin (Pl. XIV, Figs. *A*, C_1-C_2, th_1m, th_2m; Figs. 14 *A*, B_1-B_2 th_1m) are a form the simplest morphologically. Each microfusellar addition is composed of numerous, densely crowded, but rather regularly arranged usually gently bent arcuately and very narrow strips (Fig. 14 *A*). The arrangement of these strips is only rarely more irregular, displaying discordances and the presence of separated wedge-shaped patches or

Plate XVIII

Bohemograptus bohemicus tenuis (Bouč.). Proximal part of rhabdosome and its variation *A* details of structure of the proximal part, *B* — variation in the shape of the proximal part (Mielnik, depth 863.80 m, *kozlowskii* zone); *A*×50, B×25.

ap apex of prosicula, *dp* dorsal process of metasicular aperture, r_1—r_8 successive black rings of sicula, *reg* regeneration of damaged periderm, th_1—th_3 successive thecae, *thr* thecal black ring, *v* virgula, *vi* virgella.

PLATE XIX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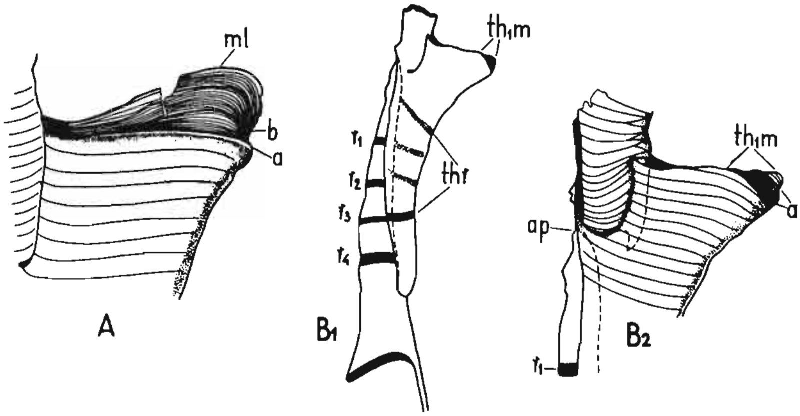

Fig. 14. — *Bohemograptus bohemicus tenuis* (Bouček). Morphological patterns of microfusellar additions. *A* microfusellar addition in a proximal theca in form of paired, almost symmetric apertural lobes, B_1 sicula with first theca showing early stage of formation of microfusellar addition, B_2 details ofthis addition (Mielnik, depth 854.60 m, *kozlowskii* zone); *A*, $B_2\times50$, $B_1\times25$.

a aperture of fusellar part of theca, *ap* apex of prosicula, *b* basal part of microfusellar addition, *ml* microfusellar addition forming apertural lobe. r_1—r_4 successive sicular black rings, th_1m microfusellar addition laid down on aperture of the first theca, *thr* thecal black rings.

bundles of microfuselli ("lenses" of the tissue, comp. Fig. 14*A*). The microfusellar tissue lies here on a thickened apertural margin of the theca proper, which suggest its delayed formation. In some cases, the microfusellar addition on each side of the theca is independent and separated ventrally by an incision, that is, the ventral notch. Such additions are, therefore, paired lobes (Figs. 13, *A*-*B*; Pl. XIV, Fig. C_1; Figs. 14, *A*-*B*; Fig. 15 *B*, *ml*, th_1m). In some other cases, microfusellar systems on both sides of the thecal aperture are continuous, with microfusellar elevations or lateral walls also being fused ventrally (Pl. XIV, Fig. C_2, th_2m; Figs. 14 *A*, B_1, B_2, *ml*, th_1m, *thm*). The further growth of the structure described above may result in the formation of a rather high "collar", dorsally connected with ventral wall of adjacent theca (Fig. 14 B, th_2m).

In more extreme cases, microfusellar additions form more complex

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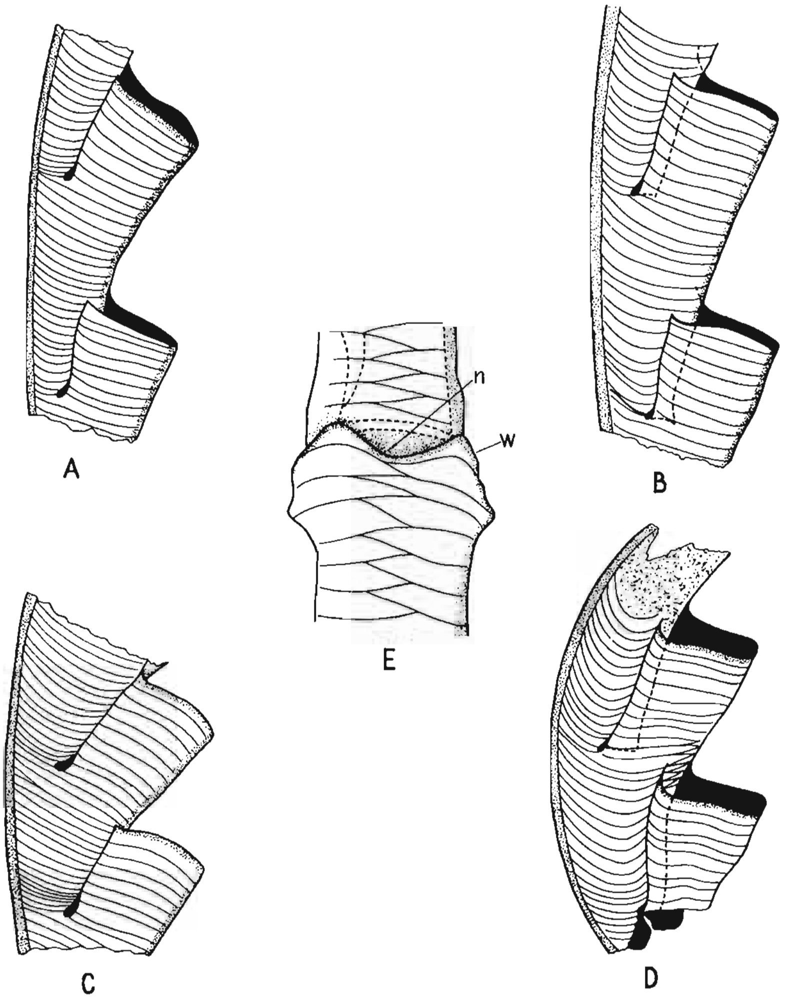
Plate XIX

Bohemograptus bohemicus aff. *tenuis*. Siculae showing a trumpet-like expansion of aperture and a medial theca with pseudomicrofusellar addition. *A* sicula with expanded aperture and initial bud, *B* sicula with expanded aperture and fully grown first theca, *C* sicula with expanded aperture provided with strong dorsal process. Fusellar structure in the upper part of sicula and first theca not discernible. *D*—*E* variation in shape of dorsal apertural process of metasicula, *F* apertural part of a medial theca with pseudomicrofusellar addition (erratic boulder S. 234, Mochty); $F\times63$, all remaining$\times50$

a aperture of theca provided with marginal thickening, *adp* asymmetric elevation of margin (abnormal form of a dorsal process), *ap* apex of prosicula, *dp* dorsal process of metasicular aperture, *ib* initial bud, *ms* microfusellar addition laid down on apertural margin, *n* ventral notch on the margin of dorsal process, r_1—r_4 successive sicular black rings, *w* wing-like lateral part of a dorsal process, *v* virgula, *vi* virgella.

PLATE XX



Bohemograptus Přib., distal thecae of the rhabdosome (*A—D*), and ventral view of distal theca in *Neolobograptus auriculatus* n.sp. (*E*), *A*. *B.b. bohemicus* (Barr.), *B B. b. tenuis* (Bouč.), *C B. praecornutus* n.sp., *D B. cornutus* n.sp., *E* details of aperture in *Neolob. auriculatus* n.sp. (*A* erratic boulder S. 32, Gdańsk-Wrzeszcz, *parascanicus* zone, *B* Mielnik, depth 887.20 m, *inexspectatus* zone, *C* same, depth 919.10 m, *praecornutus* zone, *D* same, depth 910.10 m, *cornutus* zone, *E* same, depth 894.20 m, *auriculatus* zone); *A—D*×25, *E*×92.

n ventral apertural notch, *w* wing-like portion of apertural elevation.

structures which may consist of paired, large and extremely thin-walled apertural lobes (Pl. XXI, Figs. A_1-A_3, th_1m, th_2m; Pl. XXII, Figs. A_1-A_3, th_1m), or form single membranaceous platforms or webs, joined with thecal aperture, and spread around it (Pl. XXI, Figs. B_1-B_2, th_1m).

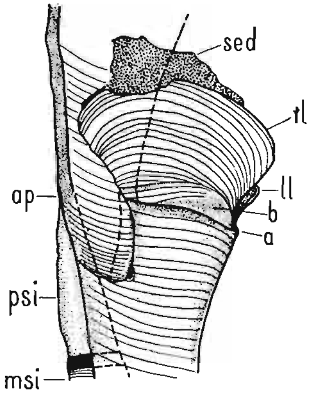
The first type of these advanced microfusellar additions displays a remarkable and irregular variation and even adjacent thecae of same rhabdosomes display microfusellar lobes quite different in shape (Pl. XXII, Fig. *A*, th_1m, th_2m). In the specimen in question, th_1 is provided with asymmetric microfusellar lobes, the right (Pl. XXII, Fig. A_2, *rl*) of them being larger than the left (Pl. XXII, Fig. A_3, *ll*). They also differ in shape and structural details. The right apertural lobe is damaged on its ventral and upper margins, as it is indicated by its jagged edges, extroverted in the upper part. It spreads on both sides beyond the dorsal and ventral walls of th_1. It is peculiar structurally in the irregular arrangement of growth-bands, some of them being very narrow and approaching the normal microfuselli and some much wider, exceeding even the width of normal fuselli in metatheca. Both kinds of bands are markedly gathered into a kind of patches or bundles, separated by certain discordancies or discontinuities, which are marked by strongly pigmented bands, or a number of particularly narrow and densely packed strips. The lobe is clearly attenuated, almost membranaceous and it also differs in this respect from normal periderm of the theca proper. This irregular tissue, which differs in certain respects from true microfusellar tissue, has here been called a pseudomicrofusellar tissue (see terminology).

The left apertural lobe (Pl. XXII, Fig. A_3, *ll*) is smaller, ovate in outline and dorsally it stretches only slightly beyond the aperture. A strongly damaged ventral margin suggests that initially the left lobe was spread much further in this direction. The main part of the lobe consists of pseudomicrofusellar tissue and does not differ in this respect from the right one, except for the structure of its basal part (*b*), which forms a darkly pigmented elevation most probably consisting of densely crowded microfuselli which, due to the state of preservation (strong "carbonization"), are unidistinguishable in the specimen under consideration. Basal parts of both lobes were resting on a strongly thickened apertural margin (*a*) of the theca proper, and suggested a lagged formation of an entire microfusellar addition.

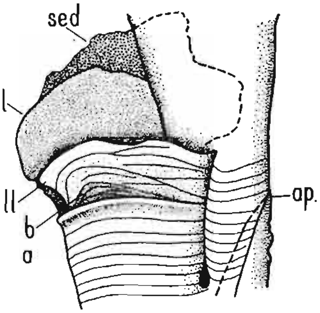
Microfusellar addition in adjacent theca (th_2) of the same rhabdosome (Pl. XII, Fig. *A*, th_2m) differs sharply from that previously described. The right apertural lobe is ovate and composed of a pseudomicrofusellar tissue. Smoothed margins suggest that this lobe is completely preserved. The left apertural lobe in this theca is smaller, ovate and similar in outline to left lobe in th_1 described above. Its smaller size may, however, be also caused by its partial preservation.

The specimen figured in Pl. XXI, Figs. A_1-A_3 represents a somewhat

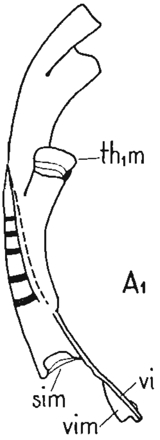
PLATE XXI



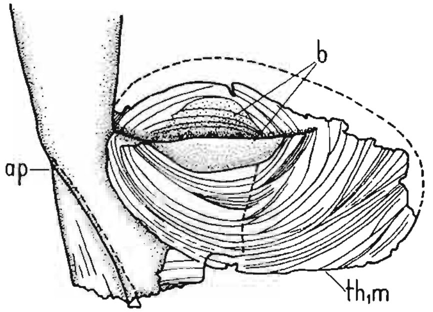
A$_2$



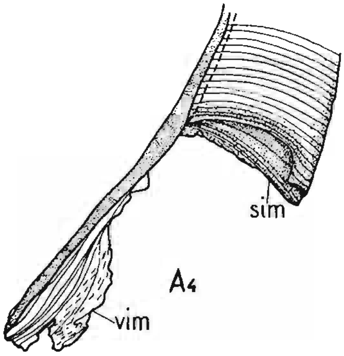
A$_3$



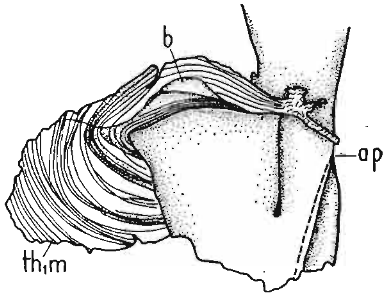
A$_1$



B$_1$



A$_4$



B$_2$

different pattern of paired microfusellar lobes. The right, larger lobe, connected with a thickened apertural margin of th_1 (*a*), consists of a basal part (*b*), darkly pigmented and probably composed of condensed microfusellar strips and the lobe proper, which consist of numerous growth bands almost as wide as normal fuselli, but conspicuously thin-walled (*rl*). The left, smaller lobe (*ll*) differs only in size.

The second type of the advanced microfusellar addition in a theca is represented by the specimen figured in Pl. XXI, Figs. B_1-B_2, th_1m. In this case, the microfusellar addition forms a continuous, extremely thin-walled, horizontal platform around the aperture. Its jagged edges suggest that only part of the structure is preserved and primarily it spreads much wider, being most probably extremely attenuated marginally. The preserved part of the structure allows one to distinguish, on each side of aperture, darkly pigmented, opaque basal part (*b*) most probably produced by densely packed microfuselli.

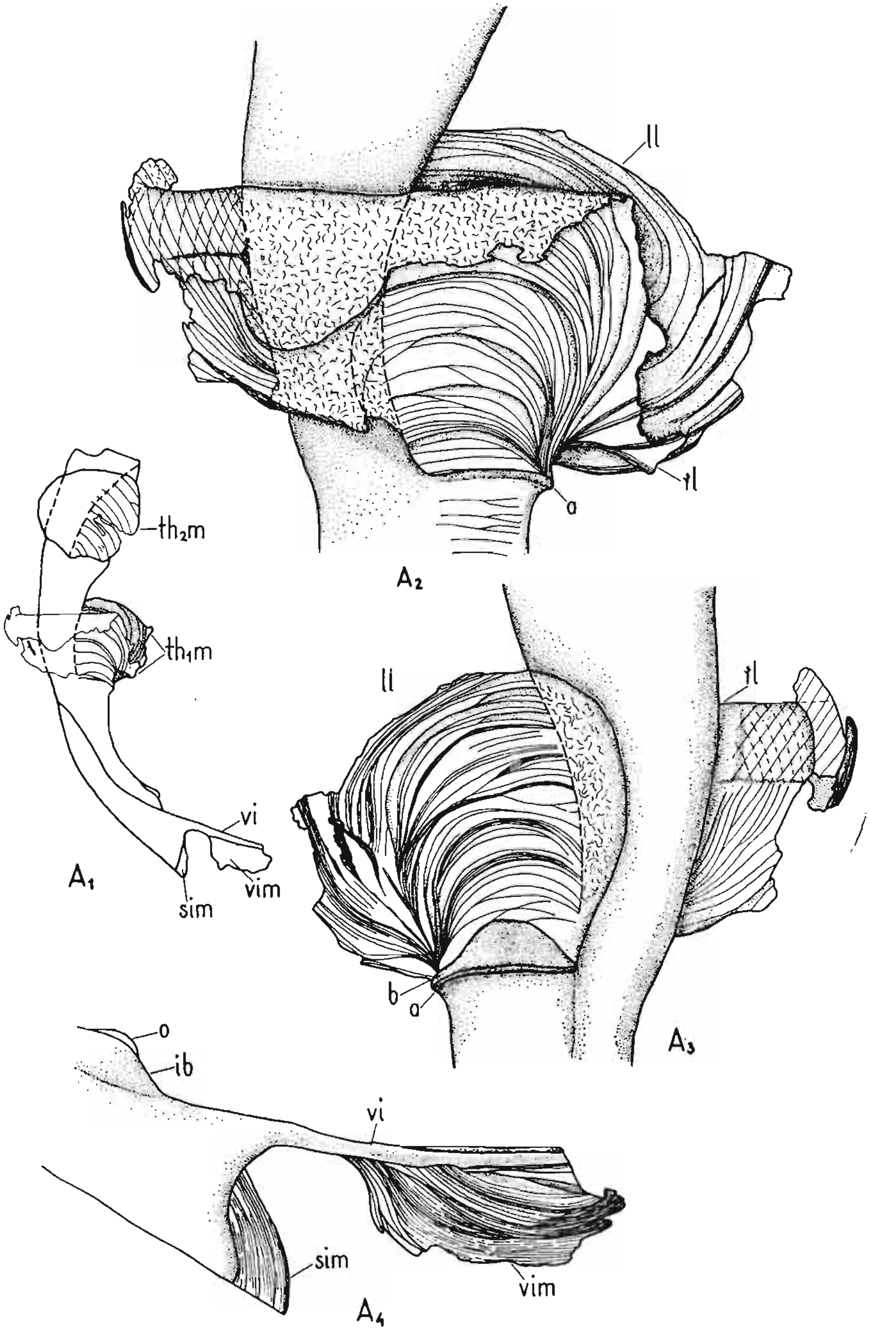
The rest of the structure, *i. e.* the apertural membrane proper, is composed of a pseudomicrofusellar tissue, in which both wider and narrow, rather irregularly arranged strips participate. There is, however no discordance in the trace of these strips across the midline of the platform and the whole structure is primarily entire (Pl. XXI, Fig. B_2). The structure of microfusellar additions in succeeding theca (th_2) of the same rhabdosome (here not figured due to its poor state of preservation), differs strongly as it consists of paired lobes, not unlike those figured in Pl. XXI, Figs. A_2, A_3. The preserved parts of both lobes suggest that they were separated along midline on ventral side and only secondarily they closely touched each other. As concerns their function, they form a platform-like addition, but less horizontally oriented and which consists structurally of two independent lobes. This sharp contrast in structure of microfusellar additions in adjacent thecae reveals their great and capricious (without a definite spatial pattern) variation in a single rhabdosome.

Plate XXI

Bohemograptus bohemicus tenuis (Bouček). "Velum", as an extreme form of microfusellar additions. A_1 general view of the proximal part of rhabdosome from reverse side, A_2—A_3 pseudomicrofusellar apertural structures in same specimen, forming paired apertural lobes in first theca, seen from reverse and obverse side, A_4 pseudomicrofusellar structure on apertural margin of metasicula and on virgella in same specimen, seen from obverse side, B_1—B_2 pseudomicrofusellar structures in another first theca forming continuous platform around the apertural margin seen from reverse side and top (B_1) and from obverse side and below (B_2). Mielnik, depth *A* — 885.00 m, *B* 883.60 m, *inexspectatus* zone); $A_1 \times 14$, remaining×50).

a apertural margin, *ap* apex of prosicula, *b* basal, strongly pigmented part of pseudomicrofusellar structure, *ll* left pseudomicrofusellar apertural lobe, *rl* right pseudomicrofusellar apertural lobe, *sed* grains of sediment attached to the periderm, *sim* pseudomicrofusellar addition on aperture of sicula, th_1m pseudomicrofusellar structures in form of paired lobes (*A*) or membranaceous platform (*B*) on aperture of the first theca, *vi* virgella, *vim* pseudomicrofusellar addition on virgella.

PLATE XXII



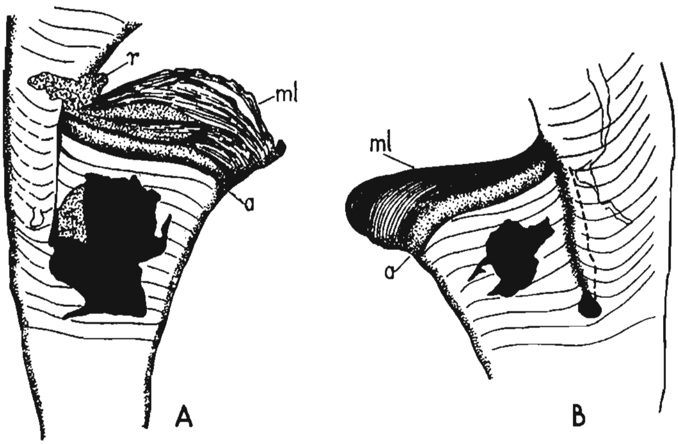


Fig. 15. — *Bohemograptus bohemicus tenuis* (Bouček). Morphological form of microfusellar addition in two successive thecae of the same rhabdosome (A_1 reverse side; B obverse side), representing essentially unpaired (A) and paired structure (B). (Mielnik, depth 925,10 m, *aversus* zone, *rostratus* subzone); ×63.

a thickened margin of the aperture, *ml* microfusellar lobe paired or unpaired, *r* remains of membranaceous part of the lobe.

The question arises: what a relation may exist between less and more advanced microfusellar additions in the thecae of *B. b. tenuis*? The most reasonable interpretation seems to be that both structures simply represent differencies in growth stage. Apertural elevations, walls and "collars" produced by the deposition of microfusellar tissue may be considered as younger, less advanced growth stages of the same structure which in a definite stage takes the form of larger lobes or platforms. Incipient structures of the clearly paired nature (the presence of the ventral notch separating the elevations!) would continue to form bilateral lobes, while primarily single incipient structures (a junction between microfusellar systems on ventral side) would produce, by further growth, unpaired apertural platforms. In both cases, this continued growth is related with the transformation of a deposition of true microfusellar tissue into a secretion of strongly attenuated membrane consisting of a pseudomicro-

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Plate XXII

Bohemograptus bohemicus tenuis (Bouček). "Velum", as an extreme form of microfusellar additions, A_1 general view of the proximal part of rhabdosome from reverse side, A_2—A_3 pseudomicrofusellar apertural structures in same specimen, forming a velum in first theca, seen from reverse and obverse side, A_4 pseudomicrofusellar structures on apertural margin of metasicula and on virgella in same specimen, reverse side (Mielnik, depth 891.20 m, *auriculatus* zone); A_1×14, A_2—A_4×57.

a apertural margin, *b* basal part of pseudomicrofusellar addition, *ib* initial bud, *ll* left pseudomicrofusellar apertural lobe, o peridermal outgrowth on initial bud, *rl* right pseudomicrofusellar apertural lobe, *sim* pseudomicrofusellar addition on aperture of sicula, th_1m, th_2m pseudomicrofusellar apertural lobes in first and second theca, *vi* virgella, *vim* pseudomicrofusellar addition on virgella.

fusellar tissue. Incipient stages are here preserved in the form of basal parts, composed of the true microfusellar tissue (comp. Figs. 15, *A—B*).

The interpretation suggested would require the conclusion that each rhabdosome, showing the capability to form microfusellar additions, also as a rule capable to produce, by further growth, its more extreme derivatives. In fact, more extreme forms were observed as associated with proximal thecae only, and there is no evidence that such structures were formed in all thecae, throughout the rhabdosome, in any growth stage. Most probably, microfusellar additions — if present in distal thecae — were arrested in their earlier growth-stages and represented by apertural elevations or microfusellar "collars". Moreover, it is also possible (but difficult to prove on the basis of existing data) that in certain rhabdosomes even proximal thecae never exceeded, in the development of their microfusellar additions, the limits of a less advanced stage, their growth being thus also restricted.

Nevertheless, the difference between a more or less advanced microfusellar addition in sicula and thecae of *B. b. tenuis* seems to be secondary and both represent only different degrees of expression of essentially the same (homological) structure. This is indicated by the fact that less advanced additions may rise to a more advanced stage as a result of further growth and of the share of microfuselli in both kinds of structure. The extreme form of microfusellar additions so strongly differ, in its outer morphology from others that a suggestion is here made to introduce a special term to denote it — a "velum" (from Lat. *velum* — covering, a veil). This term previously suggested by the present writer (Urbanek, 1968, *in press*) pay attention to its membranaceous nature, broadly lobate or annular form, bordering the thecal aperture and projecting outward like a veil. In certain cases, specimens of *B. b. tenuis* preserved on rock surface display thecal apertures surrounded by light-brownish, "misty" mass of partly damaged velum. Isolated parts of these structures, broken of the thecal apertures, are common in samples etched from the Mielnik core from a depth of 925.10 m (*aversus* zone, *rostratus* subzone) upwards. These represent lobate fragments of periderm with a peculiar microstructure.

The structure of advanced microfusellar additions in thecae, helps classify the nature of these additions in siculae. Microfusellar elevations or bands, superimposed on metasicular aperture, may be compared with basal parts of "velum" which in most specimens is composed of densely crowded microfuselli. In both cases discussed, the microstructure is very much the same. "Pelta" attached to virgella is more similar morphologically and structurally (pseudomicrofusellar tissue!) to membrane of the velum. As compared with those in thecae, the peculiarity of microfusellar additions in sicula consists in the disjunction of these two components of velum, each of them being formed separately. In the case of sicula, the separation of these two parts of velum may be connected with different conditions of growth and the presence of virgella.

In the erratic boulder (S. 234), microfusellar additions were found in the form determined as *B. b. aff. tenuis* (see p. 263—4). An example of this is figured in Pl. XIX, Fig. *F*, in which it forms a fairly high "collar", composed of numerous, very fine strips, conspicuously gathered into a number of clearly discordant bundles (*ms*). The whole structure is superimposed on a thickened apertural margin of the theca proper (*a*) and joins dorsally the ventral wall of adjacent theca, which is separated ventrally by a deep incision. Other specimens found in the same boulder are indicative of the presence of similar microfusellar additions in proximal and medial thecae.

The occurrence of microfusellar additions in *B. b.* aff. *tenuis* from Baltic drift clearly indicates that the appearance of this character was not local geographically.

Populations of *B. b. tenuis* display a somewhat peculiar variation, determined by the coexistence of two sharply contrasted morphological forms: one incapable of producing microfusellar additions ("typical" form), and the other — capable. From this viewpoint, the variation in *B. b. tenuis* is truly discontinous, as there are no intermediates, and no overlap in the character considered. This abrupt difference is caused by the mere nature of the changes involved (sharp contrast of peridermal fabric in normal and additional thecal structures, delayed formation of the latter). The discontinuous pattern apart, the variation in *B. b. tenuis* is marked by proportions in the share of the two forms, the "typical" form being far more common, the other much less frequent but persistent.

This character of the variation in *B. b. tenuis* is very suggestive as a probable instance of the genetic polymorphism (comp. p. 208). This polymorphism has been created phenotypically on the basis of the appearance, during a given period of the history of *B. bohemicus* (probably in *hemiaversus* zone, of a new morph capable to produce the microfusellar tissue, of which velum is the most extreme structural derivative. The suggestion is here made to name this morph a "veliger" morph (after Lat. *velum* — a veil, and *gerere* — to bear).

The polymorphism of *B. b. tenuis* is caused by the presence in one and the same chronodeme of two abruptly different forms — the "typical" and the "veliger" morph. The proportions of both morphs were kept at approximately the same level throughout the stratigraphic range, which seems to be indicative of a balanced nature of polymorphism in the case under study. Possible evolutionary consequences of this polymorphism are discussed in chapter on phylogeny.

The erection of a new taxon of specific rank, based on considerable morphological differences and the lack of intermediate forms ("morphological species" of authors) is perhaps an alternative of this interpretation of variation in *B. b. tenuis.* For the reasons indicated elsewhere (see chapter on phylogeny), the concept of veliger (in systematic sense) as a neutral term introduced only to denote a group of sharply defined intrapopulationary variants seems preferable. The suggestion that "veliger" is "rather an infrasubspecific morph, which appeared in different subspecies of *B. bohemicus* group" has previously been done by the present writer (Urbanek, 1968, *in press*).

Stratigraphic range. — In the temporal subdivision of *B. bohemicus* here suggested, its subspecies *tenuis* occurs from the bottom of *aversus* zone to the top of *kozlowskii* zone (from a depth of 940.50 m to 854.60 m in the Mielnik core).

It seems to be markedly more frequent throughout its distribution range, than *B. b. bohemicus,* being usually one of the chief or predominating elements in graptolite assemblages from particular samples. In the lower part of its stratigraphic range (*aversus-auriculatus* zones) it may be commonly associated with *Cuc. aversus* cf. *aversus* (Eisenack), *Saet. leintwardinensis* (Hopk.), *Cuc. aversus rostratus* Urb., *B. praecornutus* n. sp., *Neolob. auriculatus* n. sp., *Prist. dubius frequens* Jaekel, *Prist. dubius tumescens* (Wood), *Monoclim. haupti* (Kühne). Curiously enough, it has never been find directly associated with *B. cornutus* n. sp.

In the upper part of its stratigraphic range (*inexspectatus-kozlowskii* zones), it is commonly associated with index fossils: *Neocuc. inexspectatus* (Bouč.), *Neocuc. kozlowskii* n. sp. and, moreover, with *Prist. dubius frequens* Jaekel, *Monoclim. haupti* (Kühne).

Populations from particular horizons display some changes in quantitative characters which could be tentatively ascribed to certain zonal evolution in *B. b. tenuis.* We could distinguish:

1) a group of lower zonal populations (*aversus-auriculatus* zones), with a relatively higher frequency of large-sized siculae ($\geqslant$ 1.70 mm, especially in *aversus* zone), higher frequency of specimens with th_1 placed below apex prosiculae, wider range of variability in diameter of the metasicular aperture and its dorsal process;

2) a group of higher zonal populations (*inexspectatus-kozlowskii* zones), which displays a relatively lower frequency of largesized siculae and specimens with th_1 placed below apex prosiculae, a stabilization of diameter of the metasicular aperture (lack of extremely expanded forms), more common elaboration of thecal apertures in form of gentle elevations.

Particularly striking is the reduction of the dorsal process in metasicula, which in the lower group of populations is 0.10—0.19 mm (0.143 mm in average) and in the higher 0.04—0.14 mm long (on the average 0.099). This indicates a certain progressive tendency to decrease in the dorsal process. The first specimens with strongly reduced dorsal processes (0.04 mm long!) appear in *inexspectatus* zone, representing a very characteristic morphological type of *B. b. tenuis* in the last mentioned and higher horizon. This may indicate a certain secondary trend toward an almost complete reduction of the dorsal process and the first appearance in *inexspectatus* zone (comp. p. 254). This seems especially true when comparing mean values of the length of the dorsal process in *B. b. bohemicus* (a total for subspecies from *parascanicus-hemiaversus* zones) with that in the lower-zonal group of populations in *B. b. tenuis*, which almost do not differ from each other (a mean for the former 0.144 mm and for the latter 0.143 mm). A decrease in the length of the dorsal process in metasicula seems to be a remarkable feature of the higher-zonal forms in *B. b. tenuis*, resulting in a distinct and easily recognizable morphological form (Pl. XVII, Figs. *A-D*). The dorsal process of metasicula seems to be fairly often affected by evolutionary changes (comp. Urbanek, 1966, p. 315, for a progressive decrease in this process in most advanced Cucullograptinae and modifications in other lineages — e. g. divergence of trends; and Jaeger, in Jaeger *et al.*, 1969, p. 182, for a progressive increase in the same structure in "*M.*" *aequabilis* Přib.). Jaeger (*ibidem*) reached the conclusion that the differences in size of the dorsal process in sicula, associated with mutually excluding stratigraphic occurrence, are a basis for the discrimination of the temporal subspecies in "*M.*" *aequabilis*. In the case of *B. b. tenuis*, it seems preferable to treat a similar pattern of variation as an infrasubspecific one (the occurrence of transients in one and the same population and a gradual character of reduction), but strongly indicative of populations the youngest geologically.

Bohemograptus praecornutus n. sp.

(Pl. XX, Fig. *C*; Pls. XXIII—XXIV; Fig 16)

Holotype: Pl. XXIII; Figs. C_1-C_3.

Paratype: Pl. XXIII, Fig. *A*; Pl. XXIV, Fig. *A*.

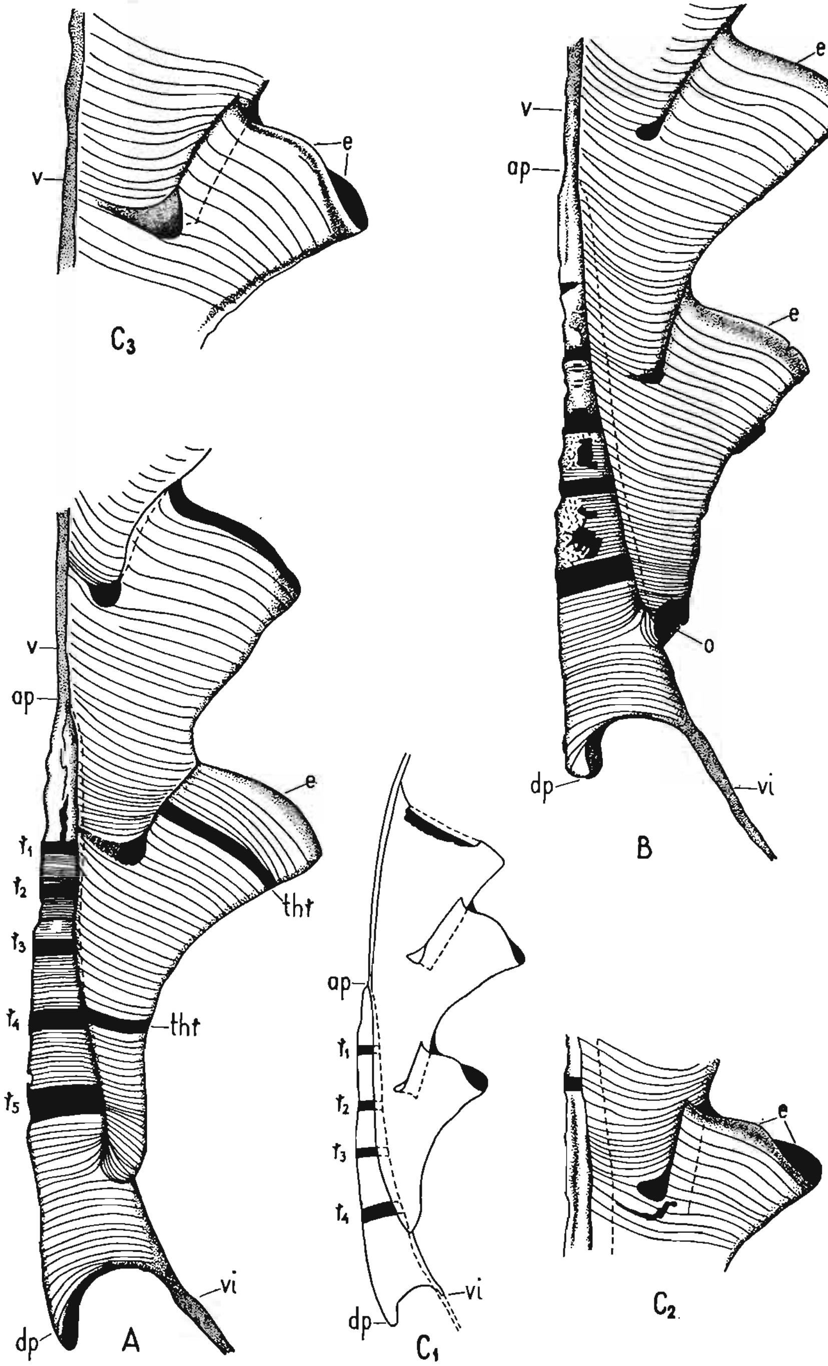
Type stratum: Greenish-blue mudstones in the core of the Mielnik deep-boring at a depth of 919.10—905.60 m. (*B. praecornutus* zone and surviving into the lower part of *auriculatus* zone, lower part of the Siedlce Beds).

Derivation of the name: Lat. *prae* — in front, earlier; as preceding the *B. cornutus* in stratigraphic occurrence.

Diagnosis. — A *Bohemograptus* with robust, short and wide thecae, provided with gentle lateral elevations on apertural margin. Aperture of th_1 placed well below the apex of prosicula. Microfusellar additions present only occasionally and forming simple apertural lappets. Sicula robust, with wide aperture and strong dorsal process. In proximal part, rhabdosome strongly curved ventrally.

Material. — Mostly proximal, flattened fragments of rhabdosome. Distal fragments very few. Material, obtained by chemical treatment from a number of samples taken mostly at a depth of 919.10—911.10 m from the Mielnik core, enables the analysis of sicula and thecal structure. From the Baltic drift material unknown.

PLATE XXIII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Description. — Sicula robust, with rather strongly expanded aperture 1.40—1.71 mm long, almost straight or displaying a gentle ventral curvature (Pl. XXIII, Figs. *A*, *B*, C_1).

Prosicula 0.36—0.51 mm long its apex situated markedly above the apertural level of the first theca (0.15—0.38 mm above it), which seems to be characteristic of the species. Prosicular aperture some 0.11 mm wide usually at the level of the beginning of the first interthecal septum, occasionally somewhat higher up. (Pl. XXIII, Figs. *A*, *B*, C_1. In certain cases, prosicula without black rings, the first sicular black ring (r_1) being then situated usually right at the boundary of pro- and metasicula (Pl. XXIII, Fig. *A*, r_1). There is, however, a certain indication that in some cases r_1 may be somewhat shifted from this boundary onto the metasicula proper. In some other cases, prosicula is provided with a black ring (r_1) more or less pronounced and situated approximately in the middle of it (Pl. XXIII, Figs. *B*, C_1). Neither longitudinal threads, nor a helical line were discernible, most likely due to a poor state of preservation.

Metasicula 1.00—1.20 mm long, almost straight or gently curved ventrally, provided with 3—4 sicular black rings. The ring situated at the boundary of pro- and metasicula, may be r_1 (Pl. XXIII, Fig. *A*), or r_2 (Pl. XXIII, Fig. *B*). Sometimes r_2 is, however, placed at a certain distance from this boundary (Pl. XXIII, Fig. C_1).

Metasicula widens gradually from 0.22—0.23 mm at the level of the primary notch, to approximately 0.33—0.35 mm at definite aperture, which has a strong virgella and a pronounced dorsal apertural process. The latter is 0.09—0.15 mm long and tongue-like or somewhat shovel-like (Pl. XXIII, Figs. *A*, *B*, C_1, *dp*). No traces of any microfusallar addition have been found on metasicula.

The normal monograptid pattern of budding of the first theca is suggested by the structure of the primary notch region and its relation to initial bud (Pl. XXIII, Fig. *A*). The latter displays a relatively low position in the sicula, distinctly shifted toward its aperture. Consequently, it is situated at a distance of 0.84—0.94 mm from the aperture of prosicula and only 0.16—0.21 mm from the aperture of metasicula. This rather delayed manner of budding may be in a way correlated with the low

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Plate XXIII

Bohemograptus praecornutus n.sp. Structure of proximal part of rhabdosome. *A*—*B* proximal parts of rhabdosome with less marked elevations on apertural margin, C_1 general view of another proximal part with thecae showing distinct lateral elevations of apertural margins and C_2—C_3 details of their structure in first and second theca (Mielnik, depth 919.10 m, *praecornutus* zone); C_1×25, remaining×50.

ap apex of prosicula, *dp* dorsal process of metasicular aperture, *e* lateral elevations of apertural margin of thecae, *o* opening secondarily formed in initial bud, r_1—r_5 successive sicular black rings, *thr* thecal rings, *v* virgula, *vi* virgella.

position of aperture in the first theca, characteristic of the whole species and found also in *B. cornutus* n. sp.

The first theca has a characteristic shape, which may be roughly described as very broadly obtriangular (Pl. XXIII, Figs. *A*, *B*, C_1-C_2). Its ventral wall is steeply sloping, with a certain tendency, in metathecal part, to form a bell-like expansion (Pl. XXIII, Figs. C_1-C_2). The first theca is 0.94—1.20 mm, the metathecal segment 0.25—0.33 and prothecal one 0.69—0.87 mm long. The prothecal part occupies therefore approximately 72—76% of the total thecal length. Occasionally, the first theca has thecal rings (Pl. XXIII, Fig. *A*, *thr*). One of two such rings may be situated on the prothecal part, the other on metathecal one. They are similar to each other and probably homological with sicular black rings. Over its entire length the metatheca is adnate to the ventral wall of the second theca, the latter being inclined to the axis of protheca at an angle of 30—40°.

Very slightly elaborated aperture has paired elevations laterally situated on the margin (Pl. XXIII, Figs. *A*-C_1-C_2, *e*).

Proximal fragments, as long as 8 thecae, display no further differentiation of aperture in the first theca. Strongly thickened and "carbonized" proximal parts (which most likely belong to old rhabdosomes), do not differ in structure of thecal termination. It seems thus, that in the vast majority of rhabdosomes, apertural elaborations in the form of lateral elevations mark the final growth stage in the first theca.

The remaining proximal thecae are 1.04—1.28 mm, their metathecal segment 0.35—0.45, and prothecal 0.59—0.83 mm long. Prothecal part occupies thus about 59—68% of the total thecal length. There is a distinct (Pl. XXIII, Figs. *A*, *B*) and rather rapid increase in width of proximal thecae, which are in their prothecal part 0.34—0.70 mm, and in metathecal 0.33—0.45 mm wide. Diameter of apertures of proximal thecae reaches 0.39—0.50 mm. Like the first theca, the remaining proximal thecae have the apertural margins slightly elaborated in the form of two lateral elevations, separated by a shallow ventral notch (Pl. XXIII, Figs. C_1, C_3 *e*). These elevations 0.03—0.06 mm high are produced by the addition to the apertural margin of usually one short, both dorsally and ventrally free fusellus.

In more distal thecae, the length increases to 2.20 mm, metathecae and prothecae being almost exactly equal in length. Rhabdosome, measured above the apertural level, is 0.80—0.90 mm metatheca 0.55—0.60 mm wide. Apertures of distal thecae, such as the more proximal one have paired lateral elevations, in some specimens rather gentle, in others more pronounced, separated by a fairly deep ventral notch and occasionally even somewhat pointed (Pl. XX, Fig. *C*).

Very rare microfuseller additions were observed only in the uppermost part of the distribution range of *B. praecornutus* n. sp. (samples taken at a depth of 909.10—906.60 m)[11]. These is no direct evidence for their occurrence in a population from the lower part of the distribution range of the subspecies in question, but for the theoretical reasons one might expect that the microfusellar additions were most probably inherited from ancestral bohemograptids, and should already be present in earlier populations. Further considerations on this problem are given in chapter on phylogeny.

Microfusellar additions display a remarkable variation (Pl. XXIV, Figs. *A*-*B*). Their morphological form does not indicate a stable astogenetic succession, so characteristic of other thecal characters, the shape and size of these additions in particular thecae being to a considerable extent irregular. The best preserved proximal part (Pl. XXIV, Fig. *A*) displays it in five thecae (1—5). The microfusellar additions of the first theca are less advanced then those on the remaining thecae and form only small lobes composed of microfusellar tissue laid down on apertural elevations (Pl. XXIV, Figs. A_1-A_{10}). The shape and size of microfusellar additions on the remaining proximal thecae are very variable. Occasionally they display a considerable asymmetry, resulting in a strong differrence between apertural lobes on the reverse and obverse sides (comp. apertural apparatus of the third and fourth theca, Pl. XXIV, Figs. A_5-A_8). This asymmetry pattern is, however, completely random and not followed by successive thecae. In each case, it is characteristic of a given theca. The morphological form of particular microfusellar additions differs greatly, from a simple, ear-like lobe (Pl. XXIV, Figs. A_1, A_2, A_5, B_3-B_4) to more advanced lappets, forming broad, tongue-like structures, stretching out from aperture (Pl. XXIV, Figs. A_3-A_4), or to wide platforms connected with the margin of aperture (Pl. XXIV, Figs. A_8-A_9).

In spite of these great differences in size and shape of microfusellar additions, *B. praecornutus* n. sp. displays a relatively stable structural pattern. A basal part, which consists of numerous, but rather regularly arranged, microfusellar strips (with few unconformities) may be distinguished in each apertural lappet (Pl. XXIV, Figs. A_3, A_{10}, B_4, *b*). It is strongly brownish pigmented, occasionally completely opaque, and probably rather thick-walled. The rest of the lappet is strongly attenuated, almost membranaceuos, strongly transparent and probably due to it fragility, rarely complete preserved (Pl. XXIV, Figs. A_3-A_4, A_7-A_8 *m*.). It is com-

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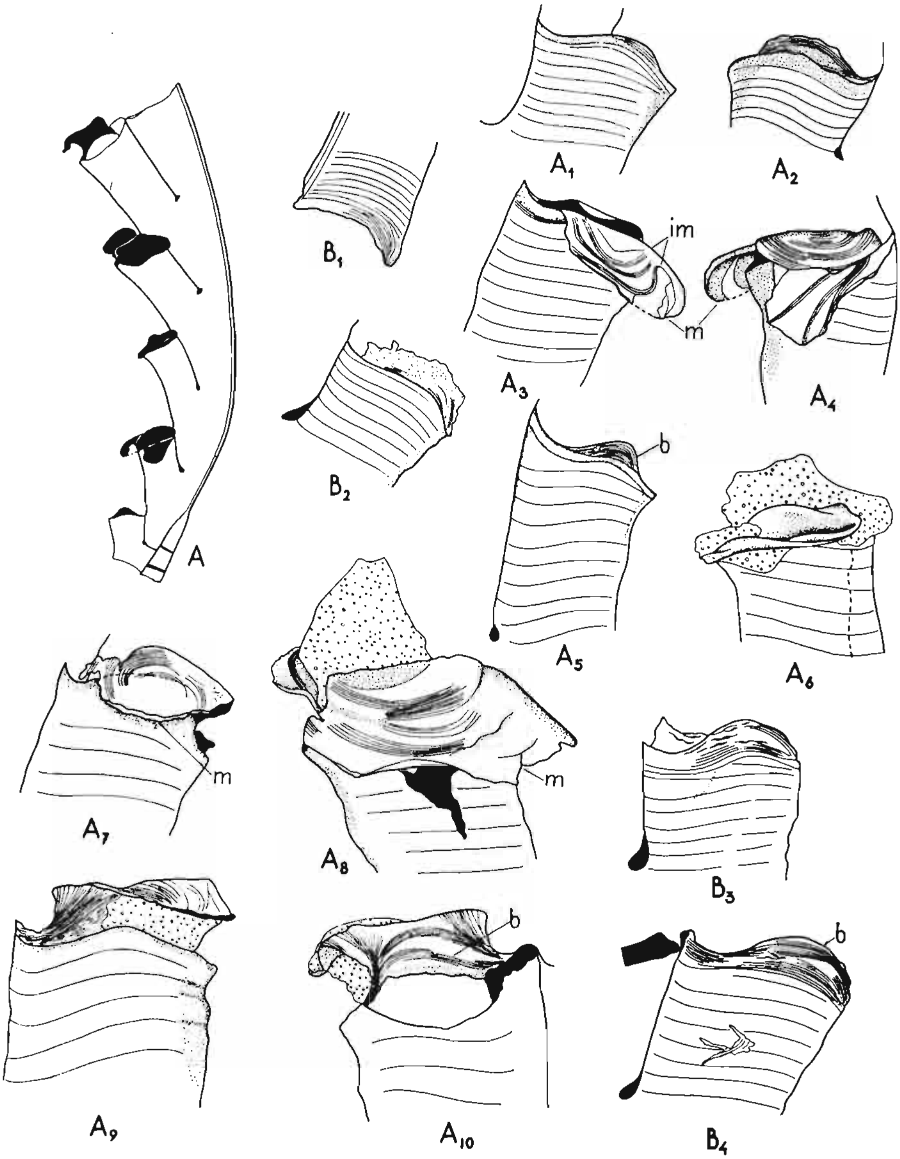
[11] The significance of these specimens requires a certain consideration. Their assignment to *B. praecornutus* n. sp. is based 1) on the resemblance of the thecal structure to *B. praecornutus* n. sp. lacking, microfusallar additions and 2) on a strong difference in microfusellar additions of proximal thecae from their characteristic form recognized in *B. cornutus* n. sp. The stratigraphic occurrence (above the *cornutus* zone) may, however, suggest that here described specimens with microfusellar additions represent an only aberrant form of *B. cornutus* n. sp. This interpretation is, in my opinion, less likely, because these microfusellar additions approach structurally their form in the earlier *Bohemograptus* rather then the specialized form characteristic of *B. cornutus* n. sp.

PLATE XXIV



Bohemograptus praecornutus n.sp. Morphological form of microfusellar additions. *A* general appearance of proximal part of rhabdosome with microfusellar additions, seen from obverse side. Microfusellar additions in solid black, A_1—A_{10} details of structure of microfusellar additions on successive thecae as seen from reverse and obverse side; B_1—B_4 microfusellar additions in another specimen, seen on metasicula (B_1) and successive thecae (B_2—B_4) (Mielnik, depth *A* 909.60 m, *B* 906.60 m, *auriculatus zone*); $A \times 16$, A_1—$A_{10} \times 47$, B_1—$B_4 \times 50$.

b basal part of microfusellar addition made of microfusellar tissue proper, *im* intercalated microfusellar strips forming pseudomicrofusellar tissue, *m* membranaceous part of microfusellar addition.

posed of pseudomicrofusellar tissue. Characteristic of it is a combination of rather wide strips, differing little in this respect from normal fuselli, with more or less irregularly intercalated bands of microfusellar strips, or strongly pigmented narrow bands which delimits the bundles of widely spaced strips (*im*). These faint details are sometimes not discernible at all and the membrane seems to be structureless. It is rarely preserved complete and its jagged margin and certain traces preserved on the surface of the sediment around thecal apertures in the form of a brownish mass, in flattened specimens suggest that in the primary state, these structures were extended into a broadly spread, extremely attenuated membrane.

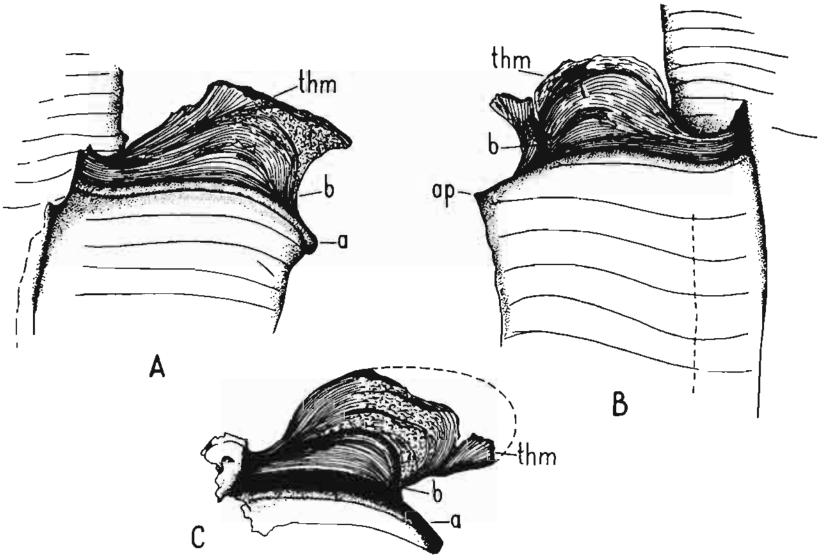


Fig. 16. — *A-C* Morphological forms of microfusellar additions on thecal apertures in *Bohemograptus praecornutus* n.sp. (*A-C*), *C* seen from inside (Mielnik, depth 909.10—909.60 m); ×63.

a apertural margin, *b* basal part of pseudomicrofusellar addition placed on apertural margin of thecae.

Few fragments available having distal thecae provided with microfusellar additions, show that they do not differ greatly from those described above. They form lobate structures broadly joined on each side by the apertural margin (Fig. 16, *A-C*). Strongly pigmented basal part consisting of microfusellar tissue and a more transparent, thin mebranaceous part might were easily distinguishable (*b*, *thm*). The latter part most probably corresponds to a pseudomicrofusellar tissue, recognized in more proximal thecae. The upper margin is in all cases damaged and irregularly jagged, which suggests that the structure is incompletely preserved. Preserved parts indicate, however, a roughly ear-like shape of these apertural processes (Fig. 16*C*, broken line).

Microfusellar additions in *B. praecornutus* n. sp. clearly differ in shape from that noted in *B. cornutus* n. sp. An especially sharp contrast is observed in these additions in proximal thecae. In spite of this difference, there is a remarkable resemblance in general structural pattern of microfusellar addition in both species (for considerations on significance of this resemblance see description of *B. cornutus* n. sp.).

The fragmentary material does not enable determining the size and shape of a complete rhabdosome. Proximal fragments with as much as seven thecae preserved display a distinct ventral curvature. Its degree varies, however, in particular specimens from almost straight to strongly curved. In most cases, the greatest curvature occurs at the apertural level of the second theca, where prothecal part of the third theca is slightly bent angularly. Another peculiar character is a rather rapid increase in width of rhabdosome, which, measured above the apertures of a succeeding theca (from 1—7 *th*), is as follows (in mm): 0.35; 0.48; 0.45—0.59; 0.50—0.55; 0.70; 0.80. Remarkable is a rather quick widening of rhabdosome from the fourth theca onwards, resulting in a width of some 0.90 mm. measured in distal thecae. Thecal number approximately 10 (in proximal part of rhabdosome) to 11 (in distal part) in 10 mm.

Stratigraphic range. — *B. praecornutus* n. sp. makes its first appearance at a depth of 919.10 m; shorts after the last occurrence of *Cucullograptus aversus rostratus* Urb. (at a depth of 920.80 m). The subspecies in question, together with "*M*". *egregius* n. sp. are the first new elements of graptolite fauna, which may be ranked taxonomically as separate species and which appear after a great extinction of Lower Ludlow fauna in and above the *leintwardinensis* zone. Thus they start a new phase of the development of graptolite fauna, that is, the phase of the Upper Ludlovian.

The extinction of such a characteristic Lower Ludlow element as *Cucullograptus* and the appearance of the first new element of Siedlce Beds (*B. praecornutus* n. sp.) nearly coincide with each other, being separated by a small gap 1.70 m in thickness.

B. praecornutus n. sp. continues to occur to a depth of 905,60 m. It survives well above the top of *B. cornutus* n. sp. range. This long persistence of earlier and more primitive species is a remakable feature of the stratigraphic distribution of *cornutus*-offshoot. Another peculiar feature, however random it may be (comp. chapter on phylogeny), is the distribution of "veliger" morphs (specimens provided with microfusellar additions). So far, they were found only in the upper part of the *B. praecornutus* n. sp. range, above the occurrence area of the true *cornutus* (at a depth of 910.60—906.60 m).

In the scheme of subdivision of Siedlce Beds here suggested, *B. praecornutus* n. sp. is considered to be an index fossil for the lowermost zone of Siedlce Beds (*praecornutus* zone). It is, however to remember that in its vertical distribution it also surpasses the *cornutus* zone and penetrates into the lower part of *auriculatus* zone here distinguished.

Systematic position. — *B. praecornutus* n. sp. differs only in few qualitative characters from earlier representatives of *Bohemograptus* Přib. They are, however, very distinctive (a low position of the aperture of the first theca, robust, short and wide thecae provided with apertural elevations) and indicate that 1) this subspecies represents a separate line of descent, which starts a new trend; 2) it may be easily derived from the representatives of *Bohemograptus* which, as *B. b. bohemicus* (Barr.), display similar thecal characters — short and wide thecae, low position of the large-sized sicula (Pl. IV).

B. praecornutus n. sp. (Pl. IV, Fig. C) represents an only small advance in thecal structure on this robust form of *Bohemograptus* (a certain change of proportions and a slight elaboration of aperture). *B. b. bohemicus* (Barr.) as here defined (comp. Table II) may for morphological and stratigraphical reasons, be regarded rather safely as an ancestor of the entire *cornutus* lineage (represented by *B. praecornutus* n. sp. and *B. cornutus* n. sp. as successive links).

Deriving *B. praecornutus* n. sp. from late populations of *B. b. bohemicus* (occurring in the *hemiaversus* zone) rather than from robust variants of nearly contemporaneous or contemporaneous *B. b. tenuis* seems preferable for the reasons indicated elsewhere (comp. chapter on phylogeny with other speculations on a mechanism possibly involved in the origin of *B. praecornutus* n. sp.). Although the latter possibility cannot be precluded, it seems less probable because of the fact that *B. b. tenuis* on the whole displays quite a different trend in changes and that both taxa coexist synchronically the same area, e. g. behave as already separate species. The form and structure of microfusellar additions, which only sporadically occur in the former subspecies, do not differ in principle from those known in earlier bohemograptids. We may believe therefore, that capability of producing this kind of apertural superstructures, has been transmitted from ancestral populations rather, than appeared as a result of an independent mutation. Such a process may only be effective after the earlier bohemograpti acquired the capability of producing microfusellar tissue and its derivatives. The sequence of events here suggested is supported by stratigraphic data, which indicate that *cornutus* lineage has in fact originated after the *B. b. bohemicus* group was acquired by the last-named cability (in *hemiaversus* zone, Fig. 11).

In regard to the fusellar structures, the derivation of *B. cornutus* n. sp. from its probable forerunner, *B. praecornutus* n. sp. is rather easy. The thecal characters of the former species are only slightly more advanced, the orientation of changes being the same (still more robust thecae). The main changes were, however, expressed in the structure of microfusellar additions, especially so in proximal part of rhabdosome. In the form of microfusellar additions in these thecae, *B. cornutus* n. sp. strongly differs from other bohemograpti. The microstructure of these apertural additions is, however, as indicated earlier fundamentally the same. It is suggested that bizarre microfusellar additions in *B. cornutus* n. sp., are in fact deriveable by relatively few changes from similar structures of earlier bohemograpti (comp. description of *B. cornutus* n. sp.). On the other hand, the resemblance of fusellar structures and stratigraphic occurrence also indicate *B. praecornutus* n. sp. as a forerunner of *B. cornutus* n. sp.

Bohemograptus cornutus n. sp.

(Pl. XX, Fig. *D*; Pls. XXV—XVIII).

Holotype: Pl. XXV, Figs. A_1-A_2.

Paratype: Pl. XXVII. Fig. *H*.

Type stratum: Greenish-blue mudstones and marls in the core of the Mielnik deep-borings at a depth of 911.60—910.10 m (*B. cornutus* zone, lower part of the Siedlce Beds).

Derivation of the name: Lat. *cornutus* — horny; as having long apertural projections resembling horns.

Diagnosis. — A bohemograptus with robust, short and wide thecae, terminating, at least in proximal and medial parts, in a pair of ventro lateral lappets in the form of gradually widening membranaceous tapes, composed of micro- and pseudomicrofusellar tissue. Sicula robust, with a wide aperture and strong dorsal process. Rhabdosome in proximal part conspicuously curved ventrally.

Material. — Most proximal, flattened or semiflattened fragments of rhabdosome. Medial and distal fragments scanty, damaged or deformed. The material, although obtained by chemical treatment from a few samples in a limited thickness of the Mielnik core, enables the analysis of thecal structure including microstructure of apertural process. From the Baltic drift material unknown.

Description. — Sicula robust, with strongly expanded aperture, 1.61—2.14 mm long, displaying a gentle ventral curvature (Pl. XXV, Fig. A_1; Pl. XXVI, Fig A_1).

Prosicula 0.40—0.54 mm long, with apex markedly above the apertural level of the first theca (0.20—0.37 mm above). Prosicular aperture some 0.12—0.17 mm wide, usually lying right at the apertural level of the first theca (Pl. XXV, Fig. A_1), or occasionally somewhat below (Pl. XXVI, Fig. A_1). Prosicula lacking black rings, the first ring (r_1) being situated as far as the baundary of pro- and metasicula. Neither longitudinal threads nor helical line are discernible, most likely due to a poor state of preservation.

Metasicula 1.21—1.60 mm long, usually gently curved ventrally, provided with 4—6 sicular black rings, the first (r_1) being situated on the boundary of pro- and metasicula, the rest irregularly scattered over its length. A strongly widening metasicula is some 0.29—0.33 mm wide at the level of primary notch and some 0.35—0.45 mm at the definite aperture.

The latter displays usually strong virgella and a pronounced dorsal apertural process. Sometimes it is more elaborated and with a certain tendency to form two lateral, wing-like outgrowths (Pl. XXV, Fig. A_1, *dp*), but a shovel-like of tongue-like shape is much more common (Pl. XXVI, Figs. A_1, B_1, C_1; Pl. XXVII, Figs. A_1, B_1, E_1). No microfusellar additions on metasicula.

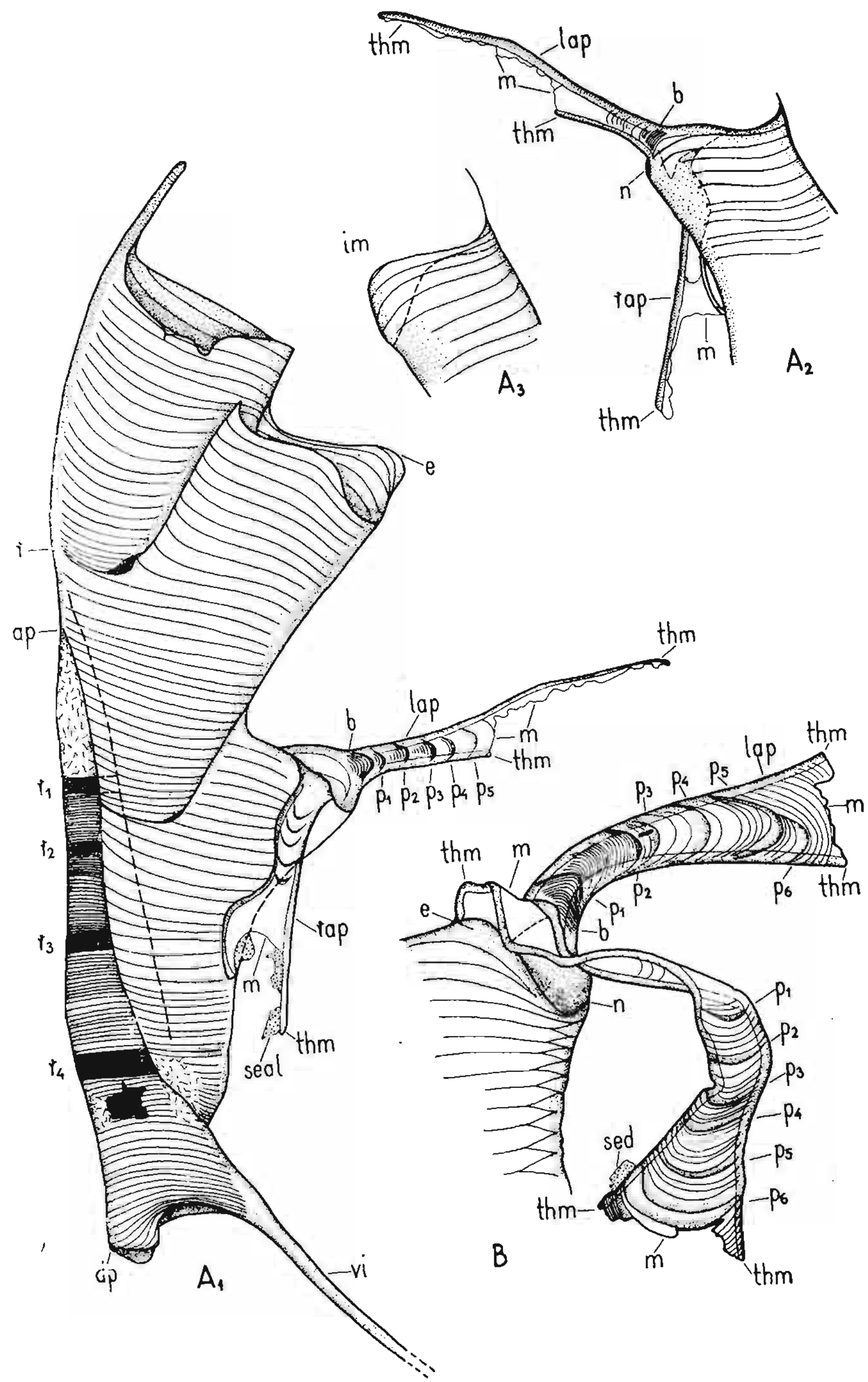
As shown in Pl. XXVI, Fig. B_3, the structure of the region of primary notch indicates a normal monograptid pattern of budding of the first theca. The initial bud strongly displaced toward the aperture of metasicula, which is situated only some 0.20—0.37 mm from it. Pl. XXVI, Fig. B_3, ib). On the other hand, it is rather distant from the aperture of prosicula (1.00—1.23 mm). This low position of the primary notch may exert a certain influence on characteristic proportions of the first theca (a low position of the aperture in th_1 characteristic of the species).

The first theca has a characteristic shape, which may be described roughly as very broadly obtriangular (Pl. XXV, Fig. A_1, Pl. XXVI Figs. A_1, B_1, C_1; Pl. XXVII, Figs. A_1, E_1). Initially only slightly elevated, at a certain point its ventral wall rather rapidly grows up, forming its characteristic outline. The first theca is some 1.10—1.40 mm long, the subapertural segment of metatheca being 0,26—0.40, and the prothecal 0.75—1.00 mm long. The prothecal part takes, therefore, about 68—77% of the total thecal length.

The basal part of the protheca may occasionally have thecal rings (Pl. XXVI, Fig. A_1, *thr*) in the form of dark bands similar to sicular black rings. Over its entire length metatheca is adnate to the ventral wall of subsequent theca, which is inclined to the axis of protheca at an angle of some 30—50°.

Aperture of complete first theca is characteristically elaborate. In the early stage of development of rhabdosome ($1^1/_3$ theca stage), the apertural margins of this theca form only slightly outlined, paired lateral elevations, involving 1—2 fuselli (Pl. XXVI, Figs. B_1, B_2, *e*) and separated ventrally by a notch. Before the growing second theca reaches its metathecal stage, the first microfusellar strips are laid down on the ventral slope of these elevations (Pl. XXVI, Figs. C_1, C_2, *im*). A further deposition of densely crowded microfusellar strips results in the formation of low, ear-like projections of apertural margins (Pl. XXVII, Figs. A_1, A_2, *im*). In a more advanced growth stage (which roughly coincides with a simultaneous final stage of the formation of second metatheca and budding of third protheca) — it takes the form of a more or less projecting proturberance (Pl. XXVII, Figs. B_1, B_2, ip, C_1-C_2 *is*). This incipient apertural outgrowth is composed of many densely crowded, arcuate and therefore relatively dark-pigmented microfuselli. During a further growth of these processes, when rhabdosome reaches the fourth prothecal stage (Pl. XXVII, Figs. D_1-D_2, E_1-E_2, as), they produce relatively long structures stretching out on

PLATE XXV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both sides of aperture and somewhat shifted ventrally. More complete apertural lappets in the first theca are shown in Pl. XXV, Figs. A_1-A_2; Pl. XXVI, Figs. A_1-A_2, *lap*, *rap*). Preserved parts of these apertural outgrowths are 0.45—0.90 mm long. Their fine structure is discussed below in connection with apertural processes of other proximal thecae.

Proximal thecae broadly obtriangular, 1.07—1.45 mm in length with metathecae 0.36—0.68 mm long and inclined at an angle of some 40° to the axis of protheca. The prothecal segment of these thecae, 0.68—0.77 mm long, occupies therefore about 55—62% of the total thecal length. At the level of aperture of the preceding theca, the prothecal part is 0.33—0.43 mm wide, reaching some 0.34—0.44 mm at the base of metatheca.

Aperture of proximal thecae is 0.40—0.47 mm wide, in earlier growth stages provided only with gentle lateral elevations consisting of two fuselli and separated ventrally by a distinct apertural notch (Pl. XXV, Fig. A_1; Pl. XXV, Figs. A_1, *D*, *e*, *n*). A later growth continues on these lateral elevations with narrow microfusellar strips producing lateral apertural processes in exactly the same manner as in the first theca.

A fine structure of apertural processes in proximal thecae of *B. cornutus* n. sp. deserves a special attention. In many respects it is peculiar and without close analogies to other known monograptids. In at least 6 (±1) most proximally situated thecae, these processes take the form of long tapes, gradually widening and more or less expanded terminally (Pl. XXV, Figs. A_1-A_2, *B*; Pl. XXVI, Figs. A_1-A_2, and especially Pl. XXV, Fig. *B*). Each lappet consists of a rather thin peridermal membrane (*m*), framed by roll-like, thickened margins placed on both sides of the process (*th m*; comp. Pl. XXV, Fig. *B*, Pl. XXVI, Figs. *A*, *B*). These margins seem to be produced by a condensation of many minute stripes making up the membrane, converging toward both sides and traceable even on thickened frames (Pl. XXV, Figs. *B*, *t*, *h*, *m*).

In the preserved parts of apertural process, a proximal and a terminal part may be distinguished, which differ from each other in certain

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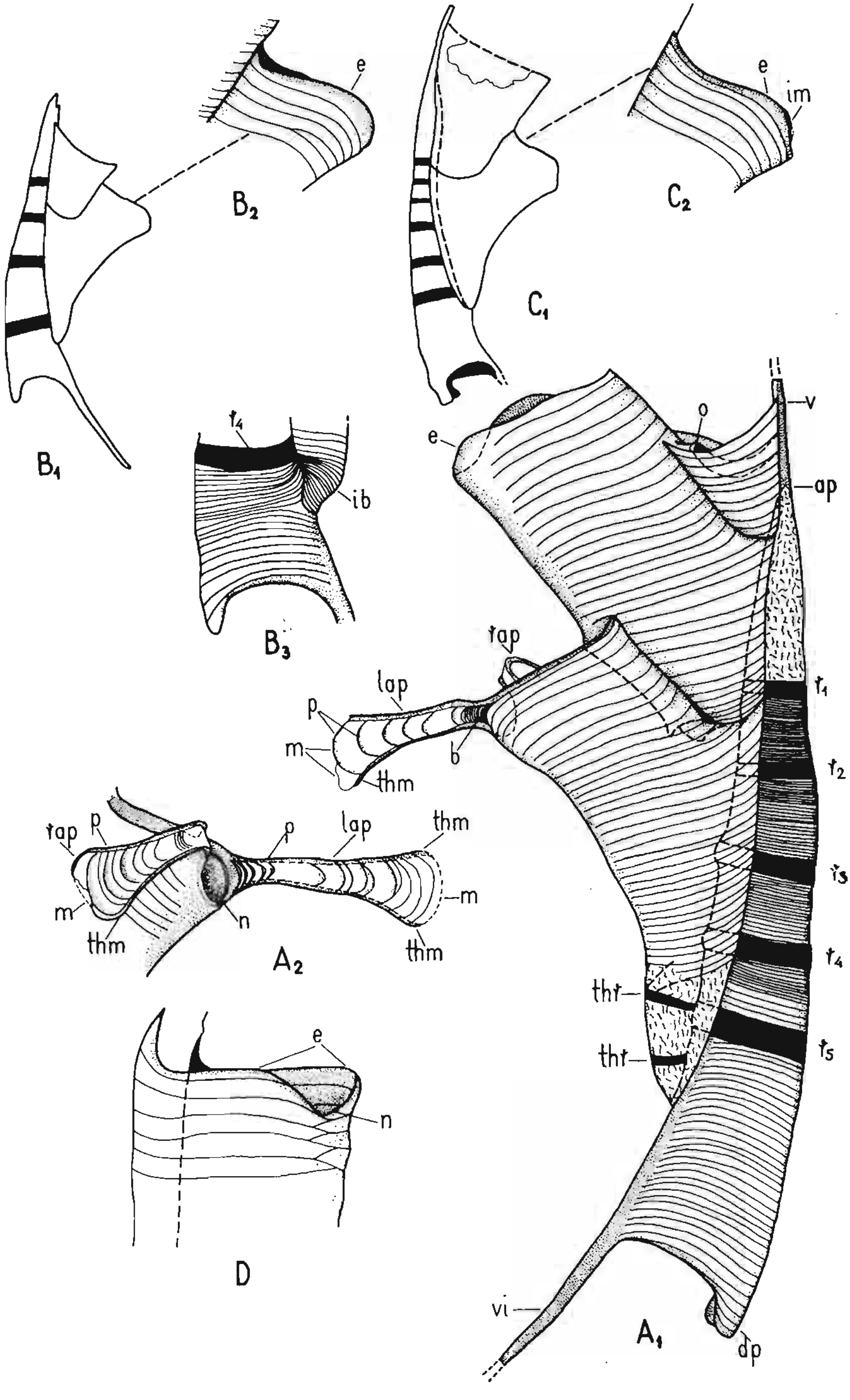
Plate XXV

Bohemograptus cornutus n.sp. Sicula with first theca and structure of apertural apparatus in proximal thecae. A_1 proximal fragment of rhabdosome with growing third theca in reverse aspect, A_2, A_3 apertural part of first and second theca in same specimen, obverse aspect, *B* apertural apparatus of a second theca in reverse aspect (Mielnik, depth 911.60 m, *cornutus* zone); *A*×50, *B*×97.

ap apex of prosicula, *b* basal parts of apertural processes made of densely crowded fuselli, *dp* dorsal process of metasicular aperture, *e* lateral elevation of apertural margin, *im* incipient microfusellar addition laid down on apertural elevation, *lap* left apertural process, *m* membranaceous part of apertural processes, *n* ventral apertural notch, p_1—p_6 strongly pigmented bands on surface of apertural processes, r_1—r_4 successive sicular black rings, *rap* right apertural process, *sed* grain of sediment attached to the surface of periderm, *thm* thickened margin of apertural processes, *v* virgula, *vi* virgella.

PLATE XXVI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aspects of microstructure (Pl. XXVIII, Fig. *A*, *p*, *t*). The proximal part is composed of more densely crowded, arcuate microfuselli, whose arrangement is, therefore, similar to a typical microfusellar tissue. An initial series of especially narrow and compact strips with strong arcuate curvature, laid down immediately over the fusellar apertural elevations, permits to distinguish it as a base of the process (Pl. XXV, Figs. *A*, *B*; Pl. XXVI, Fig. *A*; Pl. XXVIII, Figs. *A-C*, *b*). It corresponds to a structure formed in early growth stages and described previously as an ear-like-projection or protuberance. The dense packing of microfuselli results in the opacity of the base, which is hardly bleachable.

A tissue displaying a variable structural pattern occurs directly above the base. It consists of many microfusellar strips, gathered into bundles separated by distinct boundaries (Pl. XXV, Figs, A_1, *B*, Pl. XXVI, Figs. A_1, A_2; Pl. XXVIII, Figs. *A*, *B*, *C*). These boundaries are marked by dark-brownish bands (P, P_1-P_4...), which are probably local thickenings produced by the peridermal material. Most probably they correspond to certain periodicity of the growth. A rapid deposition of a series of microfuselli making a bundle, is succeeded by a certain arrest of the growth, resulting in the thickening of the edge. The pigmented bands are irregularly scattered over the surface of the membrane, the number of microfuselli in particular bundles being considerably variable.

The occurence of two secretionary units, that is, microfusellar strips (secretionary units of the first order) and the bundles of microfuselli, separated by strongly pigmented bands (secretionary units of the second order), seems to be, however, the main feature of this peculiar tissue, which in certain aspects is similar to the pseudomicrofusellar tissue, distinguished previously (see terminology).

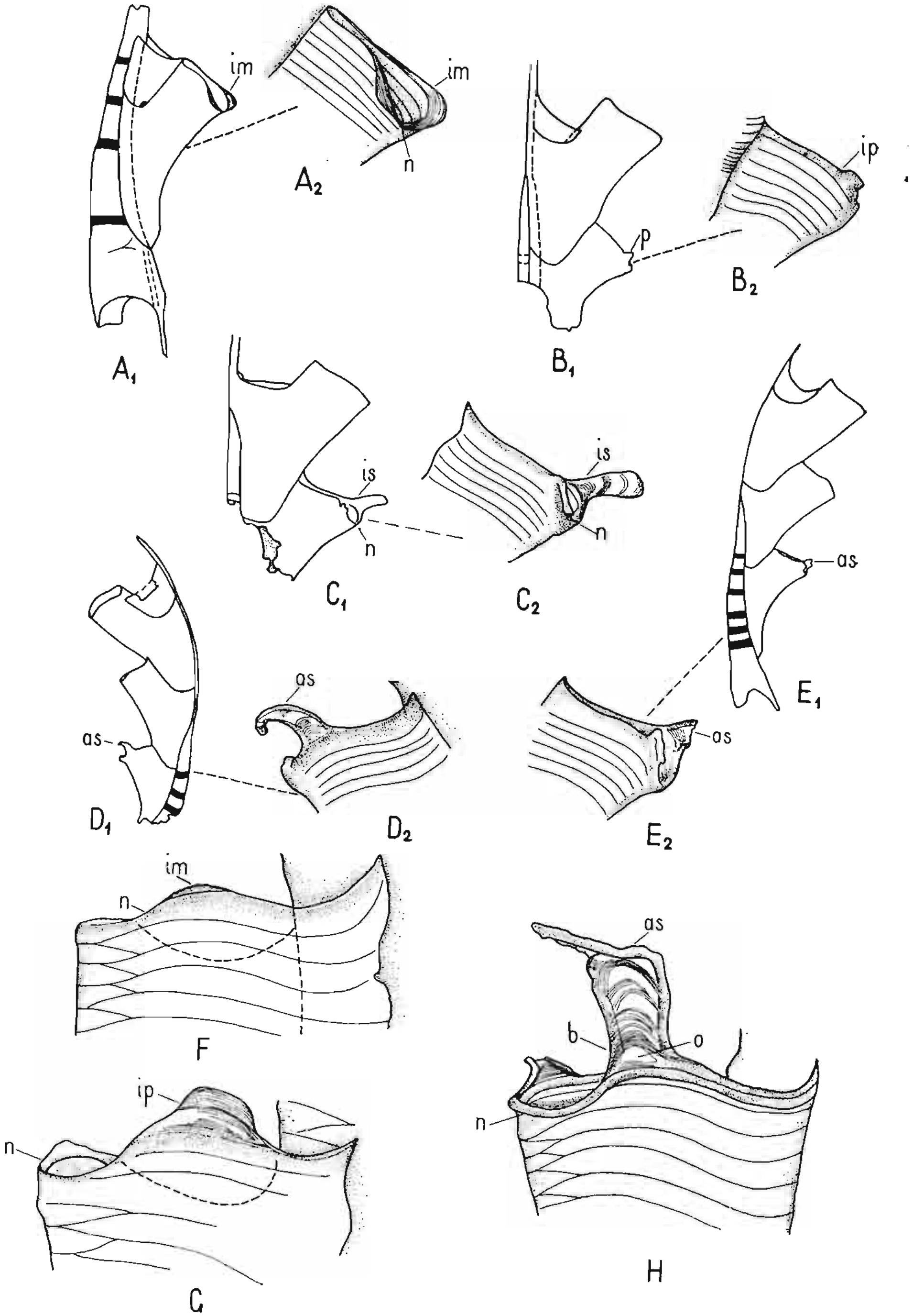
The terminal parts of the processes have a somewhat different struc-

Plate XXVI

Bohemograptus cornutus n.sp. Sicula with first theca, structure and development of apertural apparatus in proximal thecae. A_1 proximal part of rhabdosome with growing second and third theca seen from obverse side, and apertural apparatus of first theca in reverse aspect (A_2), *B*—*C* early growth stages of first theca, B_1 general appearance of the specimen, B_2 structural details of apertural margin in its first theca provided only with lateral elevations, B_3 structural details of primary notch area and initial bud, C_1 general appearance of specimen showing slightly more advanced growth stage of first theca provided with incipient microfusellar addition (C_2), *D* early growth stage of the third theca showing only the presence of lateral apertural elevations (Mielnik, depth *A*, *D* 911.60, *B*, *C* 910.10 m, *cornutus* zone); B_1, C_1×26, remaining×50.

ap apex of prosicula, *b* basal parts of apertural processes made of densely crowded fuselli, *dp* dorsal process of metasicular aperture, *e* lateral elevations of apertural margin, *ib* initial bud, *im* incipient microfusellar addition laid down on apertural elevation, *lap* left apertural process, *m* membranaceous part of apertural process, *n* ventral apertural notch, *o* prothecal opening for bud of the second theca, *p* strongly pigmented bands of surface of apertural processes, r_1—r_5 successive sicular black rings, *rap* right apertural process, *thm* thickened margin of apertural processes, *thr* thecal black rings, *v* virgula, *vi* virgella.

PLATE XXVII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tural pattern. The presence of more pronounced, pigmented bands also permits to distinguish two secretionary units of the membrane. The units of the first order are, however, much wider than normal microfuselli, which are half the width of a normal fusellus of metatheca, or in certain cases as wide as a normal fusellus. The limits of particular strips of the first order are hardly discernible in terminal part and the membrane of the process is distinctly attenuated. In certain cases, the strips of the first order are absent (Pl. XXV, Figs. A_1,A_2; Pl. XXVI, Figs. A_1A_2), the membrane displaying only more or less scattered pigmented bands (*p*). The latter condition seems, however, to be caused by a poor state of preservation and the situation shown in Pl. XXV, Fig. *B*, Pl. XXVIII, Figs. *A-B* to be primary one. The greater width the strips of the first order may be partly a primary structural character and partly may also be caused by its faint limits, which allow one to trace only certain strips in a bundle.

The terminal part of the process is strongly expanded by the divergence of its thickened margins. Pl. XXV, Fig. *B*; Pl. XXVI, Figs. A_1—A_2; Pl. XXVIII, Figs. *A* and especially *B*). The membrane is there strongly attenuated, its free margin being usually jagged. It seems therefore, that in the primary state, each complete apertural process in proximal thecae terminates in a fanlike expansion, composed of an extremely thin, membranaceous periderm, mostly not preserved.

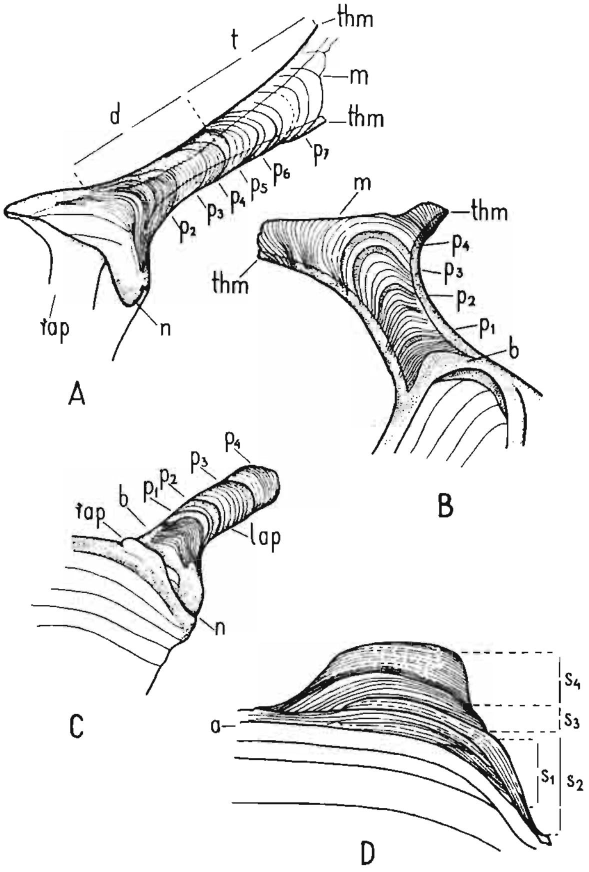
True distal thecae in the material investigated are very scanty, partly deformed or damaged and on the whole representing young growth stages. Judging from the few available thecae, they are 1.60—1.82 mm long, with metatheca 0.65—0.92 mm and protheca some 0.90—0.95 mm in length. Prothecal segments occupy, therefore, about 50—60% of the total thecal length. Thecae are 0.43—0.48 mm wide in prothecal part, measured at the level of aperture of preceding theca, 0.40 at the base of metatheca and 0.43—0.48 mm at the aperture (Pl. XX, Fig. *D*).

Plate XXVII

Bohemograptus cornutus n.sp. Growth stages of apertural processes in proximal and distal theca. *A*—*C* delayed formation of apertural processes in the first theca in successive stages of the development of rhabdosome, A_1—C_1 general appearance of growing rhabdosome, A_2—C_2 details of apertural structures in the first theca, *D*—*E* form attained by apertural processees in the first theca after reaching by rhabdosome the three-thecal stage, D_1—E_1 general appearance of growing rhabdosome, D_2—E_2 details of apertural structures in the first theca, *F*—*H* successive growth stages in formation of apertural processes in distal theca (Mielnik, depth *A*, *F*—*H*, 911.60 m, all remaining 910.10 m, *cornutus* zone); A_1, B_1, C_1, D_1, E_1×26, all remaining ×50.

as apertural spine, *b* basal part of apertural spine made of densely crowded fuselli, *im* incipient microfusellar elevation formed on apertural border, *ip* incipient apertural spine forming a protuberance or wing, *is* more advanced growth stage of apertural spine, *n* ventral apertural notch, *o* secondary (accidental) opening formed in result of a damage of the periderm.

PLATE XXVIII



Bohemograptus cornutus n.sp. Structural details of apertural processes. *A* microstructure of the proximal part of a left apertural process with rather distinct boundary between darker thickened part (d) made of densely crowded microfuselli, and a transparent, attenuated terminal part with hardly discernible microfuselli (*t*), *B* microstructure of an apertural process in a proximal theca showing fan-like expansion at the terminal end, *C* early growth stage in formation of a left apertural process in the first theca showing a distinct basal part made of densely crowded microfuselli, and more attenuated terminal part, *D* incipient microfusellar structure laid down on apertural margin of a distal theca (Mielnik, depth *C* 910.10 m, all remaining 911.60 m, *cornutus* zone); ×97.

a apertural margin made of normal fuselli, *b* basal part of apertural process made of densely crowded microfuselli, *d* darker, semitransparent part of apertural processes, *lap* left apertural process, *m* membranaceous wall of apertural process, *n* ventral apertural notch, *rap* right apertural process, p_1—p_7 strongly pigmented bands of surface of apertural processes, s_1—s_4 successive secretionary units of second order deposited on aperture of fusellar metatheca, *t* terminal, attenuated part of apertural processes, *thm* thickened margin of apertural process.

In early growth stages, aperture, like more proximal thecae displays gentle lateral elevations, separated by a shallow ventral notch (*n*). In further growth stages, an addition of microfusellar strips, laid along these elevations, results in incipient, earlike, apertural processes (Pl. XXVII, Figs. *F*, *G*, *im*, *ip*).

In thecae, placed more medially, such an addition of more strips results in tapelike apertural processes, which do not differ much from those in proximal thecae, and probably are only shorter (Pl. XXVII, Fig. *H*, *as*). Because of the scarcity of the material available the shape and structure of apertural processes in true distal thecae are uncertain. Associated in samples with typically *cornutus* proximal fragments, and tentatively assigned on the basis of their robust appearance to *B. cornutus* n. sp., lack microfusellar additions. This may indicate that most distal thecae are devoid of these structures throughout their life-time. It seems however more probable, that such additions present in fact, were delayed in their formation, their absence on the distal thecae examined being thus connected with their early growth stages. In the latter case, one may expect that microfusellar additions in distal thecae are similar to their morphological form considered to be medial thecae, the processes being probably progressively shorter (Pl. XXVII, Fig. *H*, *as*), or more strongly differing structurally. In this latter case the processes may be more similar to microfusellar additions in the distal thecae of *B. praecornutus* n. sp. and take the form of broad, earlike lappets (comp. Fig. 16).

The fragmentary material does not enable establishing the shape and size of rhabdosome. Proximal fragments of rhabdosome are distinctly curved ventrally, with the strongest curvature probably at the third theca. Thecal number in 10 mm cannot be reliably established, but it seems safe to suggest that in its general characteristic rhabdosome only slightly differs from that in *B. praecornutus* n. sp.

Stratigraphic range. — *B. cornutus* n. sp. has been recognized in few samples from a thickness limited by a depth of 911.60—910.10 m (1.50 m). It is associated there with *Neolobograptus auriculatus* n. sp., *Prist. dubius frequens* Jaekel and *Prist. dubius tumescens* (Wood).

A rather narrow vertical range of *B. cornutus* n. sp. marks a highly characteristic horizon in the lower part of the Siedlce Beds. In the present paper a suggestion is made to distinguish these strata in the sequence investigated as the range zone of *B. cornutus* n. sp. (see distribution table on Pl. I, and comp. p. 177).

As compared with the distribution of earlier and more primitive *B. praecornutus* n. sp. the distribution of the species in question marks only a short episode. *B. praecornutus* n. sp. displays a long persistence over the last occurrence of *B. cornutus* n. sp. The overlap in time in the distribution of the two forms mentioned above is a fact, but the restriction of the *cornutus* zone may have a local character.

Systematic position. — *B. cornutus* n. sp. is strongly similar in size, shape of thecae and rhabdosome to *B. praecornutus* n. sp. The presence of apertural elevations in thecae throughout the rhabdosome is a characteristic feature common to both species. The delayed formation of microfusellar additions described above results in a "*praecornutus*" stage of growth of thecae. This seems to be a recapitulatory effect, the growing theca of *cornutus* passing through a stage approaching the final growth stage in *praecornutus*. Stratigraphic data are in a complete conformity with the phylogenetic sequence here suggested, *B. cornutus* n. sp. originating later than *B. praecornutus* n. sp. (comp. Pl. I, range chart). In the light of these data it seems very likely that, since *B. praecornutus* n. sp. was the earlier form to occur and the fuselar part of its thecae displayed a great similarity to the thecae of a true *cornutus*, this species was the ancestor.

The most significant difference between the species in question is that in the structure of their microfusellar additions. In *B. praecornutus* n. sp., they seem to occur sporadically. Only some relatively few rhabdosomes display the capability of producing microfusellar tissue and its derivatives. The morphological form of microfusellar additions is strongly variable, the prevailing structure being an earlike process, broadly joining the apertural margin.

In contrast to *B. praecornutus* n. sp., in *B. cornutus* n. sp. microfusellar additions are remarkably constant and reach a specifically characteristic morphological form. It seems that the development of these additions became a rule in all or most of the rhabdosomes in *B. cornutus* n. sp. A tapelike process with a contracted base and a fanlike expansion at the free end is the fundamental morphological pattern of apertural microfusellar additions [12].

Despite these significant morphological differences, the microstructure of the apertural apparatus is in both cases fundamentally similar. A base, consisting of densely crowded and rather regularly arranged microfusellar strips (a normal microfusellar tissue) may be distinguished (comp. diagram Pl. V, Fig. B_1—D_1) in all cases. The extension of this structure consists of a thin membrane with wider and narrow, irregularly arranged strips (pseudomicrofusellar tissue) and is followed by an extremely attenuated membranaceous expansion at the free end of the process (comp. diagram Pl. V, Figs. B_1—D_1). In the light of these important similarities, in microstructure of processes in both species, it seems reasonable to derive microfusellar apertural processes of *B. cornutus* n. sp.

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[12] It should be remembered that the known examples of microfusellar additions in *B. praecornutus* n. sp. were found above the place of appearance of *B. cornutus* n. sp. They appear, therefore, too late to be directly related to the origin of the latter form. It is however very likely that the earlier population of the former species also included specimens with the capability of producing such additions.

from homological structures in *B. praecornutus* n. sp. The analysis of generalized patterns of these processes, as shown diagramatically in Pl. V, Figs. C_1—D_1, indicates that the only necessary changes were: 1) the contraction of the base, 2) the appearance of a framing in the form of roll-like thickenings at both margins of apertural processes.

Since the marginal frame was formed by a certain convergence, condensation and coalescence of the free ends of the strips, both changes are mutually interrelated. This is responsible for the simultaneous narrowing of the process.

The change from a very broad, platformlike apertural addition (Pl. X, Fig. B_1), to narrower, rather earlike process (Pl. X, Fig. C_1) fits into the range of variations in a single rhabdosome of *B. praecornutus* n. sp. The latter type of microfusellar addition was most probably the starting-point of further transformation (Pl. V, Fig. C_1) which quite naturally may be reduced to a single change, that is, the formation of lateral framing and narrowing of the process. The adaptive significance of this framework was probably connected with its possible mechanical role (the strengthening of the processes).

B. cornutus n. sp. is a form extreme morphologically and strongly differing from other representatives of *Bohemograptus*, probably also specialized adaptively. It is a final link in a short-living offshoot of *B. cornutus* n. sp. (comp. Pl. VIII).

Genus *Neolobograptus* n. gen.

Type species: Neolobograptus auriculatus n. sp.

Diagnosis: As in type species (see below).

Species assigned: At present monotypic.

Stratigraphic distribution: B. praecornutus — Neolob. auriculatus zones, and bottom of *Neocuc. inexspectatus* zone; the lower part of Siedlce Beds, Upper Ludlovian.

Remarks on the concept of Neolobograptus n. gen. — This at present monotypic genus is distinguished as a distinct link in evolution of Neocucullograptinae n. subfam. It differs from *Bohemograptus* Přib. in a strong elongation of thecae, placing thecal aperture in a stabilized position above the apex of prosicula, and by a formation of strong bilateral elevations of thecal margin provided with dorsolateral incisions. From *Neocucullograptus* n. gen. it differs in a sporadic occurrence of microfusellar additions and simple nature of apertural apparatus made of this tissue.

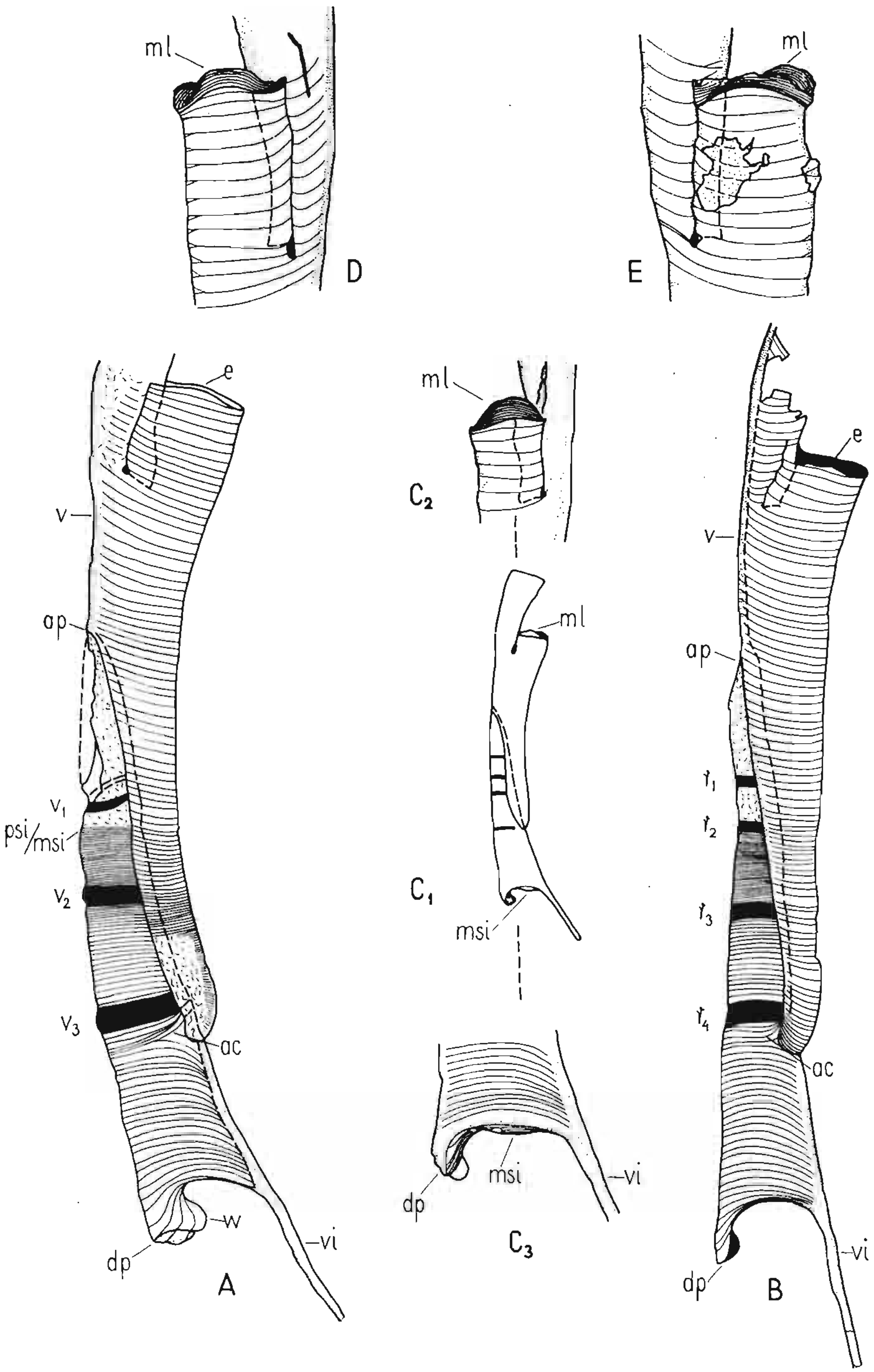
Neolobograptus auriculatus n. sp.

(Pl. XXIX—XXX)

Holotype: Pl. XXIX, Fig. *B*.

Paratype: Pl. XXX, Figs. C_1—C_2

PLATE XXIX


ml
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r_3
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ac
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B

Type stratum: Greenish-blue mudstones and marls in the core of the Mielnik deep-boring, between 914.60—889.20 m of depth (*Bohemograptus praecornutus* to *Neolob. auriculatus* zones, lower part of the Siedlce Beds).

Derivation of the name: after Lat. *auricula* — an ear; resembling an ear in shape of its apertural elevations.

Diagnosis. — Monograptid with sicula of the *Bohemograptus* type, proximal part of rhabdosome strongly curved ventrally and consisting of slender, elongated thecae. Thecae provided, throughout the rhabdosome, with lateral elevations of the apertural margin composed of a fusellar tissue. Simple microfusellar additions occur sporadically.

Material. — Many fragments of rhabdosome, including siculae and most distal thecae etched from samples of the Mielnik boring mainly at a depth of 904.60—893.70 m. Best preserved, flattened specimens were obtained from a sample taken at a depth of 904.60 m and the best unflattened ones at a depth of 893.70 m. The material obtained enables the analysis of the detailed structure of sicula and thecae. From the Baltic drift material unknown.

Description. — Sicula straight or very slightly curved ventrally, 1.43—1.55 m long, provided with 3—5 sicular black rings and a strongly marked dorsal apertural process (Pl. XXIX, Figs. *A*, *B*, *C*, C_3).

Prosicula some 0.45—0.55 mm long and, at its aperture 0.15—0.17 mm wide. No traces of longitudinal threads or helical line discernible on it, most probably due to a poor state of preservation. Adult prosicula provided with a sicular black ring (r_1) situated approximately in the middle of prosicular segment (Pl. XXIX, Figs. *B*, C_1, r_1), or displaced towards its aperture and, occasionally, situated obliquely (Pl. XXIX, Figs. *A*, r_1). In the case of the presence of several sicular black rings (4—5), the second of them lies right on the boundary of pro- and metasicula. (Pl. XXIX, Figs. *B*, C_1, r_2).

When, however, only 3 sicular black rings are present, the second one, distant from the boundary ocurs already on the metasicula proper (Pl. XXIX, Fig. *A*, r_2).

Metasicula about 0.97—1.05 mm long, gradually widening and reaching 0.17—0.27 mm at the level of primary notch and 0.30—0.36 mm at its definitive aperture. The latter is provided with a strong dorsal

Plate XXIX

Neolobograptus auriculatus n.sp. Sicula and proximal thecae with their microfusellar additions. *A*—*B* Sicula with first theca devoid of microfusellar additions, *C* sicula with first theca provided with microfusellar additions *D*—*E* proximal thecae with microfusellar additions on the apertural margin (Mielnik, depth *A*, *C* 904.60 m, *B* 901.80 m, *D*, *E* 894.00 m, *auriculatus* zone); $C_1 \times 14$, remaining $\times 50$.

ac fuselli showing archline arrangement, *ap* apex of prosicula, *dp* dorsal process of metasicula, *e* elevations of apertural border, *ml* microfusellar lobes of thecae, *msi* microfusellar lobes of metasicula, r_1—r_4 successive black rings of sicula, *v* virgula, *vi* virgella.

process and a virgella (Pl. XXIX, Figs. *A, B, dp, vi*). Dorsal process 0.12—0.17 mm long (*long.*), shovel- or tongue-like, occasionally provided with wing-like, lateral outgrowths, separated by a median notch and situated on a dorsal, zigzag suture (Pl. XXIX, Fig. *A, w*).

As indicated by the structure of the primary notch region (Pl. XXIX, Figs. *A, B, ac*), the first theca is formed from sicula in normal monograptid manner of budding. The initial bud begins a some 0.55—063 mm from the aperture of prosicula and is situated some 0.40—0.42 mm from the lateral margin of metasicular aperture.

The first theca is elongated, slender and terminating well above the apex of prosicula (Pl. XXIX, Figs. *A, B,* C_1). In these characters it clearly differs from the known species of *Bohemograptus* Přib. and is similar to *Neocucullograptus* n. gen. It is 1.51—1.82 and its free part, stretching above the prosicular apex, 0.50—0.70 mm long. The subapertural segment of metatheca ranges from 0.20 to 0.25 mm in length, theca reaching a width of some 0.21—0.25 mm at the level of prosicular aperture and some 0.16—0.25 mm at the base of its metatheca. Over its entire length metatheca is adnate to the basal part of the second theca and inclined to the axis of protheca at an angle of some 20—30°. The prothecal segment, 1.29—1.57 mm long occupies about 70—86% of the total thecal length.

Aperture of the first adult theca is 0.17—0.26 mm wide and provided on both sides with low apertural elevations, each of them consisting of only one fusellus separated on the ventral side by shallow notch (Pl. XXIX, Figs. *A, B, e*).

As compared with the species of *Bohemograptus* Přib., sucessive proximal thecae are relatively slender. They are 1.54—1.55 their subapertural segment 0.26—0.47 prothecae 1.08—1.28 mm long. The prothecal segment occupies therefore about 72—85% of the total thecal length. At the level of aperture of a preceding proximal theca prothecae are 0.15—0.25 mm wide. Metathecae are 0.25—0.28 mm wide at the base. Metathecal segment, inclined to the axis of protheca at an angle of 10°, is adnate to the base of an adjacent theca. Apertures of adult metathecae are provided with gentle lateral elevations on the margin, each of them made up of a single fusellus (Pl. XXX, Figs. A_1,A_2, *B, e*). The fuselli are separated on the ventral side by a shallow notch. Usually, they do not join dorsally the wall of a succeeding theca, thus forming a small recess. The lateral apertural elevation, still very slightly marked, increases gradually up to a height of 0.03—0.04 mm (*long*).

Still more elaborated are the elevations on distal thecal apertures (Pl. XXX, Figs. *C—E*).

Usually, 3 fuselli make up the elevations which reach 0.05—0.16 mm in height (*long.*). The elevations are separated on the ventral side by a distinct, ventral, apertural notch (Pl. XX, Fig. *E, n*) and, sloping gently to the dorsal end, they form characteristic dorso-lateral incisions (*li*) on both sides of the aperture. This characteristic shape of a thecal aperture is a result of a certain arrangement of fuselli making up the elevations which dorsally terminate freely, becoming successively shorter and resting mostly on the ventral slope of the apertural elevation (Pl. XXX, Fig. *D, e, li*).

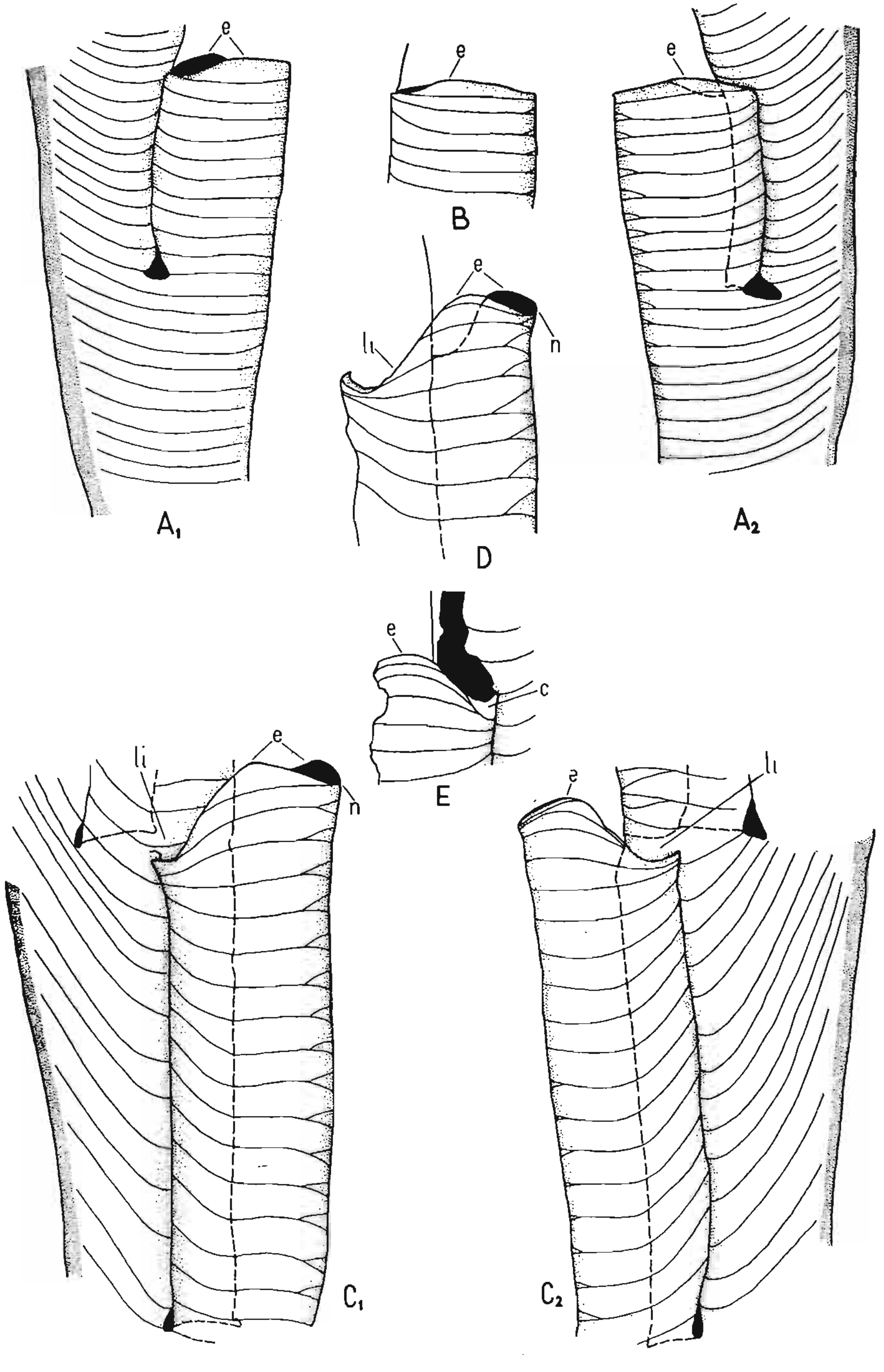
Sometimes, a dorso-lateral incision on the obverse side of aperture may be partly filled with a crescentic, peridermal material secondarily deposited in its corner (Pl. XXX, Fig. *E, c*). Such a filling has however never been noted on the reverse side of the thecal aperture.

Distal thecae are elongate and rather slender their ventral walls being almost straight, except in the most distal theca which probably may be assigned to this species but is marked by a certain sigmoid curvature of its ventral wall. They are 1.85—2.33, their metathecae 0.85—1.20 and prothecae 1.00—1.15 mm long. The protheca takes about 47—55% of the total length of distal thecae. At the level of the aperture of a preceding theca (measured therefore due to overlap accross the metatheca of a given theca and protheca of succeding theca) rhabdosome is 0.57—1.00 mm wide. Metatheca is 0.26—0.70 mm wide.

The simple picture of thecal structure in *Neolob. auriculatus* n. sp. presented above is occasionally complicated by the appearance of microfusellar additions. Judging from the rarity of specimens affected by these changes, microfusellar additions occur sporadically, only very few specimens of the population investigated being capable of developing them (comp. chapter on phylogeny). The specimen in Pl. XXIX, Fig. C_1 displays microfusellar additions on metasicula (*sim*) and on the first theca (*ml*). In the case of metasicular aperture, a microfusellar addition forms on both sides a slightly marked elevation consisting of few, densely crowded strips (Pl. XXIX, Fig. C_3, *sim*). It is situated between the virgella and the dorsal apertural process (*vi, dp*). A microfusellar addition on the first theca is relatively more conspicuous, produced by a number of narrow and densely crowded strips, arcuately curved and deposited along each of the lateral apertural elevations (Pl. XXIX, Fig. C_2, *ml*) Thus these additions form two symmetric, ear-like, apertural lobes.

A number of medial thecae, provided with microfusellar additions on distinct apertural elevations, may be surely assigned to *Neolob. auriculatus* n. sp. (Pl. XXIX, Figs. *D, E*). They are associated with numerous thecae of *Neolob. auriculatus* n. sp. devoid of microfusallar additions. As in the first theca, these microfusellar additions form paired, symmetric, earlike lobes (Pl. XXIX, Fig. *D, ml*), or bands connected dorsally with the ventral wall of a succeeding theca (Pl. XXIX, Fig. *E, ml*). There is no indication of an asymmetry of these microfusellar structures. No exagerated form of microfusellar additions (“*velum*”, comp. terminology) has ever been observed in *Neolob. auriculatus* n. sp.

PLATE XXX



In general appearance, the rhabdosome in *Neolob. auriculatus* n. sp. strongly resembles the *Bohemograptus* Přib. In the proximal part rhabdosome is strongly curved ventrally with the strongest curvature at the level of the second theca. The distal part of rhabdosome is straight or almost straight. The degree of thecal overlap increases distally (from 1/6 to almost 1/2 of thecal length). Thecae number 9—10 in 10 mm in proximal and medial parts and 8—9 in distal one (Pl. VII, Fig. *A*).

Due to the fragmentary material, the size of a complete rhabdosome cannot be estimated, but it was probably fairly long.

Stratigraphic range. — In the core of the Mielnik boring, *Neolob. auriculatus* n. sp., makes its first appearance at a depth of some 914.60 m, at which however, only few thecal fragments, which might be assigned to this species, were found. More fragments were found in samples taken right 1 m higher up (913.60 m) and the first richer assemblage was recorded at a depth of 909.60 m. Assemblages containing numerous siculae, proximal and distal thecae were obtained from samples taken at a depth of 904.60—903.60 m. The last occurrence, marked by few distal fragments, was noted at a depth of 889.20 m. The entire vertical distribution of *Neolob. auriculatus* n. sp. in the Mielnik core seems, therefore, to be limited to a range of of 914.60—889.20 m (see distribution table, Pl. I).

Over its entire distribution range, *Neolob. auriculatus* n. sp. is commonly associated with *Bohemograptus praecornutus* n. sp., *B. cornutus* n. sp. (only in lower part), *B. bohemicus tenuis* (Bouč.), *Pristiograptus dubius frequens* Jaekel, *P. dubius tumescens* (Wood), "*Monograptus*" *egregius* n. sp., (throughout or almost throughout its range).

In the upper part, its distribution range overlaps that of the succeeding *Neocuc. inexpectatus* (Bouček), but they have never been found directly associated.

In the subdivision of the Siedlce Beds here suggested a partial range of *Neolob. auriculatus* n. sp. has been used as a basis for a partial range-zone of *N. auriculatus* (comp. range chart Pl. I). It comprises the belt of strata between the top of *cornutus* zone and the bottom of *inexspectatus* zone. In this biostratic unit, *N. auriculatus* n. sp. is the most cha-

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Plate XXX

Neolobograptus auriculatus n.sp. Structure of medial and distal thecae. A_1—A_2 apertural part of medial thecae in reverse and obverse aspect, *b* aperture of a theca adjacent to *A* and placed proximally to it, C_1—C_2 metathecal part of a distal theca in reverse and obverse view, *D* aperture of a distal theca with normal lateral apertural incision, *E* fragment of distal theca showing lateral apertural incision partly filled by crescentic fusellar addition (*C*) (Mielnik, *A*—*B* 903.60 m, *C*—*E* 894.00 m, *auriculatus* zone); ×63.

e lateral elevations of apertural margin, *li* dorso-lateral incision of apertural border, *n* ventral apertural notch.

racteristic fossil, although it appears much earlier, being present as early as the *praecornutus* zone.

Systematic position. — A general appearance of rhabdosome, shape of sicula and stratigraphic occurrence leave no doubts that *Neolobograptus auriculatus* n. sp. may be derived from *Bohemograptus* Přib., only few changes being necessary for its origin. These changes may be summarized as follows: 1) elongation and gracilization of thecae, especially proximal and medial ones, 2) appearance of distinct, paired, lateral elevations on thecal apertures throughout the rhabdosome. These progressive changes are, however, combined with certain others, common with the representatives of *Bohemograptus* as 1) shape and size of sicula, 2) strong ventral curvature of rhabdosome, 3) capability of forming microfusellar additions.

The predominant trend toward elongation and gracilization of proximal thecae displayed by *Neolob. auriculatus* n. sp. seems to suggest an ancestry of *Bohemograptus* having relatively elongated proximal thecae. Since it displays a remarkable trend toward a certain elongation of proximal thecae and precedes *Neolob. auriculatus* n. sp. in stratigraphic appearance, *Bohemograptus bohemicus tenuis* (Bouč.) seems to be a probable ancestor. Further elongation of proximal and partly medial thecae, expressed, among other features, by a characteristic uplift of the aperture in the first theca (Pl. II) an appearance and spreading of thecal elevations along the rhabdosome are in practice the only changes necessary to separate the line of *Neolob auriculatus* n. sp. from bohemograptids. While the first trend (gracilization of thecae) seems to be a phylogenetic novelty introduced to the rhabdosome proximally (as the proximal thecae are affected by this change to a greater extent), the second seems to be rather introduced distally. There is a distinct distal increase in apertural elevations, which are hardly discernible in most proximal thecae but strongly marked and deeply notched in distal ones. This evidence may suggest two different trends operating simultaneously according to different phylastogenetic modes (comp. chapter on phylogeny).

The presence of microfusellar additions also throws some light on the origin of *Neolob. auriculatus* n. sp. Since the microfusellar additions were quite common as early as in *B. b. tenuis*, it may be safe to believe that the *auriculatus* lineage separated itself from *B. bohemicus tenuis* populations. This seems especially true since the inheritance of microfusellar tissue from some earlier monograptid is more likely than its independent development due to a new mutation. In this connection, it is noteworthy that in *Neolob. auriculatus* n. sp. microfusellar additions consist exclusively of the microfusellar tissue proper, with a well-ordered arrangement of strips. This seems to represent a more advanced stage in the evolution of microfusselar additions (comp. chapter on phylogeny).

On the other hand, *Neolob. auriculatus* n. sp. might be ancestral to *Neocucullograptus* n. gen. This possible line of evolution implies a further development of microfusellar additions. These are, however, built up on a distinctly *auriculatus* foundation as indicated by the *auriculatus* growth stage recognized in *Neocuc. inexspectatus* (Bouč.). Especially remarkable is here the presence of dorsolateral incisions on apertural elevations of *Neocullograptus* n. gen., which indicate that this resemblance has a value of true homology. The dorsolateral incision on the obverse side of theca is later simply filled by microfuselli, which here join the ventral wall of a suceeding theca. The fate of the same incision on reverse side is, however, quite different. It remains deeply notched and later serves as a base for a peculiar structure, or what is known as a lateral process (comp. description of *Neocuc. inexspectatus*).

Genus *Neocucullograptus* n. gen.

Type species: Neocucullograptus kozlowskii n. sp.

Diagnosis: Monograptids with rhabdosomes, strongly curved ventrally in proximal part and invariably provided in adult growth stages with microfusellar additions, composed of the microfusellar tissue proper. These additions are simple, bilaterally symmetric lobes in sicula, but they produce a complex apertural apparatus in thecae, consisting of a smaller right and a larger left lobe, sometimes provided with certain superstructures such as gular, rostral and lateral processes.

Species assigned: Neocuc. inexspectatus (Bouček, 1932), *Neocuc. kozlowskii* n. sp.

Stratigraphic distribution: Neocuc. inexspectatus — Neocuc. kozlowskii zones, the lower part of Siedlce Beds, Upper Ludlovian.

Remarks on the concept of Neocucullograptus n. gen. — This genus represents the most specialized and terminal link of Neocucullograptinae n. subfam., marked by the presence of microfusellar additions as stabilized morphological character and by the complex nature of apertural apparatus in thecae, composed of only the microfusellar tissue proper.

Neocucullograptus inexspectatus inexspectatus (Bouček, 1932)

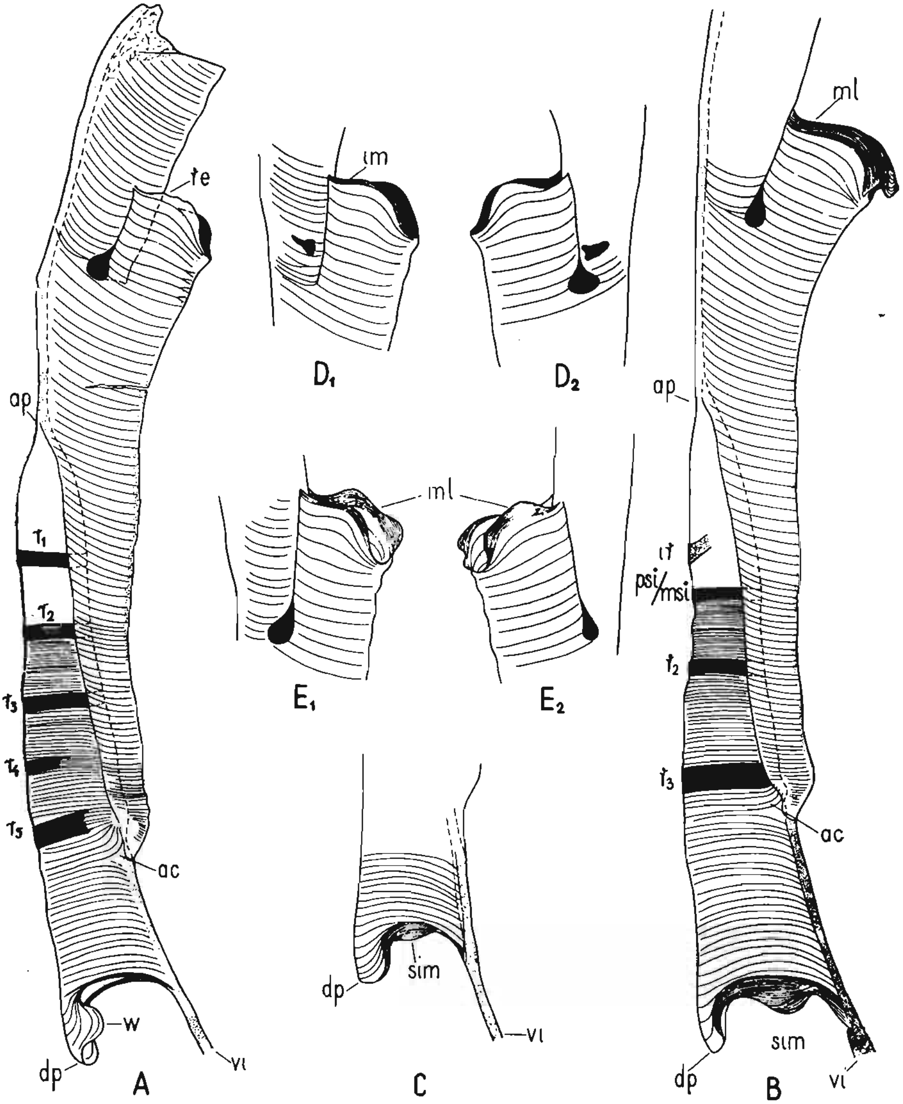
(Pl. XXXI—XXXIV, Fig. 17)

1932. *Monograptus inexspectatus* Bouček; B. Bouček, Předbězna sprava... II; Fig. 1, E-f, pp. 151—153.

1936. *Monograptus scanicus* Tullberg, B. Bouček, Graptolitová fauna... pp. 21—22 (*M. inexspectatus* Bouč. mentioned as junior synonym of *M. scanicus* Tullb.).

Material. — Numerous siculae; proximal and distal fragments of rhabdosome mostly flattened or semiflattened, etched from core samples of the Mielnik boring at a depth of 890.70—887.00 m. The material allows one to examine the astogeny, details of structure and growth stages of sicula and thecae. From the Baltic drift material unknown.

PLATE XXXI



Neocucullograptus inex. inexspectatus (Bouček). Sicula with the first theca and development of their microfusellar apertural additions. *A* young sicula and the first theca without microfusellar additions, *B* same in advanced growth stage, provided with microfusellar apertural additions, *C* aperture of metasicula with incipient microfusellar apertural lobe, D_1—D_2, E_1—E_2 apertural parts of the first thecae in less (*D*) and more (*E*) advanced growth stages seen in reverse and obverse aspect (Mielnik, depth 888.20 m, *inexpectatus* zone); *A*—*C* ca × 50, *D*—*E* ca × 63.

ac fuselli showing archline arrangement, *ap* apex of prosicula, *dp* dorsal process of metasicula, *im* incipient microfusellar lobe, *ir* incipient black ring, *ml* microfusellar apertural lobes, *psi/msi* boundary of pro- and metasicula, r_1—r_5 successive black rings of sicula, *sim* microfusellar additions on metasicular aperture, *vi* virgella, *w* wing-like outgrowth on the dorsal process.

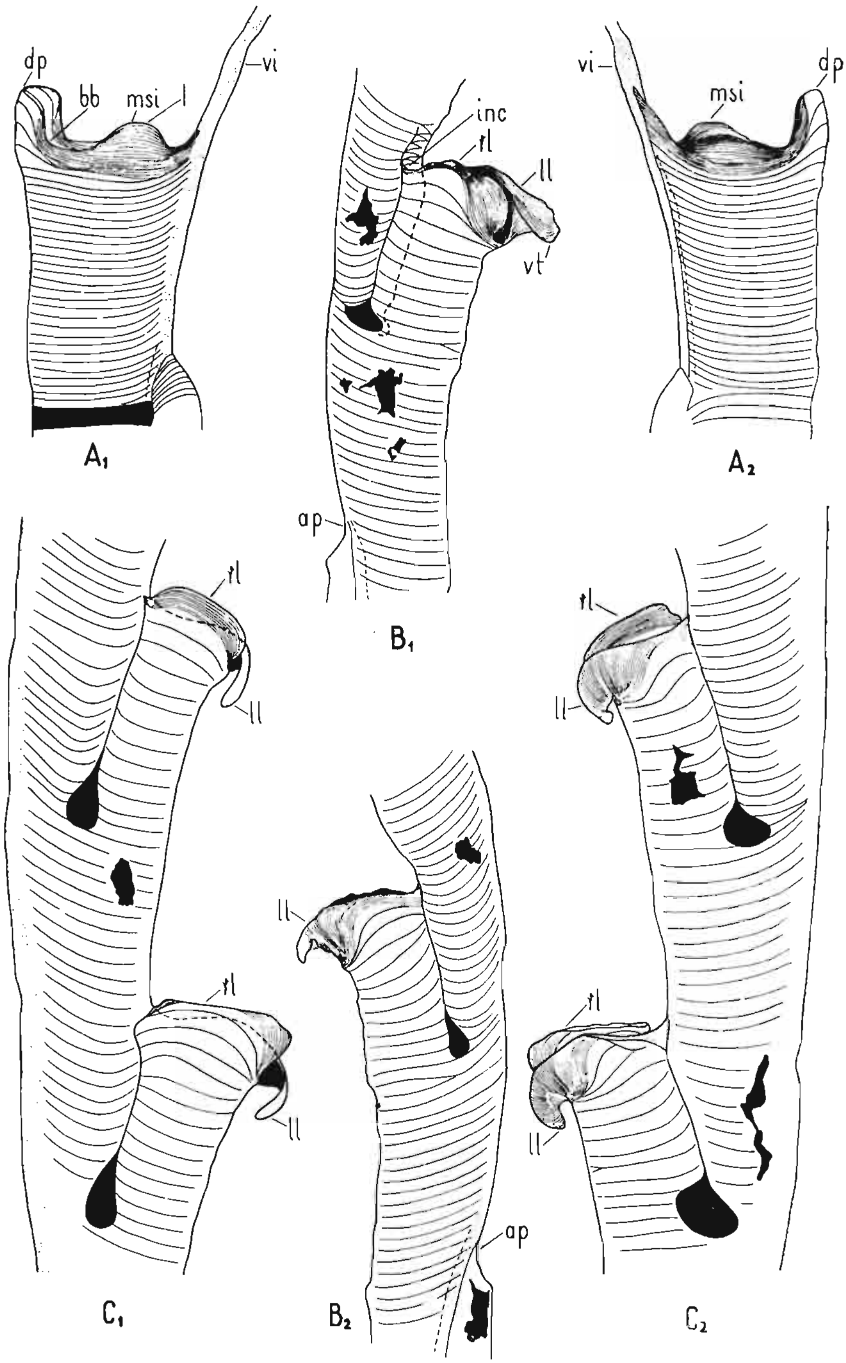
Description. — Sicula (Pl. XXXI, Figs. *A*, *B*) straight or only very slightly curved ventrally, 1.39—1.64 mm long and similar in shape to siculae of *Bohemograptus*. In five of the specimens measured prosicula ranges in length from 0.45 to 0.61 mm. In some cases, it is provided with a sicular black ring (r_1) approximately in the middle of prosicular segment (Pl. XXXI, Fig. *A*, r_1) and r_2 on the boundary of pro- and metasicula. Such arrangement was noted in siculae with a greater number (4—5) of sicular black rings only. In siculae with a number of sicular black rings reduced to 3, the first of them (r_1) is situated at the boundary of prosicula and metacicula, the prosicula lacking any black ring, or having an only incomplete and obliquelly situated (dark-brown) incipient ring (Pl. XXXI, Fig. *B*, *ir*). The apertural width of prosicula amounts to 0.17 mm. Probably due to the poor state of preservation of periderm, neither helical line nor longitudinal threads are discernible on the prosicula.

Adult 0.94—1.06 mm long metasicula, expands gradually toward the aperture, reaching 0.24—0.29 mm in width at the level of the primary notch and some 0.30—0.39 at a definitive aperture. It is provided with 3 or 4 sicular black rings, one of them (r_1 in the case when there are only 3 black rings in sicula and r_2 when their total number is 4 or 5) being invariably placed on the boundary of pro- and metasicula. Nevertheless as shown on transparencies under strong transmitted light (Pl. XXXI, Fig. *A*, r_2), r_2 is situated already on the metasicular segment, where translucent fuselli are visible through it. Some of the black rings situated on metasicula, may be incomplete (Pl. XXXI, Fig. *A*, r_4, r_5).

The aperture of metasicula displays the presence of virgella and a strong 0.15—0.20 mm long, dorsal process, which due to a shallow medial notch, separating two lateral, winglike elevations (Pl. XXXI, Fig. *A*, *dp*, *w*), may be slightly bifid at the end. In other cases, the dorsal process is shovellike and subtriangular (Pl. XXXI, Figs. *B*, *C*, *dp*).

In addition to the dorsal process, the aperture of a complete metasicula has two, laterally situated lobes composed of microfusellar tissue (Pl. XXXI, Fig. *B*, *sim*). The latter are conspicuously smaller than those in *Neocuc. kozlowskii* n. sp., which reach no more than 0.08—0.10 mm in height (*long.*). A basal band (*bb*), spread between virgella and the dorsal process, and a low, ear-like elevation, that is, the lobe proper (*l*), may be distinguished in this microfusallar structure (Pl. XXXII, Fig. *A*, *bb*, *l*). No distinct asymmetry of these lobes has been noted, and their small size differences seem to be accidental. The specimens in Pl. XXXI, Figs. *A*, *C* show that this microfusellar material was laid down on the apertural margin of metasicula with a considerable delay, after the sicula has reached maturity. The specimen figured in Pl. XXXI, Fig. *A* indicates that the first strips of microfusellar tissue appear on the lateral margin of metasicular aperture only during the growth of the second theca (or later). The condition seen in Pl. XXXI, Fig. *C*, *sim*, clearly displays a slightly more advanc-

PLATE XXXII


dp
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C_2

ed growth stage of this addition, which consists of numerous microfusellar strips. The sequence, seen in Pl. XXXI, Figs. *A, C, B*, represents, therefore a complete course of the growth of microfusellar apertural lobes of metasicula. Clearly, then, in earlier growth stages, sicula lacks any microfusellar additions and is similar in shape and size to adult siculae of *Bohemograptus* (bohemograptid stage). The next growth-stage (neocucullograptid stage) is reached after a gradual formation of the microfusellar addition. This pattern of adding the microfusellar material to the latteral apertural margins of sicula, after the growth of its fusellar tissue was finished, is marked by a certain delay. The suggestion is made therefore to describe this additional growth as "a postmatural growth" (comp. chapter on comparative-anatomical analysis).

The structure of the primary notch region indicates that the initial bud was produced in the normal monograptid manner (Pl. XXXI, Figs. *A, B, ac*). The initial bud begins 0.60—0.68 mm from the aperture of prosicula and is situated some 0.30—0.45 mm from the lateral margin of the metasicular aperture.

The first theca is 1.82—2.00 mm long. The free part of the theca, stretching above the apex of prosicula, is 0.69—0.85 mm long and the more elongated this theca, the longer is its free part. The subapertural segment of the metatheca is 0.28—0.40 mm long, the theca being some 0.25—0.28 mm wide at the apex of prosicula and 0.19—0.21 mm at the base of the metatheca. Over its length the metatheca is adnate to the basal part of the second theca and inclined to the axis of protheca at an angle of some 20—30°. The 1.54—1.63 mm long prothecal part of the theca occupies, therefore, about 85—80% of the thecal length.

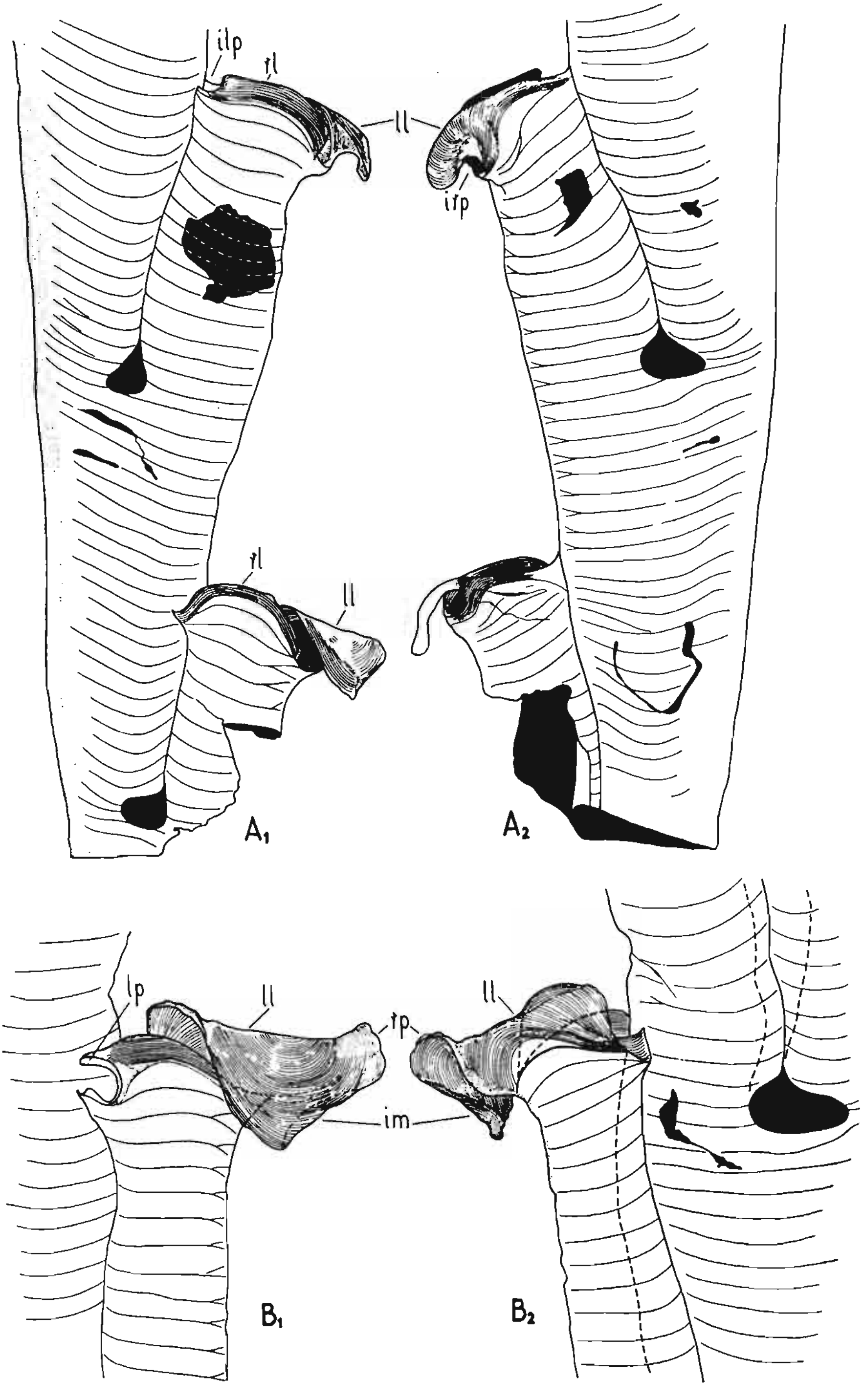
In earlier growth stages, the aperture of metatheca is provided with two lateral elevations on the margin (Pl. XXXI, Fig. *A, re*), each of them consisting of 2—3 fuselli slightly curved upwards and separated by a ventral notch.

Later, the microfusellar strips have been laid down gradually on either apertural elevation to form an initially narrow microfusellar band, that is, the incipient form of microfusellar apertural lobes (Pl. XXXI, Figs. D_1—D_2, *im*). This microfusellar addition continues to grow by fur-

Plate XXXII

Neocucullograptus inex. inexspectatus (Bouček). Structure of thecae compared with apertural part of metasicula. A_1—A_2 apertural part of metasicula in reverse and obverse aspect, B_1—B_2 first theca in reverse and obverse aspect, C_1—C_2 medial theca in reverse and obverse aspect. (Mielnik, depth 888.20 m, *inexspectatus* zone); ×63. apex of prosicula, *bb* basal band of microfusellar addition, *dp* dorsal process of metasicula, *inc* dorso-lateral incision in the right lobe, *l* lobe proper of the microfusellar addition, *ll* left microfusellar apertural lobe, *rl* right microfusellar apertural lobe, *sim* microfusellar additions on metasicular aperture, *vi* virgella, *vt* ventral termination of the left lobe.

PLATE XXXIII



ther deposition of microfuselli, the bands widening to form microfusellar apertural lobes of equal size and shape (Pl. XXXI, Figs. E_1—E_2, *ml*).

The next stage in the formation of apertural apparatus in the first theca is connected with a differential growth of microfusellar lobes, the left one becoming larger and partly curved over the aperture and the right forming only a low elevation. This results in a characteristic shape of apertural apparatus (Pl. XXXI, Fig. *B, ml;* Pl. XXXII, Figs. B_1—B_2 1, *rl*).

As described above, an earlier, "*auriculatus*" stage (Pl. XXXI, Fig. *A*) and a later "*inexspectatus*" stage may be distinguished (Pl. XXXI, Fig. *B*) in the development of the apertural apparatus of the first theca. The phylogenetic significance of this pattern of development is discussed below). below).

The left microfusallar apertural lobe is markedly larger, incurved over the aperture and terminating ventrally in shovel-like process (Pl. XXXII, Figs. B_1—B_2, *ll*). This lobe consists of 1) a basal band of microfuselli initially deposited over the entire margin of the left apertural elevation and dorsally joining the ventral wall of an adjacent theca (Pl. XXXII, Fig. B_2,) and 2) a shovel-like process mentioned above, produced by an arch-like arrangement of microfuselli (Pl. XXXII, Fig. B_1, *rt*).

The right microfusellar apertural lobe consist of a very narrow basal band, displaying a shallow incision in its dorsal part (Pl. XXXII, Fig. B_1, *rl, inc*) and a more ventrally situated elevation.

Proximal thecae are tubular, 1.25—1.85 mm long, with a straight ventral wall, some 0.28—0.54 mm wide in the prothecal part (at the level of the aperture of a preceding theca) and reaching some 0.20—0.35 mm in width at the base of matetheca. The protheca is 0.85—1.15 and the subapertural segment of metatheca 0.40—0.70 mm long. The prothecal part occupies, therefore, about 70—60% of the total thecal length. Metatheca is inclined to the axis of protheca at an angle of some 20°.

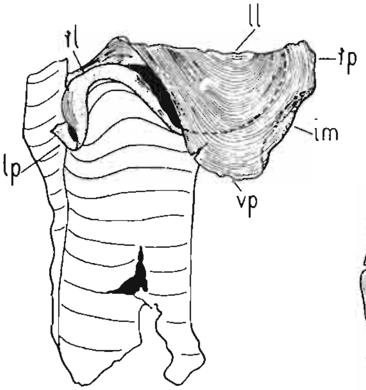
Astogenetic changes are expressed mostly in the structure of the apertural apparatus of thecae (Pl. XXXII, Figs. C_1—C_2). The hypertrophied left microfusellar apertural lobe, situated on the apertural elevation formed by 2—3 last fuselli, has a more pronounced ventral termination than that of the first theca. Dorsally it is fused with the ventral wall of adjacent theca and curved over the aperture (Pl. XXXII, Figs. C_1—C_2, *ll*).

Plate XXXIII

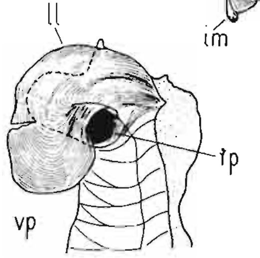
Neocucullograptus inex. inexspectatus (Bouček). Structure of distal thecae. A_1—A_2 distal theca in reverse and obverse aspect, B_1—B_2 apertural part of more distally placed theca in reverse and obverse aspect (Mielnik, 888.20 m, *inexspectatus* zone); ×63.

ilp incipient lateral process on the right lobe, *im* introverted margin of the left lobe, *irp* incipient rostral process on the left lobe, *ll* left microfusellar apertural lobe, *lp* lateral process on the right lobe, *rl* right microfusellar apertural lobe.

PLATE XXXIV



A₁



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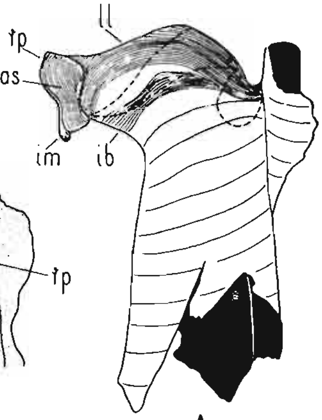
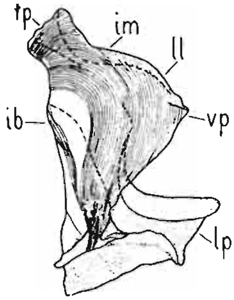
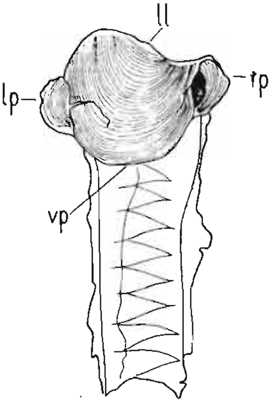


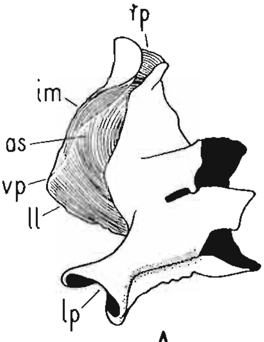
A₂



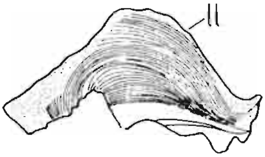
A₄



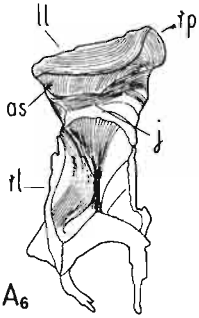
A₃



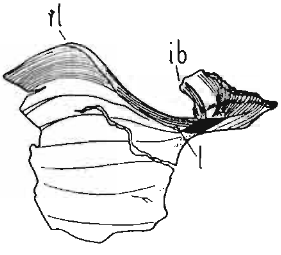
A₅



B



A₆



C

The right microfusellar apertural lobe forms a rather narrow band which ventrally is gradually tapering into the ventral notch. At its dorsal end only a few lowermost microfusellar strips join the ventral wall of adjacent theca, thus forming a more pronounced dorsolateral incision.

In thecae situated more distally, the ventral termination of the left lobe displays a certain tendency to overlap the aperture and the dorsolateral incision in the right lobe may be distinctly marked with its margins somewhat elevated (Pl. XXXIII, Figs. A_1-A_2, *ilp*). In the distal thecae (Pl. XXXIII, Figs. B_1-B_2), the degree of asymmetry of apertural apparatus increases as a result of a strong hypertrophy of the left microfusellar apertural lobe (*ll*). A very strong ventral termination covers, to a great extent, the aperture its free margin being even somewhat introverted (*im*). The dorsolateral incision in the right lobe is deeply notched and its anterior elevated margin produces a prominent semitubular lateral process, stretching out from aperture (*lp*).

The details of structure of apertural apparatus in a distal theca are shown in Pl. XXXIV, Figs. A_2, A_4, which illustrates a common case in which, on the obverse side, the left microfusellar apertural lobe begins with a certain transitional zone between the microfusellar addition and the normal fusellar theca. The secretion of the first band of microfusellar strips (*ib*) is disrupted in this place by a sudden retrogress to wedge-shaped, intercalary fuselli. The rest of the lobe is, however, invariably composed of a normal microfusellar tissue. The free margin of the lobe is usually slightly introverted (Pl. XXXIV, Figs. A_1, A_4 *im*). Owing to its curvature the left lobe forms ventrally a widely gaping ventral apertural slit (Pl. XXXIV, Figs. A_5, A_6, *as*). The upper margin of this slit is slightly elevated thus forming a short (0.05—0.07 mm) extention, that is, an incipient rostral process (Pl. XXXIII, Figs. B_1-B_2; Pl. XXXIV, Figs. A_1-A_7; *rp*). This semitubular projection of the left lobe communicates with the apertural slit (Pl. XXXIV, Figs. A_2, A_5, A_6).

The right microfusellar apertural lobe forms an only narrow band, framing the elevation of apertural margin consisting of 3—4 fuselli. This

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Plate XXXIV

Neocucullograptus inex. inexspectatus (Bouček). Structural details of distal thecae. A_1—A_7 apertural part of a distal theca in reverse (A_1), obverse (A_2), ventral (A_3) aspect and seen in top view (A_4) from below and right side (A_5), from below (A_6) and from ventral and left side (A_7), *B* isolated left microfusellar apertural lobe in lateral view, *C* ventral part of the right microfusellar apertural lobe the left lobe being removed by the needle preparation (*B*) to show the extroverted ventral apertural lip. (Mielnik, depth 888.20 m, *inexspectatatus* zone); ×63.

as ventral apertural slit, *ib* intercalary microfusellar band, *im* introverted margin of the left lobe, *j* junction between microfusellar systems of the left and right lobe, *l* extroverted apertural lip, *ll* left microfusellar apertural lobe, *lp* lateral process on the right lobe, *rl* right microfusellar apertural lobe, *rp* rostral process on the left lobe, *vp* ventral process of the left apertural lobe.

fusellar elevation may be more pronounced than that on the opposite side (Pl. XXXIV, Fig. A_1), although a reversed situation may be also the case when the left elevation is more prominent (Pl. XXXIII, Fig. B_2). The low fusellar elevation on the obverse side seems to be related with the presence of intercalary fuselli and the transitional zone (Pl. XXXIV, Fig. A_2, *ib*) mentioned above, whereas the sharp contrast between the fusellar and microfusellar tissue is associated with the presence of a rather higher fusellar elevation (Pl. XXXIII, Fig. B_2).

About a half of the free margin of the right microfusellar lobe is involved in the apertural lip, an extroverted, slightly rolled brim situated ventrally (Pl. XXXIV, Fig. *C*, *l*) and usually covered almost completely by the left lobe. It is visible after the removal of the left lobe (e. g., by means of a needle) (Pl. XXXIV, Fig. *B*). On the ventral side microfusellar system of the right and left apertural lobe concordantly join each other above the zigzag suture (Pl. XXXIV, Fig. A_6, *j*). The dorsal end of the right microfusellar apertural lobe is provided with a deep dorsolateral incision, bordered by projecting edges which form a distinct lateral process 0.20—0.25 mm long. It is, therefore, more pronounced than the corresponding rostral process (Pl. XXXIV, Figs. A_1, A_4, A_5, *up*). Like the latter, it is semitubular opening dorsally in the form of a slit. The structure of this dorsolateral process may be examined only in strongly bleached specimens (Figs, A_1, A_2, *lp*). The microfusellar strips of the right lobe curve round the edge of the dorsolateral incision to form a shovel like, partly rolled projection.

After the removal of apertural apparatus from the theca proper (needle preparation), it can be seen from underneath, that the apertural slit is almost completely hidden under incurved and overlapping microfusellar lobes (Pl. XXXIV, Fig. A_6).

The distal thecae reach 2.15—2.68 mm in length, their metathecae being 1.13—1.68 mm and prothecae 0.92—1.17 long. The prothecal segment occupies, therefore, about 50—40% of the total thecal length. The width of rhabdosome measured just above the aperture (across a protheca and metatheca) amounts to 0.65—0.95 mm and of metatheca at its base — to 0.30—0.35 mm. The right apertural lobe is 0.35—0.47 mm, the left apertural lobe (including the incipient rostral process) 0.45—0.68 mm long (*trans.*) the rostral process being 0.05—0.07 mm long.

Clearly, then, the distal thecae grow in the same manner as that observed in the first theca. The specimen in Figs. 17, B_1-B_3 indicates that their apertural apparatus is formed with a certain delay as a result of the postmatural growth. This specimen most probably represents the growing tip of rhabdosome with different growth-stages of its thecae. The lowermost (most proximal) of them has a complete apertural apparatus with the left lobe overlapping the aperture. The next theca (magnified in Fig. 17, B_3) is right midway the formation of its apertural apparatus. It consists

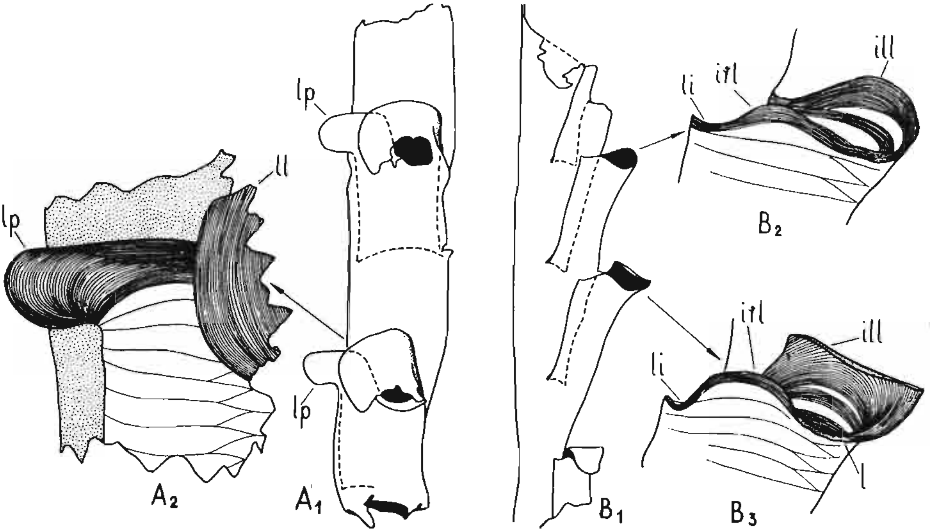

Fig. 17. — *Neocucullograptus inexspectatus* (Bouček). Details of structure and growth relations of apertural apparatus in distal thecae. A_1 fragment of rhabdosome in ventral view to show the protruding lateral processes on right lobe, A_2 minute structure of lateral process seen in reverse aspect on a theca (marked by an arrow), B_1 growing tip of rhabdosome showing thecae with apertural apparatus on different growth stages, B_2, B_3 details of structure of apertural parts in thecae on less (B_2) an more advanced (B_3) growth stages (Mielnik, depth 888.20 m, *inexspectatus* zone); $A_1 \times 26$, $A_2 \times 52$, $B_1 \times 14$, B_2, $B_3 \times 50$.

ill incipient left microfusellar apertural lobe, *irl* incipient right microfusellar apertural lobe, *l* extroverted apertural, lip, *li* lateral incision of apertural margin, *ll* left microfusellar apertural lobe, *lp* lateral process on right lobe.

of a narrow microfusellar brim around the right fusellar elevation of the apertural margin (*irl*) and a much larger left lobe which just begins to curve over the aperture, thus producing, on its free margin, a kind of a flange (*ill*). The ventral part of the right lobe is already extroverted to form an apertural lip (*l*). The adjacent theca, enlarged in Fig. 17, B_2, has its apertural apparatus in a still earlier stage of development, but both lobes already display a distinct asymmetry due to different growth rate of the microfusellar material on either side of aperture (*irl*, *ill*). Unfortunatelly the most distal theca is damaged, but judging from the remains preserved it shows more or less complete subapertural segment of metatheca. A growing prothecal segment is still visible behind it (Fig. 17, B_1). As described above, the growth relations of distal thecae indicate that no less than three thecae were formed behind until a given distal theca reaches a complete apertural apparatus.

Judging from the fragments of rhabdosome preserved, rarly exceeding 10 mm, a complete rhabdosome was fairly long, in proximal part strongly curved ventrally and with the greatest curvature in the region of the second theca. The medial part of rhabdosome is only gently curved ventrally and the distal part almost completely straight. The degree of thecal overlap increases distally (from about $^1/_6$ to more than $^1/_2$ of thecal length). Thecae number 10—11 in 10 mm in proximal and medial and 9—10 in distal part (Pl. VII, Fig. *B*).

Stratigraphic range. — In the Mielnik core, *Neocuc. inex. inexspectatus* has been recorded at a depth of 890.70—888.20 m. The richest assemblages were obtained from samples taken at a depth of 888.20 where the subspecies in question occurs abundantly. Few, poorly preserved specimens, which may still belong to this form were noted at a depth of 887.00 m (see distribution table, Pl. I). Even in its first appearance, *Neocuc. inex. inexspectatus* is rather frequent. It disappears also rather abruptly. It occurs in fairly scanty assemblages of other graptolites, the most frequent of them being *B. b. tenuis* (Bouč.).

In the lower part of its distribution range it is also occasionally associated with *Neolobograptus auriculatus* n. sp.

In the zonation of the Siedlce Beds here suggested the subspecies in question, together with *Neocuc. inex. supernus* n. subsp. delimits the *Neocuc. inexspectatus* zone, which overlies the *Neolob. auriculatus* zone and underlies the *Neocuc. kozlowskii* zone (comp. distribution chart, Pl. I). The vertical ranges of *Neocuc. inex. inexspectatus* and *Neocuc. inex. supernus* n. subsp. rather excluding each other, suggest that in future, after accumulating more data, a subdivision of this zone into a lower subzone (*Neocuc. inex. inexspectatus*), and higher subzone (*Neocuc. inex. supernus*) may be possible.

The examination of graptolites, collected by Prof. dr B. Bouček (Prague) in the key-section of Barrandian in Čertovy schody near Koněprusy, and kindly offered the present writer for a comparative study, reveals in the uppermost part of Kopanina Beds (some 15 m below the horizon of brecciated limestones which form the base of overlying Přidoli Beds) the presence of a not uncommon but poorly preserved *Neocuc.* cf. *inexspectatus* (Urbanek, 1968 *in press*). Despite the poor state of preservation, it is clear that these forms from Čertovy schody are conspecific with the form described above (comp. p. 185). Earlier suggestions placing *Neocuc. inexspectatus* much lower (in *nilssoni* zone as results from the presence of *Colonograptus colonus* mentioned in association by Bouček, 1932, p. 153 or in *scanicus* zone as results from its identification with *M. scanicus* Tullb. indicated by Bouček, 1936, P. 14) are, therefore, probably misleading [13].

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[13] In the material from Pankrác (Barrandian; type locality of *Neocuc. inexspectatus*) housed in Národni Muzeum (Prague) and in an additional material from this locality in possession of Prof. B. Bouček (Prague), kindly offered for comparison by him, I never found *Colonograptus colonus* (Barr.) (or other saetograptids!) associated with *Neocuc. inexspectatus*. Typical association of the latter form in Pankrác probably includes: *Prist.* ex gr. *dubius* Suess, *Bohemograptus bohemicus* (Barr.) and a form probably conspecific with "*Monograptus*" *egregius* n. sp.

It is, therefore, beyond any doubt that *Neocuc. inexspectatus* is an index fossil of the upper part of Kopanina Beds and its time equivalents (lower part of the Siedlce Beds).

Some of the enigmatic monograptids mentioned by Horný (1962, p. 893, also Fig. 6 on p. 882), from the upper part of Kopanina Beds (Barrandian) (in strata immediately underlying the *ultimus* zone) and tentatively identified by him as "*Monograptus* ex gr. *scanicus* Tullberg", may in fact be partly conspecific with *Neocucullograptus inexspectatus* (Bouč.) and partly correspond to other cucullograptids (comp. Urbanek, 1968, *in press*, also the present paper pp. 199).

Systematic position. — *Neocuc. inex. inexspectatus* being the most primitive of the known members of *Neocucullograptus* n. gen. seems to derive from *Neolobograptus auriculatus* n. sp.

This opinion is supported by a number of resemblances in structure of fusellar part of rhabdosome between *Neolob. auriculatus* n. sp. and *Neocuc. inex. inexspectatus*. These characters which may be inherited from *Neolobograptus* n. gen. are primarily: shape and size of sicula, elongation of thecae (slender proximal thecae, the first theca being especially elongated with aperture situated high above the apex of prosicula) and the presence of fusellar apertural elevations with very characteristic and indubitably homologous dorsolateral incision in the right apertural margin. Especially remarkable in this connection seems to be the *auriculatus* stage in the development of apertural apparatus in *Neocuc. inex. inexspectatus*, which strongly resembles the apertural elevations in adult thecae of *Neolob. auriculatus* n. sp. (comp. chapter on comparative-anatomical analysis). This stage may be considered to be recapitulatory, the elevations in *Neocuc. inex. inexspectatus* being, however, somewhat more pronounced than in the latter species. Also the stratigraphic occurence fully agrees with the phylogenetic relationships suggested, *Neocuc. inex. inexspectatus* appearing later, but displaying a certain overlap in stratigraphic range with *Neocuc. auriculatus* n. sp. (comp. distribution chart Pl. I).

These strong resemblances in structure of fusellar parts are, however, accompanied by remarkable differences in structure of microfusellar additions, which in *Neolob. auriculatus* n. sp. occur rather sporadically and are generally strongly variable, while in *Neocuc. inex. inexspectatus* they reach a stable, specifically characteristic form. In *Neolob. auriculatus* n. sp. they occur in the form of simple bands or lobes without distinct asymmetry, while in *Neocuc. inex. inexspectatus* they are complex lobes with certain superstructures (lateral and rostral processes) and a distinct, stable asymmetry. The only exception is here the microfusellar addition on sicula, which being symmetric and simple lateral lobes still approaches a primitive form of microfusellar structures found in the thecae of

Neolob. auriculatus. n.sp. These conditions may reflect the general rule that sicula, even when involved in the same evolutionary changes as thecae, is affected by them later and to a smaller extent (comp. p. 199) and therefore the shape of sicular microfusellar addition has probably also a certain significance for tracing the ancestry.

The similarities in structure of fusellar foundation of thecae, connected with distinct differences in structure of their microfusellar additions, seem to indicate that the main changes between *Neolob. auriculatus* n. sp. and *Neocuc. inex. inexspectatus* were expressed in the pattern of forming the latter structures. It is not unlikely that a certain so far unknown intermediate form was not unlikely that a certain so far unknown intermediate form was a transient link filling up some morphological discontinuity in the structure of microfusellar additions recorded in the species mentioned above. In theory, one could expect a form with habitus generally the same as that in *inexspectatus* but lacking the superstructures (such as rostral and lateral processes) and displaying a leer degree of asymmetry in apertural apparatus.

An early stratigraphic appearance and certain structural characters (less advanced development stage of apertural processes, lack of gular process) clearly indicate that *Neocuc. inex. inexspectatus* is most primitive of all known representatives of the genus. Its kinship with *Neocuc. kozlowskii* n. sp., which seems certain, is also indicated by the presence of intermediate morphologically (appearance of gular process) and stratigraphically (comp. distribution table) *Neocuc. inexspectatus supernus* n. subsp.

Neocucullograptus inexpectatus supernus n. subsp.

(Pls. XXXV—XXXVI)

Holotype: Pl. XXXVI, Fig. *C*.

Paratypes: Pl. XXXV, Figs. *A*, C_1-C_2.

Type stratum: Greenish-blue mudstones and marls in the core of the Mielnik deep-boring between 887.00—886.00 m of depth (upper part of *Neocuc. inexspectatus* zone, lower part of the Siedlce Beds).

Derivation of the name: Lat. *supernus* — higher, overlying, superior; as occurring above the *Neocuc. inex. inexspectatus* (Bouč).

Diagnosis. — *Neocucullograptus* with slightly developed rostral and lateral processes, but with a pronounced gular process on the left microfusellar apertural lobe.

Material. — Three fairly well preserved siculae and numerous thecae or short rhabdosome fragments, which, although flattened in some cases, are well preserved. The material available enables an analysis of the main features of sicula and thecal structure. Larger fragments and complete rhabdosomes have not been found. From the Baltic drift material, unknown.

Description. — Sicula, associated with thecae of *Neocuc. inex. supernus* n. subsp., which therefore may be assigned to the subspecies mentioned above, is 1.26—1.45 mm long, almost straight and with a faint curvature in metasicular part (Pl. XXXV, Fig. *A*).

Prosicula 0.50—0.60 mm long and, at the aperture, 0.18 mm wide, provided with one sicular black ring approximately in the middle of the prosicular segment (r_1). Three partly preserved, hardly discernible longitudinal threads have been recognized.

Metasicula 0.74—0.89 mm long, almost stable in width, about 0,25 mm wide at the level of primary notch and 0.28—0.37 mm at the aperture. It has three sicular black rings, the first (r_2) right on the boundary of pro- and metasicula. Aperture of metasicula provided with a distinct dorsal process (*dp*), virgella (*vi*) and microfusellar addition, forming distinct lateral apertural lobes (*sim*). In size (approx. 0.05—0.09 mm in height) and shape they are more similar to microfusellar additions on sicula of *Neocuc. inex. inexspectatus* (Bouč.) then to those of *Neocuc. kozlowskii* n. sp.

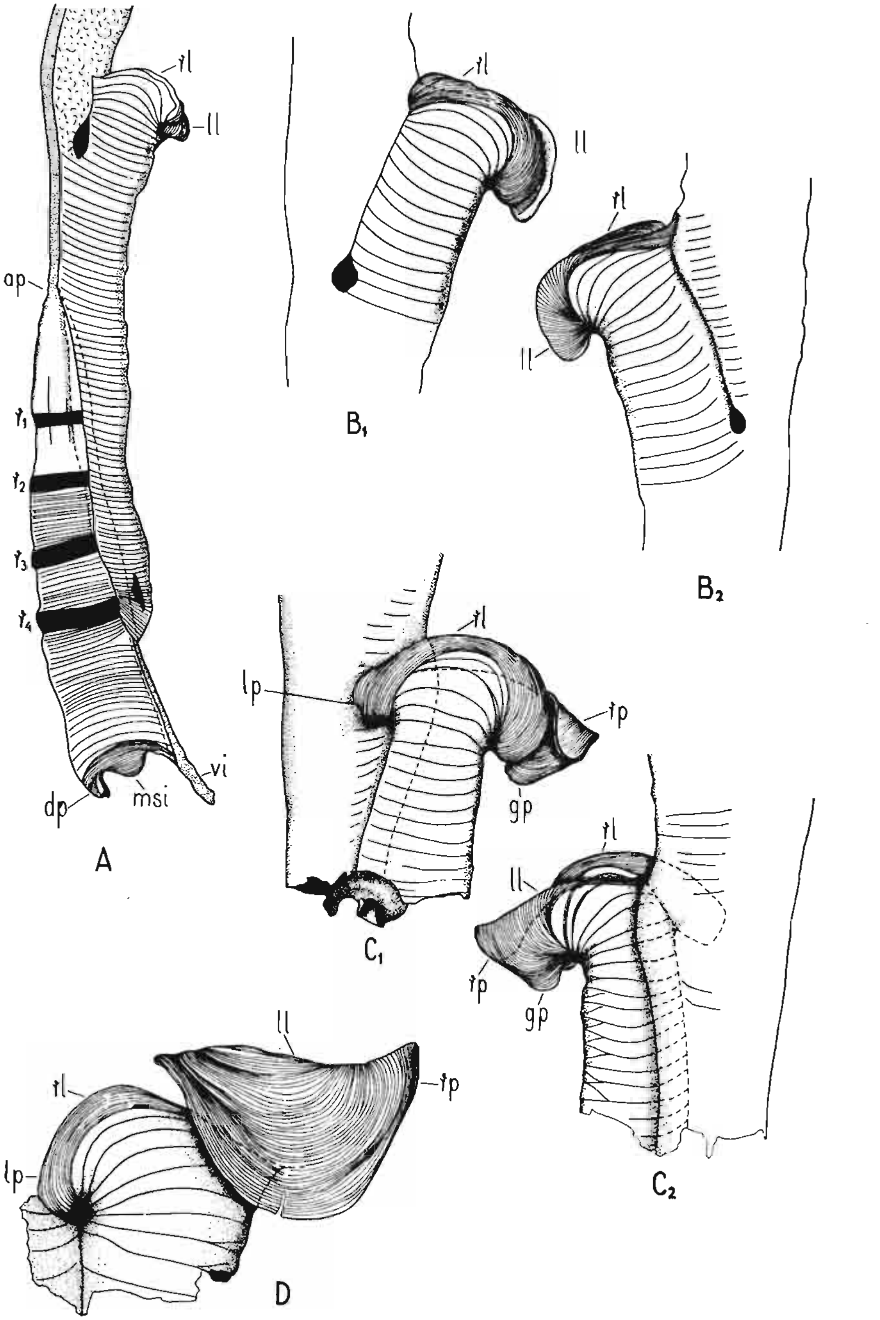
The initial bud formed according to a normal, monograptid pattern and situated 0.52—0.98 mm from the apex of prosicula and some 0,26—0.30 mm from the lateral borders of the metasicular aperture.

The first theca is 1.45—1.50 mm, the subapertural segment of metatheca 0.20—0.22 mm and the protheca 1.25—1.28 mm long. The width of the first theca at the level of the apex of prosiculae and at the base of metatheca amounts to 0.19 mm and to some 0.23 mm at the aperture. Rather high fusellar elevations of the apertural margin (some 0.10 mm in height), bordered by fairly narrow microfusellar bands, are a remarkable feature of the specimen figured.

The remaining thecae display a combination of characters, in some respects intermediate between those recognized in *Neocuc. inex. inexspectatus* and in *Neocuc. kozlowskii* n. sp.; in some others rather typical of the form in question.

In the degree of the development of microfusellar additions proximal thecae (Pl. XXXV, Fig. *B*; Pl. XXXVI, Fig. *A*) are similar to *Neocuc. kozlowskii* n. sp. rather than to *Neocuc. inex. inexspectatus*, which is markedly less advanced. In most proximal thecae (Pl. XXXV, Fig. *B*) the asymmetry of microfusellar apertural lobes is only slight, but later on, the left apertural lobe (*ll*) becomes conspicuously larger with a certain tendency to overhang the aperture (Pl. XXXVI, Figs. A_1-A_3). In ventral part, it stretches well beyond the right apertural lobe (*rl*), forming, at its free termination, two gently marked elevations: an incipient gular process (*gp*) and an incipient rostral process (*rp*). The left microfusellar apertural lobe joins dorsally the wall of a succeeding theca.

PLATE XXXV


rl
ll
ap
r1
r2
r3
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vi
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rp
gp
C1
rl
ll
rp
gp
C2
ll
rl
rp
lp
D

The right microfusellar apertural lobe forms a rather narrow band 0.04 mm), bordering the underlying fusellar elevation, which terminates free at both ends. The ventral end is somewhat beak-like and, overhanging the margin, is attached to the ventral wall of theca. The dorsal end is gently rounded, without traces of a dorsolateral incision (Pl. XXXVI, Fig. A_1). In other respects proximal thecae resemble those in *Neocuc. inex. inexspectatus* (Bouč.). They are 1.56—1.80 mm long, with metathecal parts some 0.40—0.67 and with prothecae some 1.13—1.16 mm long. The prothecal part takes thus about 70% of the total thecal length. The width of proximal thecae above the apertural level of a preceding theca amounts to 0.24—0.42 mm, and at the base of their metathecae to 0.22—0.27 mm.

In the thecae placed probably more medially (Pl. XXXV, Fig. *C*), the apertural apparatus is marked by a further increase in asymmetry, which is due to an increasing hypertrophy of the left microfusellar lobe (*ll*). It forms a distinct folding in the upper part of its free termination, producing in this place a more pronounced rostral process (*rp*). Also the gular process (*gp*) in correspondingly better marked off, being about 0.05 mm long. A transient zone between the normal fusellar tissue and the microfusellar system of the lobe proper may be seen, along with a number of intercalated microfusellar bands.

The right microfusellar apertural lobe has its margin still uncovered by the left lobe overhanging the aperture (Pl. XXXV, Fig. C_1, *rl*). Noteworthy are the changes at its dorsal end which is transformd into a short semitubular outgrowth, a slightly marked lateral process (*lp*).

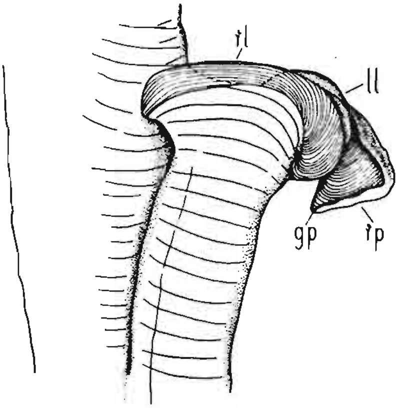
Further astogenetic changes in distal thecae are limited in practice to a strong increase in the left microfusellar apertural lobe (Pl. XXXV, Fig. *D*, Pl. XXXVI, Figs. *B-D*, *ll*), which curves over the aperture and overlaps by its strong ventral process the right lobe over $^1/_3$ to $^1/_2$ of its length (*vp*). The gular process takes the form of an elongated, tongue-like outgrowth (*gp*) 0.15 mm in length. There are, however, surprisingly small changes in size and shape of rostral and lateral processes. In true distal thecae the former does not differ from that in the medial one, being marked only as a slightly elevated fold of the upper margin (*rp*). Due to the overhanging of the left apertural lobe and its strong folding, it forms an apertural slit, widely gaping on the ventral side (Pl. XXXVI, Figs.

Plate XXXV

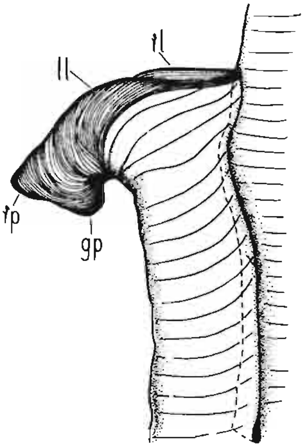
Neocucullograptus inexspectatus supernus n.subsp. Sicula and structure of thecae. *A* sicula with the first theca, B_1—B_2, C_1—C_2 apertural parts of proximal and medial thecae in reverse and obverse aspect, *D* apertural apparatus in a distal theca (Mielnik, depth *B* 886.00 m, *A*, *C—D* 887.00 m, *inexspectatus* zone); *A*×50, *B—D*×63.

ap apex of prosicula, *dp* dorsal process of metasicula, *gp* gular process, *ll* left microfusellar apertural lobe, *lp* lateral process of right lobe, *msl* microfusellar lobes of metasicula, r_1—r_4 successive black rings of sicula, *rl* right lobe, *rp* rostral process, *vi* virgula.

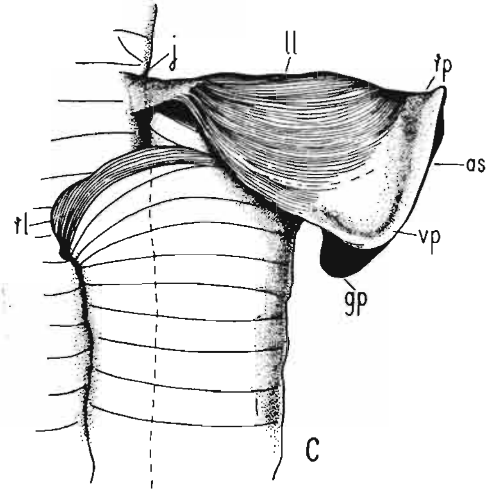
PLATE XXXVI



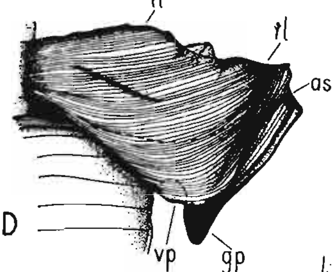
A₁



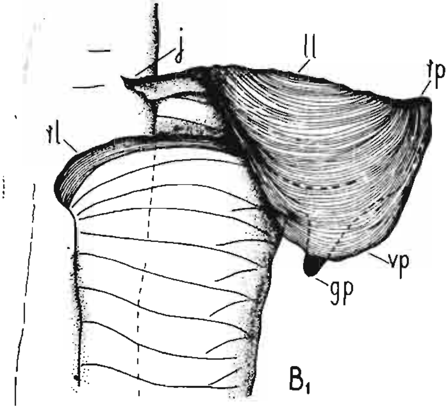
A₂



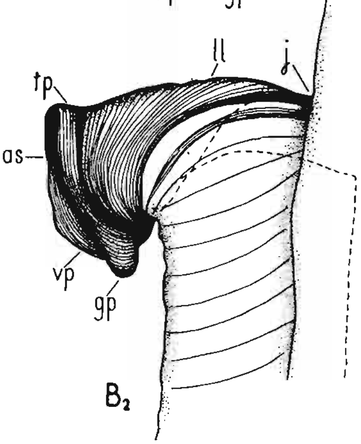
C



D



B₁



B₂

B_2, *C-D*, *as*). The left microfusellar lobe joins dorsally the wall of an adjacent theca, is fused with it over a considerable distance and due to its curvature form there a sort of a roof over the aperture (*j*).

The right microfusellar apertural lobe remains in the forms of a narrow band, covered in its ventral part by the ventral process of the left lobe (Pl. XXXV, Fig. *D*; Pl. XXXVI, Figs. B_1-*C*, *D*, in which this margin, marked by broken line is seen through the strongly bleached and, therefore, transparent left lobe. The medial part and dorsal end are visible in specimens viewed laterally. This latter may be rounded, without any differentiation (Pl. XXXVI, Fig. B_1), or display a shallow incision (Pl. XXXVI, Fig. *C*) and it is only occasionally provided with conspicuously elevated margins which thus form a short semitubular outgrowth slightly projecting laterally, that is, the incipient lateral process (Pl. XXXV, Fig. *D*, *lp*).

The distal thecae which in general shape resemble those in *Neocuc. inex. inexspectatus* (Bouč.) are 2.20—2.50 mm long, with metatheca 1.25—1.50 mm and prothecae 0.95—1.00 mm long. The prothecal part occupies, therefore, about 60⁰/₀ of the total thecal length. The width of rhabdosome above the level of aperture increases to 0.65—0.82 mm, thecae being 0.30—0.36 mm wide at the base of their apertures. In a strong development of gular process the thecal structure in *Neocuc. inexspectatus supernus* n. subsp. is similar to *Neocuc. kozlowskii* n. sp., but strongly differs from it in a much less marked rostral and lateral processes, which in turn seem to be even less conspicuous that those in *Neocuc. inex. inexspectatus* (Bouč.) This may be seen even in the thecae which in regard to size and shape seem to be truly distal. This combination of thecal characters is therefore considered in the present work to be typical of *Neocuc. inex. supernus* n. subsp.

In its general appearance rhabdosome differs but little from that in *Neocuc. inex. inexspectatus* (Bouč.). A certain curvature of proximal fragments may indicate a ventral curvature of rhabdosome in the proximal part similar to that in other representatives of *Neocucullograptus* n. gen. The number of thecae in 10 mm comes to 9 proximally and to 10 distally.

Stratigraphic range. — In the Mielnik core, *Neocuc. inex. supernus* n. subsp. has been found in samples from a depth of 887.00—886.00 m.

Plate XXXVI

Neocucullograptus inexspectatus supernus n.subsp. Structure of medial and distal thecae. A_1—A_2 apertural part of a medial thecae in reverse and obverse aspects, B_1—B_2 same in distal theca, *C* another distal theca in reverse aspect, *D* anteroventral part of the left lobe (Mielnik, depth 886.60 m, *inexspectatus* zone)' × 63

as anteroventral apertural slit, *gp* gular process, *j* point of junction between microfusellar lobe and thecal wall, *ll* left microfusellar apertural lobe, *rl* right microfusellar apertural lobe, *rp* rostral process, *vp* ventral process.

being thus limited to 1 m of thickness. It is relatively abundant in particular in the lower part of these strata, where it is associated with *Monoclim. haupti* (Kühne) and *B. b. tenuis* (Bouč.).

Neocuc. inex. inexspectatus (Bouč.) and *Neocuc. inex. supernus* n. subsp. seem to exclude each other in their stratigraphic distribution. The former is limited to the lower part of *Neocuc. inexspectatus* zone, the latter to its upper part. If these data, so far based on one bore-core would be confirmed by further evidence, the *inexspectatus* zone could be subdivided into a lower subzone of *Neocuc. inex. inexspectatus* and a higher subzone of *Neocuc. inex. supernus* (see range chart, Pl. I). In a tentative scheme of subdivision of Siedlce Beds here suggested, *Neocuc. inex. supernus* n. subsp. is considered to be a fossil characteristic of the upper part of the *inexspectatus* zone (the lower part of the Siedlce Beds).

Systematic position. — In certain aspects of thecal structure (appearance of gular process, combined with the *inexspectatus* stage of development of other parts of apertural apparatus and in its stratigraphic occurrence) the form in question may be considered as truly intermediate between *Neocuc. inex. inexspectatus* (Bouč.) and *Neocuc. kozlowskii* n. sp. Only two features may contradict this presumption these being: 1) a certain decrease in size of sicula and the first theca and 2) the lack of further advance in the development of the rostral and lateral processes, which certainly are not more advanced than those in *Neocuc. inex. inexspectatus* (Bouč.), or even display a certain decrease in size.

The significance of these purely quantitative differences must not be overestimated, especially in regard to the apertural processes which in *Neocuc. inex. inexspectatus* (Bouč.) are also very slightly marked. Moreover, the evaluation of the degree of their development is, to a certain extent, subjective. The origin of the gular process, a structural detail very characteristic of *Neocuc. kozlowskii* n. sp., and the stratigraphic occurrence seem to be far more impressive. It seems safe, therefore, to generalize that *Neocuc. inex. supernus* n. subsp. is a transient link between two representatives of *Neocucullograptus* n. gen. mentioned above and which only slightly differs from a theoretical intermediate. Due to the lack of distinct processes in apertural apparatus and its stratigraphic distribution (immediately overlying the *Neocuc. inex. inexspectatus*), it is here described as a subspecies of the latter.

Neocucullograptus kozlowskii n. sp.

(Pl. XXXVII-XXXIX, Figs. 18-20)

Holotype: Fig. 20, *A-B*.
Paratype: Fig. 18.

Type stratum: Greenish-blue mudstones and marls in the core of the Mielnik deep-boring between 873.40—854.60 m of depth (*Neocuc. kozlowskii* zone, lower part of the Siedlce beds).

Derivation of the name: in honour of Professor Roman Kozłowski — an eminent Polish palaeontologist and the writer's master in graptolitology.

Diagnosis. — *Neocucullograptus* whose left apertural lobe in distal thecae terminates in a long, semitubular rostral process and the right one is provided with a similar dorsolaterally situated outgrowth.

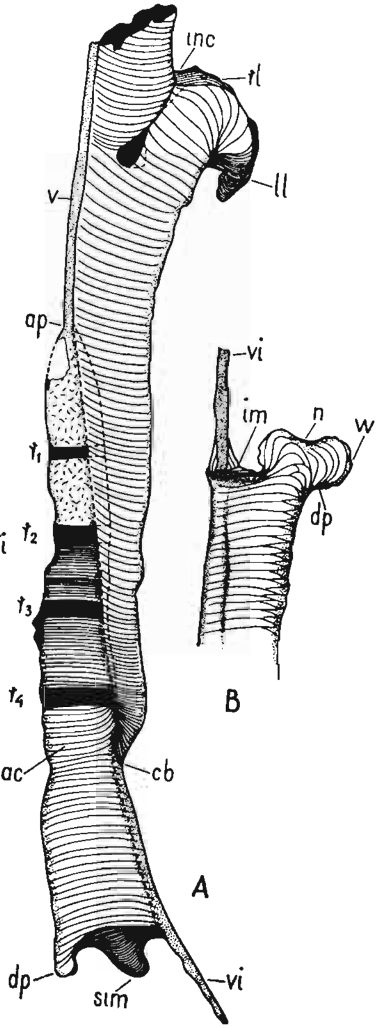


Fig. 18. — ***Neocucullograptus kozlowskii*** n.sp. Sicula with the first theca. *A* fully grown sicula and first theca in reverse aspect, *B* apertural part of a young metasicula with incipient microfusellar apertural lobes (Mielnik, depth 873.40 m, *kozlowskii* zone); *A* ca×50, *B* ca×63.

ap apex of prosicula, *bb* basal band of the microfusellar addition, *dp* dorsal process of metasicula, *im* incipient microfusellar lobe of metasicula, *inc* dorso-lateral incision in the right lobe *l* lobe proper of the microfusellar addition, *msi* microfusellar apertural lobe of metasicula, *n* median notch of dorsal process, *psi/msi* boundary of pro- and metasicula, r_1—r_4 successive black rings of sicula, *v* virgula, *vi* virgella, *w* lateral wing of the dorsal process.

Material. — Numerous fragmentary rhabdosomes, including siculae etched from samples from the Mielnik boring at depth of 873.40—854.60 m. Best preserved, unflattened specimens were sampled at a depth of 873.40 m. The material obtained allows one to analyse the detailed structure and development of rhabdosomes. From the Baltic drift material unknown.

Description. — Sicula almost straight or only slightly curved ventrally in its metasicular part, rather long (1.63—2.02 mm), provided with 4 sicular black rings (Fig. 18, *A*).

Prosicula some 0.57—0.74 mm long and at its aperture some 0.15 mm wide. Due to a rather poor preservation state, neither the longitudinal threads nor the helical line are distinguishable. Adult prosicula invariably provided with a black ring approximately in the middle of the prosicular segment (Fig. 18, *A*, r_1). The next sicular black ring (r_2) is situated just on the boundary of pro- and metasicula.

Metasicula, 0.98—1.28 mm long, gradually widening to reach 0.20—0.28 in width at the level of the primary notch and 0.29—0.38 mm at its definitive aperture. Dorsally it is provided with a rather strong dorsal process (Fig. 18, *A*, *dp*) projecting some 0.07—0.10 mm beyond the lateral margin of metasicular aperture. Usually this strong dorsal process is slightly bifid (Fig. 18, *B*) displaying two wing-like lateral lobes (*w*), separated by a shallow median notch (*n*).

Aperture of adult metasicula has moreover two, laterally situated lobes composed of microfusellar tissue (Fig. 18, *A*, *sim*). The lobes are markedly larger than those in *Neocuc. inexspectatus* (comp. Pl. XXXI, Fig. *B*, *sim*), and consist of a basal band (*bb*), laid down on both sides of the aperture of fusellar metasicula between the virgella, the dorsal process and the lobe proper (*l*). The latter is roughly ovate-triangular and directed slightly toward the ventral side (Fig. 18, *A*, *sim;* Pl. XXXVII, Fig. *A*, *sim*). No distinct asymmetry in size of these lateral, microfusellar lobes has been noted. The presence of siculae with microfusellar additions in the form of narrow, bilaterally placed bands, which most probably represent an early stage of the formation of metasicular apertural lobes (Fig. 18, *B*, *im*), indicates their gradual growth. In all likelihood, the origin of these microfusellar structures was somewhat delayed, the same as in *Neocuc. inexspectatus* and their growth began, with a certain delay, after the growth of fusellar metasicula definitely ceased. As indicated by the structure of the primary notch region in the metasicula (Fig. 18, *A*, *ac*, *cb*) the origin of the initial bud and the budding of the first theca follow a normal monograptid pattern.

The initial bud begins some 0.59—0.75 mm from the aperture of prosicula, and is situated some 0.44—0.65 mm from the lateral margin of metasicular aperture.

The first theca is 1.96—2.16 mm long, its free part stretching above the apex of prosicula being 0.78—0.94 mm long. The subapertural segment of the metatheca is some 0.82—0.30 mm long, the theca reaching ca 0.22—0.23 mm in width at the level of the apex of prosicula (prothecal segment), and ca 0.21—0.23 mm at the base of metatheca. Over its entire length metatheca is adnate to the basal part of the second theca and inclined to the axis of protheca at an angle of some 35°. The prothecal part occupies about 83—88⁰/₀ of the total thecal length. The adult metatheca terminates in the apertural apparatus which is composed of 1) fusellar elevations of the lateral margins of the aperture consisting of 5—6 arched fuselli (Pl. XXXVII, Figs. B_1—B_2, *e*) and 2) apertural lobes composed of microfusellar tissue and making up an extension to the former structure (Pl. XXXVII, Figs. B_1—B_2, *ll*, *rl*).

In contrast to the lateral fusellar elevations of the apertural margin, which are rather symmetric, the microfusellar additions display a distinct asymmetry in shape and size. The left microfusellar apertural lobe (Pl. XXXVII, Fig. B_2, *ll*) is markedly larger, 0.36—0.40 mm long (*trans.*), incurved over the aperture, and provided with a distinct, somewhat beak-like, ventral termination (*vt*). This lobe consist of numerous microfuselli laid down initially over the entire margin of the left apertural elevation and therefore forming a kind of basal band joining dorsally the ventral wall of adjacent theca. Further, the microfuselli are deposited only on its anteroventral edge and, through their arch-like bending from the ventral termination of the lobe mentioned above.

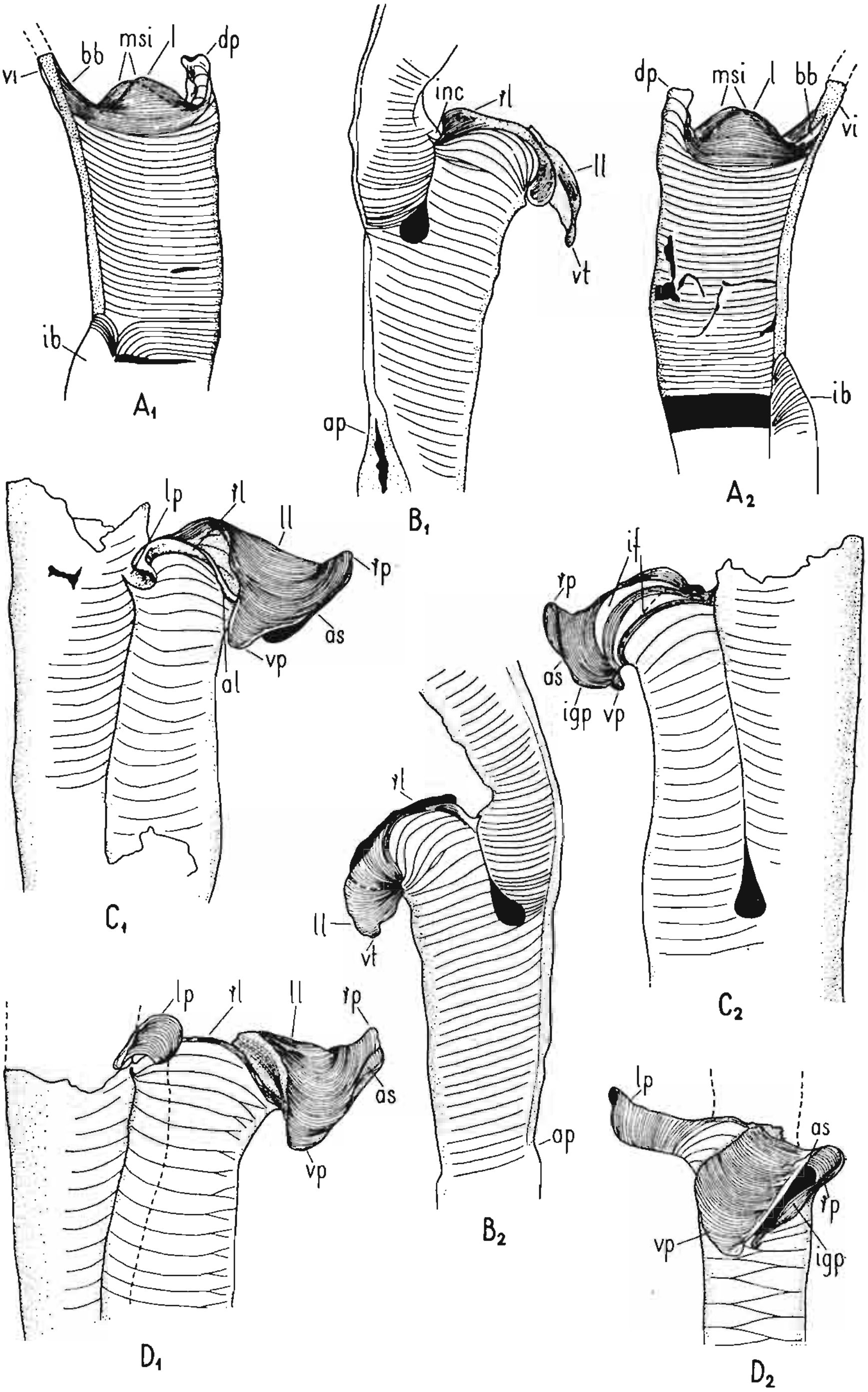
The right, clearly smaller, 0.30—0.33 mm long (*trans.*) apertural lobe, forms an only narrow band over the fusellar elevation (0.03—0.05 mm high) and terminates ventrally in the form of a short tongue-like process. In contrast to the left lobe, the right one is attached dorsally to the wall of adjacent theca only in its lower part. Usually, it even terminates freely, forming in this place a small, more or less pronounced incision with slightly risen margins (Fig. 18, *A*, *inc*; Pl. XXXVII, Fig. B_1 *inc*).

The remaining proximal thecae occur in the form of rather long (1.66—1.72 mm) and slender tubes, gradually widening distally to reach some 0.22—0.33 mm in width and having an almost straight ventral wall. The protheca is 1.04—1.35 mm and the subapertural segment of metatheca ca 0.50—0.68 mm long. The latter is inclined at an angle of some 20° to the axis of the protheca. The prothecal part occupies therefore about 60⁰/₀ of total thecal length.

The most striking astogenetic changes are observed in the structure of apertural apparatus of thecae. They are shown in Pl. XXXVII, Figs *C*, *D*.

On the whole, the degree of asymmetry in apertural apparatus of thecae, increases distally. From the third theca onward, the left microfusellar apertural lobe is strongly hypertrophied as compared with the right one. The former is markedly incurved over the aperture and partly covers

PLATE XXXVII



with its ventral termination the right lobe (Pl. XXXVII, Fig. C_1, *rp*). Due to this overlap, the left microfusellar apertural lobe forms, on its ventral margins, a slit-like opening that is, the ventral apertural slit (Pl. XXXVII, Fig. C_1, *as*). The upper margin of this slit is slightly elevated to form an incipient only 0.05 mm long rostral process (Pl. XXXVII, Figs. C_1—C_2, *rp*.). In regard to the microstructure of the left lobe, one could distinguish a basal part, consisting of a number of wide fusellar bands separated by intercalated bands. The latter consist of densely deposited microfuselli, thus forming a kind of a transient zone between the fusellar and microfusellar part of the theca (Pl. XXXVII, Fig. C_2, *if*). The remaining part, that is, the lobe proper is composed of a normal microfusellar tissue.

The right microfusellar apertural lobe forms only a narrow band laid down on the fusellar elevation of apertural margin (Pl. XXXVII, Fig. C_1, *rl*). In its ventral part the lobe is slightly extroverted, forming a narrow apertural lip (*al*); at the dorsal end it forms a deep incision surrounded by a markedly elevated margin which makes up a distinct projection. This is an incipient lateral process of the right lobe (*lp*).

In successive proximal thecae, the lateral process of the right lobe elongates rather rapidly as compared with the rostral process of the oposite lobe. A stage is soon reached in which the rostral process is still only 0.05—0.06 mm long, while the lateral process already forms a prominent semitubular outgrowth some 0.15—0.20 mm long (Pl. XXXVII, Figs. D_1—D_2, *rp*, *lp*). Both processes are widely open from underneath and communicate with the inner cavity of aperture with which the lateral process is connected through the dorsal incision in the right lobe mentioned above.

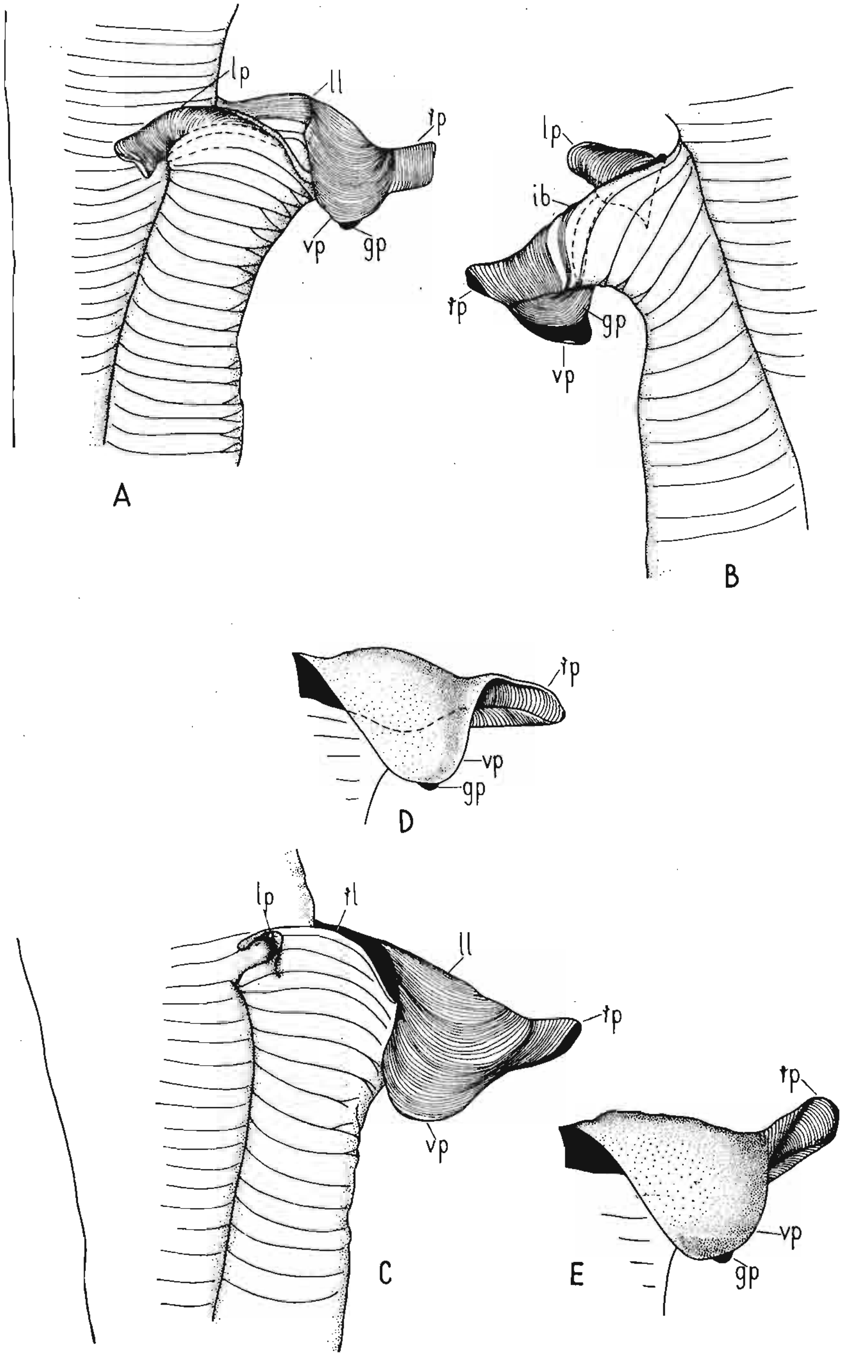
Thecae placed more distally (Pl. XXXVIII, Figs. *A*—*E*) display the prominent form of the lateral process (*lp*) referred to above and a gradual increase in the rostral process (*rp*), which gradually reaches a length of ca 0.15—0.17 mm and, through an appropriate arrangement of microfuselli, forms (Pl. XXXVIII, Figs. *D*, *E*, *rp*) a semitubular outgrowth. The cross section of this process is thus approximately semilunar (crescent), the slit facing downwards or slightly displaced towards the lateral (reverse) side.

Plate XXXVII

Neocucullograptus kozlowskii n.sp. Structure of proximal thecae compared with of metasicula. A_1—A_2 apertural part of metasicula in reverse and obverse aspect, B_1—B_2 upper part of the first theca in reverse and obverse aspect, C_1—C_2 proximal theca in reverse and obverse aspect, D_1—D_2 medial theca in reverse and in ventral view. (Mielnik, depth 873.40 m, *kozlowskii* zone); ca×63.

ap apex of prosicula, *as* ventral apertural slit, *bb* basal band of microfusellar addition, *dp* dorsal process of metasicula, *ib* initial bud, *ig* incipient gular process, *inc* dorsolateral incision in the right lobe, *l* lobe proper of the microfusellar addition, *ll* left microfusellar apertural lobe, *lp* lateral process, *msi* microfusellar apertural lobe of metasicula, *rl* right microfusellar apertural lobe, *rp* rostral process, *v* — virgula, *vi* virgella, *vp* ventral process of the left apertural lobe, *vt* ventral termination of the left apertural lobe.

PLATE XXXVIII



The left lobe is more strongly hypertrophied than the right one and its structure is complicated by the appearance of the gular process (Pl. XXXVII, Fig. *B*, *gp*), that is a tongue like portion of the left lobe, situated below the rostral process and continued into the right lobe. The gular process consists of many arcuate microfuselli and, in rear view, is almost completely concealed by the ventral process of the left apertural lobe (Pl. XXXVIII. Figs. *A*, *C—E*, *gp*), which is clearly visible only from the opposite side (Pl. XXXVIII, Fig. *B*, *gp*).

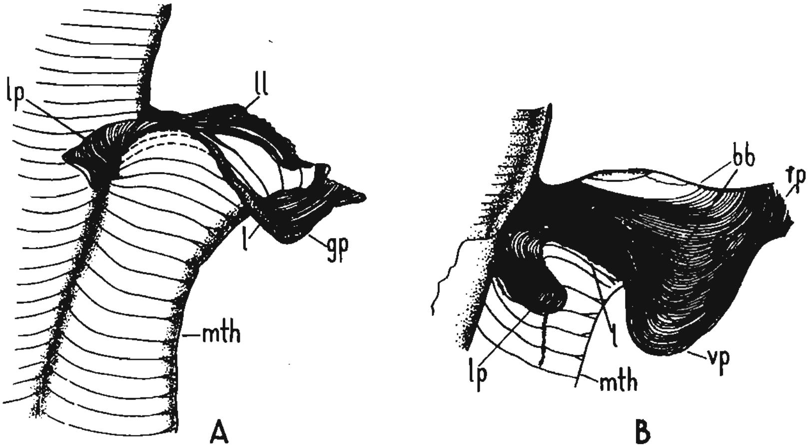


Fig. 19. — *Neocucullograptus kozlowskii n.*sp. Structural details of the apertural apparatus in distal thecae. *A* needle preparation, with left microfusellar apertural lobe removed, to show the internal structure of apertural apparatus, *B* apertural apparatus with terminal part of its lateral process removed by the needle to show relations of its base (*lp*) to internal cavity of the aperture (Mielnik, 873.40, *kozlowskii* zone); ×63.

gp gular plate, *l* apertural lip on border of the right microfusellar apertural lobe. *ll* left microfusellar apertural lobe, *lp* lateral process on right apertural lobe, *mth* distal part of metatheca, *rp* base of rostral process, *vp* ventral termination of the left lobe (translucent gular plate marked with broken lines).

In order to explain the relation of the gular process to the remaining microfusellar apertural structures in the specimen figured in Pl. XXXVII, *A*, a larger part of the left lobe has been removed by a needle (Fig. 19, *A*, *gp*). The microfusellar system of gular process, making up a distinct elevation, is continuous with the basal part of the left lobe and with an

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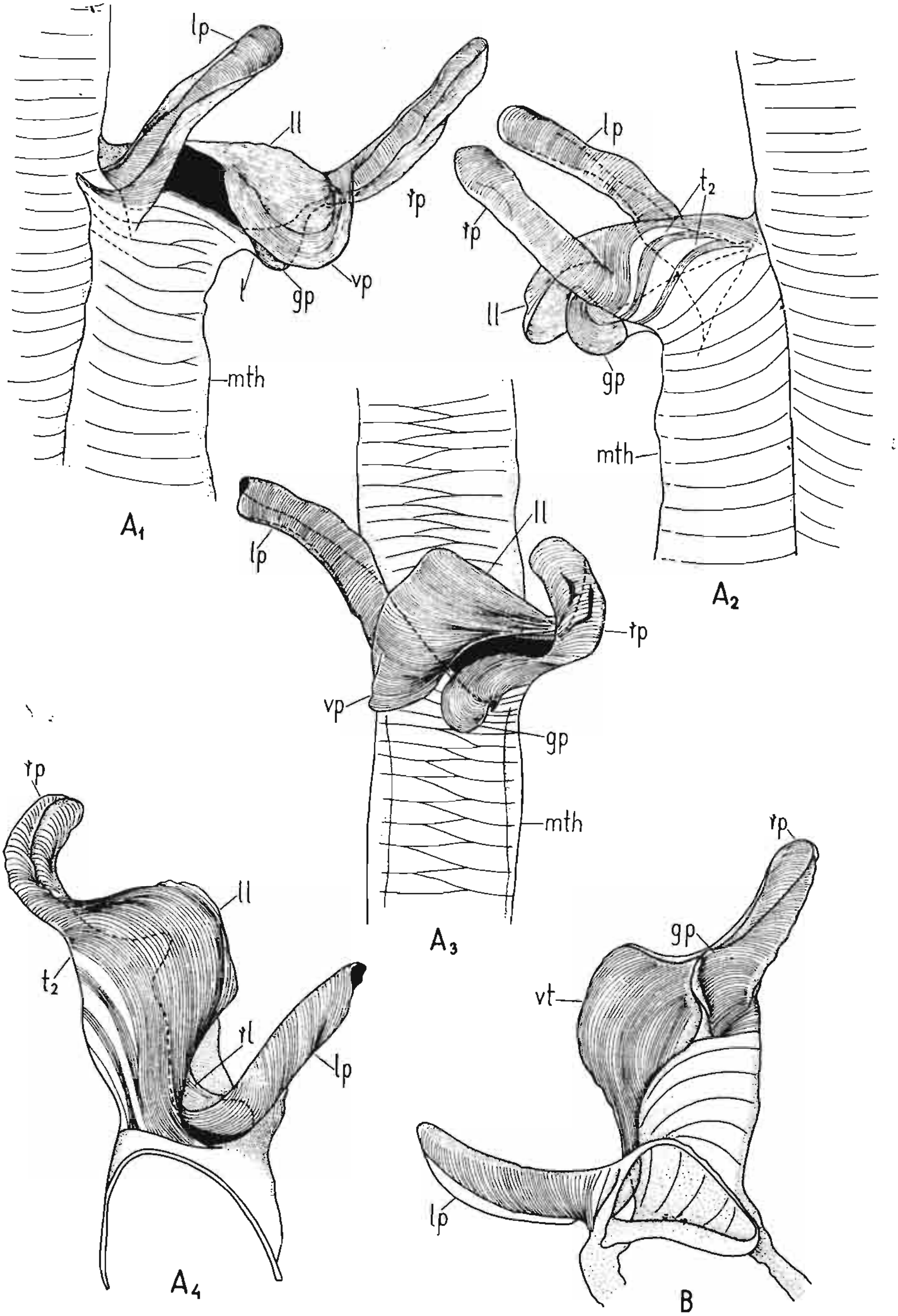
Plate XXXVIII

Neocucullograptus kozlowskii n.sp. Structure of distal thecae. *A—C* apertural parts of distal thecae, in reverse (*A*, *C*) and obverse (*B*) views, *D—E* variation in form of the rostral process (Mielnik, 873.40 m, *kozlowskii* zone); ×63.

ib intercalary band of microfuselli, *gp* gular process, *ll* left microfusellar apertural lobe, *lp* lateral process, *rl* right microfusellar apertural lobe, *rp* rostral process, *vp* ventral process of the left lobe.

PLATE XXXIX


lp
ll
rp
l
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mth
A_1
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t_2
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ll
gp
mth
A_2
lp
ll
rp
vp
gp
mth
A_3
rp
ll
t_2
rl
lp
A_4
rp
gp
vt
lp
B

extroverted apertural lip of the right lobe (Fig. 19, *A, l*). This extroverted margin of the right lobe is, to a considerable extent, concealed by the overlapping left lobe (Pl. XXXVIII, Fig. *A*).

The gular process, a remarkable feature of distal thecae in *Neocuc. kozlowskii* n. sp. develops in the course of astogeny from an incipient structure which already occurs in medial thecae in the form of a slight elevation below the rostral process (Pl. XXXVII, Fig. D_2, *igp*).

The distal thecae reach a length of 2.33—2.87 mm, their metathecae being 1.12—1.27 mm and prothecae 1.12—1.27 mm long. The prothecal segment occupies, therefore, about 48—40% of the total length of distal thecae. The width of rhabdosome beyond apertures amounts to ca 0.67—0.83, the metatheca being 0.20—0.28 mm wide at its base. The length (*trans.*) of the right lobe is 0.40—0.45 mm, its dorso-lateral process being 0.40—0.50 long. The length (*trans.*) of the left lobe proper reaches 0.48—0.61 mm, its rostral process being 0.28—0.40 mm long.

The structure of apertural apparatus in a true distal theca is shown in Pl. XXXIX, Figs. *A, B*). Due to the presence of strongly elongated rostral and lateral processes (*sp, lt*) these thecae are remarkably "spinose". The processes of both types are of nearly the same length, the lateral process being only slightly longer.

The left microfusellar apertural lobe, strongly hypertrophied, domed and curved over the aperture, is provided with a strong, tongue-like ventral process (Pl. XXXIX, Fig. A_1, *rp*), a very distinct gular process (Pl. XXXIX, Figs. A_2, *B, gp*) and a long rostral process (*rp*), which sometimes is almost straight (Pl. XXXIX, Fig. *B*) and sometimes variously curved (Pl. XXXIX, Figs. A_3, A_4). The lobe begins with a certain transitional zone between the fusellar and microfusellar part displaying the presence of intercalated microfusellar bands, separated by broader, more or less complete fuselli (Pl. XXXIX, Figs. A_2, A_4 *t*).

Beyond this transitional zone, the microfusellar system of the lobe may be subdivided into 1) the basal band (bb) continuous along the left apertural margin, 2) ventral process made up of arcuate microfuselli and 3) independent systems of rostral process (*rp*) (Fig. 19, *B, bb, vp, rp*) and of 4) gular prosess.

On the contrary, the right apertural lobe consists only of a narrow

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Plate XXXIX

Neocucullograptus kozlowskii n.sp. Structural details of distal thecae, A_1—A_4 apertural part of a distal theca in reverse (A_1), obverse (A_2), ventral (A_3) aspect, and in top view; *B* apertural part of another specimen seen from below (Mielnik, depth 873.40 m, *kozlowskii* zone); ×63.

gp gular process, *l* apertural lip, *ll* left microfusellar apertural lobe, *lp* lateral process on the right lobe. mth distal part of metatheca, *rl* right microfusellar apertural lobe, *rp* rostral process, *vp* ventral process of the left apertural lobe, *tz* transient zone between fusellar and microfusellar tissue, with intercalary bands of microfuselli.

microfusellar band laid down on the margin of the fusellar theca. On its more ventral part it is extroverted to form an apertural lip (Pl. XXXVIII, Fig. *A*, *lp*) which in turn forms on its dorsal margin a deeply incised notch, whose anterior margins are stretched into a long lateral process. The relation of this process to the aperture of theca is especially clearly visible in Pl. XXXIX, Figs. A_1, A_4, *B*. To show the relation of the lateral process to the inner cavity of aperture (solid black), the distal part of it was removed by a needle (Fig. 19, *B*, *lp*). The figure clearly shows how the semitubular lateral process communicates with this cavity through a deep dorso lateral incision in the right lobe.

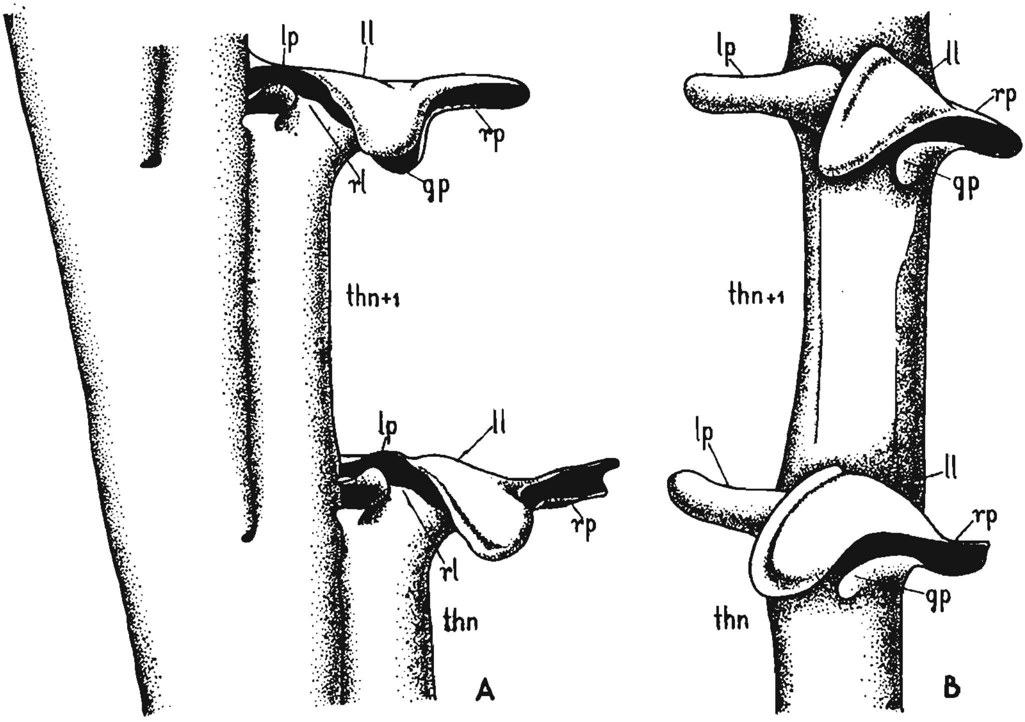

Fig. 20. — *Neocucullograptus kozlowskii* n.sp. Distal thecae of the rhabdosome in reverse (*A*) and ventral (*B*) views (Mielnik, depth 873.40 m, *kozlowskii* zone); ×47. *gp* gular process, *ll* left microfusellar apertural lobe, *lp* lateral process, *rl* right microfusellar apertural lobe, *rp* rostral process, th_n — th_{n+1} successive thecae.

No complete rhabdosome has been found, but, judging from the fragments preserved, it was fairly long, in proximal part strongly curved ventrally, with the greatest curvature in the region of the second theca. The medial part is only gently curved and distal almost straight or straight. The degree of thecal overlap increases distally (from 1/5 to about 1/2 of the thecal length). Thecae number from 10 in 10 mm in the proximal to about 9—9.5 in the distal part (Pl. VII, Fig. *C*).

Stratigraphic range. — In the Mielnik core, *Neocuc. kozlowskii* n. sp. has been recorded at a depth between 873.40 and 854.60 m. Even in its first appearance, the subspecies in question is represented by abundant populations, displaying typical morphological characters. This fact, as well as the separation from the last occurrence of *Neocuc. inex. supernus* n. subsp. by an interzone more than 7 m thick, seem to indicate that this subspecies occurred here only after its speciation was completed (comp. range chart Pl. I). There is, however, the possibility that in fact the vertical range of *Neocuc. inexspectatus* and *Neocuc. kozlowskii* n. sp. do contact, and that the lack of such contact in the distribution of the two forms in the Mielnik core is due to unrepresentative sampling, or is only local in character.

In its last occurrence that is in the sample at a depth of 854.60 m, the subspecies under study is represented by a single medial theca, which may be identified only as *Neocuc.* cf. *kozlowskii* n. sp.

In its distribution range, *Neocuc. kozlowskii* n. sp. is commonly associated with *Bohemograptus b. tenuis* (Bouček), *Monoclimacis haupti* (Kühne), *Pristiograptus dubius frequens* Jaekel, *Linograptus* sp., and *"Monograptus" egregius* n. sp.

The vertical range of *Neocuc. kozlowskii* n. sp. in the Mielnik core enables a formal distinction of the zone of *Neocucullograptus kozlowskii* (comp. range chart Pl. I). The lower, and especially upper limit of this unit, has evidently only a local significance, and the corresponding range zone shown in the distribution table — has the value of a topozonite only (Pl. I, range chart).

In the sequence established in the Mielnik core the top of this range zone is separated from the lower boundary of the overlying *"ultimus — formosus"* zone by an interzone of considerable thickness (more than 30 m!), marked by a distinct impoverishment of the graptolite fauna (scanty *Prist. dubius frequens,* numerous linograptids). A specimen of *Neocucullograptus* cf. *kozlowskii* n. sp. [14], associated directly with *M. ultimus* Perner, has, however, been etched by the present writer from the core of Pajavonys deep-boring [15] (SW Lithuania, depth 841.1—841.5 m). Showing that in fact the distribution range of both species does overlap, this specimen completes the data obtained from Mielnik boring (Urbanek, 1868 *in press,* comp. also the present paper, chapter on stratigraphy).

The lack of overlap in the vertical range of both index fossils above mentioned from the Mielnik core, may be purely accidental and connected with incomplete coring (a reduction in diameter of the core, due to some technical reasons, fall precisely within these strata), intercalations

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[14] A more accurate determination of the specimen which consisted of a sicula and the first theca with a damaged aperture, was impossible. Judging from strongly developed microfusellar additions on the sicula and the 1st theca, this is doubtlessly a *Neocucullograptus,* and most likely *Neocuc. kozlowskii* n. sp.

[15] With a permission of Prof. J. Paškevičius (Vilnius, Lithuanian SSR).

with bentonite, which are also common and rather thick (comp. pp. 174) etc. On the other hand the conditions established in Mielnik may be primary but local in character, they could be determined partly by the ingression of other graptolite assemblage (marked by the predominance of *Linograptus posthumus* R. Richter which is rather rare in underlying beds).

The present writer's examination of graptolites, collected by Prof. B. Bouček (Prague) in the key-section of Barrandian in Čertovy schody near Končprusy, and kindly offered for comparative study, shows that *Neocuc. kozlowskii* n. sp. occurs there in samples collected just below the horizon of brecciated limestones which form in this locality the base of the Přidoli Beds (Urbanek, 1968 *in press*).

In the light of these observations, the writer concludes that some of the monograptids mentioned by Horný (1962, p. 893, Fig. 7 on p. 8) from the uppermost part of Kopanina Beds, and described tentatively as "*Monograptus* ex. gr. *scanicus* Tullberg" may in fact partly correspond to *Neocuc. kozlowskii* n. sp., and partly to *Neocuc. inexspectatus* (Bouč.) (comp. Urbanek, 1968 *in press*, and the present paper pp. 185).

Systematic position. — *Neocuc. kozlowskii* n. sp. may be considered to be a further development of *Neocuc. inexspectatus inexspectatus*, and to represent a terminal, most advanced link in the *Neolob. auriculatus* n. sp. — *Neocuc. kozlowskii* lineage. Such an advanced position of *Neocuc. kozlowskii* n. sp., is indicated by a high degree of development of microfusellar additions on the thecae and sicula and, moreover, by their further morphological differentiation (the appearance and elongation of lateral and rostral process, the appearance of the gular process). The same is suggested by the stratigraphic occurrence of the species in question (comp. Pl. I).

A certain morphological gap existing between *Neocuc. inex. inexspectatus* and *Neocuc. kozlowski* n. sp. is at least partly filled by the occurrence of *Neocuc. inexspectatus supernus* n. subsp., which is intermediate morphologically and stratigraphically. The phylogenetic position of the forms here described as *Neocuc. kozlowskii unicornus* n. var. is, however, uncertain. Being to some extent also intermediate morphologically, *Neocuc. kozlowskii* var. *unicornus* n. var. appears too late to fulfill the requirements of a truly transient form.

Neocucullograptus kozlowskii var. *unicornus* n. var.

(Pl. XL)

Derivation of the name: after Lat. *unus* — one, *cornus* — horn; unicorn as a *Neocucullograptus* bearing only one (lateral) apertural process.

Diagnosis. — An infrasubspecific variety of *Neocuc. kozlowskii* n. sp. distinguished by a long lateral and a very short rostral apertural process.

Material. — A few short rhabdosome fragments including medial and distal parts, well preserved, unflattened. More complete rhabdosomes unknown.

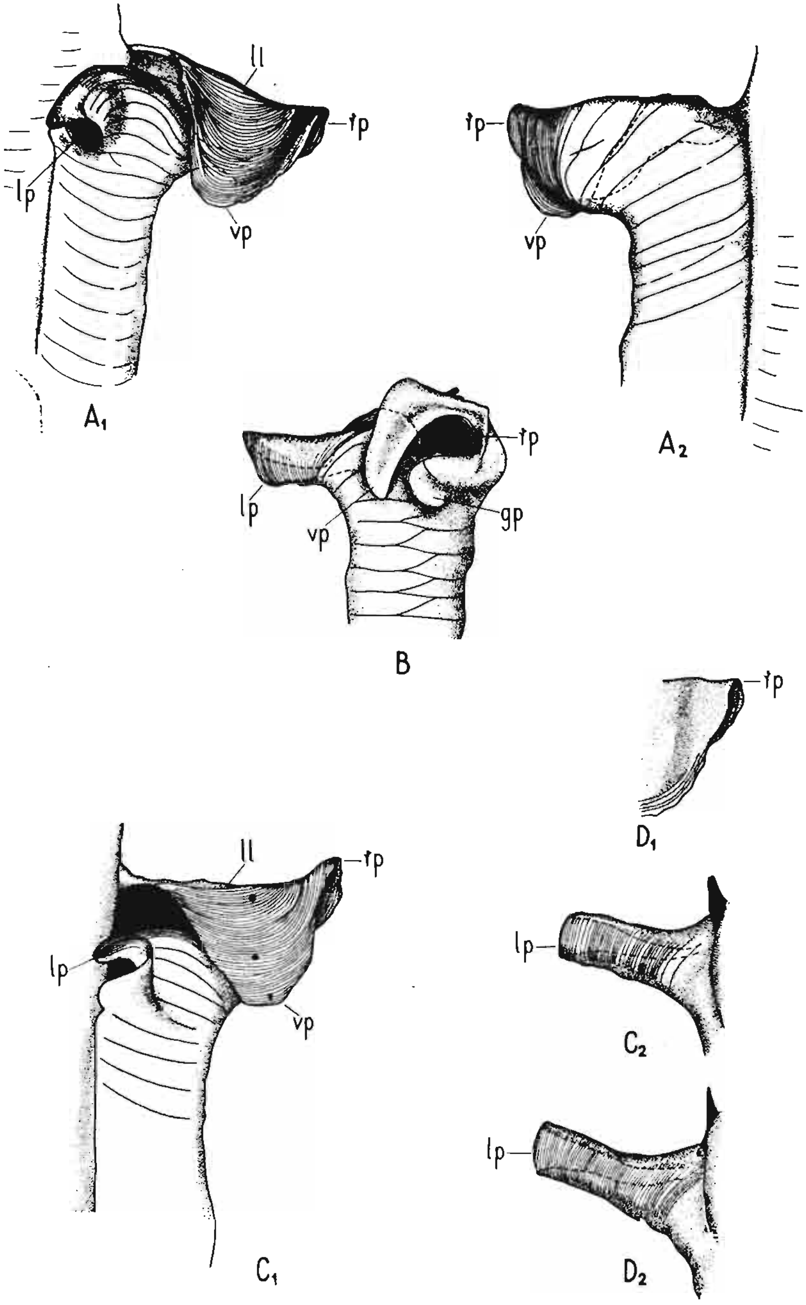
Description. — Sicula unknown, but probably undistinguishable from that in the true *Neocuc. kozlowskii* n. sp. Medial (Pl. XL, Figs. *A*, *B*) and distal thecae (Pl. XL, Fig. *C*) equaling in size and shape those in the true *Neocuc. kozlowskii* n. sp. but provided with an apertural apparatus displaying a peculiar combination of characters typical of *Neocuc. inexspectatus supernus* n. subsp. and *Neocuc. kozlowskii* n. sp. Its left microfusellar apertural lobe strongly domed, overlaps the aperture (*ll*). As in *Neocuc. inex. supernus* n. subsp. and in *Neocuc. kozlowskii* n. sp., it has a distinct gular process (Pl. XL, Fig. *B*, *gp*), which, however, placed more horizontally is sometimes not discernible in lateral view (Pl. XL, Fig. A_2). In contrast to the latter species, the rostral process of the left lobe (*rp*) is very slightly marked, projecting only some 0.05—0.10 mm upwards or laterally.

In the majority of cases the rostral process has smooth margins, without any traces of damage or breaking off. Its shortness seems to be, therefore, a primary and not a preservational feature. Due to the shortness of the rostral process, the apertural slit is widely gaping as is seen ventrally (Pl. XL, Fig. *B*). At its dorsal end, the left apertural lobe joins the ventral wall of the adjacent theca.

The right microfusellar apertural lobe (*rl*) forms a rather narrow band, framing the corresponing fusellar apertural elevation. In its ventral part, it is covered by an overhanging left microfusellar lobe. At its dorsal end, it is deeply incised to form a dorsolateral notch whose margins are stretched into or long, semitubular outgrowth, that is a strongly developed lateral process (*lp*). The last-named is especially well visible in ventral view, as it projects some 0.16—0.30 mm (Pl. XL, Figs. *B*, C_2, D_2, *lp*). It is as long as that in the true *Neocuc. kozlowskii* n. sp. A strong contrast between the incipient rostral process, which is by no means longer than that in *Neocuc. inexspectatus,* and the strongly elongated lateral process, which is not shorter than that in the true *Neocuc. kozlowskii* n. sp., seems to be the most remarkable feature of the form described (Pl. XL, Figs. C_1, C_2, D_1, D_2).

Stratigraphic range. — Thecae with characteristics described above have been found in the Mielnik core only in two samples: at a depth of 863.10 m and at a depth of 859.10 m. These occurrencies delimit, therefore, the range of *Neocuc. kozlowskii* var. *unicornus* n. var., in which it displays a discontinuous distribution (each of the two appearancies separated by a thickness of 4 m!). The vertical range of the variety in question fits within the range of the true *Neocuc. kozlowskii* n. sp. (the same zone, the lower part of the Siedlce Beds, comp. distribution table). In each case, it is associated with *B. b. tenuis* (Bouček).

PLATE XL



Neocucullograptus kozlowskii var. *unicornus* n.var. Structure of thecae. A_1—A_2 reverse and obverse views of distal part of a theca, *B* another theca in ventral view, C_1 a somewhat more distally placed theca in reverse aspect and its lateral process (C_2) seen antero-ventrally D_1—D_2 rostral process (D_1) and lateral process (D_2) of same specimen compared (Mielnik, depth 859.10 m, *kozlowskii* zone); × 63.

gp gular process, *ll* left microfusellar apertural lobe, *lp* lateral process on the right lobe, *rp* slightly marked rostral process, *vp* ventral process.

Systematic position. — The scarcity of material does not enable the discrimination between the described alternative of the form as a separate subspecies and treating it as an only infrasubspecific variety (intrapopulationary variant). The scarcity of findings, and the sporadic, discontinuous occurrence within the range of *Neocuc. kozlowskii* n. sp. may be against its recognition as a separate subspecies and suggest that it is rather an extreme variant within the variability range of *Neocuc. kozlowskii* n. sp. Nevertheless, the morphological features of this form are expressive enough to designate it as a rather non arbitrarily defined variety of a probably infrasubspecific rank.

For purely typological reasons, *Neocuc. kozlowskii* var. *unicornus* n. var. may be considered as an intermediate between *Neocuc. inex. supernus* n. subsp. and the true *Neocuc. kozlowskii* n. sp., since it inherited from the former the shape of the left lobe (the presence of the gular and absence of the rostral process) and from the latter the shape of the right apertural lobe (a prominent lateral process). This may suggest an earlier phylogenetic formation of the lateral than the rostral process. This suggestion is in fact supported by the course of astogeny in *Neocuc. kozlowskii* n. sp. in which the formation of the lateral process precedes astogenetically the elongation of the rostral process (comp. p. 353). *Neocuc. kozlowskii* var. *unicornus* n. var. appears, however, too late to be considered as a true intermediate between the phylogenetic links mentioned above, but still it may represent one of the more, primitive "morphotypes" within limits of variation of *Neocuc. kozlowskii* n. sp.

APPENDIX

"*Monograptus*" *proegregius* n. sp.

(Pl. XLI)

1955. *Monograptus* sp. Kühne; W. G. Kühne, Unterludlow Graptoliten..., pp.395—396, Fig. 17.

non 1958. *Pristiograptus* sp. Urbanek; A. Urbanek, Monograptidae..., pp. 87—88, Fig. 58, A—C.

Holotype: Pl. XLI, Fig. *A*.

Paratype: Pl. XLI, *C, F.*

Type stratum: Greenish-blue mudstones in the core of the Mielnik deep-boring between 996.90—975.90 m of depth (upper part of the *parascanicus* zone, Mielnik Beds).

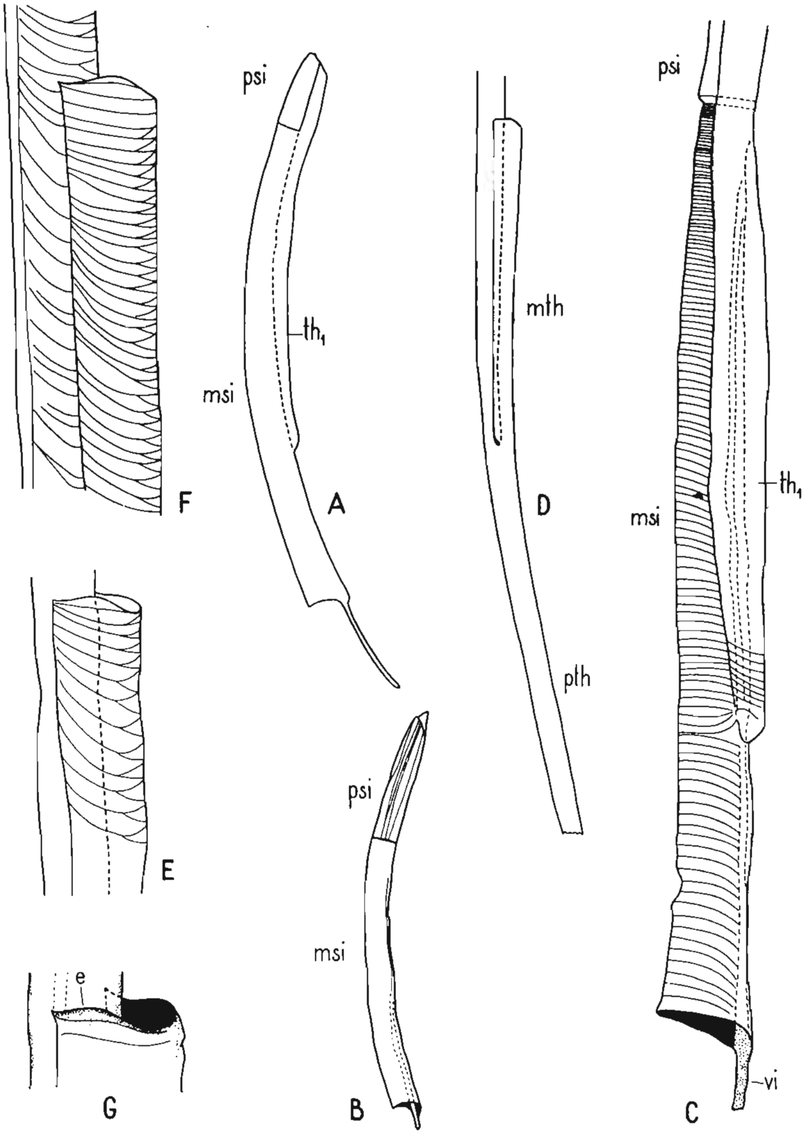
Derivation of the name: after Lat. *pro*—before; as preceding in appearance "*M.*" *egregius* n. sp.

Diagnosis. — An aberrant monograptid with extremely elongated (at
Material. — Scanty and fragmentary specimens including sicula and
least 3.28 mm long) and very narrow, tubular sicula; thecae elongated, tubular, with almost straight apertural margins.
incomplete thecae. Strongly flattened.

Description. — Sicula straight or almost straight, strongly elongated (at least 3.28 mm long), narrow and tubular, with simple aperture lacking the dorsal process (Pl. XLI, Figs. *A*—*C*).

The longest fragment of prosicula preserved measures 0.75 mm in length. Judging from its end it is, however, difficult to decide whether it is complete. A number of distinct, longitudinal threads discernible on the surface of prosicula, which measures some 0.06 mm in width at the aperture (Pl. XL, Fig. *A, l*). Aperture of prosicula provided with a distinct annular thickening, but true sicular black rings are lacking (Pl. XLI, Fig. *A, a th*).

Adult metasicula some 2.53 mm long, tubular and narrow throughout, expanding gradually and only slightly toward the aperture (0.06 mm in width on the boundary with prosicula, 0.20 mm at the level of the primary notch, and 0.22 mm at the aperture). Aperture of metasicula has a simple margin, provided only with virgella and devoid of the dorsal process (Pl. XLI, Figs. *A, C*).



"*Monograptus*" *proegregius* n. sp. Sicula and thecae. *A* almost complete sicula with fragment of first theca, *B* growing metasicula, *C* details of structure of the metasicula and basal part of the first theca, *D* diagrammatical reconstruction of a theca based on two overlapping fragments, *E* apertural part of a proximal theca, *F* apertural part of a distal theca, *G* aperture of another distal theca (Mielnik, depths *A*, *C* 977.20 m, *B* 987,90 m, *D*—*G* 996.00 m, all *parascanicus* zone); *A*, *B*, *D*× ×25, remaining ×50.

e elevation of apertural margin, *msi* metasicula, *mth* metatheca, *psi* prosicula, *pth* protheca, *vi* virgella.

Structure of the primary notch region indicates a normal monograptid pattern of the budding of the initial bud (Pl. XLI, Figs. *A*, *C*, *pn*, *ib*). Initial bud situated 1.80 mm from the boundary of prosicula and 0.73 mm from the definitive metasicular aperture. In a young metasicula, the initial bud and adapertural part of the metasicula grow simultaneously for a longer time and, judging from the specimen figured in Pl. XLI, Fig. *A*, the growth of metasicula is delayed as compared with the rate of growth of prothecal tubule in th_1.

The material of the thecae scanty and fragmentary. The fragments preserved indicate that thecae are very long, narrow and almost steady in width throughout. This results in a peculiar, tubular appearance of the thecae (Pl. XLI, Figs. *D*—*F*). A very gentle sigmoidal curvature of the ventral wall of thecae occurs at the level of the lower margin of the interthecal septum. The length of proximal thecae may be estimated, on the basis of the fragments preserved to be some 7.02 mm (about 2.52 mm for metatheca). Their width in prothecal part amounts to 0.10—0.12 mm and in the metathecal some 0.13—0.16 mm. The width of rhabdosome at the level of aperture in the proximal part amounts to 0.24 mm. A complete length of distal thecae can not be estimated, their width in metathecal part being 0.18 mm, and the width of rhabdosome measured at the aperture — some 0.28 mm. The width of prothecal part in distal thecae amounts to 0.14 mm.

The size and dimensions apart, the proximal and distal thecae are very similar morphologically. They are straight, elongated tubules with ventral wall of the theca parallel to the long axis of rhabdosome. The aperture of theca is simple, provided with very gentle lateral elevations, each of them in the form of a short fusellus which does not fuse with ventral wall of an adjacent theca. There is a shallow dorsolateral incision of the aperture, but the ventral notch is only indistinct. The apertural margin is situated perpendicularly to the long axis of the theca.

Due to the scarcity of material, neither shape nor size of a complete rhabdosome may be determined. Rhabdosome seems to be rather straight.

Stratigraphic occurrence. — "*M*". *proegregius* n. sp. has been found in the Mielnik core at a depth of 996.90—975.90 m (*parascanicus* zone, Mielnik Beds, comp. Urbanek 1966, p. 306, Pl. I, range chart [16]). It is associated with typical and rich assemblages of this zone, the most common of them being *Saet. chimaera cervicornis* Urb., *Saet. chimaera* cf. *chimaera* (Barr.), *Lobograptus scanicus parascanicus* (Kühne), *Cucullograptus pazdroi* Urb. Kühne (1955) mentioned the same association ("*chimaera* Fauna" (from

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[16] The last occurrence of "*M.*" *proegregius* n. sp. and the first appearance of "*M.*" *egregius* n. sp. are connected, on the range chart, by a dotted line, since at that time the present writer tended to lump both forms (as different zonal varieties) into one species.

the erratic boulders together with his *Monograptus* sp., here considered to be conspecific with "*M.*" *proegregius* n. sp.

Systematic position. — "*M.*" *proegregius* n. sp. is conspecific with the from described by Kühne (1955, p. 395—396) as *Monograptus* sp. from the erratic boulders of Baltic origin. Now, after comparing with a more complete material the present writer's earlier opinion (1959, p. 88) that his *Pristiograptus* sp. may be conspecific with Kühne's form seems misleading.

"*M.*" *proegregius* n. sp. is an aberrant form which strongly differs from other contemporaneous species. Its origin is obviously cryptogenetic (for comparison with "*M.*" *egregius* n. sp. and speculations on possible relationship — see below).

"*Monograptus*" *egregius* n. sp.
(Pl. XLII—XLIII)

Holotype: Pl. XLIII, Figs. D_1—D_2.

Paratype: Pl. XLII, Fig. *A*.

Type stratum: Greenish-blue mudstones and marls in the core of the Mielnik deep-boring at a depth of 922.10—854.60 m (uppermost part of *aversus* zone, uppermost part of *kozlowskii* zone, lower part of the Siedlce Beds).

Derivation of the name: after Lat. *egregius* — extraordinary, uncommon, as having unusually elongated thecae.

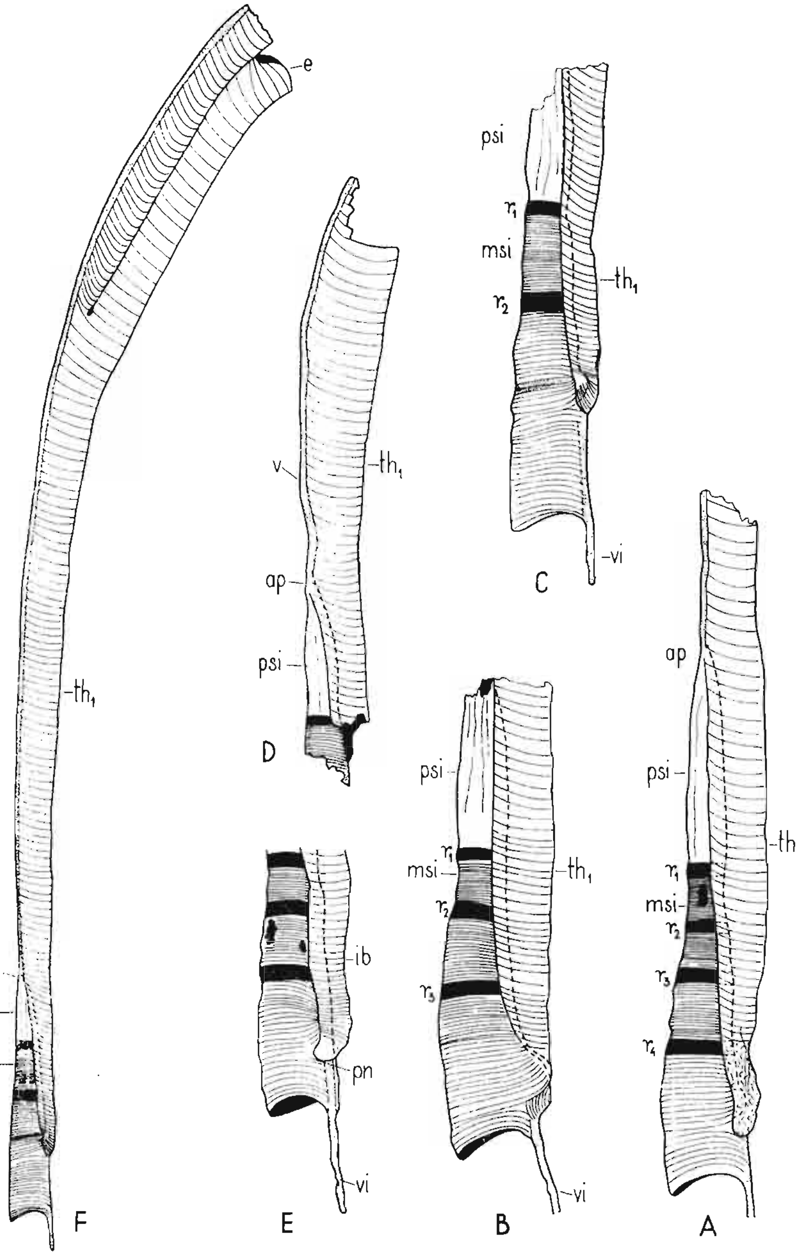
Diagnosis. — An aberrant monograptid with a normal sicula and extremely elongated thecae overlapping about one fourth in the early to two thirds in distal thecae. In the distal part of rhabdosome, the transversal section runs through the four thecae. In the proximal part rhabdosome strongly curved ventrally. Throughout the rhabdosome thecae provided with lateral apertural elevations.

Material. — Rather scanty and fragmentary material including sicula, proximal and distal parts of rhabdosome. Complete rhabdosomes unknown. The material comprises both flattened and unflattened specimens.

Description. — Sicula straight, rather small, 1.53—1.42 mm long (in one case, even 1.60 mm!), with a simple, only slightly expanded aperture and a very small, or even indistinct dorsal process (Pl. XLII, Figs. *A*—*F*).

Prosicula 0.37—0.60 mm long, with longitudinal threads (*l*). In all cases observed the first sicular black ring (r_1) is placed right on the boundary of pro- and metasicula (Pl. XLII, Figs. *A*—*D*).

Metasicula 0.80—0.82 mm long, widening gradually from about 0.10—0.12 mm on the boundary with prosicula to about 0.20—0.25 mm at the level of the initial bud and terminal aperture. Aperture, provided with a normal virgella, has a very slight dorsal process, occurring here in the form of only indistinct, some 0.03—0.04 mm long (*trans.*) elevation. A very low position of the initial bud close to the metasicular aperture



"*Monograptus*" *egregius* n.sp. Sicula and reconstruction of the first theca. *A*—*C* more or less complete siculae with fragments of the first theca. *D* structural details of the primary notch and initial bud, *E* apical portion of sicula with preserved base of the first theca, *F* reconstruction of the sicula with the first theca. All reverse aspect (Mielnik, depth *D* 916.60 m, *A*, *C* 904.60 m; *B*, *F* 854.60 m, *praecornutus-kozlowskii* zones); *A*—*E*×50, *F* ca×27.

ap apex of prosicula, *e* elevations of apertural margin, *ib* initial bud, *msi* metasicula, *pn* primary notch, *psi* prosicula, r_1—r_4 successive sicular black rings, *rdp* reduced dorsal process of sicula, th_1 first theca, *v* virgula, *vi* virgella.

seems to be characteristic of the species. It is situated 0.05—0.11 mm (and only in one case 0.25 mm) from the margin of sicular aperture.

Sicula has 4—3 black rings, the first of them right on the boundary between pro- and metasicula.

The early extraordinarily elongated and ventrally curved thecae sharply contrast in shape and dimensions with a rather small sicula.

No complete first theca has been preserved and the specimens observed have the upper part of metatheca damaged. The reconstruction of a sicula with th_1 attached shown in (Pl. XLII, Fig. *F*) is based on a combination of the fragments preserved with a metatheca of other early thecae. The length of prothecal segment in th_1 amounts to 4.00—4.20 mm while that of metatheca may be estimated to be about 1.50 mm. A complete length of th_1 was probably about 5.70 mm. As compared with its own sicula and th_1 observed in most monograptids, th_1 was unusually elongated.

The first strongly elongated theca is rather narrow and almost uniform in width (0.15 mm wide above the apex of prosicula and some 0.22 at the aperture), which result in a charasteristically tubular shape (Pl. XLII, Fig. *F*). It is also markedly curved ventrally, with the strongest curvature between half the length of prothecal segment and the base of metatheca. The curvature of thecal tube in th_1 amounts to 165°—170°.

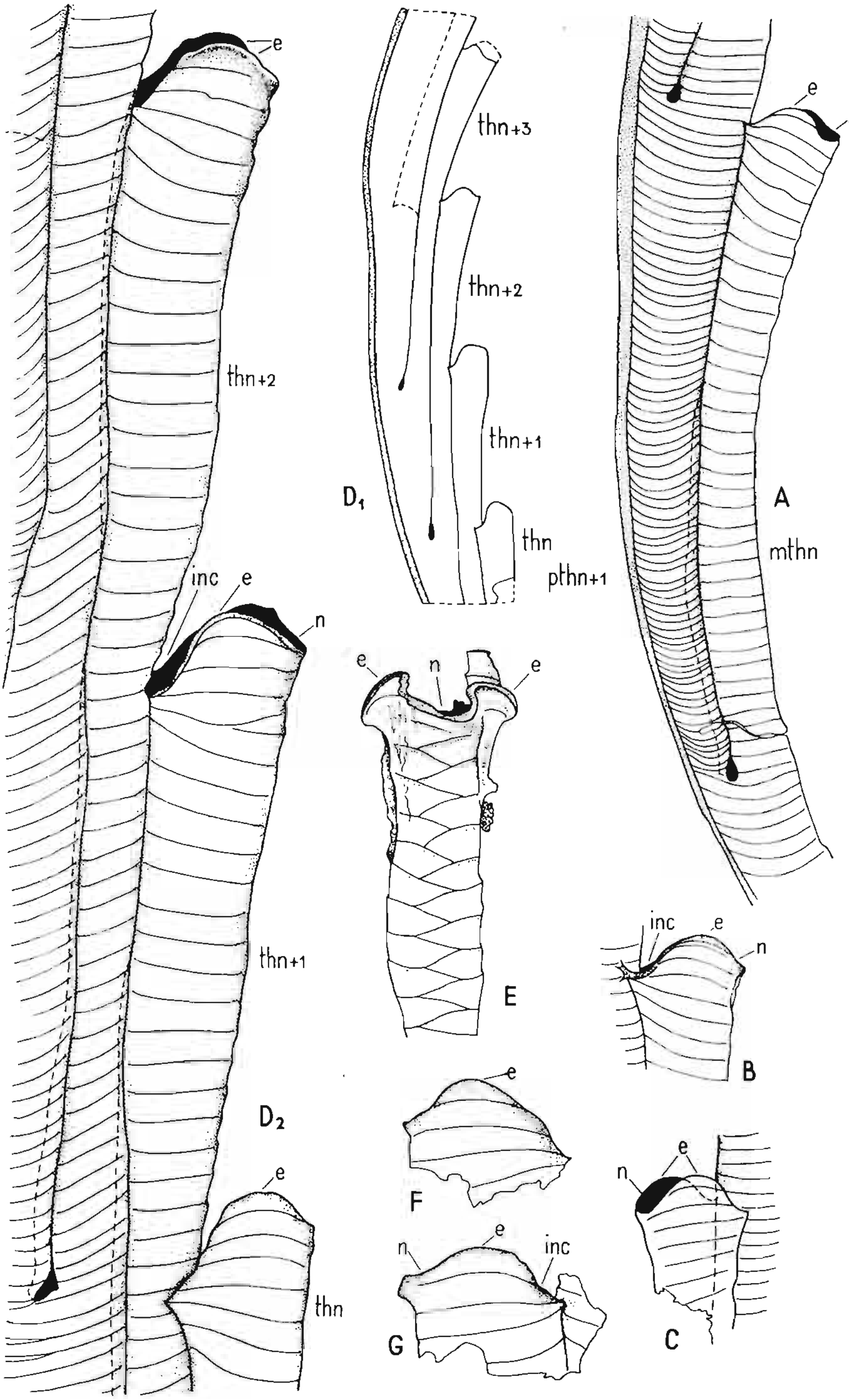
Proximal thecae are about 3.70—3.80 mm long, almost uniform in width (0.18 mm at the base of metatheca and 0. 25 mm at the aperture) and adnate throughout. Prothecal and metathecal segments are almost equal in length. Their overlap is about a half (Pl. XLIII, Fig. *A*). Aperture is provided on the margin, with paired lateral elevations 0.08—0.10 mm heigh usually consisting of 1—2 short fuselli (Pl. XLIII, Figs. *A*—*C*, *e*) and separated by a distinct ventral notch and dorsolateral incisions (*n*, *inc.*). Proximal thecae are gently curved ventrally.

Distal thecae are about 4.80 mm long, rather narrow (0.20 mm wide at the base of metatheca and 0.35 mm at the aperture) and tubular. The metathecal segment is some 3.30 mm long, prothecal being 1.50 mm in length and therefore somewhat less than one third of the total thecal length. Theca is adnate throughout and overlapping over about two-thirds of its length. Such a considerable degree of the overlap and small inclination of theca (about 20°) are responsible for mutual relations of thecae in the distal part, in which the cross section at the level of a given theca runs through four thecae (Pl. XLIII, Fig. D_1, *x*—*x*).

The width of rhabdosome in the distal part, measured across the aperture, amounts to 1.00 mm and at the base of theca to 0.70 mm.

Aperture in distal thecae display lateral elevations on the margin. They are some 0.25 mm high (*long.*), and made up of 3—4, successively shortening fuselli (Pl. XLII, Figs. D_1—D_2). The free margin of these elevations may be thickened. They are separated dorsally from the next

PLATE XLIII


e
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theca by a deep, dorsolateral incision and on the ventral margin by a ventral apertural notch (Pl. XLII, Figs. *E—G, inc., n*).

The distal part of the rhabdosome is gently curved ventrally (Pl. XLII, Fig. D_1).

The fusellar structure of the thecae is rather peculiar, particular bands being fairly wide (*long*) and measuring in the metathecal part of proximal thecae 0.05 mm and in the distal — 0.08—0.09 mm. Their upper markedly prominent edges form short "collars".

Systematic position. — *"M." egregius* n. sp. is an aberrant monograptid which strongly differs from all contemporaneous species.

In high degree of thecal overlap, length and inclination of thecae form in question approaches to *Bohemograptus? butovicensis* (Bouč.), but differs from it in smaller width of rhabdosome (1.00 mm instead 2.00—2.20 mm in distal part), and in presence of elaborated thecal aperture. Moreover last named species is accompanied by an assemblage indicative for *nilssoni* zone of Lower Ludlovian (Bouček, 1936). In the elongation of thecae and their general shape, *"M." egregius* n. sp. resembles another aberrant monograptid, occurring in *parascanicus* zone of the Mielnik Beds, that is, a form here described as *"M." proegregius* n. sp. In a peculiar pattern of the fusellar structure both forms closely resemble each other. Despite these similarities, the two forms might have distinct ancestries, as indicated by a strongly divergent structure of siculae. *"M." proegregius* n. sp. has an aberrant strongly elongated and tubular sicula. On the contrary, *"M." egregius* n. sp. displays a normal although rather short sicula with a certain expansion of the aperture. In both forms, the evolution of sicula took place in opposite direction — in the former, sicula involved in the same trend of changes as thecae (elongation), in the latter, sicula was omitted from these changes, or even modified in opposite direction (slight shortening). Although earlier *"M." proegregius* n. sp. is more specialized in structure of its sicula than the later *"M." egregius* n. sp. If there is a phylogenetic relationship between the forms under study, it seems rather less probable than *"M." egregius* n. sp. originated directly from *"M." proegregius* n. sp. than that they both had a common, but as yet unknown ancestor. The secondary loss of specialization in sicula, ne-

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PLATE XLIII

"Monograptus" egregius n.sp. Structure of thecae. *A* fragment of a proximal theca, reverse side, *B—C* apertural part in proximal thecae, seen in reverse and obverse aspect, D_1—D_2 distal fragment of rhabdosome in reverse aspect, to show general relations (D_1) and structural details (D_2) of the thecae, *E* apertural part of a distal theca in ventral view, *F—G* isolated apertural elevations in distal thecae in lateral view (Mielnik, depth 854.60 m, *kozlowskii* zone); $D_1 \times 14$, remaining $\times 50$.

e lateral elevations of apertural margin, *inc* dorsolateral incision, *mthn* metathecal segment of a given theca, *n* ventral apertural notch, *pthn+1* prothecal segment of a given theca, *thn-thn+3* successive thecae of rhabdosome.

cessary to transform the former into the latter, seems in rather unlikely. The lack of intermediate form, a considerable time interval between the last occurrence of the earlier species and the first appearance of the later may suggest a repeated occurrence of successive offshoots, arising separately from a persistently continuing stem and resulting independently in similar, but by no means identical forms (a certain similarity to the iteration).

A form which may represent a persistent stem is, however, unknown in the area investigated sympatrically. Nevertheless, the species believed to represent its offshoots might be developed allopatrically (outside the region investigated) and appear as a result of a double, independent and heterochronic migration (a combination of the iteration with the cryptogenetic origin). The speculative explanation suggested may be precocious, but on the other hand, the trend towards extreme elongation of thecae seems to be very rare among the upper Silurian monograptids, which induces one to seek a certain connection between the forms which display this tendency.

As the relationship between "*M.*" *egregius* n. sp. and "*M.*" *proegregius* n. sp. are hypothetical, it seems safer not to jump to conclusions on the question of their generic assignement and to use a general term of "*Monograptus*" (comp. a similar procedure in the case many other monograptids with unknown affinities, introduced by Urbanek, 1963, 1966).

Stratigraphic occurrence. — "*M.*" *egregius* n. sp. makes its first appearance in the Mielnik core at a depth of 922.10 m, in the uppermost part of the *rostratus* subzone (*aversus* zone). Its appearance almost exactly coincides with the extinction of the last Lower Ludlovian element (*Cucullograptus*). "*M.*" *egregius* n. sp. is itself the first entirely new element typical of the Siedlce Beds fauna (comp. p. 228).

The stratigraphic distribution of "*M.*" *egregius* n. sp., met with in the Mielnik core is discontinuous. The species in question is by no means uncommon, although never abundant in strata between depth of 922.10 m and 904.60 m (the uppermost part of *aversus* and lower part of *auriculatus* zone), afterward: absent for a number of horizons once again appearing in a rather rich population at a depth of 854.60 m (the uppermost part of *kozlowskii* zone).

Although its reappearance is separated by a thickness of some 50 m from a previous last occurrence, there is no doubt that "*M.*" *egregius* n. sp. from the lower and that from the upper part of this range are conspecific with each other. The discontinuous distribution of "*M.*" *egregius* is surely only local in character and the species in question may be considered as a fossil very characteristic of the entire range of the lower part of the Siedlce Beds. This opinion is in a complete conformity with the observations of Dr. H. Tomczyk (oral comm.) who earlier recognized in a number of borings a form most probably conspecific with "*M.*" *egregius*

n. sp. here described and noted its similar range. Very characteristic and easily recognizable, "*M.*" *egregius* n. sp. seems to be an important index fossil of the lower part of the Siedlce Beds.

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November, 1969

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NEOCUCULLOGRAPTINAE N.SUBFAM. (GRAPTOLITHINA) — ICH EWOLUCYJNE I STRATYGRAFICZNE ZNACZENIE

Streszczenie

Praca przynosi rezultaty badań nad morfologią, astogenezą i filogenezą grupy monograptidów górno-sylurskich, którą proponuje się wyodrębnić jako Neocucullograptinae n. subfam., zaliczając do niej rodzaje *Bohemograptus* Přibyl, 1967, *Neolobograptus* n. gen. oraz *Neocucullograptus* n. gen.

Opracowany materiał pochodzi głównie z rdzenia głębokiego wiercenia Mielnik nad Bugiem, I.G.1, wykonanego przez Zakład Rud Żelaza Instytutu Geologicznego w Warszawie, z serii obejmujących warstwy mielnickie i siedleckie (Ludlow), wydzielone przez Tomczyka (1962) jako jednostki regionalno-stratygraficzne dla syluru platformowego w Polsce. W mniejszym stopniu materiał pochodzi z bałtyckich głazów narzutowych, zebranych z moren Polski Północnej, głównie Pomorza. Okazy zostały wypreparowane za pomocą metod chemicznych, a następnie zbadane za pomocą standardowych metod stosowanych powszechnie do badań graptolitów o takim stanie zachowania.

W części ogólnej omawia się stanowisko stratygraficzne zbadanej fauny graptolitowej. Neocucullograptinae n. subfam. ograniczone są w swym występowaniu stratygraficznym do ludlowu, przy czym w jego części dolnej (warstwy mielnickie) reprezentowane są jedynie przez *Bohemograptus*, zaś w jego części górnej (dolna część warstw siedleckich) początkowo przez nowe gatunki tego rodzaju, a następnie przez *Neolobograptus* n. gen. i *Neocucullograptus* n. gen. Na podstawie występowania neokukullograptidów proponuje się wyróżnienie w obrębie dolnej części warstw siedleckich następujących poziomów graptolitowych (od dołu): 1) *Bohemograptus praecornutus* n. sp., 2) *B. cornutus* n. sp., 3) *Neolobograptus auriculatus* n. sp., 4) *Neocucullograptus inexspectatus* (Bouček), 5) *Neocuc. kozlowskii* n. sp.

Poniżej poziomu 1 znajduje się poziom *Cucullograptus aversus* warstw mielnickich (Urbanek, 1966), zaś powyżej poziomu 5 leży poziom *Monoclimacis ultimus* (Perner) — "*Monograptus*" *formosus* (Bouček). Najniższą część warstw siedleckich cechuje znaczne zubożenie w zróżnicowaniu fauny graptolitowej, przy licznym występowaniu *B. bohemicus* (Barr.). Bałtyckie głazy narzutowe cechujące się licznym lub masowym występowaniem *B. bohemicus*, któremu towarzyszy uboga asocjacja graptolitowa, zdają się w większości pochodzić z równowiekowego poziomu stratygraficznego. Podobny poziom licznego występowania *B. bohemicus* można stwierdzić w Barrandienie i w Turyngii. Ten fakt oraz występowanie *Neocuc.* cf. *kozlowskii* n. sp. na Litwie, zaś *Neocuc. kozlowskii* n. sp. oraz *Neocuc. inexspectatus* (Bouček) i *Neocuc.* cf. *inexspectatus* (Bouček) w Barrandienie pozwalają sądzić, że proponowany podział warstw siedleckich znajdzie zastosowanie dla rozpoziomowania równowiekowych osadów syluru całej Europy środkowej i wschodniej. Wbrew ogólnie przyjętemu poglądowi, że między poziomem *leintwardinensis* a poziomem *formosus*, rozwija się tylko zubożały zespół monograptidów, badania obecne wykazały, że w tym czasie na obszarze Niżu Polskiego istniała względnie różnorodna i liczna fauna graptolitowa, której przedstawiciele reprezentują nowe i nieoczekiwane kierunki ewolucji.

Koncepcja Neocucullograptinae n. subfam. wiąże się z wykazaniem ścisłych związków filogenetycznych między niewyspecjalizowanymi przedstawicielami *Bohemograptus* Přibyl (dolny ludlow) oraz wyspecjalizowanymi monograptidami górnego ludlowu. Początkowo grupa ta reprezentowana była przez *B. b. bohemicus* (Barr.), który wykazuje powolną mikroewolucję. Pod koniec dolnego ludlowu (poziom *hemiaversus*, warstwy mielnickie) populacje tego podgatunku wykazują znamienny polimorfizm, wyrażający się obecnością dwu odrębnych postaci morfologicznych (morf), z których jedna ma zdolność wytwarzania tkanki mikrofuzellarnej. Utwory zbudowane z tkanki mikrofuzellarnej, zwane „dodatkami mikrofuzellarnymi" (microfusellar additions), powstają z pewnym opóźnieniem po zakończeniu wzrostu części fuzellarnej teki i stanowią struktury mające postać parzystych elewacji lub płatowatych przydatków, względnie nieparzystych kołnierzy lub struktur pierścieniowatych, otaczających aperturę w postaci szerokiej platformy. Podobne struktury mogą powstawać na sikuli. W pracy uzasadnia się, że różnice między mniej lub bardziej zaawansowanymi strukturami mikrofuzellarnymi (zwanymi velum) są natury wzrostowej. Forma polimorficzna mająca zdolność ich tworzenia została określona jako morfa „veliger". Na granicy warstw mielnickich i siedleckich (poziom *aversus*) doszło do podziału jednolitej dotąd linii rozwojowej na dwa odrębne kierunki: 1) *B. b. tenuis* (Bouček), oraz 2) *B. praecornutus* n. sp. Obie wspomniane formy wywodzą się zapewne od *B. b. bohemicus* (Barr.), lecz ostatnia zjawia się w profilu Mielnika nad Bugiem nieco później.

Linię *B. b. tenuis* cechuje gracylizacja tek proksymalnych, pewne zmniejszenie sikuli, a następnie także jej wyrostka dorsalnego przy utrzymaniu się polimorfizmu. Od tego podgatunku daje się wyprowadzić *Neolobograptus auriculatus* n. sp., który obok dalej posuniętej gracylizacji tek cechuje się zróżnicowaniem apertury tek, przez powstanie wydatnych elewacji lateralnych zbudowanych z normalnych fuzellusów i opatrzonych wyraźnym wcięciem dorsolateralnym na tej krawędzi. Zdolność do wytwarzania dodatków mikrofuzellarnych zachowuje się w ramach polimorfizmu. Dalszy rozwój tej linii tworzą przedstawiciele *Neocucullograptus* n. gen. u których obecność dodatków mikrofuzellarnych staje się stałą cechą morfologiczną. Bardziej prymitywny *Neocuc. inexspectatus* (Bouček), znany jest już dawno, lecz przez długi czas błędnie był uważany za synonim *Lobograptus scanicus* (Tullb.) (Bouček, 1932, 1936). Cechuje się on obecnością na tekach aparatu aperturalnego, złożonego z tkanki mikrofuzellarnej i wykazującego przerost lewego płata aperturalnego. Bardziej wyspecjalizowany *Neocuc. kozlowskii* n. sp. cechuje się obok obecności asymetrycznych płatów aperturalnych, zbudowanych z tkanki mikrofuzellarnej także długimi wyrostkami rostralnym i lateralnym. Nadaje to „kolczastą" postać aparatowi aperturalnemu wyspecjalizowanych przedstawicieli *Neocucullograptus* n. gen., który silnie upodabnia się do takiego u *Cucullograptus aversus*, chociaż oparty jest na zupełnie innej zasadzie strukturalnej. Wykazano, że ta homeomorfia była w przeszłości przyczyną błędnych oznaczeń systematycznych. Sikule *Neocucullograptus* n. gen. wykazują również obecność dodatków mikrofuzellarnych z tym, że stanowią one zawsze proste i symetryczne elewacje aperturalne. Podczas gdy *Neocuc. inexspectatus* (Bouček) i *Neocuc. kozlowskii* n. sp. są połączone przez pośrednią formę *Neocuc. inexspectatus supernus* n. subsp., nie jest wykluczone, że między tym pierwszym a *Neolob. auriculatus* n. sp. istniało obecnie jeszcze nieznane ogniwo pośrednie.

Zupełnie inny kierunek ewolucji wykazuje linia zapoczątkowana przez *B. praecornutus* n. sp. Gatunek ten cechuje się stosunkowo niskimi i szerokimi tekami, opatrzonymi wyraźnymi elewacjami aperturalnymi. Dodatki mikrofuzellerne, o ile można wnioskować na podstawie skąpych danych, powstawały w ramach polimorfizmu wewnątrzgatunkowego i nie różniły się od takich u *B. bohemicus*. Dalszy etap rozwoju tej linii stanowi *B. cornutus* n. sp., który cechuje się zachowaniem cech poprzedniego gatunku jeśli idzie o budowę fuzellarnej części tek, przy daleko posuniętej modyfikacji dodatków mikrofuzellarnych. Obecność tych ostatnich jest stałą cechą gatunkową, przy czym przybierają one postać taśmowatych wyrostków, zakończonych wachlarzowatym i błoniastym rozszerzeniem. Sikula nie wykazuje obecności dodatków mikrofuzellarnych. Linia rozwojowa *B. praecornutus* n. sp. — *B. cornutus* n. sp. była znacznie bardziej krótkotrwała od „głównej" linii rozwoju reprezentowanej przez następstwo *Neolobograptus* n. gen. — *Neocucullograptus* n. gen.

Zbadanie rozwoju fauny graptolitowej dolnej części warstw siedleckich pozwala, przez porównanie z wcześniejszym jej opracowaniem dla warstw mielnickich (Urbanek, 1966), analizować charakter zmian tej fauny na granicy dolnego i górnego ludlowu, w otworze Mielnik nad Bugiem. Wyniki porównano z przebiegiem takich zmian na obszarach sąsiednich. W faunie warstw mielnickich wyróżniono 36 gatunków Graptoloidea, zaś w faunie dolnej części warstw siedleckich tylko 12 gatunków. Zmniejszenie się liczby gatunków do 1/3 wywołane jest wymarciem całego szeregu linii rozwojowych w poziomie *leintwardinensis*, oraz bezpośrednio powyżej niego. Wymierają saetograptidy, kukullograptidy i retiolity. Nowy zespół faunistyczny warst siedleckich rozwija się w znacznym stopniu w rezultacie specjacji z miejscowych przeżytków fauny dolnego ludlowu (7 nowych gatunków), 4 gatunki przeżywają bez zmian, zaś tylko 1 zjawia się jako kryptogenetyczny imigrant. Z fauny dolnego ludlowu bezpotomnie wymiera 19 gatunków. W sumie na proces zmian fauny graptolitowej na wspomnianej granicy stratygraficznej składa się wymieranie znacznej liczby linii ewolucyjnych, przeżycie bez zmian niewielkiej liczby takich linii oraz pojawienie się pewnej liczby nowych linii filogenetycznych. W tym ostatnim procesie uczestniczy głównie specjacja dokonująca się na podłożu tubylczych przeżytków fauny dolnego ludlowu, zaś imigracja nowego elementu faunistycznego odgrywa znikomą rolę.

Głębokie zmiany fauny graptolitowej, jakie dokonały się na granicy dolnego i górnego ludlowu na obszarze obniżenia podlaskiego, a w znacznym stopniu także całej Polski Północnej, zachodziły bez wyraźnych zmian litofacji. Zmiany takie zaznaczają się w tym czasie jednak na wielu obszarach europejskich. Zwraca się uwagę, że proces wymierania miał charakter różnicujący i na różnych obszarach poszczególne linie ewolucyjne zanikały heterochronicznie. W rezultacie heterochronicznego wymierania powstały zespoły reliktowe fauny dolnego ludlowu, które w poszczególnych obszarach geograficznych mają różny skład jakościowy (systematyczny) i ilościowy. Różny ich skład systematyczny zależny był zapewne od lokalnych warunków ekologicznych, zarazem jednak określa on za każdym razem inne stosunki biocenotyczne. Obecność zespołów reliktowych spowodowana jest faktem, że zmiany środowiska nie były w równym stopniu niekorzystne dla wszystkich graptolitów (wymieranie różnicujące). O tym samym świadczy inna cecha zespołów reliktowych, a mianowicie wielki rozkwit ilościowy niektórych ich przedstawicieli, przyjmujący niekiedy charakter eksplozji populacyjnej. Zjawisko to można tłumaczyć przyjmując, że niekorzystne zmiany środowiska były z nawiązką kompensowane korzyściami, jakie dawało osłabienie, lub wyjście spod konkurencji innych gatunków graptolitów. Fakty takie świadczą więc dobitnie o udziale i znaczeniu czynnia biotycznego w procesie różnicującego wymierania, któremu towarzyszyła konkurencja między oddzielnymi gatunkami, określona ich różnym stopniem przystosowania do zmieniających się warunków środowiskowych.

Na podstawie tych przesłanek autor nie podziela poglądów Jaegera (1959) i Obuta (1964) na przyczyny zmian faun graptolitowych i wymierania Graptoloidea w ogóle. Badacze ci przyjmują za główne, a nawet przypuszczalnie wyłączne czynniki tego procesu zmiany środowiska abiotycznego, zwłaszcza zmiany fizyczno-geograficzne, zachodzące w wyniku ruchów górnotwórczych. Uzasadnia się pogląd, że przyczyny wymierania należy pojmować kompleksowo, jako całościowy zespół abiotycznych i biotycznych warunków środowiska. Uczyniono próbę analizy tych czynników biotycznych, które mogły mieć wpływ na wymieranie Graptoloidea. Pogląd ten nie podważa ważnego znaczenia zmian środowiska abiotycznego, ale kwestionuje aby udział tego ostatniego w każdym przypadku miał znaczenie decydujące. Zmiany fauny graptolitowej na granicy dolnego i górnego ludlowu dokonują się na obszarze Niżu Polskiego bez wyraźnych zmian litofacji. Mogłoby to świadczyć, że te głębokie przeobrażenia faunistyczne dokonywały się we względnie stałych warunkach środowiska abiotycznego.

Wychodząc z pewnych metodologicznych przesłanek, opartych na poglądach Simpsona (1953), autor niniejszej rozprawy stara się wykazać, że nawet przyjęcie kompleksowych zmian środowiska abiotycznego i biotycznego nie stanowi zadowalającej teorii wymierania Graptoloidea. Te same czynniki były bowiem odpowiedzialne za rozwój, jak i za wymieranie Graptoloidea, i teoria nie wyjaśnia dlaczego w jednym i w drugim przypadku ich działanie daje przeciwny rezultat. Z tych względów postuluje się, że ostateczna przyczyna wymierania leżała w stopniowym opóźnianiu się odpowiedzi przystosowawczej organizmu na zmiany środowiska, spowodowanym przez określone mechanizmy genetyczne i epigenetyczne. Proponuje się określać ten mechanizm nazwą „histerezy ewolucyjnej" (zastępując nim mniej udany termin „lag" wprowadzony przez Darlingtona, 1939).

Jako osobne zagadnienie autor analizuje problem wyróżniania podgatunków w obrębie *B bohemicus* (Barr.). Stwierdzono, że gatunek ten tworzy długotrwałą linię rozwojową, przy czym skrajne populacje różnią się wyraźnie szeregiem ilościowych cech morfologicznych. Koncepcja wcześniej wyróżnionych podgatunków *B.b. bohemicus* (Barr.) i *B.b. tenuis* (Bouček) nie była jednoznacznie określona. Analiza literatury wykazuje, że większość autorów skłania się do pojmowania ich jako podgatunków chronologicznych, przy czym pierwszy odpowiada starszemu, drugi — geologicznie młodszemu. Jednak granice morfologiczne i stratygraficzne między tymi podgatunkami nie były określone. Na podstawie analizy cech ilościowych dokonuje się próby określenia takiej granicy. Wstępne obserwacje morfologiczne wykazały, że dla tego celu największe znaczenie mieć może analiza długości sikuli i jej języczka dorsalnego, położenie apertury teki pierwszej w stosunku do wierzchołka prosikuli, szerokość podstawy proteki u tek proksymalnej części rabdosomu. Inne cechy ilościowe mają znikome znaczenie dla rozróżniania tych podgatunków.

Pewna nieciągłość w zakresie zmienności długości sikuli, zaznaczająca się między populacjami z poziomu *hemiaversus* i *aversus*, pozwala właśnie w tym miejscu postawić granicę między obu podgatunkami. Elementarna analiza statystyczna zmienności długości sikuli pozwala stwierdzić, że próbka zawierająca populacje z poziomów *parascanicus* — *hemiaversus*, różni się wyraźnie statystycznie od próbki obejmującej takie populacje z poziomów *aversus* — *kozlowskii*, natomiast istniejące różnice morfologiczne nie uzasadniają, zgodnie z przyjętą powszechnie interpretacją „prawa 75%", wyróżniania ich jako oddzielnych podgatunków. Podobnie istotne różnice stwierdzono w położeniu pierwszej teki, która w próbie z dolnych poziomów znajduje się przeważnie poniżej apex prosiculae (tzw. warianty ujemne, stanowiące tu 80,96%), zaś w próbce z górnych poziomów leży ona na tym poziomie lub powyżej (tzw dodatnie warianty stanowiące tu 64,70%). Populacje z górnych poziomów cechuje też mniejszy wyrostek dorsalny sikuli i wyraźnie mniejsza szerokość w proksymalnej części rabdosomu.

Analiza wspomnianych cech ilościowych pozwoliła na lepsze scharakteryzowanie przedstawicieli *B bohemicus* (Barr.) pochodzących z dolnych i górnych poziomów. W świetle przyjętej procedury nie daje ona jednak wyraźnych podstaw do ich wyróżniania jako oddzielnych podgatunków. Jednak na podstawie całokształtu danych, zwłaszcza po uwzględnieniu cech o charakterze jakościowym (jak dodatki mikrofuzellarne nieobecne lub bardzo rzadkie w niższych poziomach, a stale występujące w górnych), oraz pewnych innych argumentów natury filogenetycznej i stratygraficznej, uzasadnia się wyróżnianie *B. b. tenuis* (Bouček) jako sukcesjonalnego i geologicznie młodszego podgatunku, występującego od spągu poziomu *aversus* do stropu poziomu *kozlowskii.*

W części systematycznej podano opis 11 taksonów szczebla gatunkowego, zawierający dokładną analizę morfologii, rozwoju astogenetycznego oraz rozważania na temat stanowiska systematycznego i występowania stratygraficznego. Dwa spośród tych taksonów odnoszą się do aberrantnych monograptidów o niezwykle długich tekach (przy czym 1 jest z dolnego ludlowu), pozostałe należą do Neocucullograptinae n. subfam.

АДАМ УРБАНЕК

NEOCUCULLOGRAPTINAE N. SUBFAM. (GRAPTOLITHINA) — ИХ ЭВОЛЮЦИОННОЕ И СТРАТИГРАФИЧЕСКОЕ ЗНАЧЕНИЕ

Резюме

В работе приводятся результаты изучения строения, астогенетического и филогенетического развития верхнесилурийских монограптидов подсемейства Neocucullograptinae n. subfam. включающего роды *Bohemograptus* Přibyl, 1967, *Neolobograptus* n. gen. и *Neocucullograptus* n. gen. Изученный материал происходит главным образом из керна скважины Мельник-на-Буге, I. G. 1 (Восточная Польша, Подляская синеклиза), пробуренной Геологическим Институтом в Варшаве. Вмещающие отложения включают мельницкие и седлецкие слои, выделенные как стратиграфические единицы Томчиком (Tomczyk, 1962) для платформенного силура Польши. Частично материал происходит из балтийских эрратических валунов, собранных из моренных отложений Северной Польши, главным образом Померании.

Для извлечения граптолитов из пород были применены химические методы. Исследования были проведены при помощи стандартной техники, применяемой при изучении так извлеченных граптолитов.

В общей части обсуждается стратиграфическое распространение изученных форм. Neocucullograptinae n. subfam. ограничены в своем распространении лудловом. В его нижней части (мельницкие слои) они представлены только *Bohemograptus*, а в его верхней (нижняя часть седлецких скоев) — сначала новыми видами *Bohemograptus*, а затем родом *Neolobograptus* n. gen и *Neocucullograptus* n. gen. На основании стратиграфического распределения неокукуллограптин нижняя часть седлецких слоев разделяется на следующие зоны (снизу): 1) *Bohemograptus praecornutus* n. sp., 2) *B. cornutus* n. sp., 3) *Neolobograptus auriculatus* n. sp., 4) *Neocucullograptus inexspectatus* (Bouček), 5) *Neocuc. kozlowskii* n. sp.

Ниже зоны 1 залегает зона *Cucullograptus aversus* мельницких слоев (Urbanek, 1966), выше зоны 5 — зона *Monoclimacis ultimus* (Perner) — „*Monograptus*" *formosus* (Bouček). В самой нижней седлецких слоев установлено значительное уменьшение многообразия фауны, при сильном увеличении численности *Bohemograptus bohemicus* (Barr.). Балтийские эрратические валуны, в которых присутствуют многочисленные *B. bohemicus* без сопутствующей фауны или в бедной видами граптолитовой ассоциации, вероятно происходят из одновозрастного рогизонта. Аналогичный горизонт с многочисленными *B. bohemicus* известен из Баррандена и Тюрингии. Этот факт, а также обнаружение *Neocuc.* cf. *kozlowskii* n. sp. в Литве, и *Neocuc. kozlowskii* n. sp. и *Neocuc. inexspectatus* (Bouč.) в Баррандене позволяет предположить, что введенное в настоящей работе деление нижней части седлецких слоев найдет в будущем применение для расчленения одновозрастных отложений всей Средней и Восточной Европы. Вопреки общепринятому мнению, по которому между зонами *leintwardinensis* и *formosus* развивается только обедненное сообщество монограптидов, на территории Польской Низменности выявлена многообразная и многочисленная граптолитовая фауна, представители которой демонстрируют новые и неожиданные направления развития.

Обоснование самостоятельности Neocucullograptinae n. subfam. связано с доказательством тесных филогенетических связей между примитивными представителями рода *Bohemograptus* Přibyl (нижний лудлов) и некоторыми специализированными монограптидами верхнего лудлова. В начале группа Neocucullograptinae n. subfam. была представлена *B. bohemicus bohemicus* (Barr.), который проявляет медленную но заметную зональную микроэволюцию. В конце нижнего лудлова (зона *hemiaversus*, мельницкие слои) популяции этого подвида обнаруживают замечательный полиморфизм, который выражается присутствием двух особых морфологических форм (морфы). Одна из них проявляет способность к образованию микрофузелларной ткани — перидермальной субстанции, отличающейся в типичных случаях от нормальной фузелларной ткани необыкновенно узкими полосками роста, тесно наложенными друг на друге (Urbanek, 1966). Структуры, образованные микрофузелларной тканью и определенные как микрофузелларные добавки" (microfusellar additions), появляются с некоторым опозданием после окончания роста фузелларной части теки. Они имеют вид парных боковых возвышений апертурного края, широких апертурных лопастей, непарных апертурных воротников, либо кольцеобразных структур, окружающих апертуру в виде особого рода платформ. Сходные образования могут возникать на сикуле. Таким образом, из микрофузелларной ткани на теках возникает своеобразный апертурный аппарат, отличающийся отсутствием закономерной астогенетической изменчивости. Доказывается, что различие между менее и более развитыми микрофузелларными добавками вызвано главным образом ростовыми различиями, причем для обозначения наиболее сильно развитых добавок предлагается термин „velum". Морфа, проявляющая способность к образованию микрофузелларных добавок, была названа „велигер" („veliger morph").

На границе мельницких и седлецких слоев (зона *aversus*) произошло разделение единой, до этого времени, линии развития на две: 1) линию *B. bohemicus tenuis* (Bouč.) и 2) *B. praecornutus* n. sp. Последняя появляется несколько позже, чем первая, но обе они происходят от *B. b. bohemicus* (Barr.).

Для линии *B. b. tenuis* характерна грацилизация проксимальных тек, некоторое уменьшение величины сикулы, а затем и ее дорсального отростка, при сохранении внутривидового полиморфизма (присутствие морфы „veliger"). Этот подвид можно считать исходным для *Neolob. auriculatus* n. sp., который кроме еще более отчетливо выраженной грацилизации тек, обнаруживает дифференцировку апертурного края фузелларной части теки в виде отчетливого его латерального изгиба. Способность к образованию в рамках внутривидовой изменчивости микрофузелларных добавок также сохраняется. При этом произошло некоторое изменение морфологического выражения морфы „велигер".

Дальнейший ход эволюции этой линии демонстрируют представители рода *Neocucullograptus* n. gen., у которых присутствие микрофузелларных добавок является постоянным родовым признаком. Более примитивный *Neocuc. inexspectatus* (Bouč.) известен уже давно, но ошибочно считался синонимом *Lobograptus scanicus* (Tullb.) (Bouček, 1932, 1936). Его характерной чертой является присутствие на теках сложного апертурного аппарата из микрофузелларной ткани, который асимметричен вследствие гипортрофии левой его лопасти. Более специализированный *Neocuc. kozlowskii* n. sp., кроме асимметрии этого аппарата, характеризуется присутствием апертурных шипов — рострального и латерального, сидящих на апертурных лопастях и построенных из микрофузелларной ткани. Последний признак придает шиповидный вид апертурному аппарату этих специализированных неокукуллограптин. В целом, апертурный аппарат

Neocucullograptus n. gen. становится гомеоморфным с апертурным аппаратом *Cucullograptus aversus,* хотя оба они основаны на совершенно различных структурных принципах. Эта гомеоморфия в прошлом служила причиной ошибок при определении монограптидов верхнего силура. Сикулы *Neocucullograptus* n. gen. тоже обнаруживают присутствие микрофузелларных добавок, но они всегда образуют лишь простые и симметрические апертурные лопасти.

Neocuc. inexspectatus (Bouč.) и *Neocuc. kozlowskii* n. sp. соединяются через промежуточное звено *Neocuc. inexspectatus supernus* n. subsp. Между *Neolob. auriculatus* n. sp. и первым из видов имеется некоторый морфологический пробел, который возможно заполняла неизвестная еще промежуточная форма.

Совершенно другое направление развития представляет линия, начимающаяся от *Bohemograptus praecornutus* n. sp. Этот вид характерен сравнительно низкими и широкими теками, снабженными отчетливыми боковыми изгибами апертурного края. Микрофузелларные добавки, насколько судить на основании скудных фактических данных, не отличались морфологически от свойственных для морфы велигер у *B. bohemicus,* и, как у последнего, существовали в рамках внутривидового полиморфизма. *B. cornutus* n. sp. образует дальнейший этап в развитии этой линии. При сохранении основных черт строения предыдущего вида в отношении фузелларной части теки, ему свойственно глубокое изменение формы микрофузелларных добавок. Присутствие последних становится постоянным видовым признаком, но при этом они приобрели вид лентообразных апертурных отростков, заканчивающихся веерообразным и пленковидным расширением. Сикула лишена микрофузелларных добавок. Линия *B. praecornutus* n. sp. — *B .cornutus* является значительно более кратковременной по сравнению с главной линией развития неокукуллограптин, представленной рядом *Neolobograptus* n. gen. — *Neocucullograptus* n. gen.

Изучение развития граптолитовой фауны нижней части седлецких слоев, при сопоставлении ее с ранее исследованной фауной мельницких слоев (Urbanek, 1966), позволяет провести анализ изменения граптолитовой фауны на границе нижнего и верхнего лудлова в разрезе скважины Мельник-на-Буге. Анализ сопоставляется с данными о ходе изменений фауны в других районах. В фауне мельницких слоев определено 36 видов Graptoloidea, тогда как в нижней части седлецких слоев — только 12 видов. Уменьшение количества видов до $^1/_3$ связано с вымиранием целого ряда эволюционных линий в зоне *leintwardinensis* и непосредственно выше ее. К таким вымершим линиям принадлежат саетограптины, кукуллограптины и ретиолитины. Новый фаунистический комплекс седлецких слоев развивается в значительной степени автохтонно, на базе существовавших здесь реликтов фауны нижнего лудлова (7 новых видов), 4 вида переходят из мельницких слоев в седлецкие без изменений и только 1 вид является криптогенетическим иммигрантом. Из состава фауны нижнего лудлова 19 видов вымирают, не оставив потомков. В целом, переход от одного фаунистического комплекса к другому связан со следующими процессами: 1) вымиранием значительного числа эволюционных линий; 2) переживанием без изменений некоторого количества таких линий; 3) возникновением нескольких новых линий развития.

Последний процесс основан на автохтонном видообразовании, тогда как иммиграция играет ничтожную роль.

Эти глубокие изменения состава фауны на территории Подляской синеклизы, а в значительной степени и всей Северной Польши, не сопровождались четким изменением литофациальных отношений. Однако последние проявлялись более или менее резко во многих смежных областях.

Особого внимания заслуживает тот факт, что вымирание на упомянутой границе имело дифференцирующий характер и что отдельные эволюционные линии вымирали гетерохронно. Вследствие такого гетерохронного вымирания возникали реликтовые сообщества фауны нижнего лудлова, которые в разных районах имеют разный качественный (систематический) и количественный состав. Различия систематического состава этих сообществ отражали местные экологические условия, но одновременно они связаны в каждом случае с особыми биоценотическими отношениями. Об этом свидетельствует и другая черта реликтовых сообществ, а именно большой количественный расцвет некоторых их элементов, принимающий иногда характер популяционной вспышки. Невыгодные изменения среды в этих случаях были, по-видимому, с избытком компенсированы ослаблением или почти полным выходом из конкуренции с другими видами граптолитов. Процесс дифференцирующего вымирания был неразрывно связан с явлением соревнования между отдельными видами в связи с их различной приспособленностью и соотношениями с изменяющимися условиями среды.

На основании этих рассуждений автор данной работы критически расценивает взгляды Егера (Jaeger, 1959) и Обута (1964) на причины изменений граптолитовых фаун и вымирания Graptoloidea в целом. Упомянутые исследователи принимают в качестве причины этого процесса исключительно изменения абиотических факторов среды, главным образом, изменения связанные с тектогенезом. Доказывается, что вымирание связано с комплексом абиотических и биотических факторов среды. Делается попытка определения биотических факторов, которые могли повлиять на вымирание Graptoloidea. Эти взгляды не подрывают важного значения, какое имели, вероятно, изменения абиотических условий среды, но ставят под сомнение их участие или решающее значение во всех случаях.

Исходя из некоторых методологических предпосылок, основанных на взглядах Симпсона (Simpson, 1953), доказывается, что даже принятие комплексных изменений абиотических и биотических условий среды не дает удовлетворительной теории вымирания Graptoloidea. Одни и те же факторы приводили к эволюционному расцвету в одних случаях и вымирании в других случаях и данная теория не дает удовлетворительного объяснения этому. Доказывается, что решающей причиной биологического регресса Graptoloidea было, вероятно, прогрессирующее во времени опоздывание приспособительного ответа на изменения среды, вызванное определенными генетическими и эпигенетическими факторами. Предлагается обозначать этот механизм воздействия как эволюционный гистерезис, замещая им термин „lag" предложенный в свое время Дарлингтоном (Darlington, 1939).

Особо рассматривается вопрос о выделянии подвидов *B. bohemicus* (Barr). Этот вид образует длительно существовавшую линию развития, в которой крайние популяции четко различаются рядом количественных морфологических признаков, но связаны почти непрерывистым рядом промежуточных популяций.

Концепции раньше выделенных подвидов *B. b. bohemicus (Barr.)* и *B. b. tenuis* (Bouček) не были однозначно определены. Из анализа литературных данных вытекает, что большинство исследователей скланяется к пониманию этих таксонов, как хронологических подвидов *B. bohemicus* (Barr.). Первый из них отвечает геологически более древнему, второй — геологически более молодому подвиду, но стратиграфическое и морфологическое их разграничение неясно.

На основании анализа количественных признаков делается попытка определения морфологической и стратиграфической границы между этими подвидами. Уже предварительные морфологические наблюдения указывают, что для данной цели самое большое значение имеют следующие признаки: длина сикулы; длина дорсального апертурного отростка у метасикулы; положение апертуры первой теки относительно вершины просикулы; ширина базальной части проксимальных тек. Остальные количественные признаки имеют ничтожное значение для разграничения обоих подвидов.

Некоторая прерывистость изменчивости длины сикулы, обнаруженная для популяций из зоны *hemiaversus* и зоны *aversus* (верхняя часть Мельницких слоев), позволяет проводить границу между этими подвидами именно на этом стратиграфическом уровне.

Элементарный статистический анализ изменчивости длины сикулы доказывает, что выборка содержащая совокупность популяции из зон *parascanicus-hemiaversus* отличается статистически достоверно от такой же выборки для совокупности популяции из зон *aversus-kozlowskii*. К сожалению, обнаруженные морфологические различия и степень их перекрывания не позволяют применить „правила 75⁰/₀" для их выделения в качестве подвидов. Точно так же, существенные различия обоих популяций были найдены в положении апертуры первой теки, которая для выборки из нижних горизонтов по большей части (80.96⁰/₀) находится ниже уровня apex prosiculae (— варианты), я для выборки, взятой из верхних горизонтов — преимущественно на этом уровне или выше (64.70⁰/₀ + варианты). Для популяции из верхних горизонтов характерен также меньший дорсальный отросток метасикулы и заметно меньшая ширина основания проксимальных тек.

Анализ упомянутых количественных признаков и различия в них между популяциями из нижних и высших горизонтов позволяет более точно определить эти различия, но не дает возможности основывать на них выделение отдельных подвидов. Однако на основании таких качественных признаков, как микрофузеллярные добавки (их нет, или они очень редки в нижней части стратиграфического распространения вида, но не постоянны и часты в его верхней части), и некоторых общетеоретических моментов стратиграфического и биологического порядка, основывается выделение *B. b. tenuis* (Bouč.) как геологически более молодого, хронологического подвида, существовавшего в пределах зон *aversus* — *kozlowskii* включительно.

Принятые критерии подвидовых различий были применены для определения *B. bohemicus* (Barr.) в материале из эрратических валунов балтийского происхождения. Были выделены валуны, фаунистическая ассоциация которых указывает на зону *nilssoni* (группа „N"), зону *chimaera* (группа „Ch"), а также валуны, ассоциация которых состоит из стратиграфически мало характерных видов, либо полностью лишенные ассоциации (группа „O"). *B. bohemicus* из первых двух групп валунов по морфологическим признакам сходен с *B. bohemicus* из низких горизонтов керна Мельник-на-Буге, и, следовательно, может быть определен как *B. b. bohemicus* (Barr.). Группа „O" имеет гетерогенное происхождение. Часть валунов содержит *B. b. bohemicus*, а отсутствие ассоциации является случайным. В группе „O" однако преобладают валуны происходящие вероятно из горизонта, лежащего непосредственно выше зоны *leintwardinensis*, который характерен обеднением граптолитовой ассоциации при частом или массовом присутствии *B. bohemicus* из верхних горизонтов скважины Мельник-на-Буге, что позволяет определить его как *B. b. tenuis* (Bouč.).

Систематическая часть содержит описание 11 таксонов видового и подвидового ранга, 6 видов и 1 подвид являются новыми. Два вида принадлежат аберрантным монограптидам с длинными теками, из них 1 описан из нижнего лудлова. Остальные принадлежат Neocucullograptinae n. subfam. Описание каждого вида сопровождается анализом строения и астогенетического развития, анализом его систематического положения и статиграфического распространения.

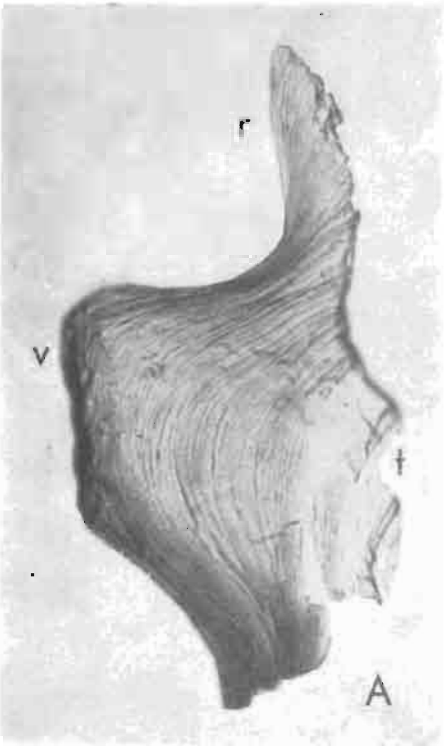
PLATES

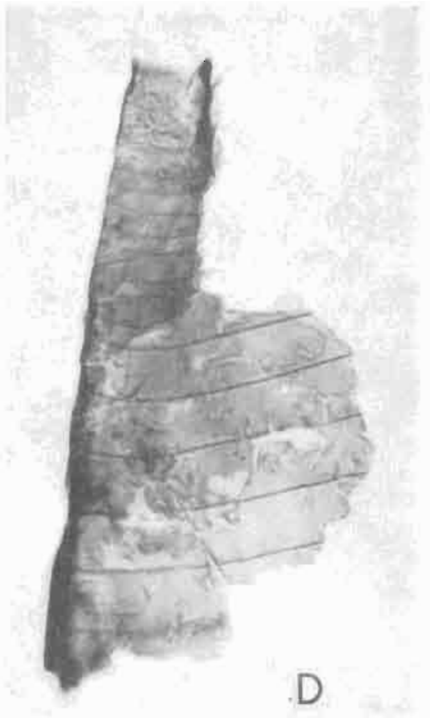
XLIV—XLV

Plate XLIV

Neocucullograptus kozlowskii n.sp., structure of microfusellar additions in distal thecae. *A—C* isolated fragments of left apertural lobe seen in transmitted light to demonstrate the microfusellar tissue proper, *D* fragment of metathecal wall made of normal fusellar tissue for comparison. All strongly bleached, needle preparations (Mielnik, depth 873,40 m, *kozlowskii* zone); ×115.

g gular process, *r* rostral process, *t* transitional zone between fusellar and microfusellar tissue with intercalary bundless of microfuselli visible, *v* ventral termination of the left apertural lobe.


r
v
t
A


D


r
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C

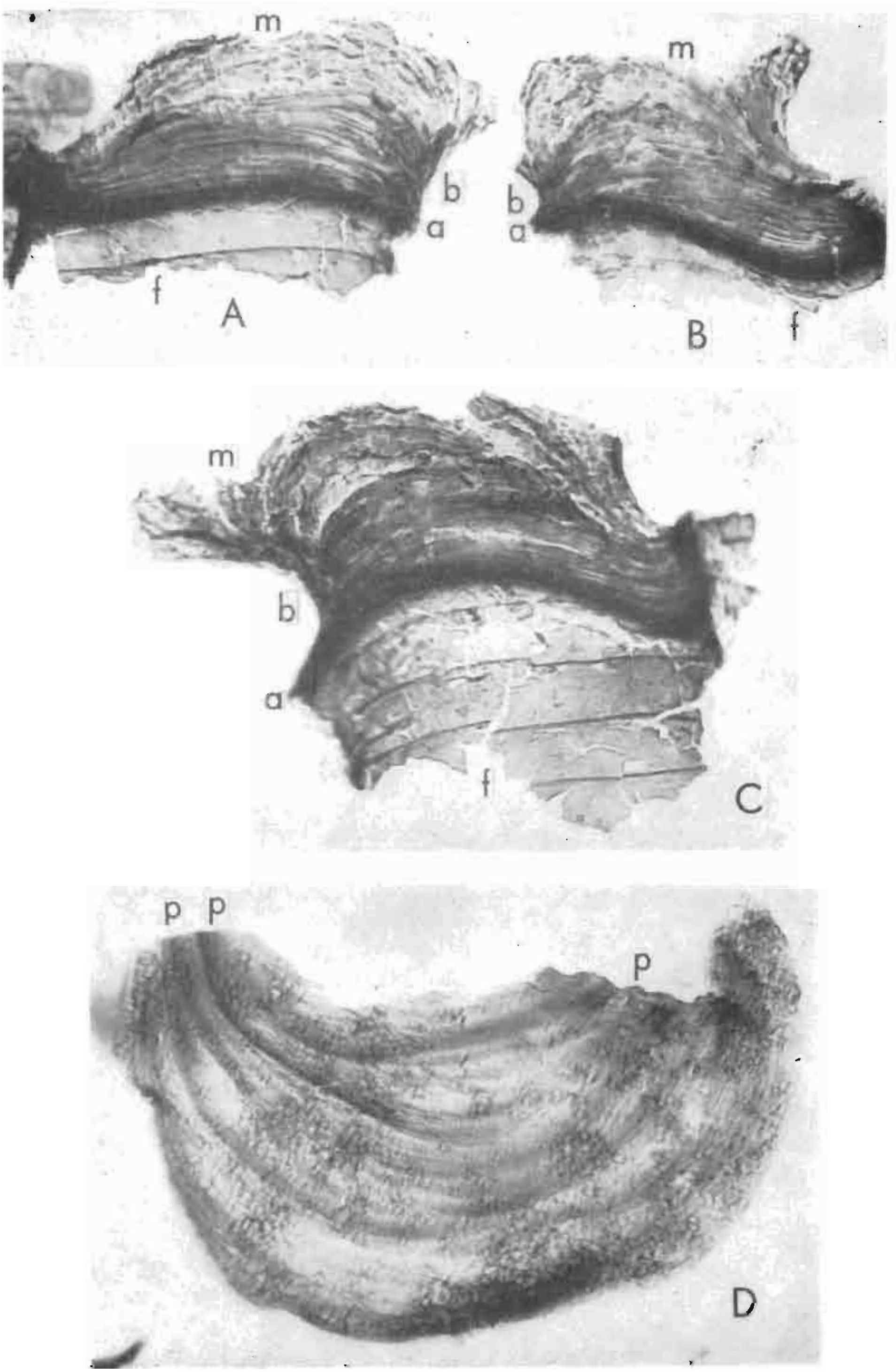
m
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Plate XLV

Bohemograptus Přib., structure of microfusellar additions in thecae. *A—C* Bohemograptus *praecornutus* n.sp., basal parts of microfusellar additions, showing its thick-walled lower part made of microfusellar tissue proper, and an outer part which consists of membranaceous pseudomicrofusellar tissue. Note a sharp contrast between fusellar and microfusellar parts of theca separated by thickened apertural margin, *D* membranaceous part of a microfusellar addition in *Bohemograptus bohemicus tenuis* (Bouč.), made of pseudomicrofusellar tissue. Note the presence of strongly pigmented bands.

All strongly bleached needle preparations (Mielnik, *A—C* depth 909.10—909.60 m, *auriculatus* zone; *D* depth 891,20 m, *auriculatus* zone); ×115.

a thickened apertural margin, *b* basal part of an addition made of microfusellar tissue proper, *f* fusellar tissue, *m* membranaceous part of an addition made of pseudomicrofusellar tissue, *p* pigmented bands seen in pseudomicrofusellar tissue.