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ON THE MORPHOLOGY AND EVOLUTION OF THE CUCULLOGRAPTINAE (MONOGRAPTIDAE, GRAPTOLITHINA)

Contents

Abstract. — A description is given of the structure, astogenetic development and evolution of the Upper Silurian Cucullograptinae. It is based on the material contained in the core samples from the Mielnik on the Bug (Eastern Poland) deep-boring and from the Baltic drift. The graptolites were prepared by dissolving the limestone and marly matrix in hydrochloric acid. For detailed study the specimens were bleached. The stratigraphic position and significance of the fauna investigated are discussed. The main trend in the evolution of sicula consists in its simplification and is interpreted as due to foetalization. In contrast with sicula, the evolution of thecae displays progressive changes which primarily consist in the development of apertural apparatus, connected, in most lines, with the elaboration of its secondary asymmetry. The biological significance of this pattern of evolution of thecal characters is discussed. The Cucullograptinae supply convincing evidence for the distal introduction of phylogenetic novelties which makes up a prevailing mode of evolutionary changes of astogeny in this group of monograptids. Problems, related to the mechanisms of evolution and organization of graptolite colonies are discussed. Using the data, now available, tentative phylogenetic relationships within the group are established. An attempt is made to show some implications of these data in the problem of origin of the Cucullograptinae. Fourteen representatives (species and subspecies) of the Cucullograptinae are described in the systematic part. Four species and two subspecies are new.

INTRODUCTION

A detailed study of the structure and astogenetic development of the representatives of the subfamily Cucullograptinae Urbanek, 1958 (Monograptidae, Graptolithina), as well as an explanation of their evolution and stratigraphic importance constitute the aim of the present work.

Despite the fact that the representatives of this subfamily have recently been subject to frequent studies (Eisenack, 1942; Bulman, 1953; Walker, 1953; Urbanek, 1954, 1958, 1960; Kühne, 1955) not all of the problems, related to this interesting group of the Upper Silurian monograptids have exhaustively been explained.

In 1960, the accumulation of a new material, coming, in part, from the Baltic erratic boulders but chiefly that, prepared from the Mielnik on the Bug boring core which, to a considerable extent, supplemented the family tree of the Cucullograptinae and threw a new light on several related problems, has induced the present writer to investigate this group once more and in a yet more exhaustive manner.

The idea of the present monograph may be summarized in the following four items: 1) a detailed investigation of the structure of the thecae and the development of the colony, carried out on the basis of adequately bleached microscopic preparations with particular consideration of the fusellar structure; 2) a comparison of the structure of different representatives with the application of the comparative-anatomical methods; 3) a determination of the main evolutionary trends and of the character of morphological changes which took place in particular phyletic lineages; 4) an investigation of stratigraphic ranges so as to be able to determine the significance of the Cucullograptinae as index fossils.

The fact that the remains of the Cucullograptinae might be etched from the rock by chemical methods was an especially important factor in the studies on their evolution. Thus isolated specimens allowed one to study several anatomical characters, otherwise inaccessible to observation by standard methods of investigation usually applied to the graptolite remains preserved on the rock surface. To obtain transparent preparations, enabling one to examine the fusellar structure of thecae and, in particular, the fusellar structure of the apertural apparatus, the present author bleached the isolated specimens. A detailed analysis of the fusellar structure is one of the main methods, applied to the present work.

In solving all these problems, the present writer aimed, in a consistent way, at the integration of all data, based on the studies of the forms from the drift material, with those obtained from the boring at Mielnik on the Bug (Eastern Poland). The latter data constituted the main basis for concluding on the evolution and stratigraphic occurrence. The material, coming from the Baltic boulders served mostly for the investigation of the morphology and astogeny of particular species.

The results of the studies on the following representatives of the Cucullograptinae are discussed in the present work:

Genus *Lobograptus* Urbanek, 1958
Lobograptus progenitor n. sp.
Lobograptus simplex Urbanek, 1960
Lobograptus exspectatus exspectatus Urbanek, 1960
Lobograptus exspectatus bicornis n. subsp.
Lobograptus scanicus parascanicus (Kühne, 1955)
Lobograptus scanicus amphirostris n. subsp.
Lobograptus scanicus scanicus (Tullberg, 1883) sensu Bulman, 1953
Lobograptus imitator n. sp.[1]
Lobograptus invertus n. sp.[1]
Lobograptus cirrifer n. sp.[1]
Genus *Cucullograptus* Urbanek, 1954
Cucullograptus hemiaversus Urbanek, 1960,
Cucullograptus aversus cf. *aversus* (Eisenack, 1942)
Cucullograptus aversus rostratus Urbanek, 1960
Cucullograptus pazdroi Urbanek, 1954

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[1] Thus marked forms are known only from the boring at Mielnik on the Bug.

ACKNOWLEDGEMENTS

In preparing the present monograph, I availed myself of much good advice, indications and stimulating suggestions, offered — during many discussions — by Professor Roman Kozłowski (Warszawa, Poland) to whom I would like to express my warmest gratitude.

My thanks are due to Professor E. Rühle, Director of the Geological Institute in Warsaw, for his consent to supply valuable materials from the Mielnik I. G. 1 bore-hole for the scientific elaboration and to Dr. H. Tomczyk from this Institute, as well as to his wife, Dr. E. Tomczyk for a friendly cooperation and aid afforded during sampling and a subsequent elaboration of the material.

My gratitude is also extended to Professor Z. Kielan-Jaworowska, Director of the Palaeozoological Institute of the Polish Academy of Sciences (Warsaw), for a friendly help and a kind assent to the technical assistance given to the present author by her scientific-technical staff. I feel particularly indebted to Mrs. K. Budzyńska and to Mrs. E. Gadomska for a careful inking of my pencil drawings, to Mrs. J. Skarżyńska and Mr. W. Skarżyński for a technical aid in the preparation of the material, as well as to Miss M. Czarnocka 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 prepared and, discussing it with the writer, offered their advice and suggestions. First of all, Professor O. M. B. Bulman (Cambridge, England), Dr. R. Thorsteinsson (Ottawa, Canada), Professor H. Whittington (Cambridge, U.S.A.), as well as Dr. S. Willefert (Rabat, Morocco), Dr. H. Jaeger (Berlin, the German Democratic Republic), Dr. B. Rickards (Cambridge, England) and Professor A. M. Obut (Novosibirsk, U.S.S.R.) are among them.

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GENERAL PART

ORIGIN OF THE MATERIAL

The material of the Cucullograptinae, studied in the present monograph, comes from: 1) the core of a deep boring at Mielnik on the Bug (Eastern Poland), drilled by the staff of the Laboratory of Iron Ore Depo-

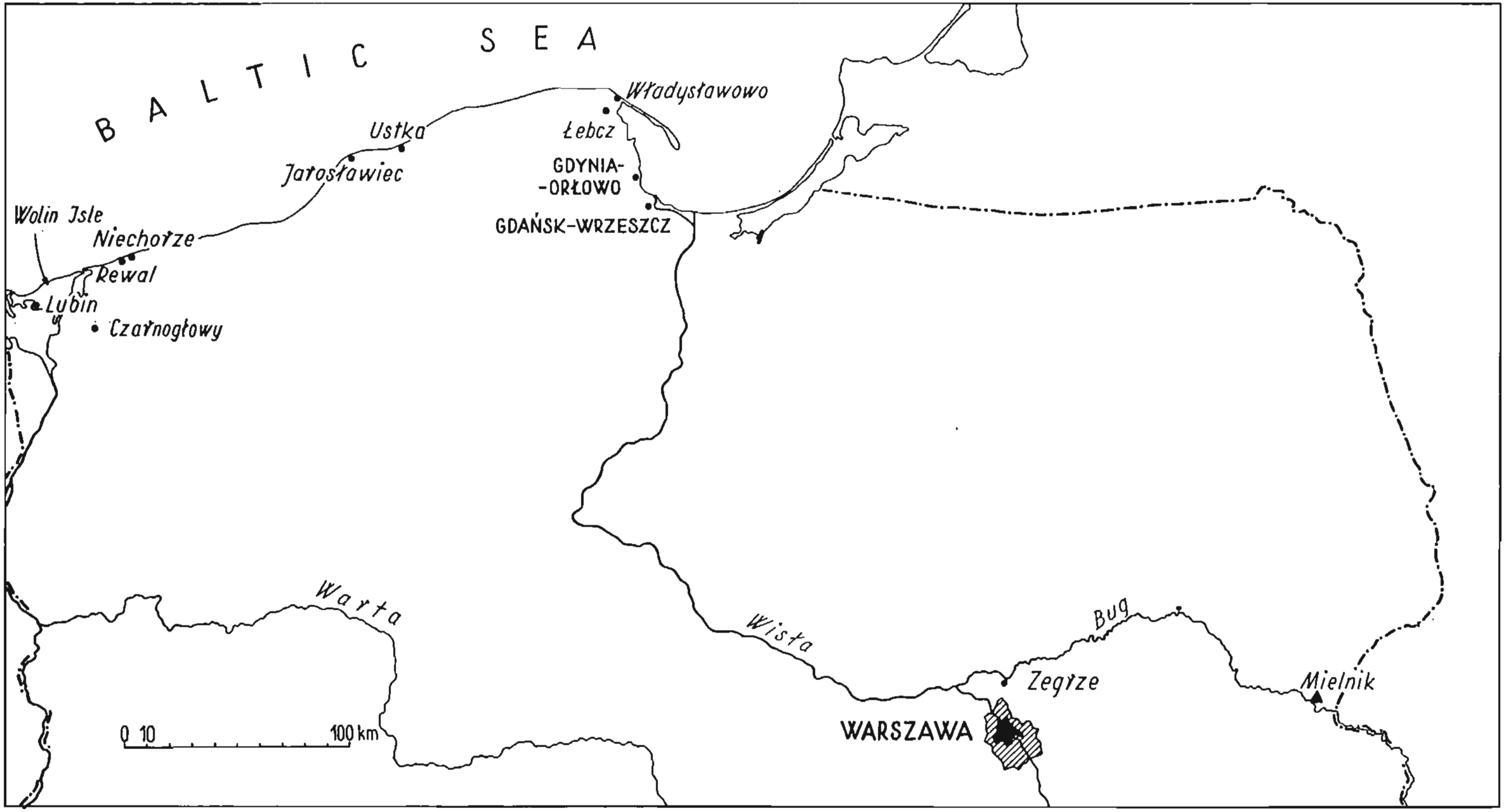

Fig. 1. — Sketch-map of Northern Poland showing: 1) localities where described erratic boulders were collected (black drops) and 2) situation of deep boring in Mielnik on the Bug River (black triangle)

sits of the Geological Institute in Warsaw, and 2) the Silurian erratic boulders of the Baltic origin, collected on Pomeranian seaside beaches and in the outcrops of the Quaternary moraines in Central Poland (Fig. 1).

Silurian deposits from the Mielnik on the Bug boring

Mielnik on the Bug (the map sheet of Biała Podlaska, scale 1:300,000) is situated in the north-western part of Polish Lowland in the platformian area, contained within the Podlasie depression (syneclize) which extends to the east, passing (in White Russia) into the Brześć syneclize (Pożaryski, 1963). This depression is one of the structural units, formed as a result of a subsidence of the crystalline substratum of the east-European platform and filled with the Cambro-Silurian deposits of a considerable thickness. In the north, the Podlasie depression borders on the Masuria-Suwałki elevation (anteclize) which makes up a western part of the White Russian anteclize. This anteclize constitutes an elevation unit (a dome, or similar positive area), marked by the predominance of the denudative processes and the lack of the Cambrian, Ordovician and Silurian deposits.

Mielnik on the Bug is situated within the marginal zone of the Podlasie depression, adjoining the Masuria-Suwałki elevation. In this zone, the Ordovician and Silurian deposits are near-shore or shallow-neritic in character (Tomczyk, 1958) and consist mostly of the calcareous and marly rocks. Within this marginal zone a regular change is also observed in the lithological character of the Silurian deposits which, in the easternmost (Krzyże boring) part of this area, is composed of calcareous sediments typical of shallow waters and, further to the west (Mielnik on the Bug boring), acquire a mixed character of marly-calcareous sediments and, to a considerable extent, mudstones. In the Żebrak boring, situated further to the west, the Silurian is developed in the form of mudstones, while marly rocks and calcareous intercalations are less developed. Thus, from marginal to central parts of the Podlasie depression, we may observe a deepening of the Silurian basin which is manifested by the change in character and increase in the thickness of its sediments. Presumably, therefore, a neritic zone extended around the Masuria-Suwałki elevation with deeper facies situated west of it. The Silurian deposits of the Mielnik boring were formed more or less in the center of the neritic zone of this basin.

The Silurian sediments, occurring in the Mielnik on the Bug borehole, have preliminarily been investigated by E. Tomczyk and H. Tomczyk of the Geological Institute in Warsaw. The results of these investigations have only in part been published (H. Tomczyk, 1962, 1964) and the rest of them, elaborated in the form of an appropriate report, have in 1963 been handed over to the archives of the Geological Institute. According to the authors mentioned above, these sediments, underlaying the Zechstein conglomerate, occur at the depths of from 583·5 m to 1,120 m, reaching about 536·5 m in thickness. With regard to stratigraphy, they include the upper part of the so-called Pasłęk Beds (corresponding to the Wenlockian), which in the Mielnik on the Bug borehole begins with the *Cyrtograptus murchisoni* zone, the so-called Mielnik Beds, Siedlce Beds, and finally the Podlasie Beds, probably their lower part only[2]. Mielnik Beds generally correspond to Lower Ludlovian (Eltonian + Bringewoodian + Leintwardinian, comp. Holland, Lawson, Walmsley, 1963), as well as to the lower part of the Kopanina Beds in Barrandian (Horný, 1962). Siedlce Beds, according to H. Tomczyk (1962) concept, include a series of sediments between the *Saetograptus leintwardinensis* zone (exclusive) and horizon with "*Monograptus*" *formosus* (inclusive) and approximately correspond to the upper part of Kopanina Beds in Barrandian. In the Mielnik boring, however, "*M.*" cf. *formosus* appears almost simultaneously with "*Pristiograptus*" *ultimus*, which is considered in Bohemia as the index fossil for the lowermost part of higher series (Přidoli Beds). Podlasie Beds, i.e. their lower part only, correspond generally to the lower part of Přidoli Beds in Bohemia, although some equivalents of Polish development may be lacking in Barrandian (comp. also H. Tomczyk, 1962, English summary, pp. 119—120, and Table 12 in Polish text).

The upper part of the Silurian series in the Mielnik boring is marked (H. Tomczyk, 1962; E. Tomczyk & H. Tomczyk, an unpublished archival report of the Geological Institute, 1963) by the occurrence of *Calymene beyeri* R. & E. Richter, of "*Pristiograptus*" *ultimus* (Perner) and of the layers, containing *Dayia* cf. *navicula* (Sow.). This identification is only preliminary and, on the basis of the investigation of this core by a chemical treatment, the occurrence has recently been stated of a rich assemblage of graptolites, situated above the layers, containing "*Monograptus*" cf. *formosus* Bouček and "*Pristiograptus*" *ultimus* (Perner). This fauna will soon allow one to state more precisely the stratigraphy of the part of the Podlasie Beds which occurs in the core of the Mielnik on the Bug boring.

The Silurian of Mielnik is developed in the form of a series of the marly-carbonate and mudstone sediments. The occurrence of many intercalations, lenses and calcareous nodules, different in size and thickness, is characteristic of the entire series, mentioned above in which they are so frequent that some of them are usually recorded on a stretch of one running meter of the core. However, some horizons are marked by the

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[2] For the stratigraphic terminology of the Silurian in Poland — comp. H. Tomczyk (1962, pp. 112—117, English summary; 1964).

presence of especially numerous and considerably thick calcareous and marly intercalations. Likewise, in definite layers, mudstones may abound in the tuffogenic material admixtures which, sometimes, pass into the tuffite intercalations (in particular, in the Siedlce Beds). Both the mudstones and marly-carbonate deposits display a different degree of lamination or layering but they are usually devoid of foliation.

The occurrence of a mixed biofacies at Mielnik was caused by the lithological character of the Silurian deposits. In addition to numerous graptolites, particularly frequent in mudstones and marly rocks, trilobites, and brachiopods, as well as, in smaller numbers, cephalopods, crinoids, pelecypods and gastropods are recorded in those strata. The presence of Eurypterida, Hydrozoa (few) and Polychaeta (scolecodonts) have been indicated by residua, obtained by the dissolution of the rock samples. In calcareous, in particular, thicker intercalations, graptolites become rather rare and their occurrence is mostly restricted to the outer marly-calcareous parts, adjoining massive layers of purer calcium carbonate.

The entire series of the Silurian sediments at Mielnik is horizontal and does not seem to be affected by the tectonic movements. It overlays the Ordovician (1,120 to 1,178 m deep) and Cambrian (below 1,178 m, also horizontal) deposits. The character of the Silurian deposits at Mielnik and the faunistic assemblage which occurs in them allow one to admit that, according to H. Tomczyk's (unpublished archival data) supposition, they were formed in a shallow-neritic or near-shore zone. The Silurian at Mielnik on the Bug is a classical example of a platformian, unfolded formation whose sediments were deposited in a relatively shallow and near-shore zone.

The section of the boring core from Mielnik in which the graptolite remains were found, assigned to the subfamily Cucullograptinae Urbanek, has been accurately examined in the present monograph. This section is contained within limits of 1,035 m (the first appearance of *Lobograptus progenitor* n.sp.) and 920·8 m (the last appearance of *Cucullograptus aversus rostratus* Urbanek) and is, therefore, 114·2 m. in thickness. Stratigraphically it corresponds to the upper part of the so-called Mielnik Beds and to the lowermost horizons of a younger series, the so-called Siedlce Beds. The conventional and provisional boundary between the last named two series has been drawn by E. Tomczyk and H. Tomczyk at a depth of 932 m[3].

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[3] After a more detailed examination of the graptolite sequence, situated between the Mielnik and Siedlce Beds, this boundary should be determined in a more precise manner. Generally speaking, there are two alternatives of drawing this boundary: 1) in the top of the zone of the *Saetograptus leintwardinensis* horizon or, 2) in the base of a horizon, marked by the appearance of one of the new species that does not occur in the Mielnik Beds. In the latter case, the boundary would run above the stratigraphic boundary accepted so far.

The examined series of sediments consists of silts and mudstones which, now and then, contain the tuffogenic material, as well as of marls and limestones. The latter form intercalations, lenses and nodules which are densely distributed and separated from each other by 5—6 to 40—50 cm thick layers of silts and mudstones. The lower part of this series (1,035—990·9 m) is marked by a certain predominance of silts and, partially, marly sediments, while the calcareous lenses and nodules are relatively rare and, sometimes, only occasional. The amount of the tuffogenic material is smaller than that in the upper part of the series investigated.

The upper part of this series (920·8—990·9 m) is more calcareous. In addition to silts and mudstones, there are many marly and even calcareous lenses and intercalations. The tuffogenic material is more frequent particularly in the uppermost part of the Mielnik Beds (932—946 m) and in the lowermost part of the Siedlce Beds (920·8—932 m).

The marly and calcareous intercalations, as well as concretional sediments consisting of them, display a pronounced lithological similarity to the graptolitiferous calcareous erratic boulders of the Baltic origin. It should be assumed, therefore, that the latter were formed under similar facial conditions. Remelé's (1883) suggestion that erratic boulders of the type of "Graptolithengestein" come probably from calcareous concretions and intercalations, which primarily were deposited within more shaly series, seems therefore to be well grounded.

Silurian erratic boulders of the Baltic origin

The Silurian erratic boulders of the Baltic origin which contain the graptolite remains are called, in German literature, "Graptolithengestein". These are mostly gray or bluish-greenish marls or marly limestones and, less frequently, pure limestones in which the graptolite remains are accompanied by a shelly fauna (crinoids, trilobites, brachiopods, Cardiola).

They occur on the area of the Central European Lowland from the western boundary of Lithuania to the Netherlands. In Poland, they are rare in the eastern part of their distribution area (Masuria) although, according to German authors' data, they are still met with in the western part of the Sambia Peninsula (Eisenack, 1942, p. 34). Occasionally, they also occur as far inland as the Masovia Region (the vicinities of Zegrze and Zakroczym, north of Warsaw) and near Poznań. It is only on the territory of Pomerania, west of Gdańsk, that they occur more frequently. They are particularly numerous in the morainic deposits of the Baltic coast in Western Pomerania from Ustka to the Wolin Island. According to Martinsson (1963, p. 4), the number of the graptolitiferous Silurian boulders in the morainic deposits increases westwards. This confirms the opinion of F. Roemer (1884—1885, p. 132) who believes that they are most frequent on the area between the Odra and the Elbe rivers. A particularly abundant occurrence of these boulders on the Rügen Island and in the vicinities of Berlin (Kühne, 1955; Jaeger, 1959) is in a full conformity with these views. The morainic deposits which contain the graptolitiferous Silurian erratic boulders may reach far to the south from the Baltic coast. This is shown by their occurrence in Lower Silesia (Mokrzeszów, Sudeten) where they are met with rather frequently.

These boulders occur in the Quaternary moraines, the most abundant being in the West Pomeranian moraines, situated more or less west of Ustka. The majority of the Silurian erratic boulders, examined by the present author, which were collected mainly on the coastal beaches in the areas of a high shore (cliff), built of a boulder clay of a considerable thickness (e.g. at Niechorze-Rewal), come from the latter region. So far, there were no detailed investigations to establish with which glaciation the most abundant occurrence of the Silurian erratic boulders is connected. However, with regard to the material, coming from Western Pomerania, it may be assumed that these boulders are mostly connected with the sediments of the last glaciation (the Baltic glaciation). According to the opinion of the Quaternary geologists, older morainic deposits are situated in this region below the sea level (oral information of Dr. K. Kopczyńska-Żandarska and Dr. Z. Lamparski from the Quaternary Geology Department of the Warsaw University). It seems to be beyond any doubt that the erratic boulders, accumulated in some places in the form of a "cobble", come mainly from the washed and destroyed morainic deposits that form a "high shore", are situated above the present sea level and may only in part derive from submerged moraines of older age. They constitute, therefore, a heterogeneous assemblage, with a probable prevalence of the material from the Baltic glaciation[4].

It has been well-known for a long time now that graptolites, contained in the Silurian erratic boulders of the Baltic origin, are stratigraphically heterogenous. Generally speaking, most boulders indicate the Lower Ludlovian age of the original matrix and make up a stratigraphic equivalent of the Mielnik Beds in the platformian Silurian of Poland. The Cucullograptinae, related to a higher part of the Lower Ludlovian horizons, occur, therefore, in many examined erratic boulders. The stratigraphic range of the graptolite assemblages in the Silurian erratic boulders is, however, much more extensive. Its lower limit is determined by the occurrence, in some boulders, of *Monograptus priodon* (Bronn) (Urbanek, 1958) and *Retiolites geinitzianus* Barrande

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[4] As to the boulders that come from the sites, located south of the Baltic coast, they may of course come and they probably do come mostly from older glaciations.

(Roemer, 1884—1885, p. 118; Kühne, 1953), which sometimes occur separately, and sometimes are associated with each other. The presence of *Monograptus priodon* may determine this limit as the Upper Llandoverian or Lower Wenlockian, while the occurrence of *Retiolites geinitzianus* — as the Upper Llandoverian or lowermost Wenlockian.

The determination of the upper limit of the range of the graptolite assemblages in the erratic material of the Baltic origin is somewhat more difficult. Until recently, it was supposed that although they exceed the level of the *scanicus* zone, as it was commonly understood, they do not reach higher than the level of *Saetograptus leintwardinensis* (Hopk.). However, the occurrence of *Cucullograptus aversus rostratus* Urbanek in the erratic boulders in a characteristically poor association (devoid of saetograptids) indicates that the stratigraphic range of this fauna extends also to the levels directly overlying the *S. leintwardinensis* zone and, therefore, it also includes the equivalents of the lowermost Siedlce Beds in the Polish Lowland. A still younger age of the upper limit of the graptolite assemblages from the Silurian erratic boulders may be indicated by the assemblages, consisting of abundant *"Pristiograptus" bohemicus* (Barrande), associated with *Pristiograptus* ex grege *dubius* (Suess) and, therefore, without cucullograptids and saetograptids. Such assemblages are very characteristic of the lower part of the Siedlce Beds in the platformian Silurian of Poland. These layers are marked by the abundant occurrence of "*P.*" *bohemicus* and related species with a simultaneous scarcity of other graptolite fauna. The possibility cannot be excluded that the erratic boulders, containing similar assemblages, are not of the Lower Ludlovian age as they have so far been believed to be but that they are much younger.

The problem of the origin of the Silurian erratic boulders has already been discussed by Roemer (1884—1885, p. 132) who was of the opinion that they come from "ein jetzt vom Meere bedektes Gebiet zwischen der Insel Oesel, der Insel Gotland und Schonen". The following facts were used by Roemer to justify his views: 1) in the North European countries, the outcropping Silurian rocks which lithologically (and, at the same time, stratigraphically and faunally) fully correspond to the erratic boulders, are unknown; 2) these boulders occur most frequently on the area, situated between the Odra and the Elbe rivers which would indicate the fact that they come directly from the bottom of part of the Baltic Sea which adjoins this area (i.e. from the region between the Bornholm and Gotland islands).

During the later period, the problem of the origin of erratic boulders was not very extensively dealt with by the investigators of their graptolite fauna. More extensive studies by older authors (Remelé, 1883; Jaekel, 1889; Stolley, 1895) have a mostly historical significance for the problem in question. A few remarks were published by, among other authors, Hucke (1917) and Kraft (1926). Urbanek (1958, p. 2) has expressed the assumption that, in addition to the Baltic Sea bottom, the Upper Silurian "Cardiolaskiffer" series in Scania and on the Gotland Island might also be a source of the erratic boulders. A similar assumption, applied only to Scania has also been expressed by Jaeger (1959). On the basis of a closer study of the Silurian sections in Scania, the present author has, however, concluded that, lithologically, these deposits differ fairly distinctly from the lithological type of the Silurian erratic boulders since the former mostly consist of clayey shales with a small number of marly and calcareous intercalations which, moreover, considerably depart from the lithological type of marly erratic limestones. At present, it seems to be less likely that the Silurian series, outcropping in Scania might be a source of the drift material.

A similar conclusion, applied to the Silurian series, outcropped on the Gotland Island, has been reached by Martinsson (1962, p. 540) who, despite the fact that the graptolite sequence of the Gotland Island and the drift material coincide with each other to a considerable extent, holds that "abundantly graptolitiferous and more shaly facies of beds of this age is foreign to the exposures of Gotland". Since the argillaceous sediment content increases south-westwards from the Gotland coast, Martinsson believes that "the source of the Graptolithengestein can nowhere be indicated more plausibly than in the SW continuation of the (Upper Wenlockian —) Ludlovian of Gotland (1962, p. 540). Considering the morphology of the Baltic Sea bottom, Martinsson has set up the interesting hypothesis that "areas around the North-Mid-Sea Bank are probably the place of origin of the Graptolithengestein" (1963, p. 9). He based his conclusion on the reconstruction of the morphology of the Palaeozoic series on the Baltic Sea bottom. In the light of Martinsson's recent investigations most erratic material seems to come from the Silurian series which presently cover the Baltic Sea bottom and, therefore, these boulders are called by the present writer by a general name of "a drift material of the Baltic origin".

The distribution of the sites which the erratic boulders, described in the present paper, come from is shown in a map (Fig. 1, p. 295).

INVESTIGATION METHODS

The dissolution of marly or calcareous rock samples in acids was a fundamental method used in the present work. According to standard methods of etching graptolite remains, mostly the hydrochloric and, less frequently, acetic acids were used for this purpose. It was only in very few cases that the hydrofluoric acid was applied to etch the remains from mudstones. Sometimes, this acid, or the HN_3+HCl mixture, were used to clean the specimens of sediment grains (arenaceous or argillaceous remainder) adhering to the periderm.

The samples from the Mielnik boring were mostly taken from marly or calcareous intercalations where graptolites are best preserved. It was only of necessity that, sometimes, the material was also sampled from mudstones and silts. Undoubtedly, such a manner of sampling caused definite distortions of quantitative ratios and of a picture of the fauna (bias sampling) but, for technical reasons, it was the most adequate method which allowed one to obtain a maximum number of well-preserved specimens and, at the same time, to save the acid and laboratory operations. On account of an abundant occurrence of intercalations, 1—3 samples were taken per one running metre of the core (the samples were 3—10 cm thick with the core diameter varying within limits of 120 mm in the upper part of the core section examined and 80—90 mm in the lower part). Depths were determined approximately, but any possible errors did not seem to exceed 30 cm.

The remains, obtained as a result of dissolution, were — together with the silty residue — washed and, hereafter, fragments of thecae and rhabdosomes were picked out by means of a pipette and put into the Petri dishes, filled with glycerine. Selected specimens were kept in glycerine in the Petri dishes 100 mm in diameter. The material, intended for detailed studies, was put into smaller vessels, made of a transparent polystyrene, approx. 35 mm in diameter and provided with airtight lids.

The specimens, destined for a detailed anatomical examination, were, prior to these tests, bleached in a mixture of potassium chlorate, nitric acid and water. Bleaching was carried out in thin glass tubes approx. 12 mm in diameter and to 45 mm high and corked up in such a manner as to leave a certain leakage (to facilitate a slow escape of Cl). The polystyrene vessels, mentioned above, were also used for bleaching. After a 10—15 hour bath, the specimens were washed in water to remove the remnants of acid and chlorine and once more put into glycerine. Studies of the internal structure of the apertural apparatus and interthecal septa were carried out by means of needle preparations. In order to exhibit certain internal details, particular fragments of periderm were removed or destroyed by means of a minute needle. In the case of *Cucullograptus pazdroi,* thin microtome sections of specimens, embedded in paraffine, were used to show details of internal structure of the apertural part of a theca.

Detailed observations were made and figures drawn by means of stereoscopic microscopes. Original drawings were linearly magnified about 150, 210 and 300 times and, for the purposes of reproduction, appropriately reduced. Few photographs of specimens, embedded in the rock surface were taken by the "Standard" type camera.

Measurements were taken by means of the "Lumipan" microscope and with the application of a properly graduated micrometre gauge or by drawing the measured sections in a proper scale.

The specimens, described and illustrated in the present paper are preserved in the writer's collections at the Palaeozoological Department of the Warsaw University (Żwirki i Wigury 6, Warszawa) and marked with successive numbers of plates and figures on which they are shown. Several specimens, particularly brittle and fragile, were damaged and, some of them, even destroyed when handled during or after drawing. Some specimens fell to pieces when not being handled at all. After bleaching, the flattened specimens displayed a strong tendency to twist or roll up which was probably caused by the tension of the periderm surface, following the oxidation of its outer layer. This process may bring about a considerable deformation of such specimens and, consequently decrease their suitability to further studies and observations. None the less, bleaching (and mostly strong one) was necessary for the investigation of the fine structure of thecae.

The destroyed specimens have been replaced in the collection by other ones, taken from similar stratigraphic horizons, which may 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, applied to the present work, is mostly modelled after a standard terminology collected by Bulman (1955). The present author's terminology is, to a certain extent, supplemented with some terms, suggested by Jaanusson (1960) (such expressions as a *geniculation,* and abbreviations as *tr.* and *long.* to denote the transverse and parallel directions in relation to the long axis of thecae and rhabdosome). With regard to the evolution of astogeny, the concepts and terms, previously introduced by the present author (Urbanek 1960, 1963), such as *expressivity, penetrance, distal and proximal introduction of phylogenetic novelties* etc., are used in the present paper. The anatomical terms are patterned after those, used before (Urbanek, 1958). However, the necessity occurred to introduce certain new terms, denoting special structures, recently found in Cucullograptinae. These terms are given below together with a brief explanation of their meaning.

The measurements of length also require a certain discussion. The numbers, representing the entire length of thecae do not comprise (unless otherwise stated) the height (*long.*) of apertural lobes. This was considered advisable because of a better comparability of these data with the species having different degree of the development of the apertural apparatus or those devoid of apertural lobes. The entire length of the sicula which does not comprise the dorsal process and the virgella, is measured from the prosicular apex to the lateral margins of the metasicular aperture.

New terms introduced or redefined

Adapertural plate — portion of apertural lobe, fused to ventral (ventral a.p.) or dorsal (dorsal a.p.) wall of theca (e.g. in the left lobe of *L. scanicus scanicus* and right lobe in *L. invertus* n.sp.).

Apertural apparatus — all derivatives of apertural segment of metatheca (comp. Urbanek 1960, p. 146) which may consist of apertural lobe (or lobes), rostral processes, gorget, gular plate and apertural lip.

Apertural elevations — incipient form of apertural lobes constituting slightly raised lateral parts of apertural margin.

Apertural incision — notch, formed on free margin of partly reduced right apertural lobe in *C. hemiaversus*, notchlike embayments in ventrobasal part of apertural lobes (e.g. in *L. scanicus amphirostris* n. subsp. and in the left lobe of *L. invertus* n.sp.).

Apertural lip — extroverted margin of aperture (e.g. in *L. invertus* n. sp. and *L. exspectatus*), or extroverted margin of partly reduced (in *C. hemiaversus*) or vestigial apertural lobe (in *C. aversus rostratus*).

Beak, beaklike process, beaklike prolongation — more or less pronounced outgrowth formed on ventral margin of apertural lobe.

Gorget — superstructure on the lateral margin of apertural lobe in *C. aversus rostratus* and forming there a collarlike prolongation which consists mainly of narrow fusellar strips. Name introduced in analogy to "gorget" being "a piece of armour defending the throat..., a kind of covering for the neck and breast worn by women" (Webster's Int. Dictionary, 1951, p. 1081).

Gracilization — process of becoming more gracile, slender and smaller. New created term, used here to describe the transformation from more robust into more gracile siculae and thecae.

Gular plate — (after Lat. *gula* — the throat) incurved portion of apertural lobe in *C. aversus rostratus*, producing a shovellike process which surrounds the ventral termination of the lobe from the ventral and lateral side.

L-cucullograptids — cucullograptids with asymmetric apertural apparatus due to hypertrophy of the left apertural lobe.

Microfusellar tissue, m. structure — structure of peridermal derivatives consisting of very narrow and densely crowded stripes (micro-fuselli), as in apertural lobes in *Monoclimacis micropoma*, described by Urbanek (1958, p. 93, fig. 68). Gorget in *Cuc. aversus rostratus* consists of tissue similar to microfusellar, see also p. 322.

Pectoral crest — narrow, spindlelike peridermal plate, fused with the ventral wall of theca and shifted somewhat asymmetrically to the obverse side (in *C. aversus rostratus).*

R-cucullograptids — cucullograptids with asymmetric apertural apparatus due to hypertrophy of the right apertural lobe.

S-cucullograptids — cucullograptids provided with bilaterally symmetric apertural apparatus.

Subapertural thickening — horseshoe shaped external swelling of periderm situated occasionally on the ventral wall of theca beneath the apertural margin (in *L. progenitor* n.sp.).

Terminations of the apertural lobe — structures formed at the ventral and dorsal ends of the apertural lobe (adapertural plate, beak).

Remark: The term *overlap* is used here to describe: 1) the mutual overlap of adjacent thecae (thecal overlap), or 2) the overlap ("overthrust") of apertural lobes.

STRATIGRAPHIC POSITION OF THE FAUNA INVESTIGATED

Stratigraphic occurrence of the investigated graptolites from the Mielnik boring

The following stratigraphic sequence, resulting from the appearance order of particular species, has been established on the basis of the particular Cucullograptinae species, found in the investigated series from the Mielnik boring, contained between depths 1,035 and 920.8 m: 1,035 m — *Lobograptus progenitor* n.sp.; 1,020.9 m — *L. simplex* Urbanek; 1,016.9 m — *L. scanicus parascanicus* (Kühne); 1,009.9 m — *L. exspectatus exspectatus* Urbanek and *L. scanicus amphirostris* n. subsp., appearing in the same layer, although it is quite possible that the former occurs even as deep as 1,015.9 m; 1,002.5 m — *Cucullograptus pazdroi* Urbanek; 988.9 m — *Lobograptus scanicus scanicus* (Tullberg) sensu Bulman; 986.9 m — *L. imitator* n.sp.; 966.85 m — *L. invertus* n. sp.; 960 m — *Cucullograptus hemiaversus* Urbanek; 952.9 m — *Lobograptus exspectatus bicornis* n. subsp.; 941 m — *L. cirrifer* n. sp.; 940.5 m — *Cucullograptus aversus* cf. *aversus* (Eisenack); 934.7 m — *Cuc. aversus rostratus* Urbanek (see Pl. I).

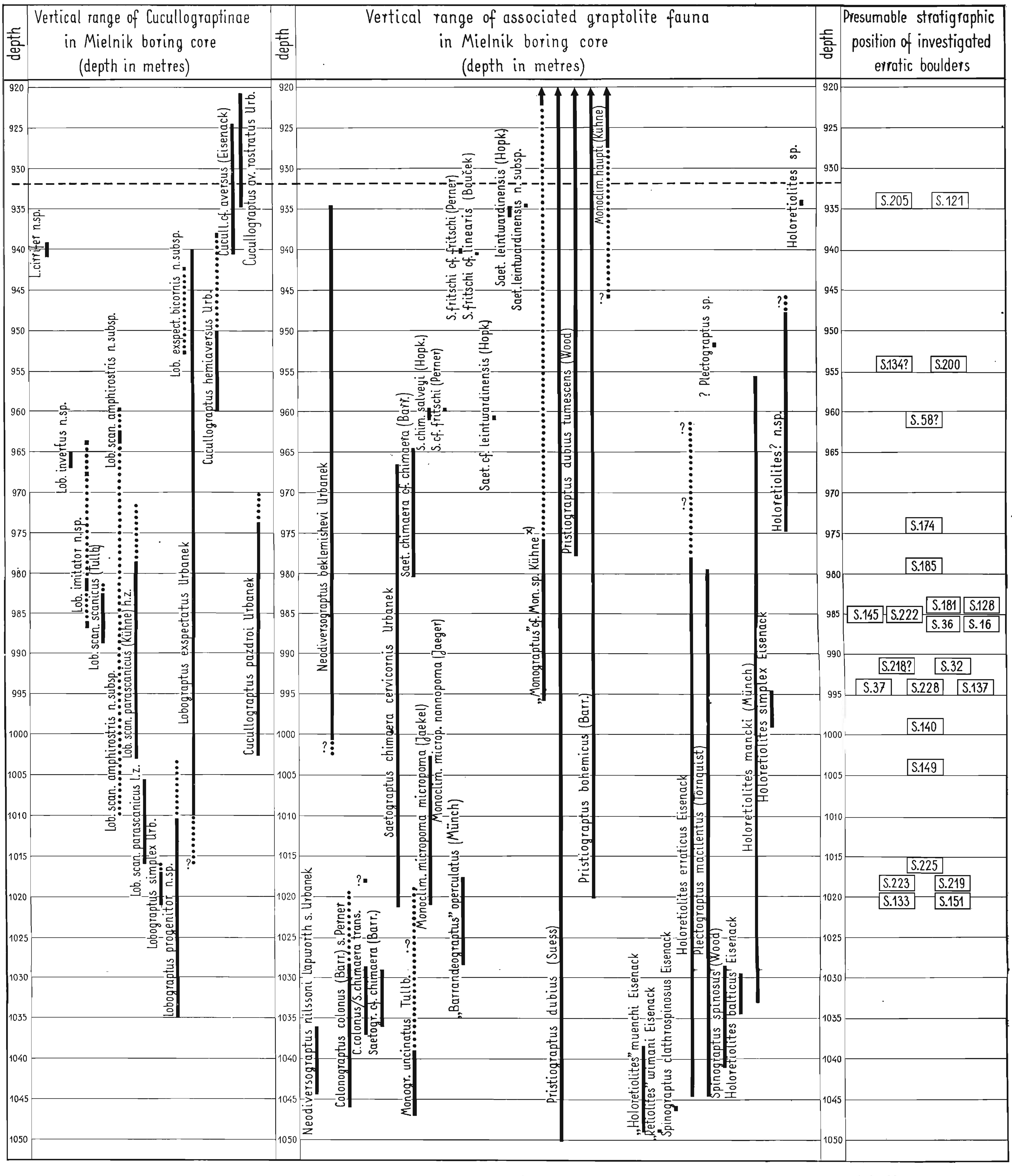
A part of this sequence may be considered an equivalent of the *scanicus* zone as it has so far been understood. This zone is marked by the occurrence of particular subspecies of *Lobograptus scanicus* and it seems that the level at which the occurrence of *L. scanicus parascanicus* is not recorded any more, might be accepted as the upper limit of this horizon. This results from the following two premises: 1) the disappearance of *L. scanicus parascanicus* coincides with the appearance of *Pristiograptus dubius tumescens* (Wood) which — in classical British stratigraphic tables — has so far been considered an index fossil of a separate and overlying *tumescens* zone; higher layers, as it is obvious from the very definition, could not be included in the *scanicus* zone as it has originally been understood (Elles & Wood, 1918; Elles, 1922, 1925); 2) at the same time, *L. scanicus parascanicus* marks a lower limit of the *scanicus* zone and is the most abundant of all the three subspecies.

The definition of the *scanicus* zone, given above, allows one for a correct comparison of the complex picture of evolution of this monograptid group, obtained as a result of recent studies, with certain classical concepts, generally accepted in the literature. It seems probable that, on account of difficulties in finding, in flattened specimens, small morphological differences by which particular species of the Cucullograptinae may be identified, the concept of the *scanicus* zone accepted in practice, was much broader and, in extreme cases, might be equal to the "range zone" of the entire subfamily. Considering all arguments, presented above, the limitation of this zone to the "range zone" of *Labograptus scanicus parascanicus* seems to be more justified. Since this subspecies is accompanied, almost over its entire range (except for the lowermost part corresponding to the layers of the lower zonal form of *L. scanicus parascanicus*), by *Cucullograptus pazdroi* Urbanek, the latter species may be considered a "satellite species" of the *scanicus* zone in its proper sense.

Isolating the *scanicus* zone, as a middle part, from the vertical distribution zone of the Cucullograptinae, we also should determine the stratigraphic status of the upper and lower part.

The lower part is marked by both the first appearance and steady occurrence of *Lobograptus progenitor* n.sp. and *L. simplex* Urbanek. With regard to their habitus, these species resemble to a considerable extent *Neodiversograptus nilssoni* (Lapworth) and there is a well-founded supposition that so far many investigators considered them to be conspecific with the latter (cf. Urbanek, 1963, pp. 151—153). Consequently, the layers containing the oldest two species of the Cucullograptinae were probably assigned to the *nilssoni* zone. In the light of recent investigations such a view becomes, however, ill-grounded. Considering the stratigraphic se-

PLATE I



Range chart showing vertical distribution of Cucullograptinae and associated graptolite fauna in the Mielnik core, compared with assemblages found in erratic boulders.

*Remark: "*Monograptus*" cf. *Monograptus* sp. Kühne is most probably conspecific with a monograptid with peculiarly elongated and very slender thecae, described by Kühne (1955, pp. 395—397, Fig. 17).

Heavy black lines with arrows indicate that given form continues above. Dotted lines indicate that given form is very rare or randomly absent in indicated horizons. Interrogative points indicate uncertainty, in majority of cases connected with rarity or imperfection of record. Thin broken lines at the depth of 932 m indicate the boundary between the Mielnik Beds and Siedlce Beds, as established by E. & H. Tomczyk (1962). Further explanations in text.

quence of the Linograptinae and Cucullograptinae, a new zone of *L. progenitor* n.sp. should be established as intercalated between the *nilssoni* and the *scanicus* zones. *L. simplex* seems to be of a lesser stratigraphic significance since it is contained within the occurrence range of *L. progenitor* n.sp. but it may also be considered an index of a corresponding subzone (an upper part of the *L. progenitor* n.sp. zone).

The upper part of the Cucullograptinae occurrence zone (above the *Labograptus scanicus parascanicus* zone) may, in turn, be divided into the following three zones: that of *L. invertus* n.sp., of *Cucullograptus hemiaversus* and of *Cuc. aversus*, with its two subspecies. Between the point where the last occurrence of *L. scanicus parascanicus* and the first occurrence of *L. invertus* n.sp. are observed, as well as between the last occurrence of the latter and the first occurrence of *Cuc. hemiaversus*, small discontinuities in their distribution (gaps) are recorded in the Mielnik boring. From the stratigraphic point of view they do not seem to be very important and, besides, they may be only accidental (local).

The last zone, containing *Cucullograptus aversus*, may presumably be divided into two subzones. It is true enough that no decisive evidence may be supplied by the Mielnik boring (since, in this boring, the occurrence of the subspecies *Cuc. aversus aversus* is not certain, comp. pp. 492—495) to confirm this supposition, but it seems likely that the lower subzone is marked by the occurrence of the type subspecies. The higher subzone would be characterized by the occurrence of *Cuc. aversus rostratus*. The evolution of this species, testified to also by the fauna from the erratic boulders (comp. pp. 517—518), was "zonal" in character and, hence, the subspecies *rostratus* is marked by the presence of more primitive lower zonal and more advanced higher zonal forms.

Considering the sequence of the Cucullograptinae, stated in the Mielnik boring, the following rough stratigraphic division may be suggested for the layers overlaying the *Neodiversograptus nilssoni* zone (from the bottom):

1) zone of *Lobograptus progenitor* n.sp. (with *L. simplex* in the upper part),
2) zone of *Lobograptus scanicus parascanicus* = zone of *Cucullograptus pazdroi),*
3) zone of *Lobograptus invertus* n.sp.,
4) zone of *Cucullograptus hemiaversus*,
5) zone of *Cucullograptus aversus*, consisting of:
    a) subzone of *Cuc. aversus aversus*,
    b) subzone of *Cuc. aversus rostratus*.

The division, suggested above, is indubitably much more complex than that, used so far, and comprising only 3 zones: *scanicus*, *tumescens* and *leintwardinensis*. Maybe, it will turn out to be unsuitable for the purposes of the practical stratigraphy, primarily for the following reasons: 1) certain difficulties may arise of a detailed specific identification of the forms which are flattened or have strongly damaged periderm; 2) the established units may be regional in character (comp. also p. 364) or too discrete for the purposes of the standard stratigraphy. In this connection, the present writer believes the use of a general concept, "Cucullograptid band", to be advisable as a designation of the entire assemblage of the zones, mentioned above. It may be much more correct in practice than the supposedly "accurate" definition, "the *scanicus* zone", as currently defined.

Another alternative of the solution of this problem may consist in basing the entire stratigraphic division on a quite different group of monograptids whose evolution allows one to develop a simpler scheme. With regard to the stratigraphic importance, the Saetograptinae (*Colonograptus* and *Saetograptus*) make up the best instance of such a group. The first of its genera, i.e. *Colonograptus* Přibyl, is indicative for the lower part of the series under study, and *Colonograptus colonus* (Barrande) sensu Perner[5] belongs to the most frequent species, accompanying *Neodiversograptus nilssoni*. More than once, the view is met with in the geological practice that this species is a facultative index form of the *nilssoni* zone whose range differs only slightly from that of the zonal species (comp. Jaeger, 1964, p. 39). Observations, based on the occurrence of *Col. colonus* in the Mielnik on the Bug boring core, reveal, however, that it reaches considerably higher than the top of the "range zone" of *N. nilssoni* (see. Pl. I). Judging by the distribution of this form at Mielnik, the zone

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[5] The name *Graptolithus colonus* was introduced by Barrande (1850). During my studies on Barrande's collection, preserved at the National Museum in Prague, Czechoslovakia, I have had an opportunity to find that none of the specimens, figured in his work (Barrande, 1850, Pl. 2, Figs. 1—5), fulfills the generally accepted concept of this species. Specimen in Fig. I, 4 (loc. Listice) is *Monoclimacis vomerina* (Nicholson). Figs. 2—3 (loc. Listice) are synthetic diagrams, based on studies of different specimens, among them, according to Perner (1899, p. 18), on fragments of cyrtograptids. Fig. 5 is based on poorly preserved specimens from loc. Borek which probably correspond to *Pristiograptus dubius* (Suess). The majority of the specimens figured were collected at Listice where, according to a recent opinion of Dr. R. Horný (Prague), there are no beds younger than the *vulgaris* zone. The name *G. colonus* was, therefore, used by Barrande to designate a number of quite different species.

Perner (1899, p. 9) was of the opinion that Barrande's Figs. 2—3 were also based on true *colonus* specimens which he refigured correctly only in part in his Pl. III, Fig. 12 and Text — fig. 12. He stated that specimens on the basis of which his figures were drawn were derived from original Barrande's collection (specimen No. 265 in Perner collection from Butovice which is preserved at the National Museum with a probably erroneous designation as Barrande's Pl. 2, Fig. 1). This specimen and Perner's description indicate that he was the first to use this specific name in its present, generally accepted, sense (most probably, Lapworth, 1876 and Tullberg, 1883 used this name to designate another collective species). To avoid any possible misunderstanding, I suggest the use of the name *Colonograptus colonus* (Barrande) sensu Perner. For the same reason, Jaeger's (1964, p. 39) suggestion to continue the use of the name *Monograptus colonus* (Barrande), which would be in conformity with a long-standing tradition, seems to be ill-grounded.

of *Col. colonus* takes in the *N. nilssoni* "range zone" and the lower part of the *Lobograptus progenitor* n.sp. zone and, therefore, it does not seem to be of the same stratigraphic importance as the *nilssoni* zone (as suggested by Jaeger, 1964, p. 39) when properly understood.

The species of the genus *Saetograptus* Přibyl are indicative for the upper part of the series investigated. In their stratigraphic distribution, a partial "overlap" with vertical distribution of *Colonograptus* is displayed by the representatives of this genus, i.e. transient forms between these two genera (*Colonograptus colonus/Saetograptus chimaera* transients, see Pl. I). Moreover questionable representatives of *S.* cf. *chimaera* (Barrande) (Pl. I) occur in the upper part of the *Col. colonus* range. These forms require further studies necessary for a closer determination of their systematic position. The occurence of *S. chimaera cervicornis* Urbanek which, in the upper part, is accompanied by another subspecies, presumably the type subspecies *S. chimaera* cf. *chimaera*[6] (Barrande), begins at a higher level (at depth of 1,020•9).

The replacement of the *scanicus* zone in its current, extensive sense by the *chimaera* zone has been recently suggested by Jaeger (1962, p. 39). He gives the following three reasons to justify his suggestion: 1) the *scanicus* group (= Cucullograptinae) has recently turned out to consist of several separate species and subspecies whose identification, in a flattened state of preservation, is very difficult; 2) the occurrence of the representatives of this group is recorded above the *Saetograptus leintwardinensis* zone; 3) the representatives of *S. chimaera* are distributed only within limits of the *colonus* and the *leintwardinensis* zones. The fact that *S. chimaera* is a species which may easily be identified in a flattened state is also taken into account by him.

In the light of data, obtained from the Mielnik boring, Jaeger's arguments are only partially correct. In particular, it turns out that, in this case, the upper limit of *Saetograptus chimaera* (at a depth of 959•6 m), determined by the occurrence of *S. chimaera salveyi*, is situated considerably lower than the base of the *S. leintwardinensis* zone (at about 936•0 m).

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[6] There is some uncertainty as to the concept of true *Saetograptus chimaera chimaera* (Barrande). A type specimen (figured in Barrande, 1850, Pl.-4, Fig. 4 and refigured in Perner, 1899, Pl. 17, Figs. 18 a-b) preserved at National Museum in Prague, Czechoslovakia, represents a young, growing proximal part of the rhabdosome (some 12 thecae). This specimen is much more robust than a form, described by Urbanek (1953) as *S. chimaera cervicornis*, and displays a rather sudden widening of the rhabdosome (amounting to 1•0 mm. in width in the most proximal part and 1•5 mm. in a somewhat more distal part). Unfortunately, this specimen does not permit to estimate the shape and size of distal thecae, but it approaches much closer to a higher zonal variety of *S. chimaera* from the Mielnik core (described here as *S. chimaera* cf. *chimaera*) than to its lower zonal form (identified as *S. chimaera cervicornis*). *S. chimaera* cf. *chimaera* is more robust than the latter subspecies and differs from it in distal thecae which are provided with broad, earlike lateral apertural lappets. The same form has also been found in some erratic boulders.

If the phenomena observed are not local in character, the *chimaera* zone is not fully substitutional for the *scanicus* and *tumescens* zones. Considering the sequence, stated at Mielnik, the following division of the series examined may be suggested on the basis of saetograptids (from bottom):

1) the *Colonograptus colonus* zone,

2) the *Saetograptus chimaera cervicornis* zone (with *S. chimaera* cf. *chimaera* in the upper part),

3) the *S. fritschi* zone (with *S. chimaera salveyi* in the lower part),

4) the *S. leintwardinensis* zone.

Thus, in supplementing Jaeger's (1964) suggestion, it seems indispensable to introduce a transient *fritschi* zone[7] between the *chimaera* (= *Saetograptus chimaera cervicornis)* and *leintwardinensis* zones. In connection with this suggestion, a certain discussion is due to the occurrence of *S.* cf. *leintwardinensis* at a depth of 960.6—960.9 m. Its position approximately coincides with the lower limit of the *fritschi* zone. The remains in question consist of a certain number of specimens, representing distal parts of the rhabdosome whose structure does not deviate from that of this same part of the rhabdosome in the typical *S. leintwardinensis* which occurs much higher (Pl. I). These specimens of distal parts are, however, accompanied by fragments of the medial and proximal parts that do not differ from those in the representatives of *S. chimaera salveyi* (Hopk.). The explanation of this phenomenon may be ascribed to the supposition that perhaps the distal parts of the rhabdosome, ascribed here to *S.* cf. *leintwardinensis*, belonged to a transient link, biform in character. Such form might have already modified thecae of the distal part with the structural type peculiar of the younger species *S. leintwardinensis* and, at the same time, not yet modified thecae of a more proximal part with the structural type that does not differ from that of the older species *S. chimaera*. There is the possibility that *S. leintwardinensis* was developed by the distal introduction of new phylogenetic characters (the form and position of apertural spines). Some traces of this phenomenon are preserved in the representatives of this species in the form of an increase in the expressivity of these characters towards the distal part[8].

A *Saetograptus fritschi linearis* zone is distinguished by Jaeger (1964, pp. 40—41) above the *S. leintwardinensis* zone. The results of observa-

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[7] In connection with this suggestion, attention should be paid to the position of *Saetograptus fritschi*, taken by this species in Barrandien. According to Horný's recent results (1962, Fig. 7, p. 883), this species occurs below the *S. fritschi linearis* zone but it does not exceed the upper limit of the *S. chimaera* range. As a result, Horný does not distinguish any separate zone for *S. fritschi fritschi*.

[8] The evolution of thecae in the Saetograptinae consisted, in most cases, in the proximal introduction of new phylogenetic characters (cf. Urbanek, 1960, pp. 187—193). The evolutionary tendency of *S. leintwardinensis* marks, therefore, a completely different trend in the phylogeny of this group.

tions of the occurrence of graptolites in the Mielnik boring considerably deviate from the sequence, found in Thuringia. At Mielnik, the occurrence of *S. fritschi* cf. *linearis* is associated with the typical form. *S. fritschi* cf. *fritschi* and, besides, the occurrence of both these forms is recorded below the zone, containing *S. leintwardinensis.*

Jaeger's (1962) suggestion to replace the Cucullograptinae with the Saetograptinae as an index group of the Lower Ludlovian may in fact be reduced to the replacement of a group whose evolutionary development has been better recognized with another, less-known in this respect. Such seems to be an apparently simple picture of the saetograptid development. It seems that, together with a more detailed and accurate recognition of the evolution of this group, the picture of its phylogenetic relationships will become as complex as that of the Cucullograptinae. There are some facts which might confirm the correctness of such a supposition (among other things, a considerable variability of *Saetograptus chimaera cervicornis*, maybe zonal in character, occurrence of *S. chimaera* cf. *chimaera* and *S. chimaera salveyi,* representing indubitably divergent differentiation trends, occurrence of transient forms between *Colonograptus* and *Saetograptus*, etc.). *S. leintwardinensis* also do not make up a uniform species but rather a group of closely related forms. This is confirmed by the presence of a presumably separate subspecies in the Mielnik boring (comp. Pl. I),. as well as by the differentiation of this group from other borings in Polish Lowland (Dr. H. Tomczyk's oral communication). Jaeger (1962, p. 40) also does not preclude the existence of a subspecific peculiarity of the forms, belonging to the *leintwardinensis* group, found in Thuringia.

A list of zones, based on the occurrence of the Cucullograptinae (and Linograptinae), together with the zonation, shown on the basis of the Saetograptinae so that mutual relationships of established units might be more clearly presented, is given in Table 1. It is clear from the diagrams presented that the separation of the *tumescens* zone established by Elles and Wood (1900) for Welsh Borderland is not justified in the case of the platformian Silurian of Poland. It has been as early as 1960 that attention was drawn by H. Tomczyk (1960, pp. 135 and 138, Table on page 136) to the fact of a slight stratigraphic significance of *Pristiograptus dubius tumescens* (Wood) in the platformian Silurian of Poland. According to this author, it results from a considerable vertical distribution of this species which passes into the Siedlce Beds, displaying a few horizons of a frequent or even mass occurrence above the zone of *Saetograptus leintwardinensis* (H. Tomczyk, 1962, Table 10; E. Tomczyk & H. Tomczyk, 1962, p. 275). A similar view was expressed by Jaeger (1962, pp. 39—40) who: 1) does not consider "*Monograptus*" *tumescens* to be an index form, 2) believes the concept of "the *tumescens* zone" to be wrong, 3) considers *M. tumescens* (Wood) to be conspecific with *M. dubius* (Suess) and to correspond to *M. dubius ludlowensis* Bouček, as well as to *M. frequens* Jaekel. The latter having a priority, *Monograptus tumescens* Wood = *Pristiograptus dubius frequens* (Jaekel, 1889).

The first and the second item of Jaeger's views are strongly justified by the materials, coming from the Mielnik boring. *Pristiograptus dubius tumescens* appears at a depth of 977.9 m (cf. Pl. I) which corresponds to the top of the *Lobograptus scanicus parascanicus* or to the upper part of the *Saetograptus chimaera cervicornis* zone but hereafter it continues to occur above the *leintwardinensis* zone, passing to the lower part of the Siedlce Beds. The specimens from the Siedlce Beds seem not to differ at all from the typical specimens of *tumescens* from a horizon, stratigraphically corresponding to the *tumescens* zone from Wales and they do not display any differences in relation to the British forms[9].

In all probability, *Pristiograptus dubius tumescens* continues to occur in yet higher layers, maybe even as high as the top of the Siedlce Beds but this problem still requires some more detailed studies.

In contradistinction to the first two, the third item of Jaeger's views, mentioned above, does not seem to be acceptable for this simple reason that among the populations of *Pristiograptus dubius* (Suess), occurring in association with a fauna typical of the *scanicus* zone (*P. scanicus parascanicus* and *Cucullograptus pazdroi*) and typical representatives of *P. dubius tumescens*, there exist certain morphological differences which allow us to state that we have to do with separate, although closely related, subspecies[10]. The possibility of *P. dubius ludlowensis* Bouček being a synonym of *P. tumescens* (Wood) seems, therefore, to be rather doubtful (although we cannot preclude another possibility, i.e. that *P. dubius ludlowensis* Bouček = *P. frequens* Jaekel).

Within the graptolite assemblage, found in the series examined, an important role is played by the Retiolitidae (see Pl. I). Many species of this family are those, described by Eisenack (1951) from the erratic boulders, whose stratigraphic ranges have not been known so far. Any preliminary statement of such ranges have only become possible on the basis of the material, coming from Mielnik. In the Retiolitidae sequence, there is a striking fact that, in the case of *Plectograptus* sp., they reach as high as the lower part of the *Cucullograptus hemiaversus* zone (= *Saetograptus fritschi* zone) and, in the case of *Holoretiolites* sp., as far as the *S. leintwardinensis* zone (= *Cuc. aversus* zone, middle part). Such

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[9] This view has been confirmed by Dr. B. Rickards (Cambridge) who had the opportunity to get to know my material as he visited Warsaw in April, 1965.

[10] In my opinion, these differences are too small to consider these forms to be separate species.

a high range of the Retiolitidae is a rather unexpected feature which makes the assemblage of the graptolite fauna, beginning with the *vulgaris* and closing with the *leintwardinensis* zone, uniform in character.

Table 1

Comparison of graptolite zones as suggested by the sequence of Cucullograptinae (plus *Neodiversograptus*) and Saetograptinae in the Mielnik boring

Cucullograptus aversus (Eisenack)	1) *Cuc. aversus rostratus* 2) *Cuc. aversus aversus*	*Saetograptus leintwardinensis* (Hopkinson)
Cucullograptus hemiaversus Urbanek		*Saetograptus fritschi* (Perner)
Lobograptus invertus n.sp.		
Lobograptus scanicus parascanicus (Kühne)		*Saetograptus chimaera cervicornis* Urbanek
Lobograptus progenitor n.sp.		
Neodiversograptus nilssoni (Lapworth)		*Colonograptus colonus* (Barrande) sensu Perner

Remark. *Cuc. aversus rostratus* survived somewhat above the *leintwardinensis* zone.

Stratigraphic position of the examined erratic boulders

The stratigraphic position of erratic boulders may be established only on the basis of the comparison of a faunal assemblage occurring in them with the assemblages of corresponding index zones, recognized from the standard Silurian sections which occur *in situ*.

The first attempt at a general stratigraphic classification of the Silurian erratic boulders has been undertaken by Kühne (1955) who distinguished certain characteristic faunistic assemblages among which "*chimaera*-Fauna", corresponding, according to this author, to the *nilssoni* and *scanicus* zones, belongs to the most frequent ones. The older assemblage is marked by the occurrence of *Colonograptus colonus* which, according to this investigator, corresponds to the lower part of the *nilssoni* zone, while the occurrence of *Monoclimacis haupti* characterizes of an assemblage younger than "*chimaera* -Fauna"[11].

At present, the comparison of the faunistic assemblage of the examined boulders with the standard section and with that of the Mielnik boring, similar to them in its lithological development, as well as with other Silurian sections of the same age, situated all over Europe, allows one for a more accurate determination of their stratigraphic position.

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[11] The "*chimaera*-Fauna" in erratic boulders corresponds rather to the *scanicus* zone (in its redefined sense) only. *Colonograptus colonus* corresponds not only to the lower part of the *nilssoni* zone, but it comprises all this zone and reaches even higher. *Monoclimacis haupti* comprises, as a matter of fact, zones which are younger than the *scanicus* zone (Pl. I).

Table 2

DISTRIBUTION OF GRAPTOLITES IN EXAMINED ERRATIC BOULDERS

No. of boulder Systematic names	S. 133	S. 151	S. 219	S. 223	S. 225	S. 149	S. 140	S. 37	S. 228	S. 137	S. 218	S. 32	S. 16	S. 36	S. 145	S. 222	S. 181	S. 128	S. 185	S. 174	S. 58	S. 134	S. 200	S. 205	S. 121
Lobograptus progenitor n. sp.	+	+																							
L. simplex Urbanek			+	+																					
L. cf. *simplex* Urbanek					+																				
L. exspectatus exspectatus Urbanek						+	+				+										+	+			
L. scanicus parascanicus (Kühne)								+	+	+		+	+	+			+		+	+					
L. scanicus amphirostris n. subsp.																					+				
L. scanicus scanicus (Tullberg)															+	+		+							
Cucullograptus hemiaversus Urbanek																							+		
Cuc. aversus rostratus Urbanek																								+	+
Cuc. pazdroi Urbanek												+				+	+			+					
Neodiversograptus beklemishevi Urbanek									+		+	+		+											
Saetograptus chimaera cervicornis Urbanek						+				+	+	+	+	+	+			+							
S. chimaera cf. *cervicornis* Urbanek								+	+								+		+		+	+	+		
S. chimaera cf. *chimaera* (Barrande)																				+					
S. chimaera cf. *salweyi* (Hopkinson)				+																			+		
Monoclimacis micropoma micropoma (Jaekel)	+	+	+			+																			
M. micropoma cf. *nannopoma* (Jaeger)											+														
M. haupti (Kühne)											+										+	+		+	
Pristiograptus dubius (Suess)	+		+	+					+	+	+	+	+				+			+	+	+	+	+	
"*Pristiograptus*" *bohemicus* (Barrande)									+	+		+				+			+	+					
Pristiograptus sp.							+																		
Holoretiolites erraticus Eisenack																			+						
H. cf. *erraticus* Eisenack			+						+				+												
H. mancki (Münch)		+		+											+		+	+							
H. cf. *mancki* (Münch)					+			+		+															
H. cf. *simplex* Eisenack										+															
Holoretiolites sp. z								+						+											
Plectograptus macilentus (Törnquist)	+											+													

A tabular list of the graptolite fauna of all erratic boulders, examined in the present monograph, is shown in Table 2.

At the same time, these assemblages make up a basis for conclusions as to the presumable stratigraphic position of the boulders (corresponding numbers are shown in the first right-hand column of Pl. I). It should be remembered that these conclusions are not free of an arbitrary element and that they cannot be safely proven in all cases (hence, the question marks accompanying the numbers of some boulders).

COMPARATIVE ANATOMICAL ANALYSIS OF THE CUCULLOGRAPTINAE AND THE RULES OF THEIR EVOLUTION

EVOLUTION OF SICULAE

Siculae, their size and shape

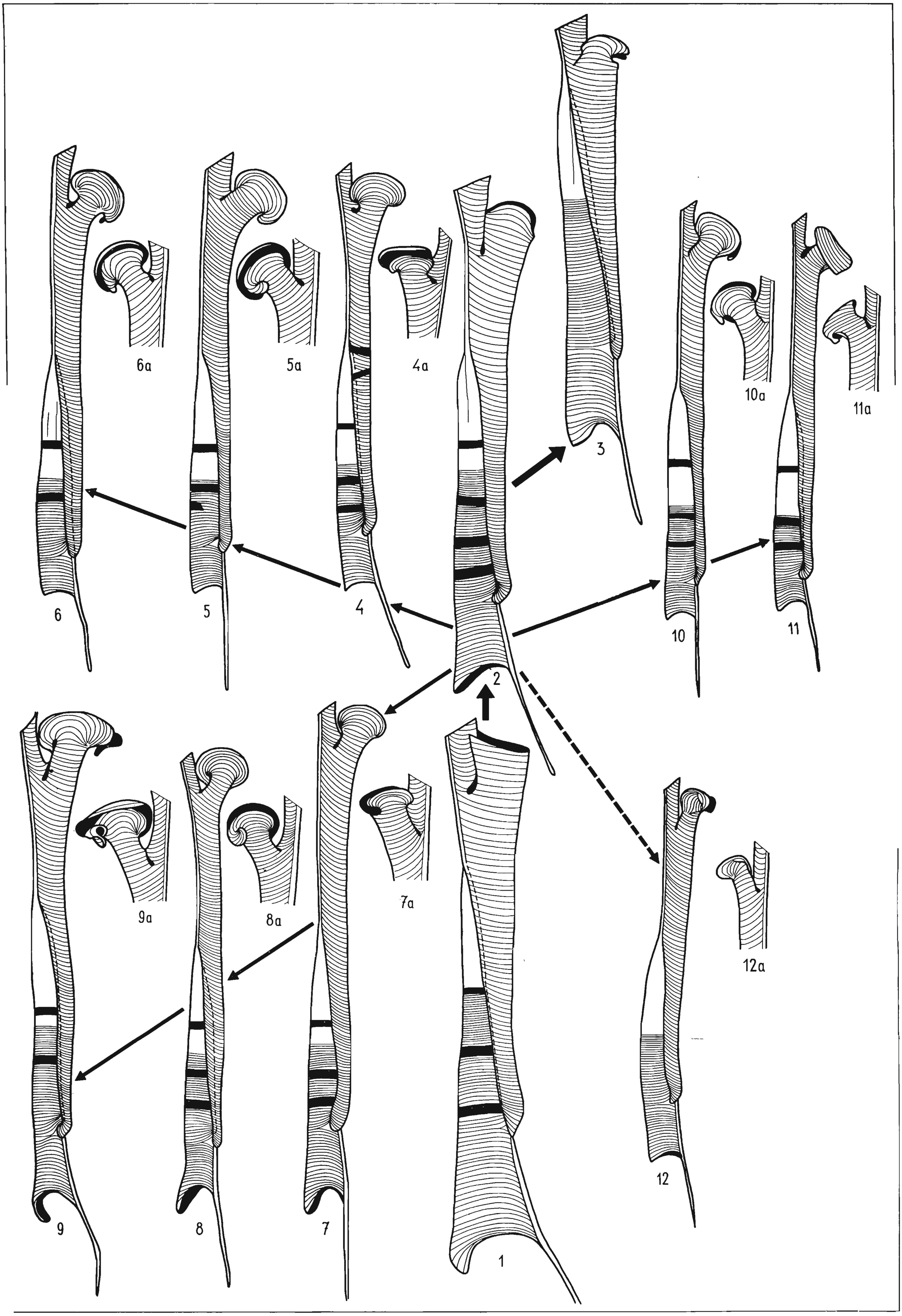
On the whole, the following two morphological types may be distinguished on the basis of the differentiation picture, displayed by the siculae in the Cucullograptinae: 1) large (robust) (Pl. II, Figs. 1—3), and 2) small (gracile) siculae (Pl. II, Figs. 4—12).

Large siculae are marked by a relatively considerable length (*long.*) and — in the adapertural part of metasicula — width (*tr.*). Metasicula is much longer than prosicula and has a distinct apertural dorsal process. The siculae of this type are recorded only in the *Lobograptus* species which are characterized by a full bilateral symmetry, such as *L. progenitor* n.sp., *L. simplex*, *L. exspectatus exspectatus*. This type of sicula may be expected to occur also in *L. exspectatus bicornis* n. subsp. which, however, no siculae have been observed so far. The occurrence of siculae of this type should presumably be considered one of many primitive characters, typical of this evolution line of *Lobograptus*.

The sicula of *Lobograptus progenitor* n. sp., in which it reaches the largest dimensions among all Cucullograptinae (comp. Table 3), may be considered especially primitive. It is marked by a strongly developed dorsal apertural process (Pl. II, Fig. 1).

The siculae of other bilaterally symmetric lobograptids display a rather slightly expressed tendency to abbreviate their length, primarily as a result of shortening the metasicula, while the length of the prosicula remains almost unchanged. At the same time, in *Lobograptus simplex,* the dorsal apertural process becomes considerably less developed, while, in *L. exspectatus,* although distinctly outlined, its shape is slightly modified (Pl. II, Figs. 2 and 3).

PLATE II



Changes in size and shape of siculae and first thecae in the Cucullograptinae. *1* — *Lobograptus progenitor* n.sp., *2* — *L. simplex*, *3* — *L. exspectatus, exspectatus*, *4* — *L. scanicus parascanicus*, *5* — *L. scanicus amphirostris* n.subsp., *6* — *L. scanicus scanicus*, *7* — *L. imitator* n.sp., *8* — *L. invertus* n.sp., *9* — *L. cirrifer* n.sp., *10* — *Cucullograptus hemiaversus* (first theca is restored on the base of preserved fragments and other proximal thecae), *11* — *Cuc. aversus rostratus*, *12* — *Cuc. pazdroi.*

a — indicate obverse (left) aspects of upper parts of first theca in asymmetric cucullograptids (e.g. *4a*). Specimens are shown semidiagrammatically, those strongly flattened are somewhat reduced in width to avoid preservational features. Heavy arrows indicate presumable direction of evolution in symmetric lobograptids, thin arrows indicate the same in other lineages.

The siculae of all other Cucullograptinae belong, without exception, to type 2, i.e. small ones. They are marked by a distinctly decreased length (total length 0.77—1.34 mm), resulting primarily from shortening the metasicula, while the length of the prosicula does not virtually differ from that of the prosiculae in the bilaterally symmetrical lobograptids (comp. Table 3).

Within this type of siculae, there occurs a distinct morphological differentiation, testifying to the existence — among Cucullograptinae — of divergent trends of specialization. In the lineage, represented by *Lobograptus imitator* n.sp., *L. invertus* n.sp. and *L. cirrifer* n.sp. the reduction of the metasicula length is not carried too far. It reaches 1.08—1.34 mm (mostly, 1.08—1.18 mm). However, like in other Cucullograptinae having type 2 siculae, the metasicula is marked by a small apertural width. The presence of a well-developed dorsal apertural process (Pl. II, Figs. 7—9) is a character in which the siculae of the species, mentioned above, differ from other asymmetric lobograptids. In addition, this process displays a certain tendency to a progressive development and, in *L. cirrifer* n.sp. it takes a slightly incurved form which is not observed even in *L. progenitor* n.sp. and acquires a length of about 0.12—0.20 mm. Much more distinct is shortening of metasicula in the *L. scanicus parascanicus* — *L. scanicus amphirostris* n. sp. — *L. scanicus scanicus* lineage. This brings about a state in which the metasicula reaches only the length of the prosicula or it may be even slightly shorter than the latter. At the same time, the apertural margins become straight as a result of an almost complete atrophy of the dorsal process (Pl. II, Figs. 4—6).

A similar trend marks the siculae in *Cucullograptus*. They display a decrease in the length of the metasicula which becomes equal to that of the prosicula (in. *C. hemiaversus*) or even slightly shorter (in *C. aversus rostratus*) (Pl. II, Figs. 10 and 11). It is only in *C. pazdroi* that the metasicula is somewhat longer than the prosicula (Pl. II, Fig. 12). Shortening of the metasicula in *Cucullograptus* is combined with a strong reduction of the dorsal process of its aperture which takes the form of a small elevation or disappears at all.

If we consider robust type of siculae to be primitive, the conclusion may be drawn that the tendency to a progressive gracilization of siculae was predominating in a further evolution of siculae in the Cucullograptinae.

Biological significance of the evolution of sicula in the Cucullograptinae

The progressive gracilization of siculae in the Cucullograptinae, probably the main trend in their phylogeny, was only to a very small extent, related to the morphological differentiation of their structure

Slight modifications of the dorsal apertural process of the metasicula in *Lobograptus exspectatus* and *L. cirrifer* n.sp. and, maybe, a certain secondary elongation of the sicula in the latter species (Pl. II, Figs. 3 and 9) might be considered the only manifestation of such a development. The other development phenomena may amount to a secondary simplification of the structure of sicula, consisting primarily in shortening of the metasicular part and the disappearance of the apertural differentiations in siculae. Such a character of the evolution of siculae in the Cucullograptinae makes up a glaring contrast with the evolution of other thecae of the rhabdosome which is primarily marked by a strong morphological differentiation, recorded first of all in the apertural apparatus of metathecae.

In general, only the species which are marked by a relatively simple structure of the apertural apparatus (i.e. bilaterally symmetric lobograptids) have siculae with a well-developed and "normal" metasicula. In all Cucullograptinae in which a strong differentiation of the apertural apparatus of thecae and the development of a secondary asymmetry took place, a more or less advanced gracilization of siculae is recorded which, as mentioned above, consists in the simplification of their structure.

The phylogeny of the Cucullograptinae displays, therefore, a fundamental divergence of general trends in the evolution of the sicula and of the rhabdosome thecae. The progressive differentiation of the structure of thecae is simultaneously accompanied by a tendency to the simplification of the structure of a sicula.

We do not know of course what significance should be ascribed to secondary shortening and simplification of the structure of siculae, i.e. to its gracilization. We may, however, presume that these phenomena were related to a partial simplification of the structure of the siculozooid and, strictly speaking, metasiculozooid which, presumably, was developed by metamorphosis from the prosiculozooid (Kozłowski, 1949, pp. 98—101). Shortening of the metasicula seems to be an evidence that the development (the growth) of the metasiculozooid was also arrested which usually results in a relative morphological underdevelopment. The tendency, displayed at the same time, to the simplification of the structure of the metasicula (except for the *Lobograptus imitator* — *L. cirrifer* n.sp. evolution line) may testify to a presumable underdevelopment of the anterior part of the body in this zooid (consisting presumably in the retrogression of the lophophore and the preoral lobe?).

Considering the premises, mentioned above, we may try to determine an approximate evolutionary mechanism which controlled the gracilization of siculae in the Cucullograptinae. This mechanism seems to resemble the process of neoteny or of foetalization. The morphological simplification of the metasiculozooid in specialized Cucullograptinae would be, therefore, caused by a certain arrest of its development. Presumably, an adult metasiculozooid resembled, in the Cucullograptinae with small siculae (type 2), a youthful metasiculozooid of primitive lobograptids in which it continued to develop for a certain time.

Obviously, on the basis of the comparison of the peridermal structures, it is difficult to answer the question if — in the case of the evolution of the Cucullograptinae — we have to do with the process of neoteny or foetalization, the more so since their ultimate morphological effects are very similar to each other. According to Remane (1956, pp. 180—186) neoteny and foetalization are not fundamentally opposite processes. In a typical case, neoteny: 1) is related to the metamorphosis it arrests, 2) does not abbreviate the development by omitting ontogenetic stages, and 3) concerns the entire organization of an animal which, in its fundamental features, takes larval characters of its ancestors. On the other hand, foetalization seems to be a simpler process which, in typical cases: 1) does not display any relationship to the metamorphosis, 2) causes the abbreviation of the development by omitting terminal ontogenetic stages, and 3) is limited to certain complexes of characters but does not change the entire organization.

Examining the evolution of siculae and siculozooids in the Cucullograptinae in the light of these considerations, we should pay attention to the following phenomena: 1) the secondary abbreviation of the development of metasicula causes the omission of terminal stages, within the limits of the stage of an imaginal metasiculozooid; 2) it does not seem to be directly related to the arrest or delay in the metamorphosis; 3) the simplification of the organization of the metasiculozooid presumably did not consist in assuming larval characters. For this reason, the present writer is inclined to believe that the gracilization of siculae in the Cucullograptinae was similar, in its mechanism, more to the foetalization than to neoteny.

Certain differences may be found if we compare the gracilization of siculae in the Cucullograptinae with the evolution of siculae in the Linograptinae (Urbanek, 1963, pp. 200—206) which, in some respects, is similar. In the latter case, the evolution takes place in a few stages and shortening of the metasicula is observed in the praelinograptid stage (1963, p. 200) while the prosicula remains unchanged. This process may be well compared with that of the gracilization of the siculae in Cucullograptinae and it presumably amounts to the foetalization of the siculozooid. On the other hand, the elongation of the prosicula is brought in the linograptid stage, while it is the metasicula that remains unchanged. As a result of this secondary elongation, the prosicula becomes distinctly longer than the metasicula. The suggestion that the "extension

Table 3

Evolutionary changes in dimensions of sicula in Cucullograptinae (measurements in mm)

Measurements Specific names	Total length of sicula	Length of prosicula	Length of metasicula	Participation of metasicula in total sicular length (%)	Apertural diameter of metasicula	Dorsal apertural process in metasicula
Lobograptus progenitor n.sp. . .	1.55—1.71	0.46—0.65	0.95—1.17	61.3—68.4	0.30—0.45	strong 0.14—0.18
L. simplex	1.38—1.48	0.45—0.58	0.80—0.93	57.9—62.8	0.24—0.30	developed 0.05—0.16
L. exspectatus exspectatus . . .	1.46—1.61	0.54—0.59	0.91—1.05	62.0—63.3	0.21—0.28	strong 0.08—0.14
L. scanicus parascanicus . . .	0.90—1.20	0.46—0.60	0.47—0.65	52.2—54.1	0.13—0.16 0.20—0.25	vestigial 0.04
L. scanicus amphirostris n. subsp.*	0.10	0.60	0.50	45.4	0.30	vestigial 0.02
*L. scanicus scanicus**	1.07	0.55	0.52	48.5	0.16	vestigial —
L. imitator n.sp.	1.08—1.18	0.48—0.50	0.60—0.67	55.5—56.7	0.18—0.20	developed 0.07—0.11
L. invertus n.sp.	1.08—1.14	0.48—0.50	0.58—0.65	53.7—57.0	0,18—0.22	developed 0.05—0.09
L. cirrifer n.sp.	1.18—1.34	0.55—0.58	0.63—0.76	53.3—57.7	0.18—0.25	incurved 0.12—0.20
Cucullograptus hemiaversus . .	1.00—1.08	0.55—0.58	0.45—0.50	45.0—47.4	0.11—0.16	vestigial —
*Cuc. aversus aversus***	0.77—0.84	—	—	—	0.08—0.15	vestigial —
Cuc. aversus rostratus	0.80—1.08	0.49—0.60	0.30—0.48	37.5—41.4	0.13—0.14	vestigial 0.03—0.06
Cuc. pazdroi	0.85—0.95	0.43—0.45	0.46—0.52	51.7—54.1	0.12—0.14	vestigial —

* Scanty material does not indicate the variation range.

** According to Eisenack's data (1942).

Note: Values in first right-hand column indicate the length of the dorsal apertural process.

of the prosicular segment may suggest a kind of embryonization of the siculozooid, represented by a delayed metamorphosis" (Urbanek, 1963, p. 251) has already been brought forward a few years ago. A possible arrest of the metamorphosis that took place during the evolution of the sicula in the linograptid stage, allows one to compare this process to neoteny. Both these modes of the phylogenetic modification of ontogeny might participate in the evolution of one phylogenetic line. In *Linograptus* they brought about a considerable simplification of the structure of the siculozooid which was transformed only into a sort of a tissue node binding together proximal zooids of all sicular cladia that branch off from the sicular aperture in a stellate manner.

The simplified, "germinal" form of the metasiculozooid in the asymmetric, specialized Cucullograptinae allows one to broach a working hypothesis that there exists a definite correlation between the development of asymmetry of thecae and the differentiation of their apertural apparatus, as well as a phenomenon of "foetalization" of the siculozooid. This might be in conformity with my previous views on the relations that take place between the evolutionary differentiation of siculae and that of the remaining thecae of a colony (Urbanek, 1960, p. 165) as e.g. in the Corynoididae (Middle Ordovician) in which a process, similar in some respect, is observed. A considerable elongation of the sicula (to about 12 mm in length) occurs here with a simultaneous differentiation of its apertural apparatus (e.g. in *Corynites;* Kozłowski, 1953, 1956). This process is, however, accompanied by a decrease in the size of the rhabdosome to 1—3 thecae which are simple in structure. The following considerations of extremely opposite evolutionary trends in the Cucullograptinae and Corynoididae allow one to suppose that the "embryonized" siculozooid was transformed in the Cucullograptinae into a more active inductor (organizer), responsible for the morphological differentiation of thecae. On the other hand, the reduction of the rhabdosome in the Corynoididae allows one to presume that the "colonial growth has been here replaced by the growth and differentiation of its first indivi-

Family & subfamily	Sicula	Thecae
Corynoididae (Middle Ordovician)	Progressive development, elongation and differentiation of the aperture	Quantitative and morphological decrease
Cucullograptinae (Upper Silurian)	Simplification of the structure by shortening and disappearance of apertural differentiations	Progressive differentiation of the apertural apparatus

dual, i.e. the siculozooid. The colonial organizer of the colony would, at the same time, become the reacting centre which might have had some bearing on the reduction of the colony. The physiological mechanism of the phenomena may, to some extent, resemble hereditary dwarfism in some plants, being an effect of the presence of some enzymes, decomposing growth substances and causing a strong decrease of their amount in tissues. The considerable use of similar substances by the growing siculozooid in graptolite colonies may have an analogous influence on the size of the whole colony" (Urbanek, 1960, p. 165).

In the light of the considerations, presented above, one might suppose that the normally developed siculozooid in primitive, symmetric lobograptids was probably less active morphogenetically than the "embryonized" siculozooid of specialized Cucullograptinae. We may ascribe these conditions to: 1) changes in the intensity of producing morphogenetic agents by the siculozooid (oozooid), as well as to 2) an increase in the reactivity of the blastozooid tissues. The latter process might also be directly related to the foetalization of the siculozooid from whose tissue, all tissues of the remaining zooids in the colony derived. An increase in histogenetic and organogenetic plasticity of tissues of the entire colony would be a consequence of a secondary "rejuvenation", i.e. a dedifferentiation of these tissues in the siculozooid caused by the arrest of its development. On the other hand, the morphological specialization of the siculozooid in the Corynoididae might also result in the drop in the reactivity of derivative tissues of the blastozooids.

Patterns of evolutionary behaviour of the sicula

Considering the whole of the evolution in the Graptoloidea, on the basis of the facts, already known, although still rather not very abundant, one may attempt to characterize the patterns of the phylogenetic behaviour of the sicula towards the remaining thecae of the rhabdosome.

1) A relatively considerable independence of the sicula from the phylogenetic modifications in the structure of thecae seems to be a most frequent case. We may observe, therefore, a relatively stable form, preserved by the sicula within large groups almost without any evolutionary changes or, with such changes, displayed to an incomparably lesser degree and by means of different morphological characters (changes only in size and proportions and no structural differentiation) than those, displayed by thecae. Such evolutionary behaviour of the sicula may be considered typical. According to Bulman (1955, p. 45): "In shape, however, the sicula varies scarcely at all and, apart from slight differences in the length-breadth ratio, or a gentle curvature, apertural spines and processes are the only modification recorded."

The conditions, observed in the Retiolitidae, may serve as an example of such extreme evolutionary conservatism of the sicula. It is well-known that, in this case, a considerable reduction of periderm comes about which takes the form of a reticula or a lacinia. An interesting stage is, however, observed in the Ordovician genus *Archiretiolites* in which the thecal periderm has a reticular form, while the sicular periderm is still normal, i.e. continuous (Eisenack, 1935). A stage of evolution, morphologically more advanced is represented by *Retiolites geinitzianus* in which only the prosicula is provided with a continuous periderm, while the metasicular skeleton is reduced to the axis of ancora only (Kühne, 1953). The Upper Silurian retiolitids (*Holoretiolites, Plectograptus*) have a periderm including the prosicula completely reduced to a system of clathria, and morphologically represent a final stage of the process.

On the basis of the conditions in *Orthoretiolites* (Middle Ordovician), investigated by Whittington (1954), I have concluded that the reduction of the periderm in the Retiolitidae was a phylogenetic character introduced distally (Urbanek, 1960, pp. 165—166). The conservative behaviour of the sicula which keeps its primary type of structure for the longest time is, in this case, understandable because of the mechanism of phylogenetic modifications in astogeny. However, in the monograptids in which new phylogenetic characters are introduced proximally, the sicula is mostly omitted in chain of morphological modifications in rhabdosome.

2) Transformations opposed in their morphological character to those which occur, at the same time, in other thecae of the rhabdosome may by considered the second mode of the evolutionary transformations in the sicula. The instances of the sicular evolution in the Corynoididae (progressive differentiation and increase in the size of the sicula with a simultaneous simplification of the structure of thecae and the reduction of the rhabdosome) and in the Cucullograptinae (simplification and partial reduction of the sicula with a simultaneous progressive differentiation of thecae), which have already been extensively discussed above, may serve as an example of this type of the evolutionary processes that take place in the sicula.

Both the first and the second mode of the evolution of the sicula testify to a considerable degree of independence of the siculozooid from other individuals forming a colony.

3) The cases of the modification of the sicula without a simultaneous distinct differentiation of thecae, which so far are rather rare, make up the third mode of the evolutionary transformations in the sicula. *Neodiversograptus nilssoni*, marked by specialized form of its sicula which is provided with a linograptid dorsal apertural spine and has simple

thecae may be a typical example of this process. Likewise, in *Neodiversograptus beklemishevi* and in *Linograptus posthumus*, considerable modifications take place in the structure of the sicula and they are accompanied by only slight modifications in the structure of thecae. However, in all forms, mentioned above, the modifications in the structure of the sicula are related with the progressive development of a colony (the formation of multibrachiate colonies).

In this connection, Jaeger's (1959, pp. 129—131) observations on the evolution of the sicula in the "*Monograptus*" *praehercynicus* — "*M.*" *hercynicus* series are very interesting. Apart from very small differences in the size of the rhabdosome, both these species distinctly differ from each other only in the structure of the sicula which, in "*M.*" *praehercynicus* is "normal", and in "*M.*" *hercynicus* — strongly modified (conical, expanded in the apertural part and provided with slightly outlined lateral marginal elevations). In the *praehercynicus* — *hercynicus* stage, the processes of sicular modifications are not accompanied by any palpable changes in the structure of thecae (Jaeger, 1959, p. 93). This opinion of Jaeger was confirmed by observations of graptolites from Morocco made quite recently by Willefert (1963, pp. 74—76). She described a transient form (*M. hercynicus* var. *subhercynicus*) of infrasubspecific rank, linking *M. praehercynicus* with true *M. hercynicus*. This transient form is characterized chiefly by an intermediate shape of sicula (less expanded at the aperture than in the typical form and still provided with a vestigial dorsal process) and it occupies a somewhat lower horizon. Willefert also noted a zonal evolution in the shape of sicula and recognized, in populations of *M. hercynicus* from different horizons, a tendency to the increase in the apertural width of sicula within a geological time. This trend is combined with a simultaneous transformation of the dorsal process into the angular corner of aperture. These important observations contribute to a better understanding of microevolutionary changes in graptolite siculae which, in this case, were almost entirely independent of thecal changes.

4) So far there was no description of a process which would consist in parallel phylogenetic modifications in the sicula and in the remaining thecae of the rhabdosome. In this connection, noteworthy are the present writer's recent investigation (so far, unpublished) on a group of species, closely related to "*Monograptus*" *inexspectatus* Bouček) comp. also Urbanek, 1963, p. 192). These species make up a phylogenetic series in which one may observe the formation and development of complex and asymmetrical apertural apparatus of thecae which, however, consist of a microfusellar tissue, microstructurally resembling the apertural lobes, described in *Monoclimacis micropoma* (Urbanek, 1958, pp. 23 and 92—96). The formation of such an apertural apparatus of thecae

is accompanied by the formation, on lateral margins of the sicular aperture, of strongly developed elevations which also consist of the microfusselar tissue and which make up a sort of apertural lobes of the sicula. The analogy of the apertural apparatus of thecae with that of sicula is not, however, complete since the latter, in contradistinction to thecae, preserves its bilateral symmetry. All the same, it is an instance of an extreme parallelism of the evolution of the sicula and the remaining thecae of the rhabdosome.

Peridermal rings of the sicula

In most cases, the siculae of the Cucullograptinae are provided with a well-developed peridermal rings. As is well-known, these rings in monograptids make up internal thickenings, formed on the wall of the sicula and consisting of a secondary peridermal substance (Walker, 1953, p. 364; Urbanek, 1958, p. 17). Earlier views that the number and position of the rings are unusually variable which deprives them of a taxonomic importance are now confirmed by the observations of the siculae in the Cucullograptinae. There are, however, some other noteworthy aspects of this problem.

All facts, collected so far, indicate that, in most cases, the peridermal rings are formed secondarily and with a certain delay as compared with the growth of the sicula itself. Young prosiculae and metasiculae are devoid of these rings which occur later on in subsequent growth stages, appearing successively from more apically situated rings to those, situated closer to the aperture. This does not preclude the possibility that, in some cases, such rings may be formed almost simultaneously with the growth of the sicula and they are located near the apertural margin of a growing metasicula or they make up a thickening on the apertural margin of a young prosicula which is still devoid of the first metasicular fuselli. Maybe, the latter case is rather an exception and not a rule.

The situation of the first peridermal ring (r_1), most apically located, claims a particular attention. In most better-known Monograptidae whose siculae are provided with such rings, the first ring is always situated on the boundary between the pro- and metasicula. Such conditions have been found in many siculae I investigated in *Monograptus priodon* (Bronn), *Monograptus uncinatus* (Tullb.), *Pristiograptus dubius* (Suess), *Saetograptus chimaera* (Barr.), *Monoclimacis micropoma* (Jaekel) and *Monoclimacis haupti* (Kühne), and in majority of examined siculae — in "*Pristiograptus*" *bohemicus* (Barr.). An exception in this respect are the Linograptinae (Urbanek, 1963), in which r_1 may also be situated on the prosicula, distinctly spaced from the boundary with the metasicula (*Neodiversograptus beklemishevi* Urb.) and, as it has been shown by recent observations, in many Cucullograptinae.

An interesting transient stage is observed in the primitive bilaterally symmetric lobograptids (*Lobograptus progenitor* n.sp., *L. simplex*). The first peridermal ring may either be situated right on the boundary between the pro- and metasicula, or may be apically set back from it and located on the prosicular segment. This situation, found in primitive lobograptids, is distinctly in contrast with that, typical of more specialized Cucullograptinae in which the disappearance of the rings (*Lobograptus exspectatus, Cucullograptus pazdroi*) or their presence is recorded with a simultaneous stabilization of the position of the first ring (r_1) which is always situated on the prosicula at some distance from its boundary with the metasicula. Such conditions are characteristic of *L. scanicus parascanicus, L. scanicus amphirostris* n. subsp. *L. scanicus scanicus, L. imitator* n.sp., *L. invertus* n.sp., *L. cirrifer* n.sp., *Cuc. hemiaversus* and *Cuc. aversus rostratus.* Thus, it should be stated that, except for *Cuc. pazdroi* which occupies a somewhat separated position among all other Cucullograptinae, the gracilization of the siculae (and probable foetalization of the siculozooid) was associated with a simultaneous change in the position of the first peridermal ring (r_1) and its displacement to the prosicula.

Changes observed in the displacement of r_1 in the Cucullograptinae may be best understood as an evolution by segregation of previously existing variability. A variable position, displayed by r_1 in stem lobograptids, may indicate that both factors (responsible for more and less apical position of this ring) were present in the genetic systems of their populations. From this ancestral pool of variability, only some factors were segregated and put into the pool of descendant populations. This had a corresponding bearing on the limitation of the range in their phenotypical variation (stabilization of the position of r_1 on the prosicula). Some factors were probably eliminated from the genetic system of more advanced cucullograptids which, on the whole, were characterized by a stable, apical position of r_1.

Certain facts may indicate that the process of these historical changes in the genetic structure of populations was gradual and rather long-ranged. Sporadic presence of r_1, situated precisely on the boundary of pro- and metasicula, observed in lower zonal populations of *Lobograptus scanicus parascanicus* (comp. Pl. XXII, Fig. A) and in *L. imitator* n.sp., may be indicative as to the presence of some "residual" genes, inherited from the ancestral pool. Similar conditions were noted in the lower zonal populations of "*Pristiograptus*" *bohemicus*, where specimens were found displaying r_1 situated on the prosicula (comp. Pl. X, Fig. D). In higher zonal forms this ring is almost invariably situated on the boundary with metasicula, and the same conditions are prevailing in populations of "*P.*" *bohemicus*, examined from the erratic boulders. In the history of this species, a shift in the population structure had an opposite direction as compared with the Cucullograptinae, but the nature of the processes was probably analogous.

A ringless condition, noted in siculae of some advanced cucullograptids, may be probably also derived from the ancestral variability of stem lobograptids, in spite of the fact that neither in *Lobograptus progenitor* n.sp., nor in *L. simplex* any ringless siculae were recorded so far. However, the examined siculae of both species are rather scanty and they doubtlessly represent an only small fraction of realized variation range. In many other monograptids, this range comprises, as is known, both ringed and ringless siculae. The suggested genetic mechanism of the appearance of ringless siculae in advanced cucullograptids from the variability pool of stem lobograptids may consist in: 1) an extremely unequal distribution of genetic factors among the descendant population, during the processes of separation of particular lines of evolution from a common ancestral stock; in some of them, therefore, the factors responsible for the formation of black rings on sicula are absent or very rare; 2) an elimination of corresponding genetic factors from the descendant populations effected by a natural selection; 3) both factors (1 and 2) combined.

The presence of slightly marked "vestigial" rings in certain siculae of *Lobograptus exspectatus exspectatus* (which, in most cases, are completely devoid of this character), may also suggest its descent from ancestral ringed forms (stem lobograptids).

In some cases, the displacement of the first peridermal ring to the prosicular segment makes the determination of the length of the prosicula difficult. This task requires well-preserved and bleached specimens in which the situation of the boundary between the pro- and metasicula may be directly determined. The observations, presented above, allow one to correct earlier data of Walker (1953, p. 224) who believed that, in *Lobograptus scanicus*, "the prosicula is probably that part above the first thickened band on the sicula..." Likewise, the length of the sicula of the *L. scanicus* group has been incorrectly estimated by Urbanek (1958, p. 73) who based this estimate on the situation of the first peridermal ring, while the fusellar part of the sicula is located only at some distance from it. Previously, I understood the lack of the fuselli directly below the first peridermal ring as a result of a poor preservation state. It has only been a recently investigated and excellently preserved material that allow me to correct this view.

EVOLUTION OF BLASTOZOOID THECAE

Thecal segments and their evolutionary changes

The thecae of the Graptoloidea consist of the following two constituent parts: 1) a proximal part or protheca which develops prior to the inception of a next theca and, generally speaking, makes up an equivalent of the stolotheca in the Dendroidea, as well as 2) a metatheca, that is a distal part, approximately corresponding to the autotheca of the Dendroidea. In forms in which a considerable mutual overlap of thecae is recorded, the dorsal wall of the metatheca consists of an interthecal septum and in others, whose metatheca is isolated, it has a dorsal wall of its own. In general, the metatheca in "Axonophora" may be defined as a segment of the thecal tube with both ventral and dorsal zigzag sutures, while the protheca has only a ventral one since the fuselli of the protheca are dorsally attached to the virgula. In the evolution of the Cucullograptinae, the prothecal segment is subject to relatively small changes which are only quantitative in character (changes in size and proportions). In *Lobograptus progenitor* n.sp. which seems to represent a primitive stage, the prothecae have the form of relatively wide tubes whose diameter considerably increases in growth (Pl. VII, Fig. 1), while in *L. simplex* they are subject to gracilization, become much slimmer and keep their diameter uniform over the entire length. Such a type of prothecae is represented by all other Cucullograptinae (Pl. VII, Figs. 2—12).

In the evolution of the Cucullograptinae, the differentiation of the metathecal segment is especially intensive. A few years ago, I have emphasized the fact that, in the case of the differentiation of the apertural apparatus, a general concept of a metatheca becomes too extensive (Urbanek, 1960, p. 146). The suggestion has, therefore, been put forwards to distinguish two components of the metatheca: 1) a subapertural part, and 2) an apertural part. The simply built thecae consists only of a protheca and a subapertural part of the metatheca (as e.g. in *Pristiograptus dubius*). In morphologically more complex graptolites, the thecal components, named above, are accompanied by an apertural part of the metatheca (*Monograptus priodon, Saetograptus chimaera, Lobograptus scanicus scanicus*, etc.).

The differentiation of thecae in the Cucullograptinae shows that the evolutionary changes consisted mostly in the modifications of the apertural part of a metatheca since the formation of a slightly outlined genicular bending of the ventral wall on the boundary of the pro- and metatheca in the distal thecae is the only noteworthy modification of the subapertural part of the metatheca. This is visible even in *L. simplex* and it is also recorded in *L. scanicus*, as well as, to a lesser degree, in *Cucullograptus*, while no tendency to produce such geniculation is observed in the *L. imitator* n. sp. — *L. cirrifer* n. sp. group.

Origin and evolution of apertural apparatus in bilaterally symmetric lobograptids

The origin and evolution of a complex apertural apparatus is one of the characters peculiar of the cucullograptids' development trend. The early stage of the origin and evolution of this apparatus may be investigated on forms making up the group of bilaterally symmetric lobograptids which, as S-cucullograptids[12], may be opposed to all other Cucullograptinae.

A fundamental structural type of the apertural apparatus in the Cucullograptinae consisted of paired apertural lobes, situated laterally on the margin of aperture. Each lobe was formed by single series of fuselli, laid down one over another, and thus devoid of a middle zigzag suture. This character distinguishes the apertural apparatus of the Cucullograptinae from hooked thecae of true monograptids in which the apertural lobe consists of two series of fuselli, united medially by a zigzag suture. All apertural apparatuses of the Cucullograptinae are derivatives of this fundamental structural type.

The apertural segment of the metatheca has probably had the initial form of two lateral and symmetric elevations, each of them consisting virtually of a single fusellus and typical only of the most distal thecae in *Lobograptus progenitor* n.sp. (Pl. III). On the other hand, more proximal thecae consisted only of a protheca and a subapertural segment of the metatheca (Pl. II, Fig. 1).

A more complex apertural apparatus of *Lobograptus simplex*, consisting of two distinct lateral lobes, each of them formed by many fuselli, may be derived from this incipient structure. Such lobes are formed in both proximal and distal thecae (Pl. II, Fig. 2; Pl. III; Pl. VIII, Fig. 2), i.e. they are recorded over the entire length of the rhabdosome.

The apertural apparatus in *Lobograptus exspectatus exspectatus* is marked by a certain hypertrophy of apertural lobes, but it may be derived from the apertural apparatus of *L. simplex* (Pl. III). The modification that took place in the phylogeny primarily amounts to the formation of a characteristic process, consisting of additional fuselli, in the anterior part of lobes and to the change in the outline of lobes. The apertural lobes in *L. exspectatus bicornis* n. subsp. may be considered a more specialized form of lobes of the type subspecies. This is expressed by a still stronger development of the anterior process and

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[12] An abbreviation of a term "symmetric cucullograptids".

by its bending (Pl. III). Lateral margins of a lobe in *L. exspectatus exspectatus*, characteristically extroverted form, in *L. exspectatus bicornis* n.subsp. strongly developed structures, protruding to the sidewards (Fig. 9).

Evolutionary changes in the apertural apparatus in S-cucullograptids may, therefore, be considered mostly as a gradual increase in the size of apertural lobes. This process consists in the occurrence of additional fuselli, increasing the area of a lobe, but, at the beginning, restricted to the ventral margin of a lobe (incomplete fuselli). Such stage is represented by *Lobograptus simplex*. Afterwards, such fuselli elongate and continue to occur along the entire margin of the lobe, thus increasing its area (complete fuselli). The formation of new fuselli and their gradual increase are the main factors of the development of apertural lobes.

Origin and evolution of asymmetry of apertural apparatus

An intensive development of apertural lobes in all advanced Cucullograptinae is always related with the asymmetry of this development. The asymmetry of the apertural apparatus in the Cucullograptinae is undoubtedly a secondary asymmetry (dissymmetry sensu Beklemishev, 1957, p. 47). This results from the following three facts: 1) a vast majority of the Graptoloidea are marked by the bilateral symmetry of their thecae and the elements of such symmetry are in general very strongly manifested in the structure of thecae; 2) the appearance of asymmetric Cucullograptinae is preceded by the occurrence of bilaterally symmetrical lobograptids; 3) in the ontogenetic development of thecae, the asymmetry appears in the last growth stages since the youthful thecae are still fully symmetrical.

The formation of the secondary asymmetry in the Cucullograptinae makes up an indubitably interesting phenomenon, rather rare among the Graptoloidea since "with minor exceptions, such as the apertural processes of certain monograptid species, a theca remains bilaterally symmetrical in the plane of the stipe, whatever modifications in form it may undergo" (Bulman, 1955, p. 46).

A divergence of the thecal asymmetry in the Cucullograptinae makes up its peculiar character. The following two types of asymmetry

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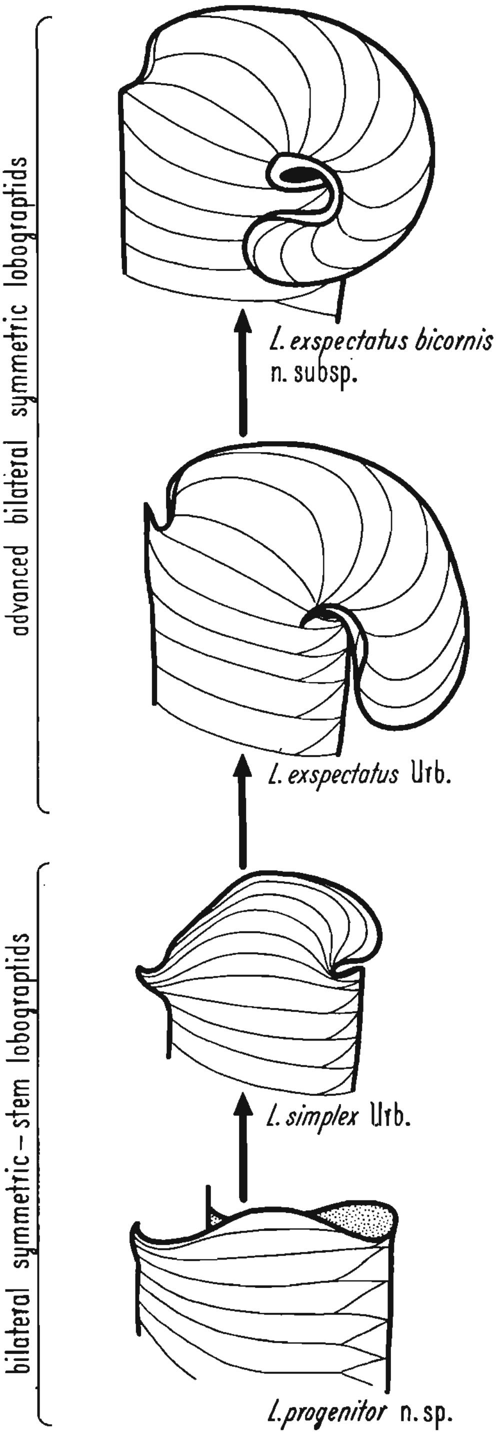
Plate III

Changes in size, shape and structure of apertural apparatus in distal thecae of bilaterally symmetric lobograptids (S-cucullograptids). Semidiagrammatic. Arrows indicate probable direction of evolution. Shape and structure of apertural apparatus for *Lobograptus exspectatus bicornis* n.subsp. are largely conjectural and restored on the base of medial and proximal thecae.

PLATE III


advanced bilateral symmetric lobograptids
bilateral symmetric-stem lobograptids
L. exspectatus bicornis n. subsp.
L. exspectatus Urb.
L. simplex Urb.
L. progenitor n. sp.

may be distinguished in asymmetric cucullograptids, 1) that, associated with a relative hypertrophy of the right-hand apertural lobe (R-cucullograptids), and 2) that, associated with a hypertrophy of the left-hand lobe (L-cucullograptids)[13].

All asymmetric species of *Lobograptus* without any exception (*L. scanicus parascanicus*, *L. scanicus amphirostris* n. subsp., *L. scanicus scanicus*, *L. imitator* n.sp., *L. invertus* n.sp. and *L. cirrifer* n.sp.) belong to the R-cucullograptids, while all representatives of *Cucullograptus*, identified so far (*Cuc. pazdroi*, *Cuc. hemiaversus*, *Cuc. aversus aversus* and *Cuc. aversus rostratus*) may be assigned to the L-cucullograptids. Thus, a distinct relationship is observed between a type of asymmetry and a general character of the structure of the apertural apparatus which determines the generic assignment of particular species. This fact allows one to assume that the asymmetry character in the Cucullograptinae was phylogenetically very stable and, in the evolution of this group, no tendencies were observed to the secondary inversion of asymmetry. In this respect, the evolution of this group of graptolites displays a certain analogy to the development of the pelecypods of the family Ostreidae which since the Triassic period have been marked by a stable and unchanged character, i.e. asymmetric hypertrophy of the left shell which is in contrast with a considerable lability of these conditions in other groups of pelecypods (Newell, 1960, p. 83).

The evolution of the thecal asymmetry in the Cucullograptinae is, however, marked by certain special features such as 1) a simultaneous occurrence of two different trends in the development of asymmetry (R- and L-cucullograptids), and 2) a generally progressive character of asymmetry, expressed by a) the formation of structural differences between the lobes in the case when no distinct increase in the difference in size of the lobes takes place in the phylogeny (R-cucullograptids) and b) the occurrence of several forms displaying regular stratigraphic sequence and, at the same time, an increase in the degree of asymmetry of the apertural apparatus in the case when a progressive increase in the difference in size does take place between particular lobes (*Cucullograptus hemiaversus* — *Cuc. aversus rostratus* line).

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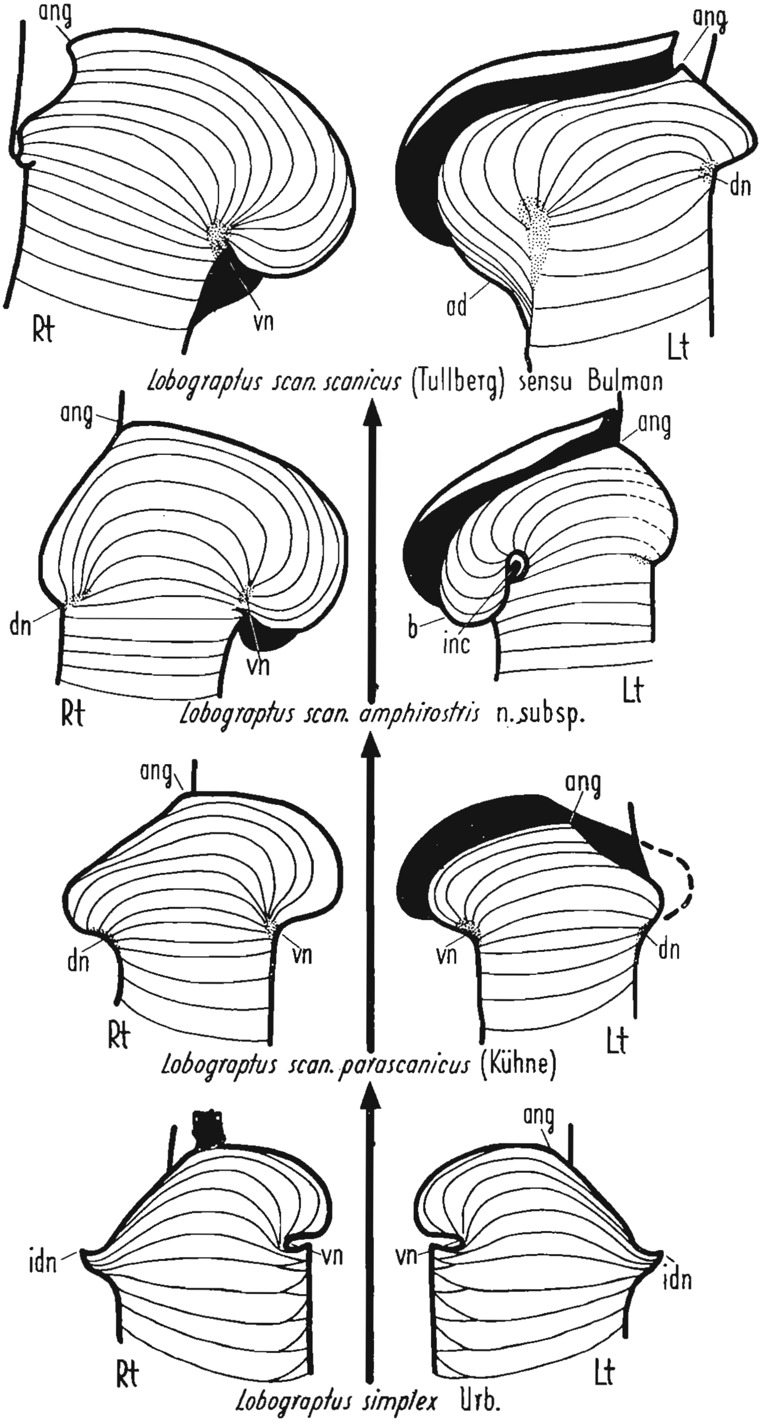
[13] *R* and *L* are abbreviations for right and left.

Plate IV

Changes in size, shape and structure of apertural apparatus in distal thecae for representatives of *Lobograptus scanicus parascanicus*—*L. scanicus scanicus* lineage. *L. simplex* shown for comparison as probable ancestor. Semidiagrammatic. Arrows indicate probable direction of evolution.

Rt right (reverse) view, *Lt* left (obverse) view, *ad* adapertural plate, *ang* angular bending of the upper margin of apertural lobe, *b* beak-like ventral termination of the lobe, *dn* — dorsal node, *idn* incipient dorsal node, *vn* — ventral node.

PLATE IV


ang
ang
dn
vn
ad
Rt
Lt
Lobograptus scan. scanicus (Tullberg) sensu Bulman
ang
ang
dn
vn
b
inc
Rt
Lt
Lobograptus scan. amphirostris n. subsp.
ang
ang
dn
vn
vn
dn
Rt
Lt
Lobograptus scan. parascanicus (Kühne)
ang
idn
vn
vn
idn
Rt
Lt
Lobograptus simplex Urb.

In the series, formed by the lobograptid sequence *Lobograptus scanicus parascanicus* — *L. scanicus amphirostris* n.sp. — *L. scanicus scanicus*, as well as *L. imitator* n. sp. — *L. inversus* n. sp. and *L. cirrifer* n. sp., no progressive increase is in truth observed in the asymmetry of the apertural apparatus, which are not more emphatically expressed by the differences in the lobe size but as a result of different structural modifications on the right-and left-hand lobe of more specialized forms (*L. scanicus scanicus*, *L. invertus* n.sp., *L. cirrifer* n.sp.). On the other hand, in the line of *Cucullograptus hemiaversus* — *Cuc. aversus aversus* — *Cuc. aversus rostratus*, an increased difference is observed in size and structure of both lobes. The presence of such series also indicates that both the R- and L-cucullograptids may be derived from primarily symmetrical lobograptids. Two divergent trends, manifested in the evolution of the asymmetry of the apertural apparatus, may be explained as a result of the evolutionary divergence. On the other hand, the subsequent gradual development of asymmetry in each phylogenetic lineage makes up an example of directional changes.

Differentiation of apertural apparatus in R-cucullograptids

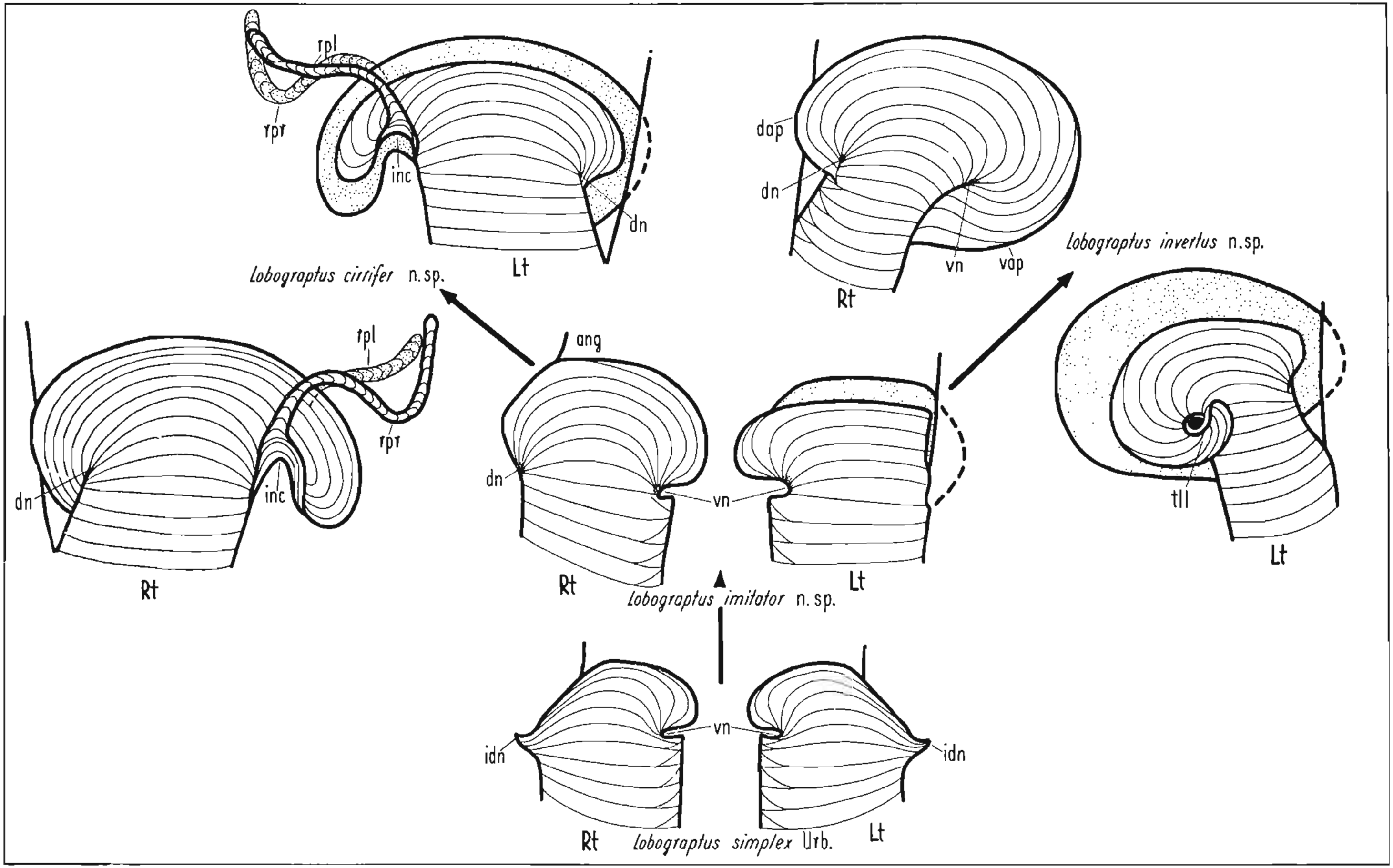
The differentiation of the apertural apparatus in asymmetric lobograptids is marked by: 1) a general tendency to a relative hypertrophy of the right-hand lobe, 2) a tendency to a partial overlap of the aperture by the upper margin of this lobe, and 3) a lack of a simultaneous tendency to the reduction of the left-hand lobe. In general, the character of the evolution may be summarized as follows: a hypertrophy of the right-hand lobe without a reduction of the left-hand lobe.

Among the R-cucullograptids, two groups of species may be distinguished which probably make up two different lines of evolution. In the *L. scanicus* species group (with three subspecies), the evolution of the apertural apparatus is limited only to a differentiating increase in the size of apertural lobes, resulting in the hypertrophy of the right-hand lobe with simultaneous slight modifications in the fusellar structure and shape of lobes (Pl. IV). In general, these changes consist in adding new fuselli to the anteroventral part of the lobes. Initially, these fuselli are incomplete (short) but, hereafter, they lengthen over

Plate V

Changes in size shape and structure of apertural apparatus in distal thecae for representatives of *Lobograptus imitator* n.sp. — *L. cirrifer* n.sp. lineage. *L. simplex* shown for comparison as probable ancestor. Apertural apparatus in *L. imitator* partly conjectural and restored on the base of medial thecae.

dap dorsal adapertural plate, *inc* incision of ventral apertural notch, *lpl* rostral process of the left lobe, *rpl* rostral process of the right lobe, *tll* termination of the left lobe, *vap* ventral apertural plate. Further explanations-as in Pl. IV.


rpl
rpr
inc
dn
Lt
Lobograptus cirrifer n. sp.
dap
dn
vn
vap
Rt
Lobograptus invertus n.sp.
tpl
rpr
dn
inc
Rt
ang
dn
vn
Rt
Lt
Lobograptus imitator n. sp.
tll
Lt
vn
idn
idn
Rt
Lobograptus simplex Urb.
Lt

the entire free margin of the lobe. This process also causes changes in the outline of the lobe. At first, both lobes terminate anteroventrally in a short outgrowth (in *L. scanicus parascanicus* and *L. scanicus amphirostris* n.subsp.) and, subsequently, the left-hand lobe of the distal thecae of *L. scanicus scanicus* fuses with the ventral wall of the metatheca, forming a corresponding adapertural plate (*ap.*). At the same time, the upper margin of the lobe overlaps the aperture and partially covers the left-hand apertural lobe.

A somewhat different type of an apertural apparatus was developed in the *Lobograptus imitator* n. sp. — *L. invertus* n. sp. — *L. cirrifer* n. sp. group. *L. imitator* n. sp. represents a stage of the development of lobes and of their symmetry which, on the whole, is analogous to that in *L. scanicus parascanicus*, except for certain differences in the shape of lobes (Pl. V). Such an apertural apparatus may be derived from that of *L. simplex*. Apertural apparatus in *L. invertus* n. sp. and *L. cirrifer* n. sp. were probably developed from apertural apparatus found in *L. imitator* n.sp. (comp. p. 371). In the former, an intensive development of both apertural lobes is noted with a distinct hypertrophy of the right-hand lobe which becomes much larger than the left-hand one. This lobe develops two well-outlined adapertural plates which are formed by the fusion of the lobe with the dorsal and ventral wall of metatheca (Pl. V, *dap, vap*). The adapertural plates are, therefore, connected with the right-hand lobe, i.e. in the opposite way as in the case of *L. scanicus scanicus* (hence its name, "*invertus*" — inverted). On the other hand, the left-hand lobe which is markedly smaller, has a well-developed ventral process in the form of a bent beak whose internal margin is strongly extroverted (Pl. V, *tll*).

A particular attention should be paid to the apertural apparatus of *Lobograptus cirrifer* n. sp. which, in addition to paired lateral lobes with a distinct hypertrophy of the right-hand one, consists of slender rostral processes, resembling bent spines (Pl. V, *rpl, rpr*). This is an additional structure which cannot be compared with other apertural parts of metatheca in R-cucullograptids. In distal thecae, each rostral process grows out of the extroverted margin of an apertural incision of each lobe (Pl. V, *inc*), constituting a sort of a supraapertural structure, formed on apertural lobes. *L. cirrifer* n. sp. is marked by the most complex apertural apparatus among the R-cucullograptids. Proximal thecae are characterized by a lower degree of development of rostral processes and even, in extreme cases, the process of the right-hand lobe may only be expressed by a small protuberance and that of the left-hand lobe — by a short spine (Pl. II, Fig. 9). The rostral processes are formed as a result of the superposition of arched and short fuselli.

A relative stability of asymmetry, distinctly marked in both the astoand phylogeny, is a feature characteristic of the evolution of the apertural apparatus in R-cucullograptids. There is no clear tendency to a progressive increase in the difference in size of apertural lobes in both the development of a colony of a given species and in the evolution of particular phylogenetic lineages (comp. pp. 347—350).

Differentiation of apertural apparatus in L-cucullograptids

The pattern of differentiating the apertural apparatus in *Cucullograptus* is marked by, 1) a general tendency to the hypertrophy of the left-hand apertural lobe, with 2*a*) a tendency to a simultaneous reduction of the right-hand lobe (the *Cucullograptus hemiaversus* — *Cuc. aversus* group with two subspecies), or 2*b*) without a simultaneous tendency to the reduction of the left-hand lobe (as in *Cuc. pazdroi*).

The divergent tendencies, mentioned above (2a and 2b), seem to allow one to consider both differentiation trends to be different phylogenetic lineages, derived — independently from each other — from symmetric ancestors (comp. p. 369). The *Cuc. hemiaversus* — *Cuc. aversus aversus* — *Cuc. aversus rostratus* group in which a regular sequence of forms is observed, which are marked by an ever increasing hypertrophy of the left-hand and a simultaneous reduction of the right-hand lobe, seems to be a particularly remarkable and interesting group. The most primitive structural stage is represented by *Cuc. hemiaversus* in whose distal thecae the left-hand apertural lobe is strongly developed and, to a considerable extent overlaps the aperture, covering about 2/3 of the margin of the right-hand lobe (Pl. VI). The right-hand, much smaller lobe, covered by the overlaping left-hand lobe, is subject to a partial reduction, represented by the formation of a marginal incision whose extroverted margins make up an apertural lip, hidden under the overlapping left-hand lobe. It is only $^{1}/_{3}$ of the right-hand lobe that has an entire margin. As a result, the area of the right-hand lobe is considerably decreased. In proximal thecae, the degree of asymmetry of the lobes is conspicuously lower and, in the most proximal ones, both lobes are almost identical in size. Correspondingly, the left-hand lobe only slightly overlaps the aperture and the margin of the right-hand apertural lobe is complete (Pl. VI).

A more advanced stage in the evolution of the apertural apparatus seems to be represented by *Cucullograptus aversus aversus*, described by Eisenack (1942). On the basis of this author's drawings, the apertural apparatus of distal thecae in this species may be reproduced in a form, shown in Pl. VI. The left-hand apertural lobe in *Cuc. aversus aversus* completely overlaps the aperture and, consequently, covers the right-hand lobe. The latter, subject to reduction, transforms, over the entire length of the right-hand apertural margin, into an extroverted apertural lip. It represents a more advanced stage of the same process of reduction whose initial stage is represented by the distal thecae in *Cuc. hemiaversus*. The apertural lip, corresponding to a vestigial form of the right-hand lobe, is formed over its entire length. As a result of a strong vaulting and overlap, the left-hand apertural lobe takes the form of a helmet with the anterior part of the lower margin characteristically turned inwards (Pl. VI, arrow). It is noteworthy that in *Cuc. aversus aversus* the proximal thecae are also marked by a distinct asymmetry, caused by the overlap of the right-hand by the left-hand lobe and by the reduction of the right-hand lobe to the form of an apertural lip.

In a structural stage, represented by *Cucullograptus aversus rostratus*, the left-hand apertural lobe is subject to further modifications (Pl. VI). There is an increase in the degree of the introversion of the anterior left-hand lobe margin which results in the formation of a distinct gular plate (*gp*), while clearly outlined eaves are formed by the posterior margin. The most important modification consists, however, in the formation of certain additional structures, such as a rostral process in the anterior part of the left-hand lobe and a structure, called in the present monograph, a "gorget" (*g*), which is developed along the free lateral margin of this lobe. The rostral process is formed as a result of the superposition of a number of short, arched fuselli, while "gorget" consists of thin fuselli concrescent with the lateral margin of the left-hand lobe and with the margin of the gular plate. Both the rostral process and "gorget" make up superstructures, formed secondarily on the apertural lobes. i.e. they constitute supra-apertural structures like rostral processes in *Lobograptus cirrifer* n. sp. The right-hand lobe in all thecae is developed in vestigial form, i.e. as an apertural lip. The proximal thecae in *Cuc. aversus rostratus* slightly differ from those in type subspecies. It is only in some populations that the presence of an additional element, a so-called pectoral crest (*pc*) is observed on the ventral side of the theca, which is more strongly developed on proximal than on distal thecae.

The apertural apparatus of *Cucullograptus pazdroi* makes this species quite different from all other representatives of the genus *Cucullograptus*. However, there are the following two characters common for this species and for the remaining species of the genus *Cucullograptus:* 1) a hypertrophy of the left-hand lobe, and 2) a domed shape of the left-hand lobe which takes the form of a cone or a hood. On the other hand, there are the following three special characters: 1) a strong transverse elongation of the internal aperture itself which takes a slit-like form, 2) a lack of the tendency to the reduction of the right-hand lobe which, although smaller, cannot be considered as a reduced one, 3) a convex shape of the right-hand lobe (while in other Cucullograptinae it is flat). *Cucullograptus pazdroi* is probably a representative of a separate evolutionary lineage whose relationship to other Cucullograptinae is not quite clear so far (comp. p. 369 and Pl. VI).

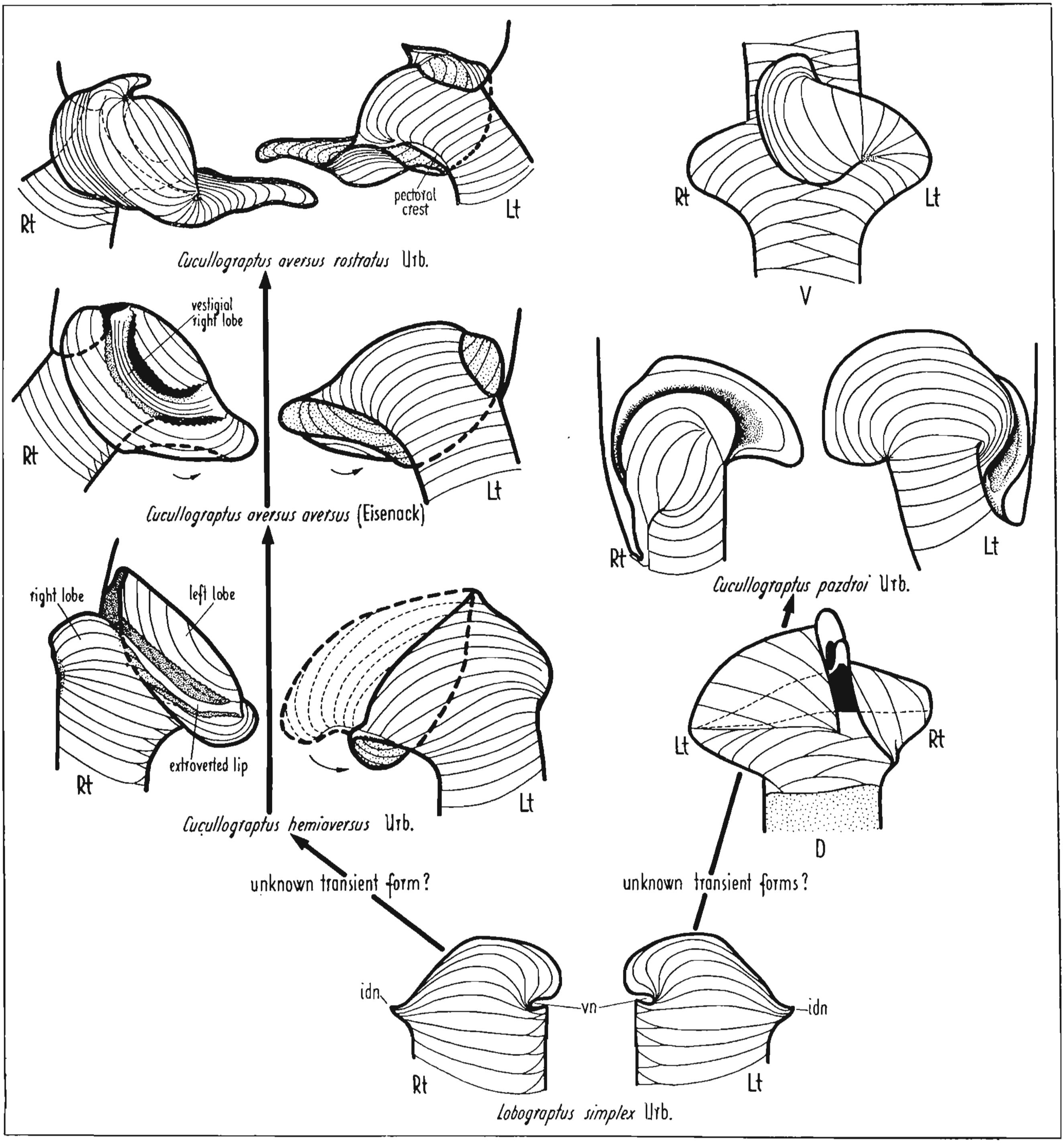
The existence of internal walls, i.e. the ventral internal wall which, making up an extension of the right-hand lobe, penetrates inside the left-hand lobe and the dorsal internal wall, extended inside the right-hand lobe (comp. Pl. XLVI, Figs. A-D) is a characteristic feature of the *Cucullograptus pazdroi* apertural apparatus. The left-hand lobe strongly overlaps the apertural slit, covering it to about $^1/_2$ of its entire length. It is provided with a strongly developed, broad ventral process which, on the upper margin, is transformed into an extroverted marginal brim. The right-hand lobe is devoid of such a process, having only an extroverted marginal brim, formed along the upper margin of the lobe. Like the left-hand lobe, it overlaps the apertural slit and covers it also to about $^1/_2$ of its length. The fusellar structure of the apertural apparatus in *Cuc. pazdroi* is discussed on pp. 524—528, and shown diagrammatically on Fig. 26.

Functionally, the apertural apparatus in *C. pazdroi* was certainly a very specialized structure. Its peridermal covers, in addition to their protective functions, probably played the role of specific "hydrodynamic tunnels", which determined an appropriate flow of water currents close to the lophophore (Urbanek, 1958, p. 25).

An attempt to interprete the evolution of the apertural apparatus

The entire picture of the evolution of thecae in the Cucullograptinae testifies in a very clear manner to the concentration of these transformations in the apertural segment of the metatheca with a relatively high stability of other thecal parts. Such nature of the evolutionary transformations allow one to conclude as to their adaptive significance. By the analogy to Pterobranchia to which graptolites are most closely related, one may assume that both the aperture and the apertural apparatus were closely connected with the lophophore, mouth and probably also preoral lobe of zooids. Definite modifications in the apertural apparatus were surely closely connected with the development of various feeding mechanisms. Furthermore, they probably corresponded to different forms of the lophophore in which the apertural structures might play the role of appropriate supports or screens which determined the flow of functional currents near the mouth. Perhaps, the hydrodynamic and the supporting-protective significance of the apertural apparatus should be taken into account alike.

PLATE VI



Changes in size, shape, and structure of apertural apparatus in distal thecae of *Cucullograptus*. Apertural apparatus in *Cuc. aversus aversus* restored on the base of Eisenack's figures (1942. Pl. 2, Figs. 1—2). In *Cuc. hemiaversus* and *Cuc. aversus aversus* the internal part of the right lobe is shown as seen through artificial fissure made in the left lobe. In *Cuc. aversus rostratus* same structure is outlined as being visible through the transparent left lobe and marked by broken lines. *V* ventral view, *D* dorsal view. Further explantations as on Plate IV.

The accumulation of the majority of evolutionary transformations on the apertural segment of the theca testifies, therefore, to a decisive importance of the feeding mechanisms for the determination of the main adaptive trends in the Cucullograptinae. It is worth while to repeat here the comparison, already cited before (Urbanek, 1960, p. 201), with the differentiation picture, displayed by famous finches from the Galapagos Islands ("Darwin's finches") (Lack, 1947; Bowman, 1961) in which, as a result of the adaptation to a definite food, the bill and head are mostly affected by the modifications while other characters of the body (such as e.g. the plumage) are much less changed. Likewise, the specialization of fishes, belonging to the family Cichlidae from Great African Lakes (e.g. *Haplochromis* from Lake Victoria) is primarily expressed in modifications, observed in the head and jaws, while other parts of the body are not subject to any major changes (Worthington, 1940).

In all these cases, there is the question of evolutionary processes in which a key, decisive role is marked of the adaptation of the food intake organs and which, as a result of the differentiation, bring about immediate changes in structure, limited virtually to one only part of an animal's body. In considering such processes, certain analogies occur to the problem of the so-called "key", or "determining" characters of organization, being of a decisive importance for the determination of the main evolutionary trends in particular groups of organisms. Opinions, indicating the existence of the adaptive characters of such type, have been expressed by Ruzhencev (1947), Rodendorf (1957) and Ivanov (1960). From the standpoint of the problem we are interested in, the most important are the latter autor's views, based on the studies on the Pogonophora because they supply us with the most direct analogy to the evolution of the Cucullograptinae. According to Ivanov (1960): "A general structural pattern in different orders and families of the Pogonophora is marked by a considerable stability, while a high degree of variation is displayed by their tentacular apparatus. As a result of a very important physiological role of tentacles..., the evolution of the Pogonophora was primarily related with a progressive development of the tentacular apparatus which, in their phylogenetic evolution, constitutes a 'key system of organs". It is precisely for this reason that the structure of this apparatus supplies us with the most important taxonomic characters necessary to characterize families and genera" (*l.c.*, p. 104). Moreover, Ivanov states: "It is beyond any doubt that tentacles fulfill functions very important in the life of an individual. The structure of the tentacular crown is variable in different forms, while the rest of the organization is marked by a relatively high degree of stability. It is precisely the tentacular apparatus that makes up a "key system of organs" in the evolution of the Pogonophora and supplies several important taxonomic characters that allow one to distinguish families and genera" (*l.c.*, p. 65).

The considerations, presented above, allow one to presume that the tentacular apparatus (the lophophore) was, also in the case of the Cucullograptinae, that "key system of organs". As a matter of fact, the occurrence of similar phenomena is not limited only to the Pogonophora and graptolites but to an equal degree of correctness they may be applied to many other groups of microphagic invertebrates, such as the Pelmatozoa in which (e. g. in the Cystoidea and Crinoidea) an essential role of the feeding system is marked by different complications of brachioles and arms.

Obviously, in each group of the "lophophorate invertebrates", the evolution of the tentacular apparatus followed its own, separate way. In this connection, the development of a complex, peridermal apertural apparatus and the formation of its asymmetry are characters, peculiar to the Cucullograptinae.

The asymmetry of the apertural apparatus of thecae seems to reflect the asymmetry of the tentacular apparatus only, while the progressive development of apertural lobes testifies to a similar development of the lophophore (Urbanek, 1960, p. 183). One may believe that, in the evolution of the Cucullograptinae, the progressive development of the tentacular apparatus was mostly correlated with the formation of its asymmetry. *Lobograptus progenitor* n.sp. and *L. simplex* were probably provided with a symmetrical but relatively slightly developed tentacular apparatus. A higher degree of the development of the tentacular apparatus, with its bilateral symmetry preserved, is a character of only *L. exspectatus* with its two subspecies, while all other Cucullograptinae were probably marked by an intensive development of the tentacular apparatus and by its asymmetry. It may be presumed that the formation of asymmetry of the tentacular apparatus was to a certain extent a basis for its continued, progressive differentiation. A similar process has been recorded in the Pogonophora of which *Spirobrachia*, marked by highly developed tentacular crown, displayed a strong hypertrophy of the right side of the base of tentacles (Ivanov, 1960, pp. 24—25). Ivanov believes that the complex and asymmetric tentacular apparatus of *Spirobrachia* (having as many as to 223 tentacles!) was formed, by the polymerization, from the simple and symmetrical tentacular apparatus, resembling that in the genus *Heptabrachia* (6—8 tentacles!). Similar processes of the development of the tentacular apparatus and of its asymmetry might take place in the Cucullograptinae. In this connection, the occurrence of the elements of asymmetry in Pterobranchia is of a considerable significance. *Rhabdopleura* is marked by a more intensive development of the base of the right-hand lophophore, forming the so-called "oral lamella" (Schepotieff, 1907). Likewise, the organs of metasome (anus, gonopore and gonad) are shifted to the right. The asymmetry of the body in *Rhabdopleura* is not, however, manifested in the structure of the theca and may be termed, a "latent asymmetry". Maybe, in the blastogenesis of asymmetric Cucullograptinae, a similar degree of asymmetry was manifested by the young zooid and during its continued growth this asymmetry was increasing until it reached a stage which caused an asymmetric development of the peridermal apertural apparatus. Certain differences were displayed in the development of the tentacular apparatus in the R- and L-cucullograptids. In the R-cucullograptids, the left-hand lobe of the apertural apparatus is only smaller but is not subject to reduction. One may presume that the asymmetry in the tentacular apparatus was also expressed only by the hypertrophy of the right side (as in asymmetric Pogonophora) without, however, a simultaneous reduction or atrophy of the left side of this organ.

This unequality in the degree of the development of the tentacular apparatus in the R-cucullograptids did not preclude a subsequent progressive differentiation of both the right- (hypertrophic) and left-hand (normal) part of this apparatus. This may be testified to by the formation of supraapertural additional structures (rostral processes), formed on both lobes in *Lobograptus cirrifer* n.sp. The fact should be emphasized that, in the proximal thecae, the rostral process on the left-hand lobe is even somewhat better-developed than that on the right-hand lobe. The asymmetry of the tentacular apparatus in the R-cucullograptids consists, therefore, in the hypertrophy of the right side of the tentacular apparatus without the reduction of its left side. Perhaps, a relatively stable character of the asymmetry of the apertural apparatus in the R-cucullograptids may be ascribed precisely to this fact (comp. pp. 347—350) because in both the astogeny of the colonies of particular species and phylogeny of separate evolutionary lineages, the degree of asymmetry of apertural lobes, determinated by the differences in their size, was always almost stable and did not displayed distinct progressive tendencies.

A principle of compensation should be considered as a basis for the development of the asymmetry of apertural apparatus. The hypertrophic part of the apparatus compensates the physiological role of the less-developed part so that together they play, to a full extent, the role which otherwise should be divided between two completely symmetrical parts of the lophophore.

The significance of the morphophysiological compensation as a mechanism of the progressive development of the lophophore is yet more clearly marked in those L-cucullograptids in which the reduction takes

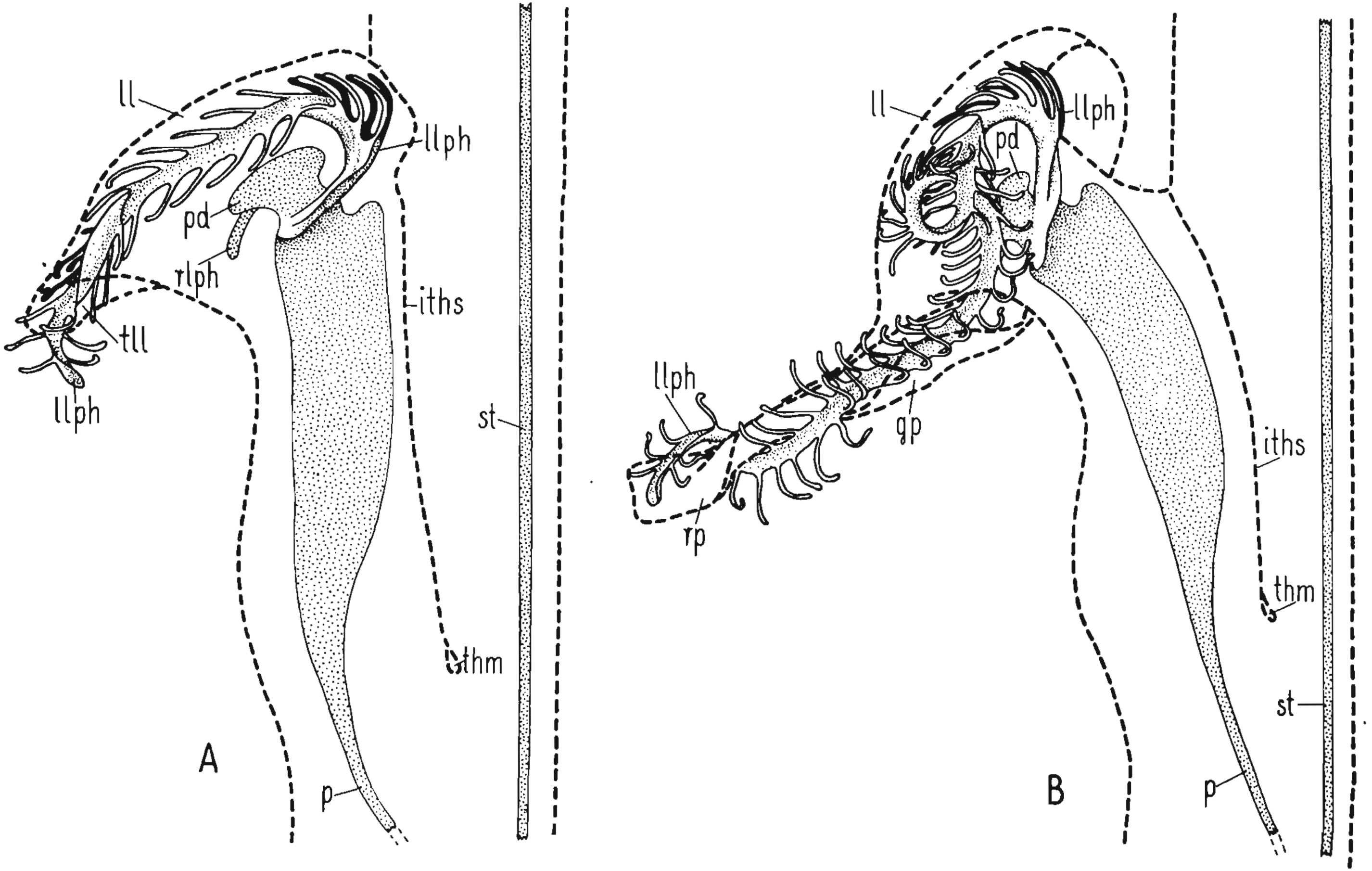


Fig. 2. — Ideogram to show general relations between supposed structure of the lophophore and the apertural apparatus in *Cucullograptus hemiaversus* (*A*) and *Cuc. aversus rostratus* (*B*). Note the presence of vestigial right lophophore (*rlph*) in *A*, and strongly hypertrophied left lophophore (*llph*) in *B*. *gp* gular plate, *iths* interthecal septum, *ll* left apertural lobe, *llph* left lophophore, *p* peduncle of the zooid, *pd* preoral disc of the zooid, *rlph* right lophophore, *rp* rostral process, *st* stolon, *tll* termination of the left lobe, *thm* thickened margin of interthecal septum.

place of the right-hand apertural lobe. It may be assumed that this was accompanied by a remarkable underdevelopment of the right-hand part of the tentacular apparatus (as in a stage, reached by *Cucullograptus hemiaversus*) and probably its subsequent atrophy (as in a stage, represented by *Cuc. aversus*). The gradual reduction of the right-hand part of the tentacular apparatus is closely related with a simultaneous compensative increase and hypertrophy of the left-hand part of this apparatus. The interpretation, presented here for the evolution of the *Cuc. hemiaversus* — *Cuc. aversus rostratus* series, is illustrated in Fig. 2. The aim of this interpretation is not so much an attempt at a reconstruction of the soft parts of graptolites, belonging to this series, as a graphic presentation of the idea of the most general relationships that occur between the degree of the development of the tentacular apparatus and the peridermal apertural apparatus. A particularly strong hypertrophy of the left-hand part of the tentacular apparatus was a character that surely marked *Cuc. aversus rostratus* and which may be estimated on the basis of the development degree of a corresponding apertural lobe.

The case of an extreme oligomerization of the tentacular apparatus in *Siboglinum* (Pogonophora), in which it is represented by one only tentacle (originally, the right-hand one) (Ivanov, 1960) makes up a certain analogy to the processes, described above. This tentacle is, however, very strongly elongated and this fact may be ascribed to the morphophysiological compensation. In the development of the *Cucullograptus hemiaversus* — *Cuc. aversus rostratus* lineage, the physiological role of the right-hand part of the lophophore was compensated by a secondary development of its left-hand part which was beginning to fulfill the physiological functions as a substitute for both parts of the lophophore (Urbanek, 1960, p. 184).

It should be, therefore, assumed that the progressive evolution of the apertural apparatus in the *Cuc. hemiaversus* — *Cuc. aversus rostratus* lineage was related with an apparently paradoxical sequence of events which, in the first phase of the process, included the oligomerization of the tentacular apparatus, taking place as a result of the reduction of the lophophore on the right side of the animal. This process evoked a compensative growth (hypertrophy) of the same organ on the left side of the zooid. Such a course of the evolution of the *Cucullograptus* lophophore, resembles to a considerable extent, the character of the oligomerization processes, occurring in the tentacular apparatus of some Coelenterata (polyps and medusae of the Hydrozoa). In analyzing these processes, Dogiel (1954, p. 21) states: "Obviously, the oligomerization of the number of tentacles to 2 or 1 exceeds the optimum limits for the species since such a decrease in their number will unfavourably rebound on an animal's capability to catch its food. In this connection, such species develop lateral or terminal branchings on the tentacles, thus increasing their prehensility. As a matter of fact, a return to the multitentacular stage occurs in this case but, according to Dollo's law, it takes place in a new manner. This phenomenon may be called a phenomenon of restitution, or compensation for the organs, lost as a result of the oligomerization".

The interpretation of the apertural apparatus in *Cucullograptus pazdroi* from the standpoint of similar assumptions, is, however, fairly difficult. Despite the fact that this apparatus was asymmetric and that it was marked by hypertrophy of the left-hand part, both the left- and right-hand part of the lophophore, were in this species subject to a strong, progressive differentiation as compared with the state which was peculiar to its presumably primitive ancestors. The transverse elongation of a fissural aperture might be related with the existence of a relatively narrow base of arms (a single one on each side?) which were branching only above this base. There is also the possibility that the development of this apparatus was not related with the secondary polymerization of the lophophore arms but rather with its secondary ramification.

EVOLUTION OF ASTOGENY

Astogenetic differentiation of thecae in the Cucullograptinae

The polarity, represented by the variation in the size and structure of thecae, different in the proximal and distal parts of each colony makes up a characteristic feature of the rhabdosomes in the Graptoloidea. Since these differences are, however, reached gradually through the directional changes in the structure and shape of thecae, it is impossible to trace the boundaries between the proximal and distal parts of the rhabdosome. The adjacent thecae differ from each other only very slightly but these differences increase gradually and in the definite direction. The successively budding zooids form thecae which display a gradual and directional morphological succession. The organization of a graptolite colony is, therefore, determined by the occurrence of morphological gradients, responsible for their polarity (Urbanek, 1960).

A glance at the enclosed reconstructions of colonies, consisting of the fragments of the rhabdosome that come from different species of the Cucullograptinae, allows one to believe that the statements, made above, are fully justified (Pl. VII).

In symmetrical lobograptids (Pl. VII, Figs. 1—3), the astogenetic varation of thecae is expressed by changes in their size and proportions. Proximal thecae are somewhat shorter (*long.*) and considerably thinner (*tr.*) than distal ones. The metathecal part of a theca is, in proximal thecae, much shorter (*long.*) absolutely, as well as in relation to the prothecal part, and the entire length (*long.*) of a theca. This causes a regular decrease in the protheca/metatheca length ratio, recorded in the astogeny. The overlap of thecae increases regularly and gradually towards the distal end which in fact is closely correlated with the elongation of the metathecal part and a simultaneous lack of its isolation. In the symmetrical lobograptids, having the apertural apparatus, its astogenetic variation is mainly manifested by a change in the size of lobes which increases towards the distal end and by slight changes in their shape. Generally speaking, these changes occur, however, only on a small scale. With regard to the changes in the direction of the growth of the rhabdosome, it is worth mentioning that a distinct, although not very strongly marked bending is observed in the dorsal proximal part. The distal part of the rhabdosome is straight or slightly curved ventrally (Pl. VII, Figs. 1—2).

In asymmetric cucullograptids, the subapertural parts of thecae display a virtually very similar astogenetic variation (Pl. VII, Figs. 4—12). However, in addition to this basic variation, there is also a variation of the apertural part of thecae. Distally, an increase is observed in the degree of asymmetry of one of the lateral apertural lobes (Pl. VII, Figs. 4—12). In ever more distally situated thecae this lobe gradually covers the aperture, overlapping of apertural lobe of the opposite side. If, in addition to the apertural lobes, there are other accessory structures (rostral processes), they increase their dimensions distally (Pl. VII, Figs. 9 and 11). In some cases, a complete lack of these structures may be recorded in proximal thecae, an incipient form on the thecae of the medial part of the rhabdosome and the greatest development — on distal thecae (Pl. VII, Fig. 11).

It was only in exceptional cases that the growing tips of the rhabdosome were found in the material investigated. Such specimens allow one to understand the relationships of growth rates between particular budding individuals. Here, we may distinguish two main types of the growing tips of the rhabdosome. In type 1, found in *Lobograptus exspectatus exspectatus* and in *Cucullograptus aversus rostratus*, only the penultimate theca reaches its final growth stage at the same moment when the growth of the last theca only begins and this is the reason why the growing tip of the rhabdosome consists here of a fully developed penultimate theca and of a barely budding last one which is formed only by the proximal part of a protheca (Figs. 8 and 23). In type 2, represented by *L. scanicus parascanicus*, the rhabdosome tip consists of as many as 5 growing thecae of which thecae 1—3 have their apertural apparatus in different growth stages, theca 4 consists only of the subapertural segment and is without apertural lobes which have not yet started their growth, while theca 5 is represented by the proximal part of the protheca. Thus, a series of thecae in different growth stages are formed on the terminal part of the stipe (Pl. XXIV, Fig. E).

Such great differences in the structure of the terminations of growing stipes occurring among particular species of the Cucullograptinae may testify to a high degree of the variation, recorded in the morphogenetic conditions of their growth.

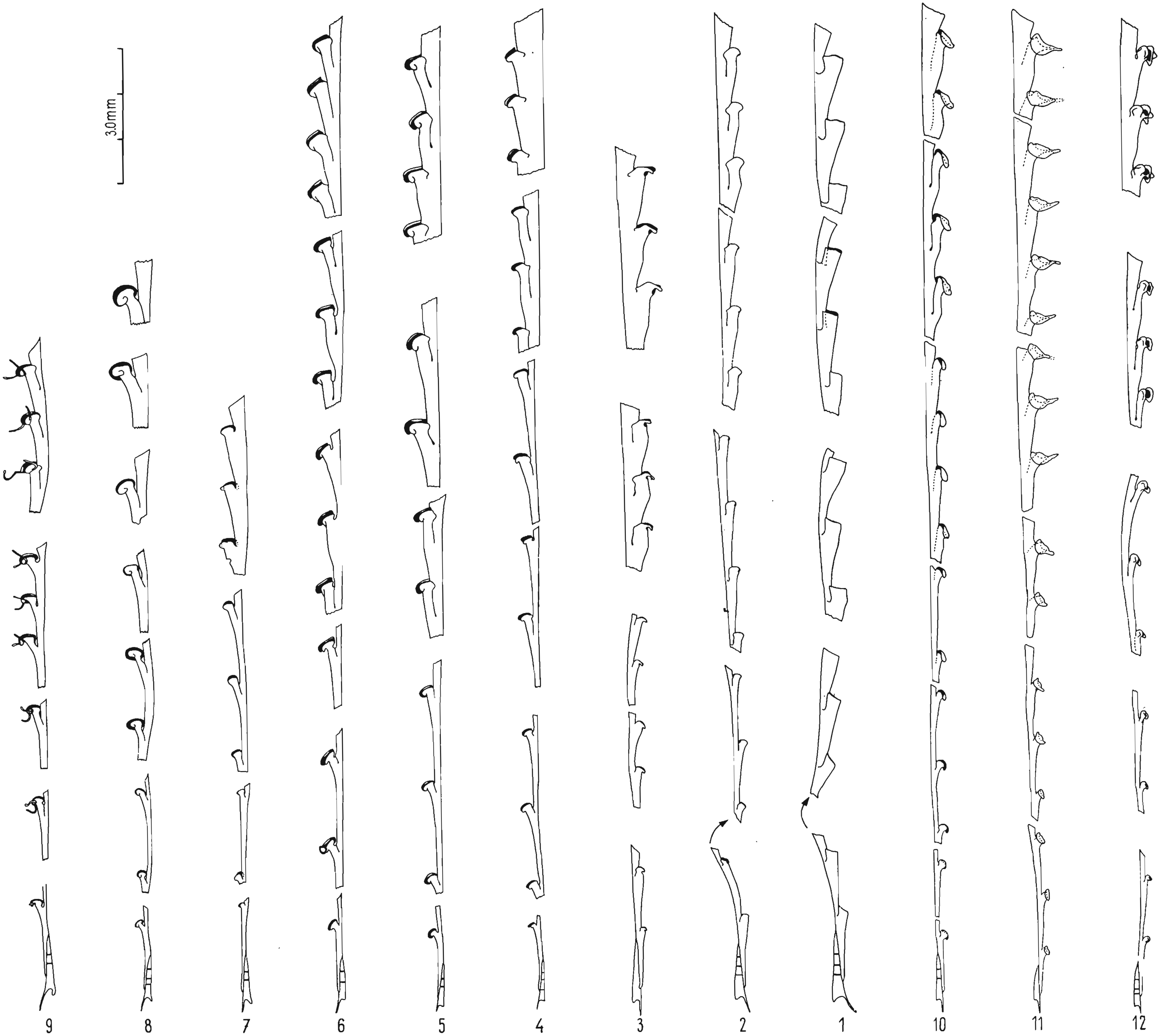
Principle of the distal introduction of phylogenetic novelties

On the basis of a comparison of the astogenetic development in several species of the Cucullograptinae, related with each other one may state that: 1) the greatest extent of variation is displayed by the distal thecae, while the proximal thecae differ from each other to a much lower degree; 2) the majority of morphological characters of the apertural apparatus are developed to the greatest extent in distal thecae, while in the proximal thecae these characters are much less distinctly expressed or even do not occur at all. It is precisely this different degree of manifesting the characters in the distal and proximal thecae that is decisive of a distinct polarity of the colonies of the Cucullograptinae (Urbanek, 1960). One may presume that the structure of individuals in the most proximal differed in many respects from that in the most distal part. In particular, this concerned probably the size and proportions, as well as the structure of the tentacular apparatus. In general, the individuals of the distal part of a colony were marked by a higher degree of modification of the primary structure of the zooids than the individuals of the proximal part. The degree of the variation of individuals decreased gradually and regularly in the proximal direction which caused the occurrence, in the colonies of the Cucullograptinae, of corresponding morpho-physiological gradients (Urbanek, 1960). Plate VII gives a convincing morphological picture which confirms the correctness of the idea of gradients as applied to the colonies of the Cucullograptinae.

The facts, discussed above, allow one to settle a presumable pattern of phylogenetic modifications of astogeny, i.e. to settle a mode of phylastogeny (Urbanek, 1963, p. 237). It seems that the evolutionary changes in the structure of the theca (mostly of its apertural apparatus) took place through the initial introduction of phylogenetic novelties from the distal end of the rhabdosome. In this respect, now, the Cucullograptinae supply the best investigated and very convincing examples of the distal introduction of evolutionary changes in the structure of thecae.

The formation of apertural lobes (in *Lobograptus progenitor* n. sp.), asymmetry and hypertrophy of a definite apertural lobe (the right-hand

PLATE VII



Changes in size and shape of thecae in the course of astogeny in the Cucullograptinae. *1* — *Lobograptus progenitor* n.sp., *2* — *L. simplex*, *3* — *L. exspectatus exspectatus*, *4* — *L. scanicus parascanicus*, *5* — *L. scanicus amphirostris* n.subsp., *6* — *L. scanicus scanicus*, *7* — *L. imitator* n.sp., *8* — *L. invertus* n.sp., *9* — *L. cirrifer* n.sp., *10* — *Cucullograptus hemiaversus*, *11* — *Cuc. aversus rostratus*, *12* — *Cuc. pazdroi*. Arrows in *1* and *2* indicate the presence of bending in proximal part of rhabdosome. Somewhat diagrammatically.

one in R-cucullograptids and the left-hand one in L-cucullograptids) and increase in the size of apertural lobes (in all Cucullograptinae above the level of *L. progenitor* n. sp.) may serve as examples of characters which appeared in particular evolutionary lines as modifications, at first limited to the distal part of the rhabdosome only. In addition, in various phylogenetic lines certain special characters of the apertural apparatus are added which are peculiar only to these lines. They also appear according to the principle of the distal introduction. The formation of an adapertural plate on the left-hand lobe in *L. scanicus scanicus* (not yet developed in *L. scanicus amphirostris* n. subsp. and in *L. scanicus parascanicus* n. subsp., as well as on proximal thecae of *L. scanicus scanicus*) is among these additional characters. Rostral processes in *L. cirrifer* n. sp. also make up a character which was presumably introduced from the distal pole of the rhabdosome.

The hypertrophy of the left-hand and the reduction of the right-hand apertural lobe in *Cucullograptus hemiaversus* constitute the most instructive instance of a distal introduction of characters, determining the asymmetry of the apertural apparatus (Pl. VII, Fig. 10). These characters are best-developed in the distal thecae and gradually decrease towards the proximal end. The gular plate, or the so-called, "gorget" in *Cuc. aversus* and, in particular, the pattern of the astogenetic variation of the rostral process in *Cuc. aversus rostratus* (Pl. VII, Fig. 11) make up excellent examples of characters introduced from the distal end. In *Cuc. aversus aversus* there is no such process and in *Cuc. aversus rostratus* it is recorded only on distal thecae decreasing towards the proximal end, so that it is still absent from proximal thecae.

The principle of the distal introduction of the phylogenetic novelties in thecae of the Cucullograptinae has been formulated a few years ago (Urbanek, 1960, pp. 144 and 176—182). More complete materials, presented above, are in full conformity with these views and, at the same time, they allow one to state that the reduction or simplification of the structure need not necessarily be related with the distal mode of the introduction of phylogenetic changes in the graptolite colonies as it has previously been claimed by Elles (1922, p. 179). The processes that, by means of this mechanism, take place in the evolution of the Cucullograptinae may undoubtedly be termed as progressive changes in the structure of thecae. With regard to morphology and adaptation they do not differ from the modifications in the structure of thecae which take place during the evolution of the Monograptinae by the proximal introduction of the phylogenetic novelties. The reduction and simplification of the structure are not, therefore, directly related with the distal mode of introduction of the phylogenetic changes in the structure of a theca.

Departures from the principle of the distal introduction in the evolution of thecae in the Cucullograptinae

The majority of the phylogenetic modifications in the structure of thecae took place in the evolution of the Cucullograptinae through the distal introduction. There are, however, certain morphological characters which in all likelihood appeared in the phylogeny of this graptolite group by the proximal introduction of the phylogenetic novelties. None the less, they make up few exceptions, departing from the predominating rules of evolution of the thecae in the Cucullograptinae.

The isolation of the metatheca, outlined in *Lobograptus cirrifer* n.sp. and in *L. invertus* n. sp. constitutes an example of such character in R-cucullograptids. In *L. imitator* n.sp., closely related with them but probably rather more primitive, all thecae are adnate, i.e. the metatheca adheres over its entire length to the prothecal segment of the next theca. On the other hand, in both species, mentioned above, the metathecal segment is, in proximal thecae, completely or almost completely isolated, i.e. inclined at a certain angle to the axis of the rhabdosome. In distal thecae, the degree of isolation is relatively smaller and a free part of the metatheca covers $^1/_3$ to $^1/_2$ of its entire length. This allows one to conclude that the tendency to the isolation of the distal part of thecae in *L. cirrifer* n.sp. and *L. invertus* n.sp. is a phylogenetic novelty which was introduced to the astogeny from the proximal end of the colony.

A pectoral crest in *Cucullograptus aversus rostratus* which is recorded in morphologically more advanced forms constitutes another example of a phylogenetic novelty which appeared in L-cucullograptids through the proximal introduction. It is best developed in proximal thecae where it forms a small plate, fused with the ventral wall of the metatheca and slightly displaced towards the obverse side, while in the distal direction the size of the pectoral crest decreases. In the most distal thecae this plate is either formed like a narrow strand, or absent at all (comp. also p. 502). Since in *Cuc. aversus aversus*, a closely related but probably more primitive subspecies, there is no pectoral crest, and in *Cuc. aversus rostratus* it is best developed in proximal thecae, one may conclude that it makes up a phylogenetic novelty, introduced to the astogeny from the proximal pole of the colony.

In one of my previous works (Urbanek, 1960, p. 172), I have also emphasized the fact that one cannot exclude the possibility of the occurrence of such a mode of evolutionary changes in astogeny in which a new character is manifested simultaneously in all individuals of the colony: "This is suggested e.g. by the structure of asymmetric thecae in *Lobograptus scanicus parascanicus* (Kühne) marked by small hypertrophy of the right apertural lobe. No distinct differences in degree of asymmetry are noted between proximal and distal thecae. This form may be regarded as illustrating full penetrance with a low and nearly equal expressivity of a factor determining the asymmetry. Nothing can be said presently whether this character was introduced proximally or distally".

A more extensive material, available at present, allows one for a more detailed analysis of this phenomenon in all R-cucullograptids. If a ratio of the height (*long.*) of the right-hand (*hr*) to the height of the left-hand lobe (*hl*) would be considered a measure of asymmetry of the apertural apparatus, no distinct distal progression in this ratio could be shown for specimens from the population of *Lobograptus scanicus parascanicus* from boulder S. 181 (Czarnogłowy). Establishing the ratio of the length (*tr.*) of the right-hand (*lr*) to the left-hand lobe (*ll*) in the form of *lr*/*ll* is another method of determining the degree of asymmetry of the apertural apparatus by means of a difference in the size of lobes. The *hr*/*hl* ratio seems, however, to be more reliable, since in part, it may also determine the degree of an overlap of the larger lobe and, therefore, in continuing these considerations, this ratio will be used as an index. However, for the purposes of comparison, Table 4 summarizes both the *hr*/*hl* and *lr*/*ll* values for all species examined.

The *hr*/*hl* ratio amounts, for both the proximal and distal thecae that have been measured to an average of about 1.3, fluctuating for the proximal within limits of 1.25 and 1.40, and for the distal thecae 1.30 and 1.50.

Analogous measurements, taken for the *Lobograptus scanicus parascanicus* (a form from the higher zonal level) population from the Mielnik boring, display in truth a more extensive range of variation (for proximal 1.25—1.40, and for distal thecae 1.25—1.60), but also they do not enable one to state a distinct increase in the degree of asymmetry of this apparatus towards the distal end of the rhabdosome.

A lack of a distinct progression of asymmetry of the apertural apparatus towards one or the other end of the colony does not allow one to state if this asymmetry was formed, in the *L. simplex* — *L. scanicus parascanicus* phylogenetic line, by the proximal or distal introduction. It may well be, therefore, that this phylogenetic character was initially formed with a relatively low degree of expressivity, but with a complete penetrance.

Such a conclusion might be fully justified by the structure of forms, morphologically transitory between *Lobograptus simplex* and *L. scanicus parascanicus,* i.e. such as for instance *L.* cf. *simplex* from boulder S. 225 (Rewal). In this case, an incipient thecal asymmetry is displayed which, however, occurs on all thecae of the rhabdosome (comp.

p. 404 and Fig. 6). The rhabdosome, although marked by the presence of asymmetric thecae, does not display here a polarity in relation to this character.

In the course of a further development of the *Lobograptus scanicus* phylogenetic line, it comes about, in truth, that the general size of the apertural lobes increases yet more but the differences in the degree of asymmetry of the proximal and distal thecae are marked only slightly. In *L. scanicus amphirostris* n. subsp., the ratio of *hr/hl* amounts: for the first theca — to about 1.5 and, for the distal thecae — to 1.6—1.7. For *L. scanicus scanicus*, these ratios amount, in all thecae, to about 1.4, some of these values being even higher for the proximal thecae (to 1.80). On the other hand, certain structural differences in which the most proximal thecae differ from the other and, in particular, from the distal ones (the formation of an adapertural plate on the left lobe in more distal thecae) appear in the latter species (comp. pp. 334, 346, 448). Owing to this phenomenon, *L. scanicus scanicus* may be even considered to be a species biform to a definite degree.

In the *Lobograptus imitator* n. sp., *L. invertus* n. sp. and *L. cirrifer* n. sp. line of evolution, no distinct progression is also observed in the degree of asymmetry of the lobes in the astogeny. In *L. imitator*, only proximal and medial thecae could be investigated, for which the *hr/hl* ratio

Table 4.

Degree of asymmetry in apertural apparatus, as indicated by *hr/hl* (upper values) and *lr/ll* (lower values) ratio

Species	First theca	Proximal thecae	Distal thecae
Lobograptus scanicus parascanicus (Kühne)	1.60*	1.25—1.40	1.25—1.60
	1.20	1.20	1.20—1.80
L. scanicus amphirostris n. subsp.	1.50	1.60—1.80	1.60—1.70
	1.20	1.40	1.20—1.40
L. scanicus scanicus (Tullberg) s. Bulman	—	1.40—1.80	1.30—1.40
	—	1.10—1.30	1.06—1.20
L. imitator n. sp.	1.41—1.66	1.30—1.50	1.50*
	1.03—1.06	1.06—1.00	1.01*
L. invertus n. sp.	1.30	1.40	1.40
	1.15	1.20	1.30
L. cirrifer n. sp.	1.60—1.90	1.30	1.40—1.46
	1.20—1.36	1.12—1.40	1.12—1.50

* Measurements made on very scanty material (1—2 specimens).

amounts respectively to 1.3—1.4 and 1.5. The same coefficient for the proximal thecae in *L. invertus* amounts to 1.3—1.4, and for the medial and distal ones — to 1.4. In *L. cirrifer* n. sp. the *hr/hl* ratio amounts: for the proximal thecae — to 1.3—1.9 and for the medial and distal ones — to 1.4—1.5. In the case of *L. cirrifer* n.sp., the asymmetry of the apertural apparatus is, however, emphasized not only by the different size of apertural lobes, but also by the occurrence of certain structural differences (rostral processes) which contribute to some distal increase in the degree of asymmetry of this apparatus. In all these cases, the differences in the degree of asymmetry of the apertural apparatus, measured by the size of apertural lobes, are contained within limits of the permissible error in measurements and do not represent a picture of a clearly directional astogenetic variation. Likewise, there is no distinct phylogenetic progression in the degree of asymmetry within the R-cucullograptids examined. Clearly, then, the asymmetry of the apertural apparatus of the lobograptids is stable in character in contrast with its labile character, displayed in the *Cucullograptus hemiaversus* — *Cuc. aversus rostratus* line.

Proximal progression of phylogenetic novelties

The tendency to a further proximal spreading is, on the whole, displayed by structural novelties of thecae which at first appeared, in the phylogeny of the Cucullograptinae, only in the distal part of the rhabdosome. As a result of this process, the phylogenetic novelties start to appear: 1) in an increasing number of thecae, and 2) also in the thecae that are situated more proximally. This proximal spreading of the novelties in the phylogenetic lines is related with changes in the number of individuals in which a given character is manifested phenotypically. These processes, occurring in the evolution of the graptolite colony may be compared with changes in the penetrance of the genetic factors (Urbanek, 1960, pp. 169—170). The phylogenetic novelties, initially limited to the modifications of thecae in the distal part and not manifested in the structure of thecae of the proximal part of the rhabdosome, display an incomplete penetrance. A further evolution, related with proximal spreading of a novelty to an increasing number of individuals may be considered as caused by an increasing penetrance of definite genetic factors. Finally, in those graptolites in which all individuals of the colony manifest a given character (although mostly to a different extent), a complete penetrance may be stated of those genetic factors which are responsible for the formation of the characters considered. The evolution of the colonies (phylastogeny) of the Cucullograptinae consists, therefore, in the changes in penetrance of definite genetic factors. Thus, the penetrance determines a quantitative (number of individuals, displaying a given character) and spacial (on account of a definite direction of spreading) characteristics of the evolution of a graptolite colony.

The following two phenomena may serve as an instance of the evolution of penetrance in the graptolites: 1) the appearance of slightly developed apertural lobes in the distal part of the *Lobograptus progenitor* n. sp. colony, followed by spreading of correspondingly more distinctly expressed apertural lobes to all thecae of the *L. simplex* colony, and 2) the formation of asymmetry of the apertural apparatus in *Cucullograptus hemiaversus,* most distinctly expressed in distal thecae, still almost imperceptible in proximal thecae and, hereafter, with an increase in the asymmetry of the apertural apparatus, spreading this character to all individuals of a colony in *Cuc. aversus aversus.*

The consideration of the instances, cited above, allows one to state that the penetrance: 1) is related, in its evolution, to a simultaneous change in the maximum degree of the phenotypic manifestation of a given character (e.g. a degree of the asymmetry or of the development of the apertural apparatus), and 2) develops gradually, by different stages, determined by the degree of spreading of a given character. The former property allows one to state that the higher the maximum degree of the phenotypic manifestation of a given character, the greater is the number of individuals in a colony which manifest the presence of this character (e.g. the higher the degree of the asymmetry of thecae, the greater is the number of individuals which display a more or less advanced asymmetry). A few years ago, the suggestion has been set forward that, analogically to solitary organisms, the degree of the phenotypic manifestation of a given character should be termed, in graptolites, an expressivity (Urbanek, 1960, pp. 170—173). An ample and conclusive evidence for the fact that an increase in penetrance was closely related, in the evolution of the graptolite colony, to an increase in expressivity, has been supplied by evolutionary changes in the astogeny of the Cucullograptinae. In these graptolites, the more intensive the expressivity of a given character, the greater is the number of individuals, displaying this character and, consequently, the more intensive is its penetrance. The latter character of the evolution of penetrance, i.e. the fact that its development takes place gradually and by different stages, determined by the degree of phenotypic spreading of given characters among the individuals that form a colony, causes the formation and development of a "biformism". The term "biform" has admittedly been introduced by Elles and Wood (1901—1918) to those monograptids in which distinct differences were recorded in the structure of thecae being parts of the same rhabdosome so that the thecae of the proximal part distinctly differed from the distal ones. Besides, these differences concern structural characters of thecae (presence or absence of definite structures, shape of a theca, etc.), but they do not involve such characters as e.g. size and proportions of a theca. In the latter respect, all Graptoloidea are, of course, biform because of the permanent gradient of size, expressed by an increase in size of thecae towards the distal end, which occurs in them (Bulman, 1950, p. 69; 1958, p. 32).

In the initial stage of evolution, the biformism is manifested as a result of the appearance of a phylogenetic novelty that displays, within the colony, a low degree of penetrance. The example of the Cucullograptinae may give every appearance that, at first, this biformism reaches only a low degree, determined by both the small expressivity of a given character and its slight penetrance. Presumably, the formation of incipient apertural lobes in the distal part of the colony, causing the appearance of a slightly marked biformism, is e.g. a novelty in *Lobograptus progenitor* n. sp. Proximal thecae are marked by the lack of these incipient lobes but, on account of a slight development of this structure and small number of individuals of a colony, having apertural lobes, the biformism is only slightly manifested. A further increase in the size of lobes (increase in expressivity) and their spreading to all other individuals of the colony (increase in penetrance) caused an obliteration of differences between the structure of thecae in the proximal and in the distal part, as well as a formation of uniform colonies, such as those in *L. simplex*. Similar phenomena enable one to presume that the biform colonies are determined by an incomplete penetrance of definite genetic factors which is simultaneously related with a relatively low expressivity of the phenotypic manifestation of a given character (e.g. the development of apertural lobes in the distal thecae of *L. progenitor*). A gradual increase in the biformism of thecae, following an increase in the expressivity of a given character and in its penetrance, may come about as a result of the subsequent evolution. *Cucullograptus hemiaversus* in which the biformism is expressed in the structure and asymmetry of the apertural apparatus may serve as an instance of a colony with a higher degree of the biformism. The distal thecae are marked by a distinct asymmetry and a partial reduction of the right-hand lobe, while the proximal thecae are still almost symmetrical without traces of the reduction of this lobe. Within a colony, a certain degree of asymmetry of the apertural apparatus is, however, displayed by a vast majority of individuals, while a considerable number of them is marked by a relatively high degree of asymmetry. Here, we can speak about a higher degree of biformism, determined by correspondingly higher degree of penetrance and expressivity of the factors responsible for the formation of asymmetry of the apertural apparatus. A continued increase in penetrance and expressivity may bring about that all individuals of the colony start to develop a new character, i.e. in such a case, a secondarily uniform colony is formed. With regard to the development of different characters, such a stage is represented by *L. simplex* and *Cuc. aversus aversus.* A continued evolution may once more cause the transformation of such uniform forms into the secondarily biform forms (e.g. by the appearance of rostral processes in *Cuc. aversus rostratus*). A course of the evolution of a colony, in the highest development stage of this process, may be as follows: uniform form (1), forms with different degrees of biformism (2), a form secondarily uniform (3), forms with different degrees of the secondary biformism (4), etc.

The processes, represented by the following species of the Cucullograptinae, had an approximately similar course: *Lobograptus simplex* (1), *Cucullograptus hemiaversus* (2), *Cuc. aversus aversus* (3), *Cuc. aversus rostratus* (4) (Pl. VII, Figs. 2, 10, 11). The latter form may be considered a "prophetic fossil", preceding a successive homogeneous form which would be marked by the presence of rostral processes on all thecae of the rhabdosome. As a matter of fact, such state has, however, never been reached in the phylogeny because of the extinction of the line, mentioned above. The adapertural plates of the left apertural lobe in *Lobograptus scanicus scanicus* which have never reached a higher degree of penetrance, make up a similar example of a character which, until the extinction of the line, was arrested at a certain degree of biformism.

In the cases in which we have to do with the occurrence of characters, both distally and proximally introduced to the same phylogenetic line, a prolonged evolution of astogeny may, as a matter of fact, consist in the occurrence of two contradictory trends of transformations. A gradual spreading of a given character in the distal direction is caused by an increase in the penetrance of a factor appearing from the proximal end of the rhabdosome, while the same process, involving the characters, displaying a distal introduction, consists in spreading them in the proximal direction (e.g. the pectoral crest and the rostral process in *Cucullograptus aversus rostratus*). The evolutionary processes of astogeny, taking place here, make up an analogy to the evolutionary processes of ontogeny in solitary organisms, e.g. in ammonites, in which, in same phylogenetic line, some characters develop, spreading from younger to older stages (e.g. modifications of the coiling of the shell, of the shape of particular whorls, etc. which are frequently developed in a proterogenetic manner). Other characters, contrariwise, they develop from older to younger stages (e.g. modifications of the lobe line, taking place as changes in the terminal stages and through the acceleration).

The causes of such a bipolar evolution of the colony may perhaps be looked for in the following three factors: 1) a different phenotypical action of active substances, produced by the siculozooid on various genetic factors (these substances act on the characters with the proximal introduction as a stimulator and on those with the distal introduction as an inhibitor), 2) changes in the degree of activity of these substances and, finally, 3) changes in the morphogenetic activity of given genes, transforming the norms of reactivity of the tissues to the action of these agents (Urbanek, 1960, pp. 172—173). Obviously, accepting a common phenotypical dependence of both factors (that, determining a character introduced proximally and that, determining a character introduced distally) on the morphogenetic substance, spreading from the sicular part, we cannot elucidate the simultaneous increase in the penetrance of both factors ascribing it only to the changes of this morphogenetic factor. Such a process was bound to consist in the changes in the first, second and third factor combined, or only in the changes in the morphogenetic activity of genes (3rd factor) with a relatively constant gradient of the morphogenetically active substances.

Morphophysiological organization of graptolite colonies

In the present writer's previous works (Urbanek, 1960, 1963), a working hypothesis has been elaborated, being an attempt to determine the morphophysiological organization and mode in which evolutionary changes took place in graptolite colonies. In general, this hypothesis consists of two fundamental parts. In the first, a polar organization of the Graptoloidea colonies and regular morphological gradient, occurring in them, are explained upon the assumption that an inductive influence is exerted by the siculozooid on all other individuals of a colony. A regular change in the quantity of morphologically active agent, produced by the siculozooid would be responsible for the occurrence of a definite morphological succession of thecae in the astogeny. The author tried to justify this view, basing his considerations on the course of a normal astogeny of uni- and multiaxiate graptolite colonies (1960), as well as on the analysis of the structure of morphoses, formed as a result of the regeneration of the stipes of a colony, broken off, i.e. as a result of the pseudocladogeny (Urbanek 1963).

The second part of the working hypothesis, mentioned above, explains in genetic terms the pattern and mechanism of phylogenetic modifications that occur in the astogeny, i.e. the mechanism of the evolution of graptolite colonies. On the basis of the premise that all individuals of a graptolite colony had the same genotype, the differences occurring between them are considered to be a result of a varying degree of the phenotypical manifestation of corresponding genetic factors, depending on the amount of the active substances mentioned above and which are probably produced by the siculozooid. The morphological gradient of thecae is conditioned upon a regular change in the amount of active substances, responsible for the modification of a phenotypical manifestation of a given genetic factor. The changes in the pattern of the development of colonies, taking place during the evolution, may be ascribed to changes in penetrance (determined by the number of individuals displaying a given phenotypical effect) and expressivity (determined by a degree of the phenotypical manifestation) of definite genetic factors (Urbanek, 1960) (comp. also p. 351).

The hypothesis, shown above, which throws a new light on the mechanism of the evolution of the graptolite colonies, has not so far called forth any wide scale response. However, it has been favourably evaluated by such eminent graptolitologist as O.M.B. Bulman (1963) who seemed to accept in general the concepts and terms suggested but it has not so far aroused any more extensive discussion of this problem as seen in its genetic aspect.

In this respect, a considerable significance should undoubtedly be ascribed to critical remarks, sent in by Dr. L. Van Valen (American Museum of Natural History, N. Y.) in his letters of October 19, 1960 and December 2, 1960 since he is both an eminent geneticist and a well-known palaeontologist.

Dr. L. Van Valen's objections may be presented in the following three items: 1) The inductive influence of the growing apexes of a colony or the cumulative effect of all zooids on the entire colony is equally likely as the sicular control. Let us cite an excerpt from this author's letter of December 2, 1960: ... "I don't object to sicular control; it seems about equally likely to me, but not proved"; 2) A colony of graptolites may, from the genetic point of view, be considered a single individual "because its components are both connected and genetically identical, and because of the possibility of at least some morphogenetic dependence on the sicula" (his letter of October 19, 1960); 3) "In regard to penetrance and expressivity, if we consider a rhabdosome as one individual, then neither term accurately expresses the common state of a reasonably constant gradient...". "Perhaps a hybrid term like "incomplete expression" would be appropriate" (his letter of October 19, 1960).

The doubts that occurred to Dr. L. Van Valen seem to be representative since similar arguments were used by some other biologists and geneticists when they discussed this problem with the present writer. Some light should, therefore, be thrown on them because they may contribute to the development of a discussion on the organization of the graptolite colony.

The first objection will not be examined in a more extensive manner since it has already been dealt with (in part, also in connection with Dr. L. Van Valen's letters) in the previous work (Urbanek, 1963). However, it is worth while to emphasize once more the significance of the analysis of the growth of bipolar morphoses which are formed after tearing apart of the original rhabdosome, resulting from the regeneration of a distal fragment. The regenerative stipe (the so-called pseudocladium) grows in a colony whose sicular part (together with the sicula) has been torn away. The pseudocladium, growing under such conditions, lacks a polar organization and a characteristic morphological sequence of thecae which occurs with a normal astogeny. The regenerative stipe grows by a simple multiplication of thecae of the same morphological (distal) type. These facts together with several other premises, mentioned previously (Urbanek, 1963, pp. 230—236), induce the present author to confirm his views that the sicular part (and probably the sicula itself) was responsible for the occurrence of the morphological gradients of thecae and, consequently, for the polar organization of the colony.

Dr. L. Van Valen's second objection, according to which a colony of graptolites is, in its genetic aspect, a single individual, deserves much closer examination. As is well-known, the problem of an individual in biology is an open problem and, in the present stage of knowledge, the only possible conclusions are arbitrary in character. The colonies of graptolites are not of course usual populations, consisting of separate individuals, but — precisely — colonies which, as I have already previously pointed out (Urbanek, 1960, pp. 129—132), in fact, basing my suggestions to a considerable extent on Beklemishev's opinions (1950), are connected by several transient stages in which the boundaries between strongly intergrated ecological populations, consisting of separate individuals (pseudo-colonies of the type of flock or swarm) and true colonies (with the tissue connections between particular individuals) are obliterated. Different degrees of integration, related with a decreasing individuality of zooids are outlined in colonies. Individual processes are not, therefore, completely abolished by reaching the colonial organization. We have here to do rather with combining them with the processes of a higher order which determine the "colonial" character of individuals' interdependence.

A similar approach to the problem of individuality of particular colonial organisms (zooids) versus individuality of the colony as a whole, is represented by Naumov (1960, pp. 69—70) who believes that a mere tendency to a certain limitation of individuality of particular zooids and its replacement with a growing individuality of the entire colony, is not a satisfactory basis for a view, ascribing a nature of a single individual of a higher order to each colony. This nature depends on a definite stage of integration of the colony which is different in each particular species [14].

A relatively high degree of the individuality of zooids (a separate theca in each individual, probably a separate oral opening and tentacular apparatus, an early separation of an individual, as a result of the blastogeny, from the rest of a colony, etc.) belongs to individual processes which have been preserved in the colonies of graptolites. The colonial processes are expressed by the presence of the tissue connection between particular individuals (mostly by means of a stolon) and, probably, by the formation of a general dependence of all individuals in a colony on its first individual (oozooid, siculozooid). This dependence is, however, no proof of a loss of individuality by zooids since it is a well-known fact that a colony may also live and develop after a loss of the siculozooid (Urbanek, 1963).

From the morphological and physiological standpoint, the organization of a colony of graptolites may be understood as a special case of the organization of a group of individuals and the processes that occur in it are mixed, i.e. both individual and populationary in character.

With regard to genetics, a colony of graptolite is of course a clone (Urbanek, 1960, p. 166) with all its individuals having the same genotype. Such groups of organisms are usually considered to make up a genetically single individual. A population of e. g. hydra, coming from a single parent individual from which it develops by budding, is therefore genetically a single individual, but ecologically and physiologically it consists of several individuals. The present considerations are not aimed at stating to what an extent such understanding of an individual in genetics may be justified, although it seems to be somewhat contradictory to the range of this concept, applied to other biological disciplines. The concept of an individual in morphology and physiology, apart from the problem of its difference from or identity with other ones, means rather its separateness or a degree of separateness. Perhaps the concept of a "genetic individual" makes up an excessive extrapolation of this concept.

On the other hand, because of genetic factors, involved in this problem, we are interested in the correct explanation of evolutionary changes that occur in a graptolite colony. The concepts of expressivity and penetrance have of course been introduced in reference to the population of individuals with different genotypes, each of them, however,

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[14] An important work on colonies in Hydrozoa by D. A. von Schenk (1965, Die Kormentektonik der Plumulariiden; Revue Suisse de Zoologie, 72, 4, 885—1021) has been sent in when the present text was prepared for printing. It contains new ideas, significant for the problem considered.

containing a gene, responsible for the formation of the character examined (Timofeeff-Ressovsky, 1931, 1934). There is an ample evidence that the "genetic environment" (the modifying genes) determines the degree of both the expressivity and penetrance of given genes. However, it is the environmental factors (primarily temperature and trophic factors) that also influence expressivity and penetrance (Hadorn, 1955). Penetrance and expressivity are not, therefore, concepts related with necessary genetic differences, occurring between individuals, because they may be shaped not only on the genotypical, but also epigenotypical basis, i. e. on the basis of differences in the course of processes that lead up to the formation of a phenotype. In graptolite colonies, following a probable occurrence of a gradient in the distribution of morphogenetically active substances, the development of each individual took place under somewhat different physiological conditions to which different processes of the realization of phenotypical characters corresponded. Among them, there were different degrees of expressivity and of penetrance of a given character as a function of this expressivity.

With regard to the third objection (comp. p. 355), I would like to state that the application of the terms, expressivity and penetrance, to the processes that occur in the evolution of the graptolite colony, seems to be fully justified for the following three reasons: 1) each individual of a colony had genes responsible for the formation of a given character; 2) these characters were, however, manifested to a different extent (expressivity) and in a different number of individuals (penetrance); 3) the differences, mentioned above, arose as a result of different development conditions of particular individuals which in turn resulted from their different position within a colony and, therefore, they are phenotypical in character.

The term, "incomplete" and, respectively, "complete expression", suggested by Dr. L. Van Valen, does not seem to be satisfactory because it attracts one's attention only to the degree of manifestation of a given character while, in the evolution of the graptolite colonies, we have definitely to do with two such processes of which the second one consists in spreading a given character on particular individuals of a colony. For many technical reasons the use of two different concepts (comp. the terms "expressivity intermediates" and "penetrance intermediates", introduced by Bulman, 1963, p. 415) is required. However, in order to avoid any misunderstandings with regard to the concept of penetrance as referred to a group of individuals in a colony, as well as that referred to a group of colonies (an assemblage of different rhabdosomes), I suggest the use of the terms: "a colonial penetrance" and "a population penetrance". In the present monograph, the term "a penetrance" has so far been meant only "a colonial penetrance".

In general, the materials, concerning the evolution of particular phylogenetic lineages of graptolites are too scanty as to allow one for an analysis of changes in the "population penetrance". It should be, however, presumed that the initial phases of evolution, related in general with a slight expressivity and an incomplete "colonial penetrance" of given genes, are also expressed by the fact that not all the colonies display phenotypically new phylogenetic characters. This would be manifested by the occurrence of "mixed populations", consisting of rhabdosomes in which new characters have not yet been manifested, as well as of those in which they have already been manifested but with a low degree of expressivity and penetrance. Such a hypothesis might be confirmed by, among other things, 1) an occasional occurrence of the forms of *Cucullograptus aversus rostratus*, provided with a "pectoral crest", in the populations from the erratic boulders of the Baltic origin, as well as by a considerable frequency of occurrence of this character in the populations of this species from the Mielnik boring (comp. pp. 517—518), and 2) an occurrence of morphologically "mixed" populations of *Lobograptus scanicus parascanicus* in the "lower zonal form" of this species (comp. p. 432).

The observations described above, which are still incomplete, may be supplemented by other findings. A process, discovered in "*Monograptus*" *deubeli* by Jaeger (1964, p. 36) who found that "*M.*" *deubeli* evolved gradually and continuously from *Pristiograptus dubius*, seems to be similar. In the lower part of the *deubeli* zone, both species are hardly distinguishable and the rhabdosomes have more *dubius* than *deubeli* appearance. However, typical *deubeli* rhabdosomes with a peculiarly shaped sicula already occur in these populations. These features, typical of "*M.*" *deubeli*, become more and more accentuated upwards.

The observations, cited above, indicate the possibility of an analysis of changes that occur not only in the "colonial penetrance", but also in the "population penetrance" of the graptolite evolution.

PHYLOGENETIC RELATIONSHIPS AND TAXONOMY OF THE CUCULLOGRAPTINAE

PHYLOGENY OF THE CUCULLOGRAPTINAE

Criteria of determining phylogenetic relationships

The conjectural phylogenetic relationships of the examined representatives of the Cucullograptinae have been determined on the basis of the following two criteria: 1) the existence of a regular morphological sequence, expressed by a consistent direction of the modifications occurring in the structure of thecae and the modifications in astogeny; 2) the existence of a regular stratigraphic sequence, expressed by an appropriate order of occurrence of particular forms, which is in conformity with their presumable morphological sequence.

The coincidence of the morphological sequence has been stated on the basis of the morphology of thecae and their astogenetic succession. Particularly significant in this respect are the apertural apparatus which, as indicated by the comparative-anatomical analysis, constituted the part of a thecae subject to the greatest changes and, at the same time, most distinctly determined the main trends in their evolution (comp. p. 339). A general type of the structure of the apertural apparatus, as well as the trend in its further differentiation, may undoubtedly be considered key characters which allow one to determine the main trends in the evolution of the Cucullograptinae.

The thecae of the distal and proximal parts of the rhabdosome differ, in their significance, to a considerable extent. The structure of thecae in the distal part of the rhabdosome of the Cucullograptinae, in particular that of their apertural apparatus, enables one to envisage, to a certain degree, a further trend in their evolution. On the basis of the structure of distal thecae, approximate conclusions may be drawn as to the structure of subsequent descendents of a given phylogenetic lineage. Thus, the structure of distal thecae and especially that of their apertural apparatus is, to a certain extent, a "prophetic character", allowing one to establish phylogenetic relationships "up" to the family tree. Such a significance of distal thecae in the evolution of the Cucullograptinae results from the mode of phylogenetic modifications of the astogeny, i. e. from the distal introduction of the phylogenetic novelties. A phylogenetic significance we ascribe to the distal thecae of this graptolite group, might be determined only after a previous understanding of a mode of phylogenetic changes in astogeny, predominating in this group of the Monograptidae. The phylogenetic significance of the same thecae may, in various evolutionary lineages, be quite different, depending on a manner in which the evolutionary changes take place in astogeny (comp. Urbanek, 1960, pp. 208—209).

Such characters as, incipient apertural lobes in distal thecae of *Lobograptus progenitor* n.sp. which enable us to consider this species as the first representative of the cucullograptid evolutionary trend, asymmetric distal thecae of *Cucullograptus hemiaversus*, allowing one to presume that, in the course of a further development of this lineage, the forms will be developed with asymmetric thecae, distributed over the entire length of the rhabdosome (such as in *Cuc. aversus aversus)*, distal thecae in *L. scanicus parascanicus*, indicating that, in the course of a continued evolution of this lineage, a progressive development of apertural lobes will take place without a distinct increase in their asymmetry, etc. may serve as instances of the "prospective" phylogenetic significance of distal thecae in the Cucullograptinae.

The structure of the proximal thecae in the Cucullograptinae has a quite different phylogenetic significance which, however, is also determined by the principle of the distal introduction of the phylogenetic novelties. Such a mode of the evolution of colonies results in the fact that: 1) the most proximal zooids are, generally speaking, structurally least modified, and 2) these modifications may be manifested in them much later than in the thecae of the distal part of the rhabdosome. Due to this fact, the proximal thecae display in the Cucullograptinae a considerably higher degree of mutual similarity and allow one to estimate their phylogenetic relationships "down" the family tree (i. e. the relationships between a given form and its ancestors). The proximal thecae in *Lobograptus progenitor* n.sp. whose structure displays a considerable similarity to that of some thecae in *Neodiversograptus* and, to a certain extent, also in "*Pristiograptus*" *bohemicus*, may serve as an example. This may testify to the existence of the phylogenetic relationships among the early representatives of these, hereafter quite divergent, development lineages (comp. pp. 380—384). The structure of proximal thecae in *Cucullograptus hemiaversus* indicates its probable descent from the bilaterally symmetrical lobograptids, while the structure of proximal thecae in *Cuc. aversus rostratus* — its descent from the forms having asymmetric thecae which, however, are devoid of apertural spines. The structure of proximal thecae in *Lobograptus scanicus scanicus* resembles that in *L. scanicus amphirostris* n.subsp. and *L. scanicus parascanicus* to such an extent that it becomes possible to presume that the first of the species, mentioned above, makes up only the most specialized link of the same development lineage to which belong the latter two forms.

Among all thecae of the rhabdosome, a particular importance should be ascribed to the sicula which, like proximal thecae, is subject to relatively slighter structural modifications. However, apart from the bilaterally symmetrical lobograptids, the siculae of the remaining Cucullograptinae were subject to the gracilization which, as a matter of fact, took place in a parallel manner, much the same as in R- and L-cucullograptids. It is only in the "*invertus-cirrifer*" development lineage that siculae display several characters of a certain specialization in the structure of the aperture of metasicula and this is a basis for stating that *Lobograptus invertus* n. sp. and *L. cirrifer* n. sp., displaying quite different trends in the evolution of their apertural apparatus, had a common ancestor, which was probably *L. imitator* n. sp. The separateness of all this development lineage is distinctly emphasized precisely by the common type of sicula and this fact still more enhances the significance of the proximal part of the rhabdosome as concerns a method of "tracing back of ancestry" in the Cucullograptinae.

The coincidence in the morphological sequence is also expressed by the coincidence in the astogenetic sequence of definite forms. On the basis of the comparison of the development degree in the progressive parts of thecae which belong to the same part of the rhabdosome (and, therefore, primarily apertural apparatus), one may determine a degree to which these forms differ in the expressivity of definite characters, as well as a trend, according to which, the expressivity of a definite character changed in the course of the family evolution. These differences do not amount, of course, to quantitative differences only (a degree of asymmetry of the apertural apparatus, degree of hypertrophy or reduction of lobes, etc.), but they may also be expressed by the appearance of qualitatively different structures (for instance, rostral spines in *Lobograptus cirrifer* n. sp. and *Cucullograptus aversus rostratus*). The determination of an approximate number of thecae, displaying the presence of definite characters, allows one to state the degree and trend of the development of penetrance. An increase in the expressivity and penetrance of definite morphological characters is, as a rule, observed in the evolution of the Cucullograptinae which, in general, is progressive in character.

Thus, the establishment of the family relationships of the Cucullograptinae is based on the following three morphological phenomena: 1) a "prospective" character of the modifications in the thecae of the distal part of the rhabdosome; 2) generally speaking, a "past" or conservative character of the structure of the proximal thecae; 3) a regular sequence in the evolution of astogeny, determined by a gradual increase in expressivity and penetrance of the progressive morphological features.

The second criterion of the phylogenetic relationships among the Cucullograptinae is supplied by all facts, concerning their stratigraphic occurrence. The most important are in this respect the data based on their occurrence in the Mielnik boring core because the stratigraphic position of particular erratic boulders might be established only approximately and, consequently, it is of an inferior value as compared with that, based on material *in situ* (Pl. I).

The graptolite sequence, determined in the present work only on the basis of a single boring core, may also be laden with a considerable error, resulting chiefly from 1) a generally unrepresentative sampling of the rock series through the single boring hole, and 2) local peculiarities of the section examined. There is, however, a markedly full conformity of the stratigraphic sequence, established on the basis of the examined samples from the Mielnik boring (Pl. I, comp. also p. 306) with the sequence, suggested by morphological similarities (Pl. VIII). The stratigraphic sequence, determined by the order of the first appearance of successive species, is in a full conformity with morphological facts and proves the correctness of most previous suppositions, concerning the course of the evolution of the Cucullograptinae (Urbanek, 1960, pp. 176—181). Such a consensus of different sources of information cannot be considered a matter of pure accident. It should be assumed that, in its main outline, the sequence of the Cucullograptinae in the Mielnik boring core, accurately reflects the course of the evolutionary events.

If a general sequence of species is, on the whole, reliable, gaps often occurring between vertical ranges of the ancestral and the descendent species seem to be accidental in character. They might result from the fact that the formation of a new species or subspecies took place in another area (allopatric speciation) and, hereafter, a new form was spread over a more extensive area, thus appearing also in the layers, pierced by the boring hole in question. A gap between the occurrence of the ancestral and the descendent forms (comp. Pl. I), for instance, between the ranges of *Lobograptus simplex, L. imitator* n. sp., the latter form and *L. cirrifer* n. sp., may correspond to a period during which these processes took place.

The stratigraphic occurrence of *L. scanicus amphirostris* n. subsp. which, in truth, precedes in its first appearance the descendent species *L. scanicus scanicus,* but occurs in very small numbers and displays considerable discontinuities, requires some closer attention. It is only above the upper boundary of the occurrence of *L. scanicus scanicus* that *L. scanicus amphirostris* n. subsp. reaches its maximum quantitative development (comp. p. 442).

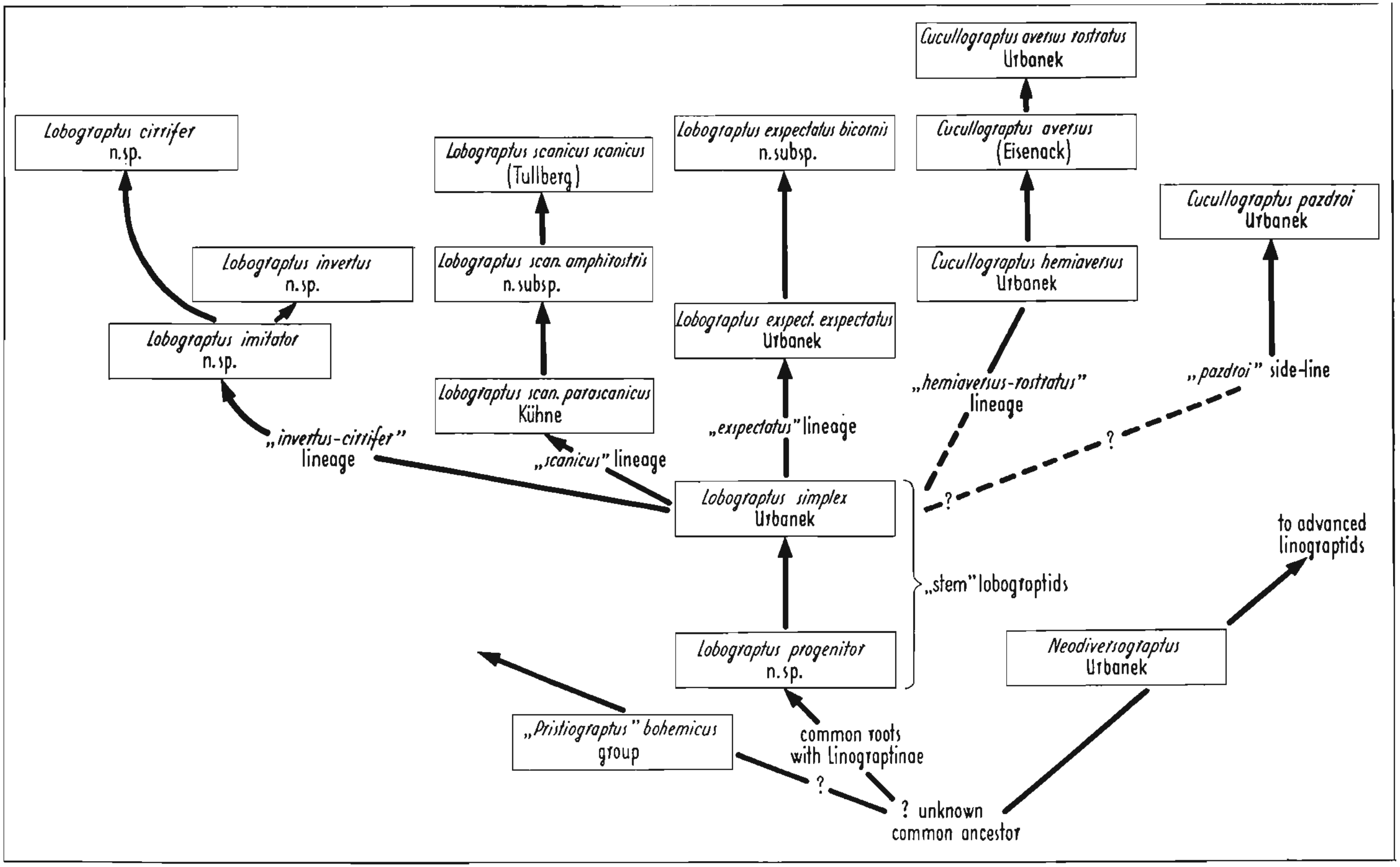
The conformity of the morphological with the stratigraphic data allow one to arrange the examined species of the Cucullograptinae in certain evolutionary series. The question arises whether or not these series, consisting of species and subspecies, successively following each other and undoubtedly closely related to each other, consequently make up phylogenetic lineages, formed by direct ancestors and descendents. There is the possibility that such series of morphologically different populations, following each other, may constitute only geographically different subspecies (geographical races) of a chronologically identical species, successively occurring on a given area as a result of an ingression (Remane, 1956, pp. 287—289; Jaeger, 1959, p. 131). In such cases, they represent an apparent phylogenetic sequence. The possibility that the phenomena of the graptolite fauna migration may participate in the process of evolution of this fauna, has already been mentioned previously (p. 363). A certain geographical differentiation of the fauna of the Cucullograptinae on a relatively small area, including the Baltic Sea and the margin of the East-European Platform, might be indicated by the fact that the entire *Lobograptus imitator* n. sp. — *L. invertus* n. sp. — *L. cirrifer* n. sp. line of evolution, is known at present only from the Mielnik boring and does not occur in the Silurian erratic boulders whose place of origin is situated presumably about 600 km to the north-west. Perhaps the origin and geographical distribution of this lineage was limited only to the southern area of the Silurian basin. Similar phenomena might also take place in the distribution of particular subspecies of the Cucullograptinae.

Considerable morphological gaps between some links, implying the existence of one or more (?) "missing links" (*Lobograptus simplex* — *Cucullograptus hemiaversus; L. simplex* — *L. imitator* n.sp., and, in particular, a great difference between *L. simplex* and *Cuc. pazdroi,* comp. p. 336), testify against the acceptance of all series, established for the Cucullograptinae, as true phylogenetic lineages. In other cases, however, transient populations are known which fill, to a considerable extent, or almost completely, the morphological gaps between adjacent species or subspecies (*L. simplex* — *L. scanicus parascanicus; Cuc. aversus aversus* — *Cuc. aversus rostratus*). It is beyond any doubt that, in such cases, we have to do with true phylogenetic lineages. These considerations allow us, therefore, to accept the "family tree" of the Cucullograptinae, shown in Pl. VIII, as a tree, represented in part by the phylogenetic series and, in part, making up anatomical series with the geological time factor taken into account. It seems, however, to be quite sure that this scheme, although a rough sketch in character, correctly presents the main structural stages in the evolution of the Cucullograptinae. Obviously, it should be born in mind that it constitutes a picture of evolution of this group only within one region. Perhaps, in other regions, there might exist other, separate phylogenetic lineages which, let us hope, will be identified as a result of continued studies. Such facts would be in conformity with the picture of microevolution of other fossil groups.

Stem lobograptids

Both morphologically (Pl. II, Figs. 1 and 2; Pl. III) and stratigraphically (Pl. I), two species, i.e. *Lobograptus progenitor* n. sp. and *L. simplex* are distinctly different from all other Cucullograptinae. They constitute two most primitive and oldest representatives of this group and make up an ancestral line of evolution which fully deserves a name "stem lobograptids".

PLATE VIII



Tentative phylogeny of the Cucullograptinae

The oldest link of this series, represented by *Lobograptus progenitor* n. sp., is marked, with regard to morphology, by the following fundamental characters: 1) a "robust" type sicula, particularly big for a cucullograptid (1.71—1.55 mm. long) and provided with a well-developed metasicula, having a differentiated aperture; 2) a dorsal curvature in the proximal part of the rhabdosome; 3) proximal and medial thecae devoid of apertural differentiation and distal ones having incipient apertural lobes in the form of characteristic apertural elevations.

It is only the latter character that indicates the cucullograptid (lobograptid) trend of specialization in *Lobograptus progenitor* n.sp. and, besides, it is morphologically still slightly developed. This shows that *L. progenitor* n. sp. represents a very primitive stage of the morphological evolution in Cucullograptinae. The progressive character of the apertural elevations which, in extreme cases, may be strongly developed and take the form, approaching that of apertural lobes, allows us, however, to assign this species to the Cucullograptinae (comp. Fig. 4, and p. 393).

The next stage of stem lobograptids is represented by *Lobograptus simplex* which is morphologically marked by: 1) a "robust" type, although, to a certain extent, gracilized sicula (1.38—1.48 mm. long), provided with somewhat less distinctly elaborated apertural differentiations; 2) a dorsal curvature in the proximal part of the rhabdosome; 3) true, bilaterally symmetrical apertural lobes on all thecae of the rhabdosome.

The latter character makes *L. simplex* the first typical cucullograptid and at the same time separates it distinctly from *L. progenitor* n.sp. in which such lobes were barely incipient (differences in expressivity) and occurred only in the thecae of the distal part of the rhabdosome (differences in penetrance). It seems, however, that *L. simplex* may be derived from *L. progenitor* which is indicated by: 1) a distinct mutual "overlap" of both these species in their stratigraphic ranges, *L. simplex* occurring later than *L. progenitor* n. sp. (Pl. I); 2) a dorsal curvature of the proximal part of the rhabdosome, occurring in both species but unknown in any other cucullograptid; 3) a similarity in the structure of the subapertural part of thecae in both species; 4) robust appearance of sicula.

Taking into account considerable differences in the degree of development of the apertural apparatus in *L. progenitor* n. sp. and *L. simplex*, one may suppose that some transient forms, unknown so far, might exist between typical forms of both species and fill a certain morphological gap now recorded. However, it is beyond any doubt that *L. simplex* constitutes a result of a further development of the same evolutionary lineage which has been initiated by *L. progenitor*.

Lobograptus simplex as a central link in the evolution of the Cucullograptinae

L. simplex, constituting the last link of the stem lobograptids, at the same time, takes a central place in the family tree of the Cucullograptinae. It is unanimously indicated by the morphological and stratigraphic facts that this species was probably a structural stage which started the differentiation of the Cucullograptinae in a few separate evolutionary lineages, i.e. which probably initiated the process of their adaptive radiation. *L. simplex* much better meets the requirements of an ancestral form for the evolutionary lineages of the Cucullograptinae, mentioned above, than *L. exspectatus* because the latter is marked by certain features of specialization (siculae without peridermal rings, strongly developed apertural lobes, provided with a ventral process, the presence of apertural incisions) which are absent from the early representatives of the remaining evolutionary lineages. With regard to morphology, the early representatives of most evolutionary lineages of the Cucullograptinae may be derived from the structural type represented by *L. simplex.* They belong to five separate phylogenetic lineages which, more or less probably, may be derived from *L. simplex* (Pl. VIII). Particularly close relationships are recorded between the latter and *L. exspectatus exspectatus* which initiates the "*exspectatus* lineage" and *L. scanicus parascanicus*, a starting link of the "*scanicus* lineage".

L. exspectatus exspectatus appearance shows coincidence with disappearance of *L. simplex* and even displays a certain stratigraphic "overlap" with the latter (Pl. I). The apertural apparatus of *L. exspectatus exspectatus* may easily be derived from that of *L. simplex* (cf. p. 327, Pl. III) upon the assumption of a further growth of lobes with their bilateral symmetry unchanged. In this respect, the *exspectatus* lineage only makes up a continuation of the stem lobograptid development trend. On the other hand, siculae are marked by certain characters of specialization (disappearance of peridermal rings, intensive development of the dorsal process, etc.). A certain specialization of the sicula and a disappearance of the dorsal curvature of the proximal part of the rhabdosome induce us to separate this evolutionary trend as a separate "*exspectatus* lineage".

It is also beyond any doubt that there exists a close relationship between *Lobograptus simplex* and *L. scanicus parascanicus,* an early representative of the "*scanicus* lineage". The extinction of *L. simplex* coincides with the first appearance of the latter species and the apertural apparatus of *L. scanicus parascanicus* may be derived from that of *L. simplex* upon the assumption of: 1) a further growth of apertural lobes, and 2) the formation of their asymmetry (comp. p. 332, Pl. IV).

The most extensive modifications are observed in the sicula which is subject to an intensive gracilization (comp. p. 316, Pl. II, Fig. 4) and in the proximal part of the rhabdosome form which the dorsal curvature disappears. The relationship between *L. simplex* and *L. scanicus parascanicus* is emphasized by the occurrence of certain morphologically transient forms such as progressive forms of *L.* cf. *simplex* from erratic boulder S. 225 (comp. p. 404, Fig. 6) and primitive populations of *L. scanicus parascanicus,* representing the "lower zonal form" of this subspecies from the Mielnik boring (comp. p. 432, Pl. XXII, Figs. A—E). On the basis of these facts, a certain supposition may be formed as to the course of the evolutionary processes that took place in the separation of this phylogenetic lineage (comp. pp. 434—435).

The relationship between *Lobograptus simplex* and an evolutionary lineage represented by *L. invertus* n. sp. and *L. cirrifer* n. sp. is less clear (Pl. VIII). An early representative of this development trend, i.e. *L. imitator* n. sp. is separated from *L. simplex* by a considerable stratigraphic gap (comp. Pl. I) and displays a fairly high degree of the morphological differentiation. The latter may be reduced to: 1) the gracilization of the sicula with a simultaneous less conspicuous shortening of metasicula than in the *scanicus* lineage and with the presence of a considerably differentiated aperture; 2) the disappearance of the dorsal curvature of the rhabdosome and advanced gracilization of thecae; 3) the development of apertural lobes and their asymmetry which, in general, is comparable with the stage, reached by *L. scanicus parascanicus.*

The original divergence of both R-cucullograptid development lineages consisted, therefore, in differences in the mode of gracilization of siculae, while the evolution of the apertural apparatus took, at first, a parallel course (*L. scanicus parascanicus* and *L. imitator* n. sp. stages). It was only when the subsequent differences appeared in the development trends of both lineages that they were still more emphasized by the divergent specialization of apertural apparatus (comp. Pl. II, Fig. 4 and 7; Pl. IV; Pl. V).

In the case of the lineage, initiated by *Lobograptus imitator* n. sp., much the same as in the "*scanicus*" lineage, the descent of *L. imitator* n. sp. from *L. simplex* seems to be the most probable. The existing stratigraphic and morphological gap may easily be explained if we accept the hypothesis that the separation of this lineage took place in another area (allopatrically), while in the Mielnik sequence later events are observed, connected with spreading of a previously separated phylogenetic lineage. On the other hand, the supposition that the *L. imitator* n. sp. lineage was formed by the specialization of *L. scanicus parascanicus* seems to be less likely.

The relationships of L-cucullograptids to *Lobograptus simplex* are, in general, not as close as those, previously stated for asymmetric lobograptids. However, in the case of "*hemiaversus-rostratus*" lineage, its descent from *L. simplex* seems to be very likely. This results primarily from the structure of proximal thecae which are still provided with an almost symmetrical apertural apparatus easily derivable from that in *L. simplex* upon the assumption of a few simple modifications. It should be stressed, however, that *Cucullograptus hemiaversus* represents an already relatively specialized evolutionary stage of this phylogenetic lineage, this specialization being marked by: 1) a strong gracilization of the sicula (Pl. III, Fig. 10); 2) a disappearance of the dorsal curvature of the rhabdosome and the gracilization of thecae; 3) a high development degree of the apertural apparatus with its simultaneous asymmetry in thecae of the medial and distal parts of the rhabdosome (Pl. VI). The supposition seems to be, therefore, fully justified that between *L. simplex* and *Cuc. hemiaversus* there existed at least one transient link, unknown so far (comp. p. 491).

The origin of the side line of "*pazdroi*" which displays considerable morphological differences as compared with *Lobograptus simplex* and all other Cucullograptinae, is still the obscurest. On account of rather peculiar morphological features and the lack of a clear relationship to other phylogenetic lineages, this evolutionary trend may be termed, a "*pazdroi* side-line". The relationship of this line to the stem lobograptids continues to be obscure and there are no transient forms, filling the gap between *Cucullograptus pazdroi* and the rest of the Cucullograptinae (Pl. VIII). This species may be: 1) cryptogenic and its similarity to other Cucullograptinae (the gracilization of the sicula, asymmetric apertural apparatus consisting of lobes) may be ascribed to the convergence or parallelism, or 2) a specialized descendent of the stem lobograptids (perhaps *L. simplex*) which was separated early and in another area (allopatric speciation) being subject to more intensive modifications than other Cucullograptinae. If we accept the latter alternative, these modifications would consist in: 1) a gracilization of the sicula with a simultaneous reduction of peridermal rings, 2) a reduction of the dorsal curvature of the rhabdosome and disappearance of the gracilization of thecae, 3) intensive modifications in the structure of the apertural apparatus, related to a) a slitlike transverse elongation of the aperture and b) a change in the shape (cones or hoods) and fusellar structure of the apertural lobes. No hypothesis, mentioned above, may be proven so far (comp. pp. 531—532).

The separate phylogenetic position of *Cucullograptus pazdroi* considerably shakes the idea of the Cucullograptinae as a homogenous phylogenetic group, derived from common ancestors. In the present stage of studies, the Cucullograptinae sensu lato (i.e. together with *Cuc. pazdroi*) are rather a sort of a morphological-taxonomic concept although it is almost certain that all other forms are connected to each other by the bonds of a close relationship.

Evolution of the "scanicus" lineage

This evolutionary lineage is represented by the stratigraphic and morphological sequence of three subspecies of *Lobograptus scanicus*, i.e. *L. scanicus parascanicus*, *L. scanicus amphirostris* n. subsp. and *L. scanicus scanicus*. There are the following three characteristic features, determining the morphological changes that occur in this evolutionary lineage: 1) a stable character of asymmetry of the apertural apparatus which — in the course of evolution — is not subject to any major changes (comp. p. 348); 2) a simultaneous progressive increase in the size of apertural lobes and a gradual increase in the complexity of their structure (comp. p. 332); 3) a stable morphological character of siculae which reach typical form as early as in the "higher zonal form" stage in *L. scanicus parascanicus* and, hereafter, are not subject to any major changes.

Since morphologically and stratigraphically *Lobograptus scanicus amphirostris* n. subsp. takes an intermediary place between the remaining two representatives of this lineage, its taxonomic position is of a fundamental significance to understand the evolution of the *scanicus* lineage.

In its first appearance, *L. scanicus amphirostris* stratigraphically precedes *L. scanicus scanicus*, but it reaches its maximum development only after the disappearance of the latter and, in addition, its occurrence is marked by a high degree of discontinuity (comp. Pl. I). Nevertheless, in view of its early appearance, less specialized apertural apparatus and, on the whole, a very high degree of mutual similarity, *L. scanicus amphirostris* n. subsp. may — in my opinion — be considered a forerunner of *L. scanicus scanicus* and included in the *L. scanicus* evolutionary series as its middle link. *L. scanicus scanicus* may be treated rather as a specialized, short-lived form which was developed from *L. scanicus amphirostris*. A supposition that *L. scanicus amphirostris* n. subsp. and *L. scanicus scanicus* represent two different development trends, whose common descent may be traced to *L. scanicus parascanicus*, makes up another alternative interpretation of the evolution picture of the *scanicus* lineage. This hypothesis seems to be, however, less strongly justified (comp. discussions on the taxonomic position of the subspecies mentioned above). A presumably continuous and gradual character of the evolutionary processes which took place in this development lineage deserves to be emphasized.

Evolution of the "invertus-cirrifer" lineage

In this phylogenetic lineage, the evolution is marked by divergent trends, occurring above its initial link which is represented by *Lobograptus imitator n.sp.* mentioned above (comp. p. 368). At present, it is impossible to state whether such tendencies started to appear directly "above" the latter species, i.e. whether both species were derived independently from *L. imitator* n.sp. or whether, for some time, they formed a common line of evolution which only later on was differentiated into two separate lineages (comp. p. 480). The specialization of the sicula, i.e. the gracilization without a simultaneous simplification of the apertural part is a feature which characterizes this evolutionary lineage as a whole (comp. p. 316, Pl. II, Figs. 7—9). On the other hand, the evolution of the remaining thecae of the rhabdosome takes place throughout the initial primitive stage which, on the whole, corresponds to a stage, represented — in the *scanicus* phylogenetic lineage — by *L. scanicus parascanicus.*

The next stage is connected with an increase in the size of apertural lobes and process of the divergence particularly distinct in the morphology of the apertural apparatus in distal thecae (comp. Pl. V):

Lobograptus invertus n.sp.	*Lobograptus cirrifer* n.sp.
1) Left-hand lobe provided with an apertural incision and a strongly bent terminal process	1) Left-hand lobe provided with an apertural incision and a rostral process, situated on the upper margin of this incision
2) Right-hand lobe provided with ventral and dorsal adapertural plates	2) Right-hand lobe provided with an apertural incision and a rostral process, situated on the upper margin of this incision

Lobograptus invertus n.sp. may, in general, be considered a less specialized species than *L. cirrifer* n.sp. This is confirmed by the following two facts: 1) the structure of the sicula which, in the former species, do not depart from that in *L. imitator* n.sp. and, in the latter, has distinct traces of a certain specialization (comp. p. 479, Pl. II, Fig. 9) and 2) the stratigraphic occurrence which, in the case of *L. invertus* n.sp., displays a distinct overlap of the *L. imitator* n.sp. range and, in the case of *L. cirrifer* n.sp., is separated from it by a considerable gap (comp. Pl. I). Considering these facts it seems to be quite possible that a transient form, unknown so far, existed between the stage, represented by *L. imitator* n.sp. and the stage of *L. cirrifer* n.sp. Such a conclusion is all the more probable since morphologically more and less advanced forms, also situated in slightly different horizons, occur among the *L.cirrifer* n.sp. populations (comp. p. 470).

Evolution of the "exspectatus" lineage

With regard to the development of the apertural apparatus, this lineage makes up a direct continuation of a development trend, represented by the stem lobograptids. The main evolutionary processes consist in: 1) an increase in the size of the apertural lobes with their bilateral symmetry unchanged; 2) a development and tendency to a strong bending of the ventral processes of the lobes; 3) a strong development of the lateral margins of the apertural lobes, forming lateral outgrowths of the apertural apparatus (in the *Lobograptus exspectatus bicornis* n.subsp. stage). *L. exspectatus*, belonging here, at the same time, constitutes a species of the longest continuance among all Cucullograptinae (cf. Pl. I) which seems to show that, in truth, it represented a relatively primitive but successful adaptive type which, morphologically and ecologically, occupied a central position among all Cucullograptinae, recorded above the *L. simplex* level.

Evolution of the "hemiaversus-rostratus" lineage

In the present state of knowledge, this lineage is represented by the following three links: 1) *Cucullograptus hemiaversus*, 2) *Cuc. aversus aversus*, 3) *Cuc. aversus rostratus*. With regard to morphology, there are much greater differences between link 1 and 2 than between 2 and 3. In the latter case, they are obliterated to a considerable extent by the occurrence of some transient forms. It might well be that between a stage, represented by *Cuc. hemiaversus* and that, represented by *Cuc. aversus aversus*, there existed some transient forms that filled the discontinuity which now is observed between them. On the other hand, the entire subsequent evolution undoubtedly constituted a gradual and almost fully continuous process ("gleitende Evolution"). Such a character of this process is most distinctly manifested in the evolution of the apertural apparatus, i.e. in the development of the left-hand lobe. The following three stages may be distinguished in this process: 1) a primitive lobe without the rostral process and with an indistinct gular plate (a typical *Cuc. aversus aversus*), 2) a "less advanced" *Cuc. aversus rostratus*, but having the rostral process and distinct gular plate, 3) the formation of secondary superstructures on the left-hand lobe, i.e. a strongly developed gular plate and "gorget", as well as the appearance of a "pectoral crest".

Links 2 and 3 of the "*hemiaversus-rostratus*" evolutionary lineage are represented by the geologically youngest species of the Cucullograptinae (Pl. I).

Anatomical-comparative analysis of the phylogeny of the Cucullograptinae

Certain key events and principal processes may be easily distinguished in the phylogenetic process of the Cucullograptinae (Pls. VIII and IX).

There were the following four key events which made up the evolution of the Cucullograptinae: 1) the separation of the stem lobograptids, closely related to the very origin of the Cucullograptinae (comp. p. 378); 2) the main radiation of the Cucullograptinae which presumably brought about the split into the five different evolutionary lineages; 3) the directional evolution of each particular evolutionary lineage; 4) the secondary divergence in the "*invertus-cirrifer*" lineage which is the only exception from the sequentional evolution processes which predominate in this phase (Pl. VIII).

The principal evolutionary processes consisted: 1) in the phenomenon of the directional evolution which was sure to make up a process, predominating in the phylogeny of particular lineages, and 2) in the divergence process which brought about the initiation of the development of different lines.

All these processes were contained within the microevolution, at the speciation level and in different stages of its advancement (the formation of morphologically more and less advanced populations of a given subspecies decisive for their "zonal evolution", the formation of subspecies and species), as well as at the level of the initial processes of the transpecific evolution (the formation of genera).

The directional evolution is most distinctly manifested in the evolution (gracilization) of the sicula, in the increase in the size of lobes and intricacy of their structure in all Cucullograptinae, as well as in the development of asymmetry of the apertural apparatus in the "*hemiaversus-rostratus*" lineage. These processes, taking place, independently from each other, in different phylogenetic lineages, constitute excellent instances of the evolutionary parallelism (the form of the sicula in *Lobograptus scanicus* and *Cucullograptus aversus* and, in particular, the formation of rostral processes on the lobes of specialized representatives of two different lines of evolution, i.e. *L. cirrifer* n.sp. and *Cuc. aversus rostratus*). The directional processes are expressed by both the progressive structural development (an increase in the size of lobes and intricacy of their structure) and the phenomena of a partial or a more advanced reduction (a reduction of the right-hand lobe in the "*hemiaversus-rostratus*" lineage, a partial reduction of the metasicula in the process of the gracilization of the sicula, a reduction of the dorsal process of the metasicula).

The divergency processes, responsible for the main evolutionary event in the Cucullograptinae, consisted mostly in the development of the divergent types of asymmetry of the apertural apparatus (the formation, of the S-, R- and L-cucullograptids) and, in less important cases, also in differences in the direction of the sicular differentiation among the R-cucullograptids), as well as in the specialization trend of the sicula and apertural apparatus (differentiation among the L-cucullograptids). The secondary divergency in the "*invertus-cirrifer*" lineage consisted in differences, marked in the specialization trends of the apertural apparatus and, to a smaller extent, in a slightly different trend in the sicula.

The "family tree" of the Cucullograptinae with the trace of main structural boundaries marked on it is shown in Plate IX. This trace allows one to observe the character of morphological changes that took place in different evolution stages.

TAXONOMY OF THE CUCULLOGRAPTINAE

GENERIC SUBDIVISION OF THE CUCULLOGRAPTINAE

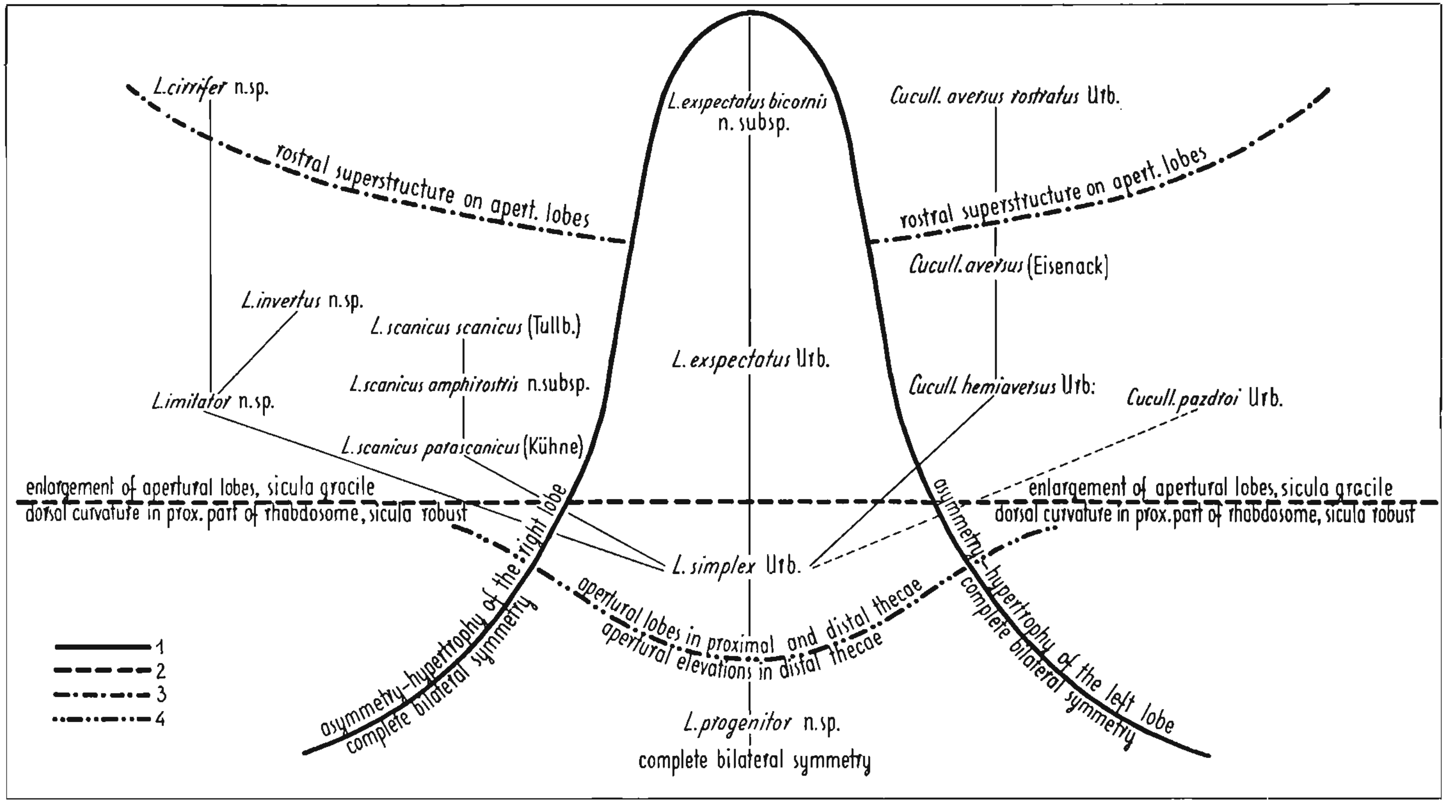
The idea of the Cucullograptinae as a separate subfamily within the Monograptidae Lapworth, 1873, has been first introduced by Urbanek (1958, pp. 10 and 11) to designate monograptids, marked by the following characters: 1) slender and thin thecae, provided, in distal part, with a straight protheca, and a metatheca having in distal thecae a ventral curvature; 2) an aperture round or fissural in cross section, provided with paired apertural lobes, formed by lateral walls of the metatheca and consisting of a single row of fuselli; 3) a tendency to asymmetry of the apertural apparatus, manifested by a stronger development of one lobe or a reduction of the other. The genera *Lobograptus* Urbanek, 1958 [*L. scanicus* (Tullberg) being a type species of this genus] and *Cucullograptus* Urbanek, 1954 (type species *C. pazdroi* Urbanek) have been assigned to this subfamily.

Lobograptus has been defined as the genus of Monograptidae whose representatives have a round aperture with flat, asymmetric or almost completely symmetrical apertural lobes, formed by the superposition of fuselli which are arched and gathered in two nodes.

As to *Cucullograptus*, it has been believed to take in monograptid forms, having slitlike apertures, provided with paired, strongly domed, apertural lobes (or with a single apertural lobe). The left-hand lobe is larger, the right-hand one smaller or reduced.

With regard to phylogeny, the Cucullograptinae have from the very beginning been understood as a group of forms, developed from the ancestors with an originally bilateral symmetry in the main two trends

Plate IX



Comparative-anatomical analysis of the "family tree" of the Cucullograptinae. Structural boundaries are marked by different lines: *1* — separates bilaterally symmetric cucullograptids (S-cucullograptids) from asymmetric ones (R-and L-cucullograptids); *2* — separates forms with dorsal curvature in proximal part of rhabdosome and robust siculae, from that without dorsal curvature, enlarged apertural lobes and gracile sicula (except *L. exspectatus* where sicula remains robust); *3* — delimitates above this line forms with rostral superstructure on apertural lobes; *4* — separates primitive bilaterally symmetric lobograptids, provided only with apertural elevations in distal thecae, from more advanced forms with true apertural lobes throughout the rhabdosome.

one of which is marked by the hypertrophy of the apertural lobes, observed on the right side and the other by that on the left side (Urbanek, 1958, p. 76, Fig. 45).

The distinction of the representatives of the "*scanicus* group" as a separate subfamily with its simultaneous division into two genera have been criticized by Jaeger (1959, pp. 82 and 83). He believes that the differences between representatives of this group are very small and, except for extreme cases, cannot be distinguished in the flattened state of preservation on the rocks. In his opinion, this deprives them of their biostratigraphic significance.

Jaeger's another objection is based on the fact that the differences between the representatives of the Cucullograptinae consist chiefly in the differentiation of apertural apparatus, whose significance is adaptive in character and which are related with the mode of feeding and small functional differences. According to Jaeger, these differences cannot be ranked higher than subspecific.

Furthermore, he believes that, for the classification of such a group as the Cucullograptinae, there is no need to erect new genera or higher taxonomic units.

The present writer sincerely hopes that the material, presented in this monograph, is, by itself, a sufficient reply to Jaeger's doubts. Within the range of the Cucullograptinae, there are considerable structural differences, probably larger than it could be presumed in 1959 by Jaeger who knew only seven forms, belonging to this group of monograptids and who, at that time, did not undertake any detailed anatomical studies on them. The varying range of differences and similarities within this group makes it necessary to apply to its taxonomy the subspecific categories, so strongly emphasized by Jaeger, as well as specific and generic ones and to integrate the entire group in a still higher taxonomic unit. Particular species and subspecies take different stratigraphic positions which, of course, enhances their stratigraphic values. The difficulties in a correct identification of some representatives of the Cucullograptinae, in particular, of those poorly preserved, may certainly be met with even by a skilled stratigrapher but they are, by no means, involved in the examination of only this graptolite group. On the other hand, the limitation of the aims of the taxonomy of fossil groups with these considerations only does not seem to be correct. In addition, the taxonomy itself should be of course established on the basis of a well- and not of a poorly-preserved material.

The least justified seems to be Jaeger's conclusion that differences in the structure of the apertural apparatus in the Cucullograptinae, as being of a definite functional and adaptive significance, cannot be considerably important as taxonomic characters. Arguments, testifying against this view, have, however, been quoted previously (comp. p. 339).

If the taxonomic units, distinguished among the Monograptina are to be comparable with the same units, distinguished among the rest of the Graptoloidea, I do not find any other way but to continue erecting new taxons which, in their range and degree of justification, approach the Cucullograptinae. Bulman (1963, p. 416) has recently been inclined to accept a similar view. He states: "The solution that would confer the greatest measure of stability on nomenclature would surely be to retain the portmanteau *Monograptus* for all general purposes (including particularly stratigraphical zone-fossil) while employing the names *Lobograptus, Colonograptus*, etc. when dealing with the phylogenies and lineages in which they are concerned".

In view of current difficulties in the taxonomy of the Monograptidae, applying a similar solution, the author of the present monograph uses quotation marks to emphasize well-founded doubts whether or not a given form may be assigned to *Monograptus* or to other genera (e.g. "*Monograptus*" *formosus*).

In the light of recent studies, certain changes should, however, be introduced to the morphological and phylogenetic concepts of the Cucullograptinae. The discovery of primitive cucullograptids which phylogenetically are probably closely related to the remaining representatives but morphologically fulfill the diagnosis of the subfamily (based on previously recognized and more specialized forms) only to a small extent, now enables us to speak more about certain tendencies than about definite morphological characters. Among such tendencies, there are: 1) tendencies to the development of lateral apertural lobes which form either a symmetrical, or asymmetric apertural apparatus, 2) tendencies to the gracilization of the sicula and, to a considerable extent, also of the remaining thecae of the rhabdosome, in particular, proximal ones, 3) a prevailing distal mode of introduction of the phylogenetic novelties.

The genus *Lobograptus* is understood in the present work as a genus, uniting the cucullograptids: 1) with a symmetrical apertural apparatus (S-cucullograptids) or those with the hypertrophy of the right-hand apertural lobe (R-cucullograptids), 2) with lobes that are either almost flat, or without a distinct convexity, or even concave, 3) marked by a stable character of asymmetry of the apertural apparatus. *Lobograptus*, put in this way, comprises forms that are undoubtedly closely related with each other. The presence of transient forms does not allow one to separate symmetrical from asymmetric lobograptids.

At present, the genus *Cucullograptus* may be defined as a genus, uniting cucullograptids, displaying: 1) a hypertrophy of the left-hand apertural lobe (L-cucullograptids), 2) a tendency to a strongly domed left-hand or both apertural lobes, and 3) as a genus which also comprises cucullograptids whose asymmetry of the apertural apparatus is progressive in character.

Cucullograptus, as understood at present, takes in the representatives of two phylogenetic lineages one of which ("*hemiaversus-rostratus*") is probably more closely related with the rest of the Cucullograptinae, while the other constitutes a side-line ("*pazdroi* line") whose relationship to the remaining representatives of the subfamily is not accurately settled. *Cucullograptus* is, therefore, to a considerable extent, a morphological-taxonomic and not a phylogenetic-taxonomic concept. In this respect, it should be emphasized that *Cuc. pazdroi* (Urbanek, 1954) is a type species of *Cucullograptus* which, in the light of recent studies, makes difficult understanding this genus as a phylogenetically homogenous one. It may well be that, in future, following a better and more accurate investigation of the origin of *Cuc. pazdroi*, one will be compelled to introduce a thorough change in the taxonomic concept of the Cucullograptinae.

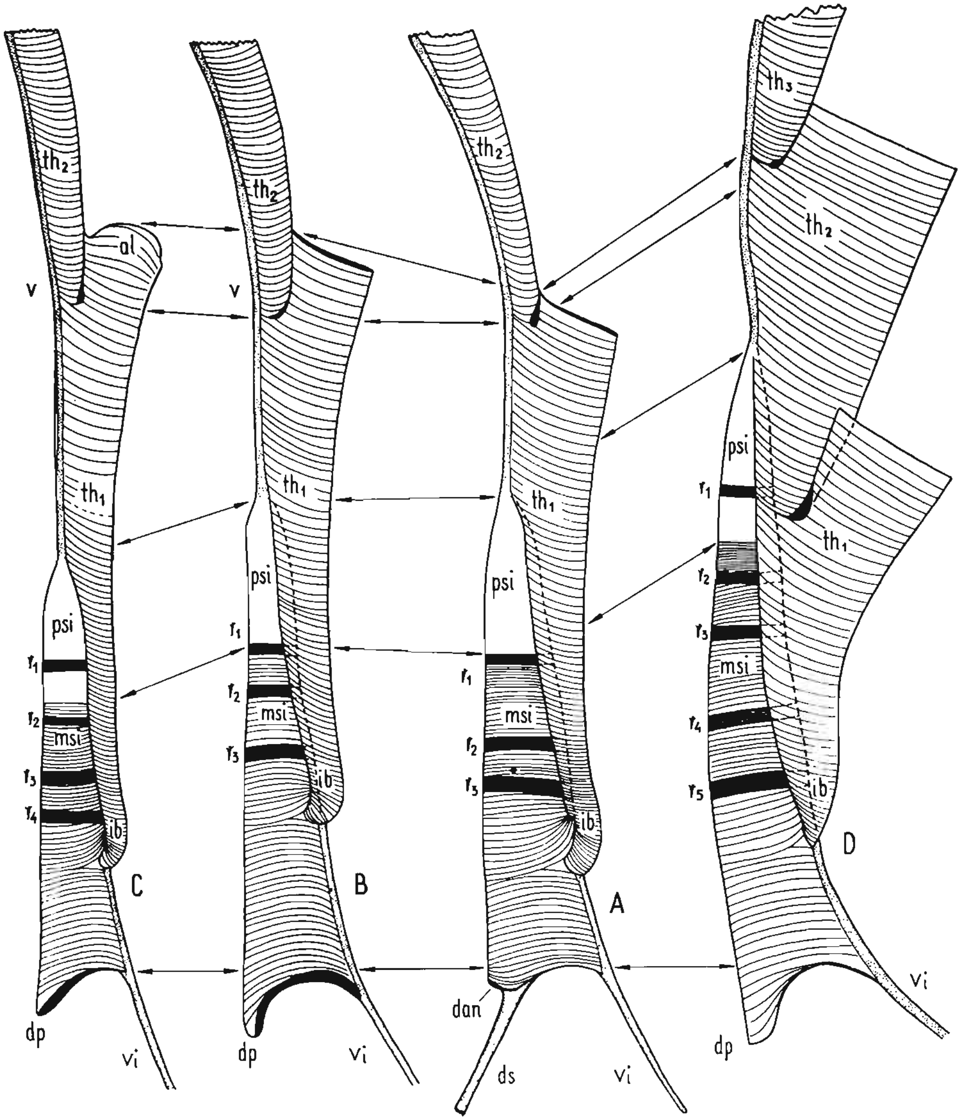
ORIGIN OF THE CUCULLOGRAPTINAE

The problem of the origin of the Cucullograptinae has, at least to a certain extent, been elucidated in a work by Elles (1922, p. 185) who supposed that *Monograptus scanicus* might be derived from monograptids "with hooked thecae". This view was, to a considerable extent, related to the fact that, since Tullberg (1883), the erroneous opinion has been accepted of *Lobograptus scanicus* having hooklike thecae. It was only as late as 1953 that Bulman (1953, p. 131) attracted attention to the true structure of the apertural apparatus in *L. scanicus scanicus*. None the less, Urbanek (1958, p. 23), who modified in some degree Elles' views, considered the Cucullograptinae (in particular, *Lobograptus*) to be likely descendents of monograptids having hooklike thecae. He suggested the division of a uniform dorsal lobe into two derivative lateral lobes (Urbanek, 1958, Fig. 8).

This view on the origin of *Lobograptus* and, through the medium of its primitive representatives, of all other Cucullograptinae, cannot be kept at present which I have previously pointed out when describing *L. simplex* (Urbanek, 1960, p. 213). There are several facts which clearly indicate that the apertural apparatus in the form of strongly developed apertural lobes has not come down to *Lobograptus* from its ancestors but it has gradually been acquired in this group of monograptids as a phylogenetic novelty.

The existing morphological data allow one for a somewhat closer analysis of the origin of the Cucullograptinae, although even now this problem cannot be ultimately solved. The structure of the proximal part of the rhabdosome in primitive lobograptids (*L. progenitor* n.sp.,

PLATE X



Comparison of sicular parts of rhabdosomes in early representatives of different trends: *A* — Linograptinae (*Neodiversograptus nilssoni*); *B-C* — Cucullograptinae (*Lobograptus progenitor* n.sp. and *L. simplex*); *D* — "*Pristiograptus*" *bohemicus* (lower zonal form from the Mielnik deep-boring, depth 1,005.9—1,005.6 m). Somewhat diagrammatically; scale approximate. Arrows indicate the position of homological points, to visualize main changes in shape of particular segments of rhabdosome.

al apertural lobe, *dan* dorsal apertural notch, *dp* dorsal process on metasicula, *ib* initial bud, *msi* metasicula, *psi* prosicula, r_1-r_4 successive sicular black rings, th_1-th_3 — successive thecae, *v* virgula, *vi* virgella.

L. simplex) as a part which should be least changed by secondary phylogenetic modifications (comp. p. 361) and facilitate "tracing back the ancestry of Cucullograptinae" (Pl. X) is of a fundamental significance to this problem.

The structure of the sicular part of the rhabdosome in the stem lobograptids (B,C), as well as in the early representatives of two other evolutionary lineages, marked by a considerable similarity of the proximal part of their rhabdosomes is shown in Pl. X. They represent a linograptid line of evolution (A, *Neodiversograptus nilssoni*) and a separate evolutionary trend of the "*Pristiograptus*" *bohemicus* group (D, "*P.*"*bohemicus*, based on a specimen from the earliest populations at the Mielnik boring). These three evolutionary trends are represented among monograptids of the Lower Ludlovian by early species, marked by a considerable similarity of the proximal part of their rhabdosomes.

Particularly noteworthy is the similarity of *Lobograptus progenitor* n.sp. as an early representative of the cucullograptid lineage (B) to *Neodiversograptus nilssoni*, as an early representative of the linograptid lineage (A). A high degree of similarity in size, shape and proportions of the sicula and the proximal thecae, the presence — in both cases — of the dorsal curvature of the rhabdosome, as well as a characteristic, obliquely inclined thecal aperture are especially remarkable.

It should be emphasized that the characteristic apertural elevations which in *L. progenitor* n.sp. make up an incipient form of apertural lobes, are very similar to the apertural structures which are hereafter developed in the Linograptinae. In particular, they resemble the lateral apertural elevations of *Neodiversograptus beklemishevi* (Urbanek, 1963, p. 165, Text-pl. 5, F), developed in distal thecae. Presumably, both structures developed parallelly in both these groups of the Monograptidae. The fact is noteworthy that the first peridermal ring of the sicula (r_1) in *N. beklemishevi* is formed on the prosicular segment which does not seem to be a frequent character in the Monograptidae, but is peculiar to the Cucullograptinae.

These similarities do not seem to be accidental and probably they indicate a closer phylogenetic relationship between the Cucullograptinae and Linograptinae. It is true that the evolutionary trends of both these groups are completely divergent but, as it has been mentioned above, their early representatives are marked by a smaller degree of divergency and, in addition, the characters are developed in both groups which may be considered a symptom of the heterochronic parallelism[15].

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[15] Similar thecal characters (apertural elevations), which appear in a later evolution stage in the Linograptinae (in *N. beklemishevi*, comp. Pl. I) and in the earlier evolution stage in the Cucullograptinae (*L. progenitor* n.sp., see Pl. I). In both cases they appeared by distal introduction

At present, it is impossible to determine accurately the character of these phylogenetic relationships. *Neodiversograptus nilssoni* appears earlier than *Lobograptus progenitor* n.sp. but it is already marked by some specializations in the linograptid direction of evolution (the presence of the dorsal spine on the metasicular aperture, Pl. X, A-*ds*; the capability to form a sicular cladium). Generally speaking, the sicula of *L. progenitor* n.sp. is, however, less specialized than that in the early representatives of the Linograptidae and it could be developed from the siculae of the latter only through the loss of their specialization characters (the "despecialization" of the sicula) which would be related with the disappearance of the capability to form a sicular cladium characteristic of primitive linograptids in the neodiversograptid stage of their evolution (comp. Urbanek, 1963, p. 200). In the light of such theoretical assumptions, the simplified structure of siculae and progressive modification trends in thecae might characterize the earliest evolution phase of the Cucullograptinae.

However, there is also another possibility of phylogenetic relationships between the Cucullograptinae and Linograptinae, i.e. the descent of both lineages from a common ancestral form unknown so far (it is precisely such a possibility that is marked in Pl. VIII).

Such a form would have to meet the conditions set for the praeneodiversograptid stage in the evolution of the Linograptinae (Urbanek, 1963, pp. 194—198, Text-pl. 13) which it represented or with which it was closely related. From this point of view, the problem of the origin of the Cucullograptinae is closely related to the "cyrtograptid theory" of the origin of the Linograptinae (comp. a more extensive discussion of this question, Urbanek, 1963). If the divergence of the Cucullograptinae and Linograptinae evolutionary trends appeared as early as in the praeneodiversograptid stage, the sicular "despecialization" process would not be necessary for the formation of the primitive, stem lobograptid structural type. The presumption may arise that the structure of the *Neodiversograptus* sicula was formed later on as an adaptation related to the capability to form a sicular cladium in the linograptid lineage. The primitive "robust" siculae of the first lobograptids may be derived from unspecialized siculae of the Cyrtograptinae.

In connection with the "cyrtograptid theory of the origin of the Linograptinae", the hypothesis was developed that *Barrandeograptus carruthersi* (Lapw.), occurring in the Upper Wenlock, was an ancestor of this group (cf. Urbanek, 1963 pp. 196—198 where several authors' views on this problem were discussed in detail). Urbanek also believed that, despite certain reservations, the "cyrtograptid theory is now doubtless the most acceptable concept of the origin of the linograptids" (1963, p. 197). In addition, it is probably *B. carruthersi* or other species, related with it and occupying a similar stratigraphic position, that should be considered a hypothetical link between *Barrandeograptus* and *Neodiversograptus.*

The following communication has been sent to me by Dr. Isles Strachan (Birmingham, England) in his letter of November 16, 1963: "Elles and Wood were wrong in describing *Cyrtograptus carruthersi* from the Upper Wenlock. The error goes back to Miss Elles's paper in 1900 when she compared *carruthersi* with *nilssoni* on the curvature of the stipe and the simple thecae. The type locality for *C. carruthersi* is in Scotland and is Lower Wenlock, probably *murchisoni* zone. Miss Elles never figured any of the Welsh material from the Upper Wenlock which she called *carruthersi* but it is possible that she was there dealing with *C. hamatus*".

It results from Dr. I. Strachan's communication that now, on the basis of British materials, one cannot be sure if *Barrandeograptus carruthersi* actually fulfills the conditions set, with regard to stratigraphy, to a transient form between the cyrto- and linograptids. On the other hand, these conditions seem to be fulfilled by forms described from Scania (Tullberg, 1883, pp. 37—38) as *Cyrtograptus carruthersi* Lapw. They occur in association with "*Monograptus*" *testis* and are considered index forms for the highest level of the "*Cyrtograptus* Series" in Scania (Regnéll & Hede, 1960, pp. 27—28). Judging by figures, given by Tullberg (in particular, Pl. 4, Figs. 17 and 18), a certain geniculation of the ventral wall is displayed by the thecae of the Scania forms, while, theoretically, they should be quite straight. This is in conformity with my direct observations of Tullberg's specimens, preserved at the Palaeontological Institute in Lund, Sweden. I have found that the thecal ventral walls are slightly sigmoidally bent and provided with a sort of a beaklike protuberance in the ventral part of the aperture. The structure of these thecae is more modified than that in the oldest linograptids.

In connection with these observations, very interesting are the materials, studied by Dr. J. Paškevičius (Vilnius, the Lithuanian S.S.R.) and which come from the Pajavonys boring, South-western Lithuania. The form, identified by Dr. Paškevičius as *Barrandeograptus carruthersi* (Lapw.) occurs in abundance in samples, taken at a depth of 1,071·75 m. Stratigraphically, this zone corresponds to that of "*Monograptus*" *testis* which has been found somewhat underneath (at a depth of 1,075 m). *B. carruthersi* occurs there in association with *Gothograptus nassa* (Holm) and *Cyrtograptus* cf. *lundgreni* Tullberg. From the samples, kindly supplied by Dr. J. Paškevičius, I etched the fragments of thecae of this form which, in its general aspect, closely resembles *B. carruthersi,* known from Scania, Sweden. The etched thecae of the medial and distal parts of the cladia are very similar to the thecae of *Linograptus posthumus* (Reinh. Richter) since they have slightly sigmoidal ventral wall and characteristic, slightly pointed lateral elevations of the aperture. Apart from the unusual homeomorphy of thecae, it should be stated that the form, designated as *B. carruthersi* from the Pajavonys boring is probably too specialized to be a direct ancestor of *Neodiversograptus nilssoni*. These facts, as well as the specific characters of the structure of thecae in *B. carruthersi* from Great Britain, discussed previously by the present author make up an additional justification of the view that the cyrtograptid theory of the origin of the Linograptinae, "though very likely, cannot however be regarded entirely proved" (Urbanek, 1963, p. 198). It might well be that another, so far unidentified representative of the Upper Wenlockian pauciramous barrandeograptids[16] was the ancestor in question.

The "*Pristiograptus*" *bohemicus* (Barrande) group makes up another Upper Ludlovian monograptid lineage which is presumably related, by its origin, to the Cucullograptinae and Linograptinae. Although formally, in view of a simple structure of thecae, these species are assigned by most investigators to the genus *Pristiograptus*, it is, however beyond any doubt that they are far from true pristiograptids, represented by the *Pristiograptus dubius* (Suess) group.

The sicular part of the rhabdosome of "*Pristiograptus*" *bohemicus* from the lower level of its occurrence in the Mielnik boring is shown in Pl. X, D. This sicula, aperturally strongly expanding, resembles more a sicula of a primitive cucullograptid than that of *P. dubius* but it is ventrally arched and not straight as in cucullograptids. Noteworthy is also the situation of the first peridermal ring (r_1) which, in this case, is disposed on the prosicula and thus resembles the conditions, predominating in this respect in the Cucullograptinae. It should be emphasized that such a situation of this peridermal ring has not been observed in "*Pristiograptus*" *bohemicus* from erratic boulders which

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[16] In this connection, attention should be turned to the divergency in understanding the genus *Barrandeograptus* which, according to Bouček (1933), takes in cyrtograptids with thecae devoid of apertural differentiations. Following this fact, *Cyrtograptus carruthersi* was assigned to the genus *Barrandeograptus* (Bouček, 1933, p. 66). Unexpected changes have been introduced to these views by Bouček's and Přibyl's work (1952), in which they indicate that the type species of this genus — *B. pulchellus* (Tullberg) — had a "dicellograptid" structure of thecae, i.e. that a spirally introverted ventral lip occurs on its aperture. On the basis of this statement, *B. carruthersi*, in view of a simple structure of its thecae, has been transferred by these authors to the genus *Cyrtograptus* (Bouček & Přibyl, 1952, pp. 18—19). Their observations so far depart from the generally accepted view on the structure of thecae in *B. pulchellus*, based on Tullberg's findings (1883, Pl. 3, Figs. 12—13) that considerable doubts arise if the Bohemian specimens are really conspecific with Tullberg's species. The concept of *Barrandeograptus*, as it has originally been formulated by Bouček (1933), should however be valid until Tullberg's originals are investigated at Sveriges Geologiska Undersökning in Stockholm.

probably represent higher stratigraphic levels (comp. p. 324). Very wide thecae depart from the form characteristic of the proximal thecae of the Linograptinae and Cucullograptinae. On the other hand, in "*P.*" *bohemicus tenuis* (Bouček), the shape of thecae is subject to a certain gracilization and becomes more similar to the thecae of the two groups mentioned above. However, judging by the occurrence of both forms at Mielnik, the subspecies *tenuis* appears later than a more massive ("robust") type variety (shown in Pl. X, D) and it may well be that it constitutes a secondary and not primary morphological form. On the other hand, taking into account the entire structure of the "*P.*" *bohemicus* rhabdosome, it may be proved that it is more closely related with the early representatives of the Cucullograptinae and Linograptinae than with *Pristiograptus* s.s. The existence of family relationships between the "*P.*" *bohemicus* groups and the former two groups might be accepted in a purely hypothetical form (Pl. VIII).

SYSTEMATIC PART

Order **Graptoloidea** Lapworth, 1875
Suborder **Monograptina** Lapworth, 1880
Family **Monograptidae** Lapworth, 1873
Subfamily **Cucullograptinae** Urbanek, 1958
Genus *Lobograptus* Urbanek, 1958
Lobograptus progenitor n.sp. [17]
(Figs. 3—4; Pls. XI—XIV)

Holotype: Pl. XIV, Fig. A (sicula and 1st theca).

Paratypes: Pl. XIV, Figs. B-E (proximal and distal thecae).

Type stratum: Greenish-blue mudstones and marls in the core of the Mielnik deep-boring, between 1,035·0—1,010·4 m of depth, on the top of the *nilssoni* zone (the lower part of Mielnik Beds).

Derivation of the name: Lat. *progenitor* = the direct ancestor, founder of a tribe, as a probable forerunner of all Cucullograptinae.

Diagnosis.—*Lobograptus* with relatively long (1·71—1·55 mm) and broad sicula, provided with a distinct dorsal process, proximal thecae

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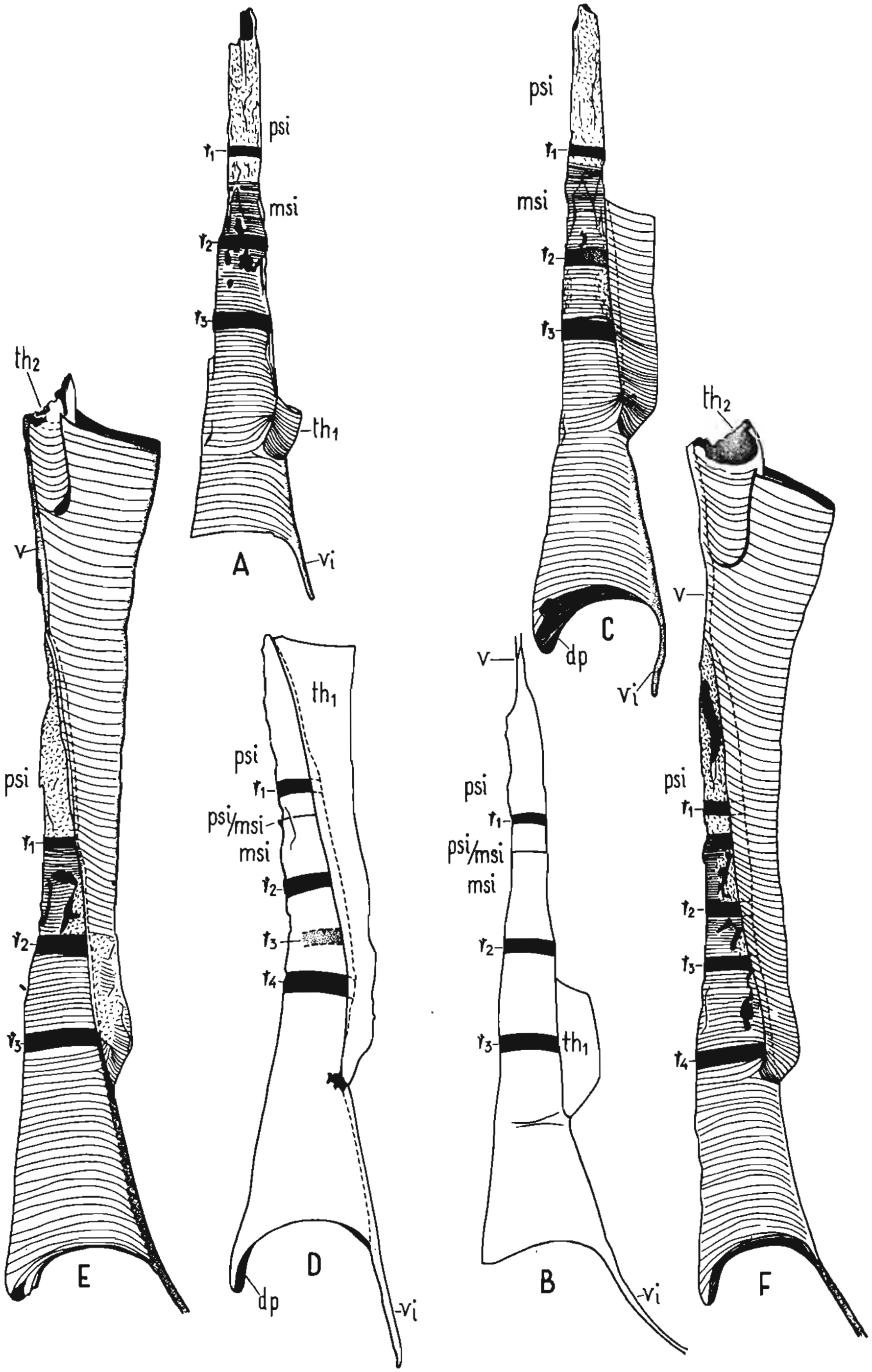
[17] Mentioned by Urbanek (1963, pp. 151—153) as "*nilssoni B*".

Plate XI

Lobograptus progenitor n.sp. Structure of sicula and successive stages in formation of 1st theca. *A* sicula and incipient 1st theca, *B* diagrammatic sketch of sicula and advanced bud of 1st theca, *C* sicula with more advanced 1st theca, *D* sicula with 1st theca reaching the apex of prosicula; *E-F* siculae with complete 1st thecae (S. 151, Jarosławiec): ca. ×50.

dp dorsal process of metasicula, *msi* metasicula, *psi* prosicula, *psi/msi* boundary between pro- and metasicula, r_1-r_4 successive sicular rings, th_1, th_2 successive thecae, *v* virgula, *vi* virgella.

PLATE XI


psi
r1
msi
r2
r3
th1
vi
A
th2
v
psi
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r1
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msi
r2
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msi
r2
r3
th1
vi
B
th2
v
psi
r1
r2
r3
r4
F

with oblique apertural margin and dorsal curvature, medial thecae with straight apertural margin and straight dorsal line, distal ones displaying slight bilateral elevations on apertural margin, distal part of rhabdosome straight or slightly ventrally curved.

Material.—Numerous siculae advanced in growth, young siculae unrecorded. Proximal and distal fragments of rhabdosomes, flattened or partly flattened, etched from the Mielnik boring core samples. Many well-preserved fragments of rhabdosomes, obtained from erratic boulders S. 133, Gdynia-Orłowo, and S. 151, Jarosławiec, allow one to examine the development and fusellar structure. Complete rhabdosome unrecorded.

Description.—Sicula (Pl. XI, Pl. XIV, Fig. A) straight and rather long (1·55—1·71 mm), in the adapertural part strongly expanded. Prosicula varying from 0·46 to 0·65 mm in length on examined specimens. In most cases, periderm secondarily damaged; two to four thin, longitudinal prosicular threads (ribs) are the only detectable details. In most cases, prosicula provided with a prosicular black ring (Pl. XI, Figs. A-D, F, r_1) which occurs at a certain distance (0·09—0·04 mm) from the prosicular aperture. In some specimens, however, the first black ring is situated precisely on the border of prosicula and metasicula (Pl. XI, Fig. E; Pl. XIV, Fig. A, r_1) as is the case of most described monograptids. This variable position of the first sicular ring (r_1) in *L. progenitor* n.sp. forms a contrast with the stability, recorded in the majority of other cucullograptids. The prosicular aperture is ca. 0·09—0·10 mm wide. The apex of prosicula usually terminates in a long virgula.

In adult siculae, metasicula is 0·95—1·17 mm long. Towards the aperture, metasicula expands gradually to reach 0·20 mm in width at the level of the initial bud and 0·30—0·45 mm in the apertural part. Metasicula is provided with some (2—4) black rings, the first of them on the boundary of prosicula and metasicula, or at some distance from it. Some rings are less dark as compared with others, or incomplete (Pl. XI, Fig. C, r_2, Fig. D, r_3). At a distance of 0·70—0·75 mm from the prosicular aperture there occurs the anterior margin of th_1. The initial bud was formed according to the normal monograptid type of development, shown by the presence of a "primary notch" (sinus) as visible on specimens—Pl. XI, Figs. A, C, in their reverse aspects. The apertural margin of an adult metasicula is provided with a distinct, shovellike dorsal process ca. 0.14—0.18 mm in length and with a strong virgella (Pl. XI,

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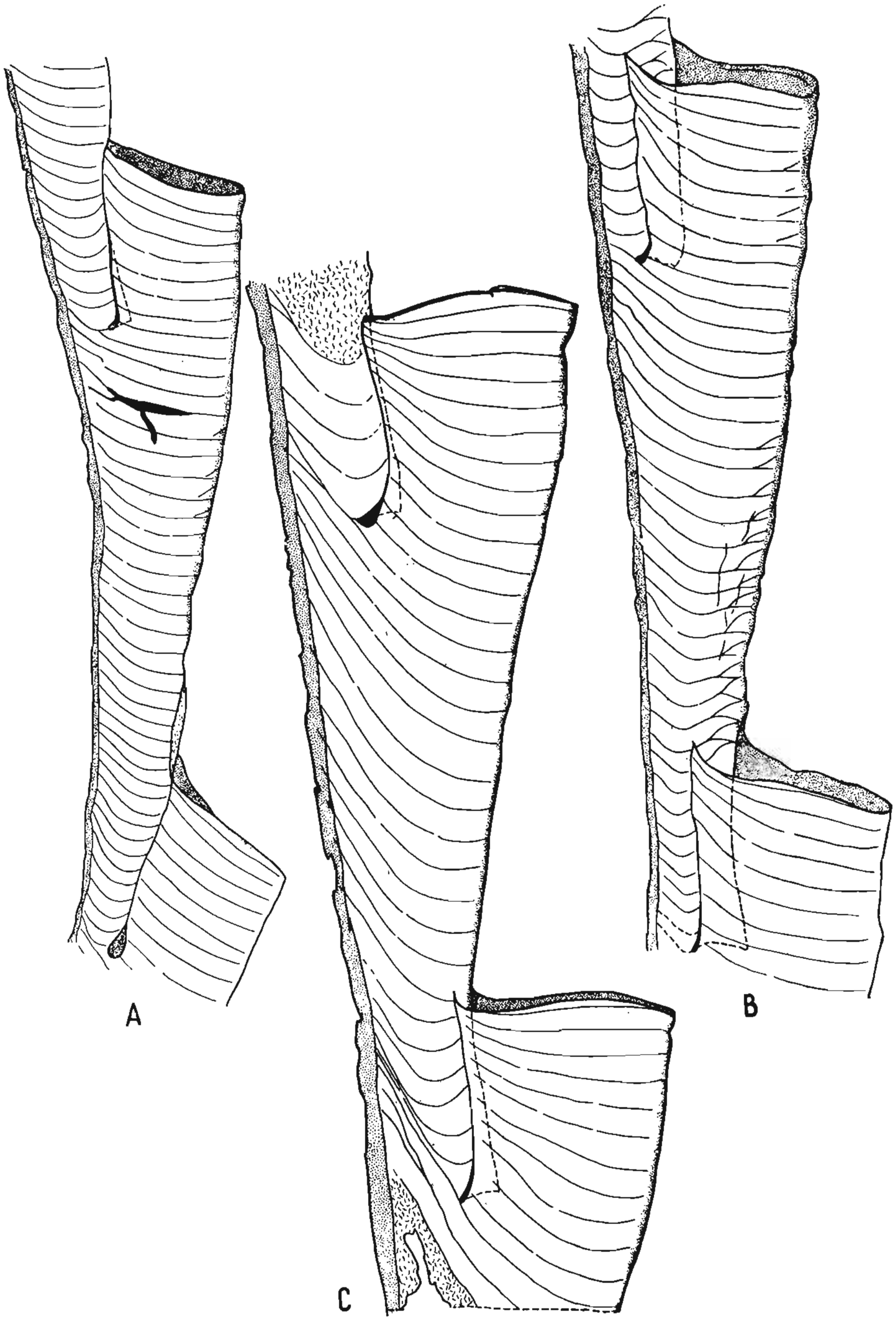
Plate XII

Lobograptus progenitor n.sp. Structure of thecae. *A* lateral view of a most proximal theca showing distinct dorsal curvature; *B* lateral view of a more medial theca with straight dorsal line; *C* lateral view of a distal theca (S. 151, Jarosławiec); ca. ×66.

PLATE XII



Figs. C-F; Pl. XIV, Fig. A, *dp*). This dorsal process is formed in a rather late growth stage of metasicula and, therefore, it is still lacking from young siculae (comp. Pl. XI, Figs. A-B). The apertural margin in adult metasiculae is situated about 0.37—0.52 mm from the anterior margin of th_1.

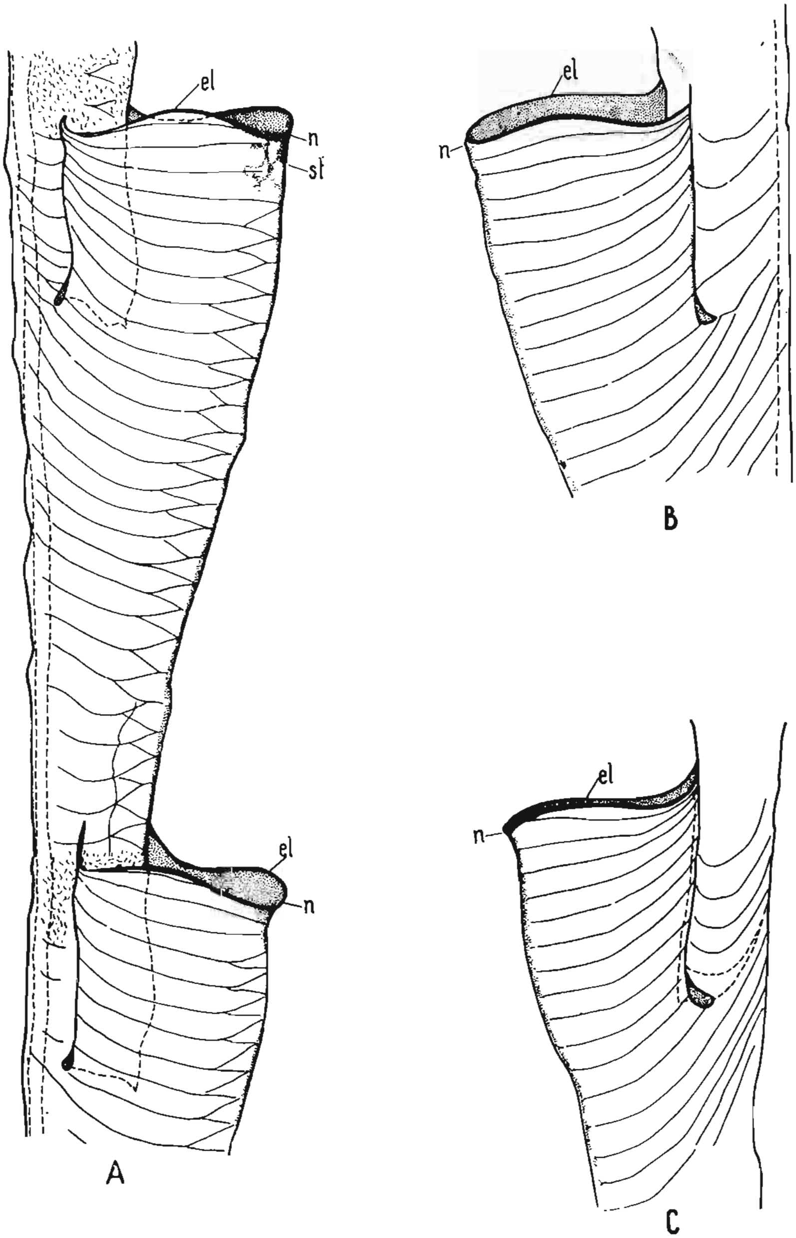
The first theca is tubular, gradually expanding towards the aperture. Its length (*long.*) ranges from 1.5 to 1.8 mm, its width (*tr.*) from 0.08 mm at the base of protheca (initial bud) to 0.23—0.25 mm at the apex of prosicula, and to 0·22—0·24 mm at the aperture. Prothecal segment is ca. 1.28—1.56 mm long, metathecal ones — some 0.22—0.28 mm. Apertural margin, usually slightly thickened, is disposed obliquely to the main axis of rhabdosome at an angle of 20—30°. The apex of sicula terminates at more than 2/3 of a total length of the first theca.

The proximal part of the rhabdosome is incompletely preserved, but on the basis of the specimens examined it may be deduced that a slight dorsal curvature was probably displayed by 3—4 most proximal thecae (th_2-th_5). The presence of this curvature is indicated by bending of the dorsal line in most proximal thecae (comp. Pl. XII, Fig. A and Pl. VII, 1). These thecae still have an oblique apertural margin inclined at about 20—40° to the main axis of rhabdosome. Their total length (*long.*) varies from 1.48 to 1.95 mm, the prothecal segment being 1.22—1.50 mm and metathecal one about 0.25—0.45 mm long. The width (*tr.*) ranges from 0.13 to 0.25 mm at the base of protheca, and from 0.21 to 0.42 mm at the base of metatheca respectively. Protheca occupies in proximal thecae 85—77% of their complete length. Metatheca in proximal thecae is inclined towards longitudinal axis of theca at an angle of 20°.

Thecae situated more medially in the rhabdosome have a less oblique or nearly rectangular apertural margin (Pl. XII, Fig. B; Pl. XIV, Fig. C) which, moreover, shows initial stages of elaboration, indicated by incipient lateral elevations situated on both sides of thecae and separated by a shallow median notch on the ventral zigzag suture.

Distal thecae attain a length (*long.*) of some 1.80—2.05 mm with prothecal segments measuring 1.40—1.58 mm, and metathecal — 0.32—0.47 mm. Their width (*tr.*) ranges between 0.23—0.46 mm at the base of protheca, and 0.35—0.50 mm at the base of metatheca. Protheca occupies in distal thecae 77—74% of their total length. Metatheca is situated almost parallelly to the main axis of theca. At the level of the free margin of interthecal septum, the ventral wall of thecae displays a slightly marked bending (incipient geniculation) which is absent from more proximal thecae (Pl. XII, Fig. C; Pl. XIII, Figs. A-C). Apertural margin has a small winglike elevations, situated symmetrically on both sides of theca. Each of them consists of one fusellus, shorter (*tr.*) than usually, or of one larger and one very short and narrow (*long.*) additional

PLATE XIII



Lobograptus progenitor n.sp. Structure of distal thecae provided with distinct lateral elevations of apertural border. *A* complete distal theca in semilateral view; *B-C* lateral view of apertural part of two distal thecae (S. 151, Jarosławiec); ca. × 66.

el lateral elevation of apertural border, *n* apertural notch, *st* subapertural thickening.

fusellus (Pl. XIII, Fig. A). On thecae, viewed somewhat more ventrally, it may be noted that each lateral apertural elevation is separated on the ventral side by a shallow notch situated just above the ventral zigzag line (Fig. A). The apertural thickened margin of thecae displays the presence of a distinct selvage.

The presence of a peculiar subapertural thickening has been noted on numerous distal thecae, in the assemblage from erratic boulder S. 151, Jarosławiec (Fig. 3, A_1-A_2). This thickening is situated on the ventral side of metatheca just below the median apertural notch and consists of the secondary external deposition of a dark peridermal substance (*sth*). The subapertural thickening is ovoid or horseshoelike in outline and, in some cases, consists of a markedly more convex marginal part (Fig. 3, *m*), surrounding a depressed central field (Fig. 3, *c*) with a thinner layer of secondarily deposited substance. In other cases, however, the subapertural thickening is more or less homogeneous, without being separated into marginal and central parts. In some cases, subapertural thickening is developed only in the form of a few anastomosing fibers, disposed on the surface of periderm (Pl. XIII, Fig. A, *st*). These fibers may also represent an initial stage in the formation

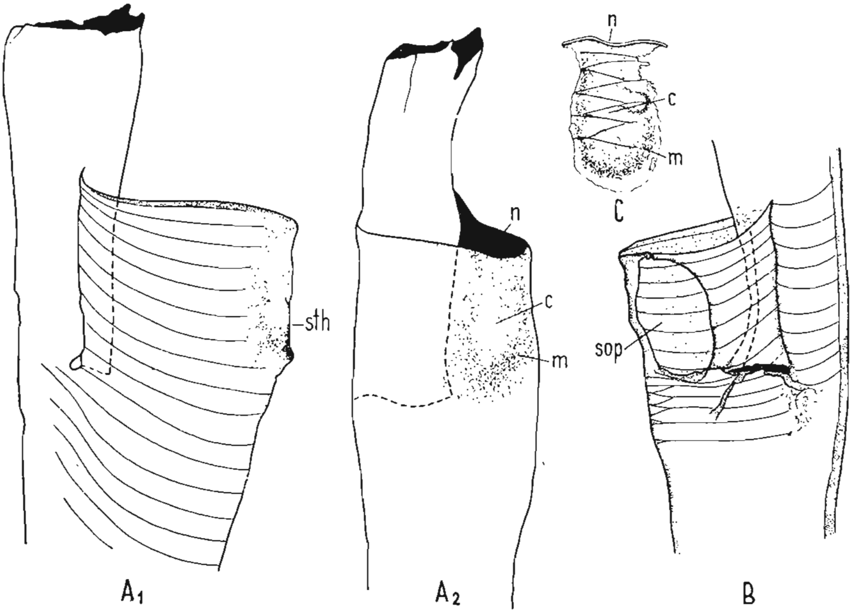
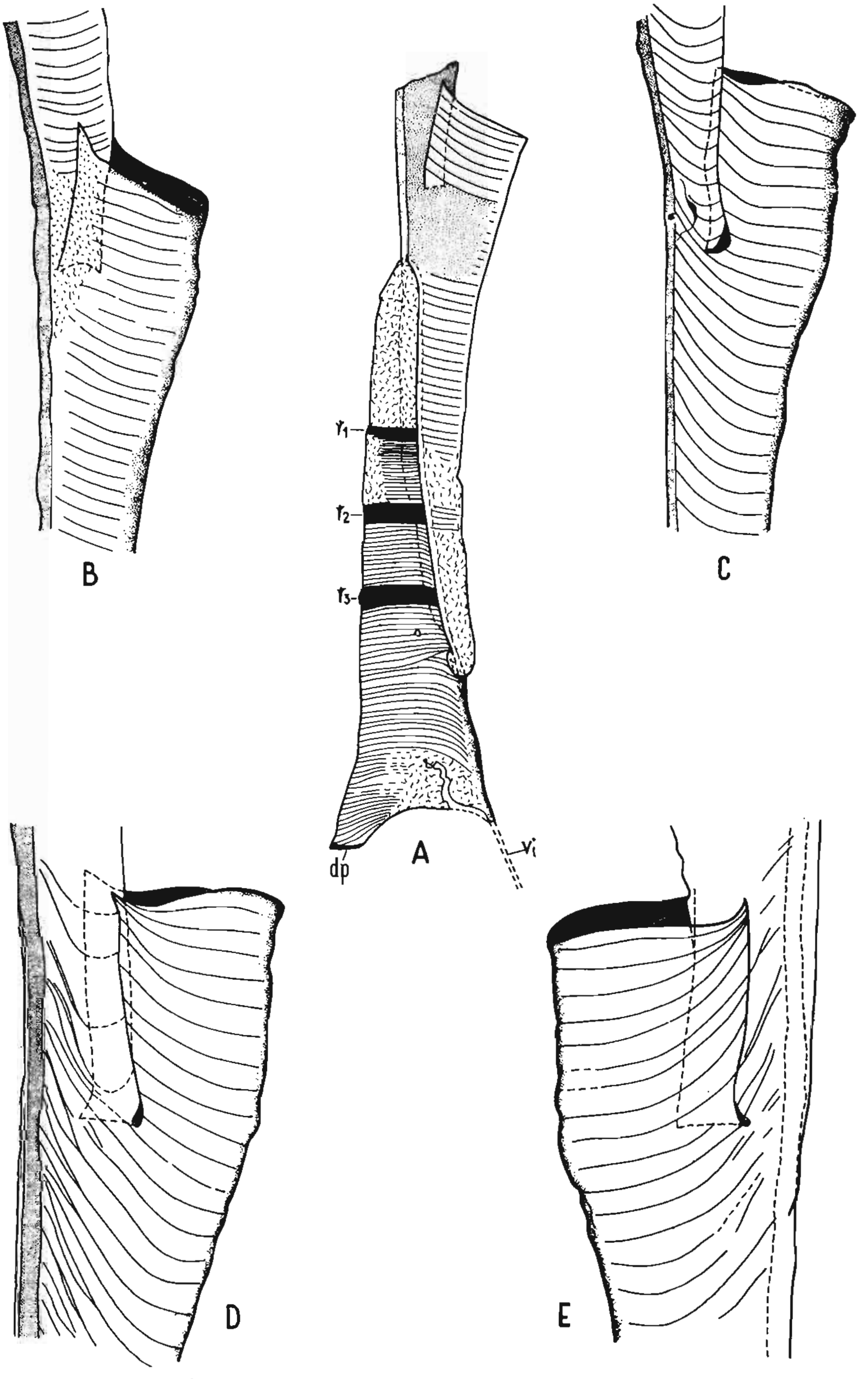


Fig. 3. — *Lobograptus progenitor* n.sp. Subapertural structures of thecae: A_1-A_2 subapertural thickening in lateral and ventral view, *B* subapertural opening, *C* naturally isolated subapertural thickening found in sample (*A*, *C* — S. 151, Jarosławiec; *B* — Mielnik, depth 1,019.0 m), ca. × 63.

c central part of subapertural thickening, *m* marginal part of subapertural thickening, *n* ventral apertural notch, *sop* subapertural opening, *sth* subapertural thickening.

PLATE XIV



Lobograptus progenitor n.sp. Structure of sicula and thecae in slightly flattened state of preservation. *A* sicula and complete 1st theca; *B* apertural part of a proximal theca; *C* more medial theca; *D-E* two distal thecae in lateral view (*A-E* Mielnik, depth 1019.9 m); *A* ca. ×50, *B-E* ca. ×66.

of a more advanced structure. The nature of subapertural thickening in *L. progenitor* n.sp. is obscure.

In contrast to specimens provided with subapertural thickening, some thecae have an opening, situated at the same place (Fig. 3, B, *sop*). The nature of this subapertural opening is still obscurer that the corresponding peridermal thickening described above, but a reasonable explanation of this structure seems to be offered by specimens as those in Fig. 3, C. The latter constitute a horseshoelike fragment of periderm, derived undoubtedly from the subapertural part of the ventral wall of theca which may be concluded from the presence of a zigzag suture and a ventral apertural notch (*n*). The periderm surface, characteristically thickened, leaves no doubt that the fragment in question represents a naturally isolated subapertural thickening. It seems reasonable to suppose, therefore, that subapertural opening is a preservational feature, formed secondarily after falling out of corresponding thickened part of periderm. The development of apertural elevations displays a considerable degree of variation. In addition to thecae with a smaller degree of elaboration of apertural elevations which were previously described from erratic boulder S. 151 and the Mielnik core samples (a depth of 1,019.9 m), the presence of specimens was noted with stronger expression of the structure mentioned above (Fig. 4, A-C). The illustrated series of thecae from the Mielnik core sample (a depth of 1,019.9 m) displays a much stronger development of lateral elevations on apertural margin which consits of 2—3 nearly complete fuselli. Particularly noteworthy is a theca, shown in Fig. 4, A which, despite its proximal character, has high apertural elevations very similar to incipient apertural

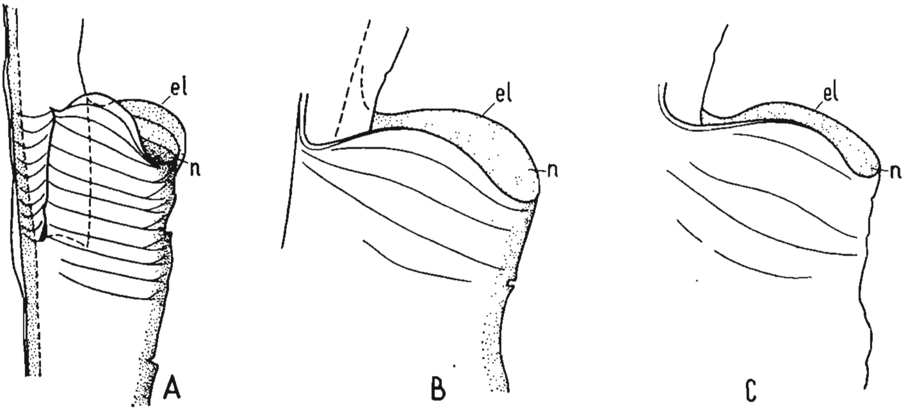


Fig. 4. — *Lobograptus progenitor* n.sp. Apertures with especially strongly developed lateral elevations: *A* in a proximal theca, *B*, *C* in distal thecae (*A-C* — Mielnik depth 1, 019.9 m), ca. × 63;
el elevation of apertural margin, *n* ventral apertural notch.

lobes in proximal thecae of *L. simplex*. A small difference in degree of elaboration of apertural elevations seems to occur also between populations of *L. progenitor* n.sp. in erratic boulders S. 151 and S. 133. In the latter boulder, thecal elevations are somewhat better expressed, but not to an extent comparable with those observed in the core material.

It seems fully justified that the picture of variation in *L. progenitor* outlined above enables one to distinguish the following two morphological types: 1) with a smaller elaboration of apertural elevations (a "normal" and probably more primitive type), 2) with a stronger elaboration of apertural elevations, probably expressed by a greater number of thecae in rhabdosome ("expressivity and penetrance intermediates") and representing a more progressive type. The latter form may be treated, at least in part, as a morphological intermediate filling of a gap between primitive *L. progenitor* n.sp. and *L. simplex*. It is, however, doubtful whether it may also be treated as a phylogenetic transient between the species mentioned above because, being associated with the true *L. simplex*, it appears somewhat too late. Moreover, the concurrence of both types in a chronodeme from the Mielnik core (at a depth of 1.019,9 m) makes the application of the subspecies concept to this material rather unsatisfactory (comp. p. 366). In general, the derivation of *L. simplex* from the progressive *L. progenitor* n.sp. seems, however, to be well-founded (comp. pp. 403—404).

Stratigraphic range. — In the core of the Mielnik boring, *L. progenitor* n.sp. make its first appearance at a depth of some 1,035.0—1,034.9 m (where the presence has been noted of a small fragment probably referable to this species) and continues to occur up to a depth of ca. 1,010.4 m. After a more detailed analysis, a few incomplete remains of similar thecae, mentioned from higher strata (a depth of 1,008,4 m, comp. Urbanek, 1963, p. 152, and a depth of 1,003.3 m) cannot be safely assigned to the species mentioned above. The entire vertical distribution of *L. progenitor* in the Mielnik core seems, therefore, to be limited to a range of 1,035.0—1,010.4 m, i.e. to about 24.6 m of thickness.

Between the last appearance of *Neodiversograptus nilssoni* at a depth of 1,035.9 m and the first occurrence of *L. progenitor* there exists a small gap of some 0.9 m in thickness from which both species mentioned above were absent. This gap of evidently short duration seems to be accidental and it is quite safe to state that the horizon occupied by *L. progenitor* is directly overlying the *nilssoni* zone proper (for more details — see the chapter on stratigraphic distribution, p. 307).

The following other three species of *Lobograptus* appear within the range of *L. progenitor* n.sp. : *L. simplex* Urbanek at depth of 1,020.9 m, *L. scanicus parascanicus* (Kühne) at 1,016.9 m and *L. exspectatus* Urbanek at 1,015.9 m. The vertical distribution of these species display a distinct overlap, in particular in the case of *L. simplex* which usually is directly associated with *L. progenitor* n.sp.

Two different assemblages may be distinguished among the graptolite fauna, associated with *L. progenitor* n.sp. The earlier of them (depths of 1,035.0—1,020.9 m) is characterized roughly by the presence of some forms intermediate between *Colonograptus* and *Saetograptus* and by the simultaneous lack of true *Saetograptus chimaera* (Barr.). There are also many associated retioloids, such as: *Spinograptus spinosus* (Wood), *Holoretiolites erraticus* Eisenack, *H. balticus* Eisenack, *H. mancki* Eisenack, *Plectograptus macilentus* (Törnquist), as well as "*Barrandeograptus*" *operculatus* Münch. An overlying assemblage (depths of 1,020.9—1,010.4 m) contains *Saetograptus chimaera cervicornis* Urbanek, *Monoclimacis micropoma micropoma* (Jaekel), as well as *Holoretiolites erraticus* Eisenack, *H. mancki* Eisenack, *Plectograptus macilentus* (Törnquist) and "*Barrandeograptus*" *operculatus* Münch (see also the distribution table, Pl. I).

In the Baltic drift material, *L. progenitor* n.sp. has been found in two erratic boulders S. 133 and S. 151, associated with the following assemblages: Boulder S. 133, Gdynia-Orłowo — *Monoclimacis micropoma* cf. *micropoma* (Jaekel), *Pristiograptus dubius* (Suess), *Plectograptus macilentus* (Törnquist). Boulder S. 151, Jarosławiec: *Monoclimacis micropoma* (Jaekel), *Holoretiolites mancki* (Münch), *H.* cf. *erraticus* Eisenack. The absence of any saetograptid, which may however be accidental, makes up a remarkable feature of both associations. In both cases, the presence of *Monoclimacis micropoma* (Jaekel) indicates a correlation with the upper part of the occurrence of *L. progenitor* n.sp. in Mielnik.

Systematic position. — *L. progenitor* n.sp. belongs to species which display an unusual combination of characters of some other Lower Ludlovian monograptids. In the structure of siculae it is almost undistinguishable from "*Pristiograptus*" *bohemicus* (Barrande), in the structure and mode of growth of proximal thecae it is similar, to a certain degree, to *Neodiversograptus nilssoni* (Lapworth), but in the structure of distal thecae it resembles markedly the *N. beklemishevi* Urbanek. In its general aspect, the species in question resembles, in many respects, the members of primitive Linograptinae (*Neodiversograptus*), although, on the other hand, it lacks corresponding specializations in the structure of siculae (dorsal spine). On this decisive point, *L. pro-*

genitor n.sp. deviates from the linograptid line of evolution, and doubtlessly represents a different trend of specialization.

The development of the apertural elevation in *L. progenitor* n.sp., being generally paralleled by that in *Neodiversograptus* and representing a morphological stage similar to that, reached by *N. beklemishevi*, has been obtained here much earlier than in any linograptid. This early tendency towards the formation of incipient apertural lobes and the lack of a linograptid specialization in structure of the sicula indicate a cucullograptid trend of evolution. The same is indicated by the pattern of an infraspecific variation, displaying the tendency to the progressive development of apertural differentiations so characteristic of the evolution of cucullograptids. As compared with the earliest, "true" cucullograptid, i.e. *L. simplex* Urbanek, the species in question differs from it mostly in the thecal structure (a degree of expressivity and penetrance in the development and distribution of apertural lobes), but strongly resembles it in the structure of sicula (in *L. progenitor* n.sp. it is only more robust) and in the presence of a dorsal curvature in the proximal part of rhabdosome. It is considered here, therefore, as the earliest and most primitive member of *Lobograptus* (for more details and implications of this assignment — see also the chapter on phylogeny (pp. 364—366).

It is very likely that *L. progenitor* n.sp., owing to its great resemblance to *Neodiversograptus nilssoni* (general appearance of thecae, dorsal curvature of proximal part) and occurrence (immediately below the *scanicus* fauna), were previously described as the latter species (comp. also Urbanek, 1963, p. 153). In this connection, the position of a form, described by Kühne (1955, pp. 384—386, Fig. 10) as *Monograptus nilssoni* but which lacks the dorsal apertural spine, is somewhat uncertain. Dr. W. G. Kühne (Berlin) advised me of the fact that he has never seen a dorsal apertural spine in his specimens of *M. nilssoni* (pers. comm., 1958). According to Dr. Jaeger's (Berlin) opinion, kindly sent me in a letter of November 30, 1959, Kühne's specimens are true *nilssoni* from the *nilssoni* zone. However, in sicula "Das dorsale Züglein is beschädigt (deutlich zerrisen). Man kan daher nicht entscheiden, ob ein Stachel vorhanden war oder nicht. Das Original ist in Kanadabalsam eingebettet."

In connection with the facts mentioned above and with a recent, more complete material, it is also likely that Kühne's species is conspecific with our *L. progenitor* n.sp. This is also indicated by the probable absence of the dorsal spine, by the shape of distal thecae, provided with a slight sigmoidal curvature of the ventral wall (geniculation) and by the presence of small elevations of the apertural margin (comp. Kühne, 1955, Fig. 10, B-C).

Lobograptus simplex Urbanek, 1960
(Figs. 5—6; Pls. XV—XVII)

1960. *Lobograptus simplex* Urbanek; A. Urbanek, An attempt ..., pp. 211—213, Pl. 1, Figs. 1 a-c; Text-figs. 13A, 14A, 19—20.

Material. — Numerous siculae, proximal and distal fragments of rhabdosome in flattened or semiflattened state of preservation, etched from core samples of the Mielnik boring. Abundant fragments of rhabdosome, including siculae in young stages of development mostly etched from erratic boulders S. 219, Lubin, and S. 223, Zegrze. A very well-preserved drift material allows one to examine the development and fusellar structure of thecae. Complete rhabdosome unknown.

Description. — Sicula (Pl. XV, Figs. H, I) straight and rather long 1.38—1.48 mm), relatively strongly expanded in the adapertural part.

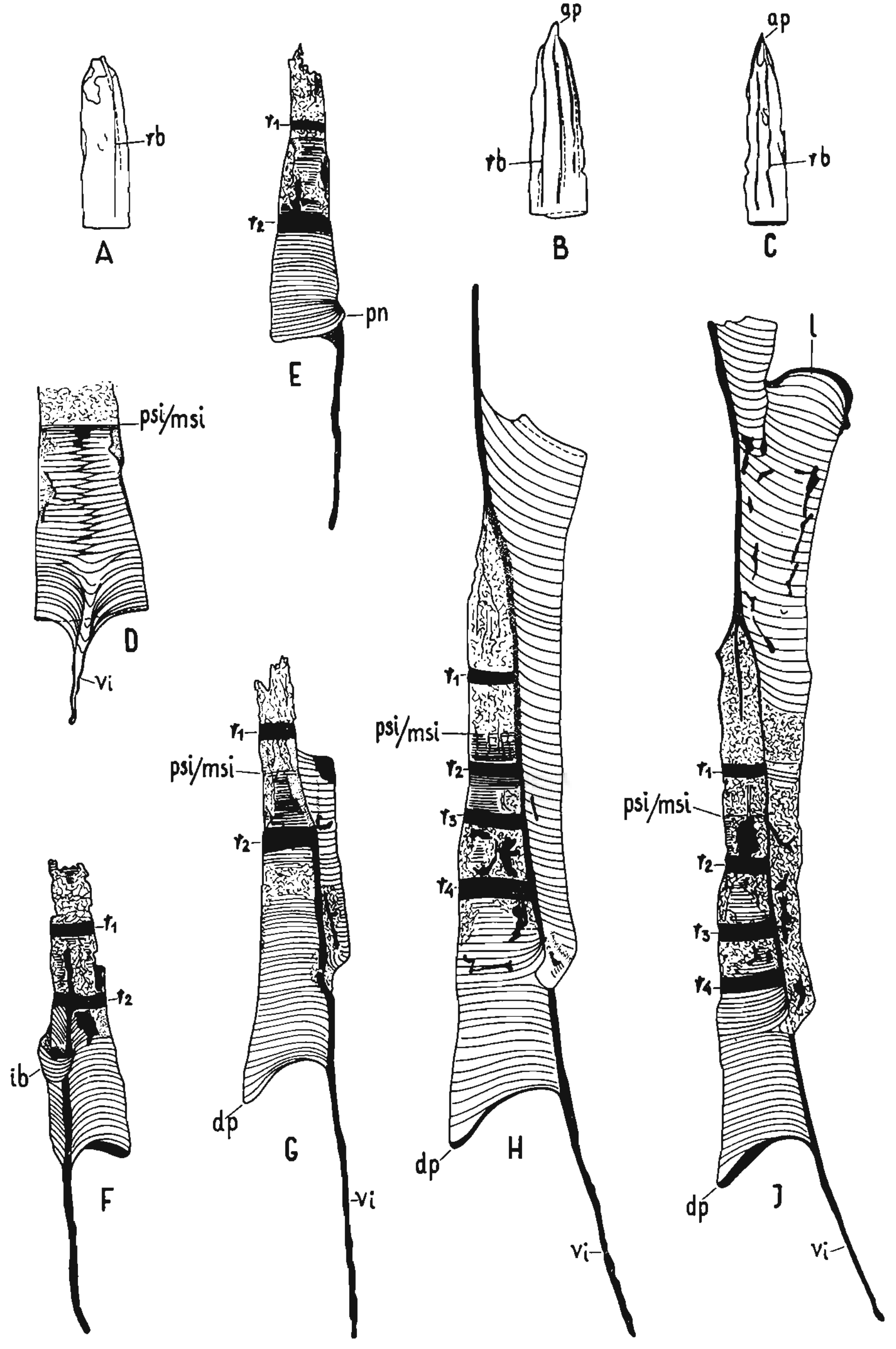
In 6 specimens examined, prosicula ranging from 0.45 to 0.58 mm in length. In most cases prosicular periderm is secondarily damaged and thin longitudinal threads (ribs) which occur in varying numbers (2—6) are the only detectable details. Young prosiculae are devoid of the black ring (Pl. XV, Figs. A-C) which is, however, developed in the majority of examined prosiculae being in later stages of development (Figs. G-I, r_1). This first black ring is mostly situated on the wall of prosicula at a certain distance (0.01—0.12 mm) from its boundary with metasicula. It has been observed in one case that the first black ring was disposed precisely on this boundary (Fig. 5, A). This shows, however, that the position of the first sicular black ring (r_1) is in *L. simplex* variable to about the same extent as in *L. progenitor* n.sp. The conditions described are in contrast with a great stability of position of the first sicular black ring in the remaining representatives of *Lobograptus*. Adult prosiculae terminate in a strong virgula at the apex. In some cases, however, the presence of a secondary, regenerative nema may be noted. These conditions (Figs. 5, A, B) are related to a secondary damage of the apex and a destruction of periderm in apical part of prosicula. The regenerative virgula (nema), in the form of an unpaired thread, is attached to one border of an apical foramen which has probably been formed by the damage of a primary peridermal membrane.

Plate XV

Lobograptus simplex Urbanek. Development and structure of sicula and 1st theca. *A-C* successive stages in development of prosicula; *D* young metasicula and early stage in formation of virgella; *E* metasicula in reverse aspect with primary notch (sinus); *F* metasicula with initial bud; *G-I* successive stages in development of first theca in reverse aspect (S. 219, Lubin), *A-C*, *E-I* ca. ×54, *D* ca. ×100.

ap apex prosiculae, *dp* dorsal process of metasicula, *ib* initial bud, *psl/msl* boundary between pro- and metasicula, r_1-r_4 successive metasicular rings, *rb* prosicular longitudinal ribs, *vi* virgella.

PLATE XV


rb
A
ap
rb
B
ap
rb
C
r_1
r_2
pn
E
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vi
l
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r_4
dp
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r_1
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r_2
r_3
r_4
dp
J
vi
r_1
psi/msi
r_2
dp
G
vi
r_1
r_2
ib
F

Virgula is irregularly twisted, most probably, due to some preservational deformation. The width of the prosicular aperture amounts to ca. 0.09—0.12 mm.

Metasicula in adult siculae is 0.80—0.93 mm long. Towards the aperture, metasicula gradually expands, but to a smaller degree than in *L. progenitor* n.sp. It reaches some 0.18—0.25 mm in width (*tr.*) at the level of the initial bud and 0.24—0.30 mm in apertural part. Metasicula is provided with a few (1—3) black rings (annular bands), the first of them being situated at some distance from the boundary of prosicula. The formation of the initial bud took place in astogeny according to the normal monograptid pattern, as indicated by the presence of a "primary notch" ("sinus" and "lacuna" stages) in Pl. XV, Figs. E-F, and the fusellar structure of adult siculae (Figs. H-I). The anterior margin of the first theca is disposed some 0.6—0.7 mm from the aperture of prosicula. Apertural part of metasicula displays the

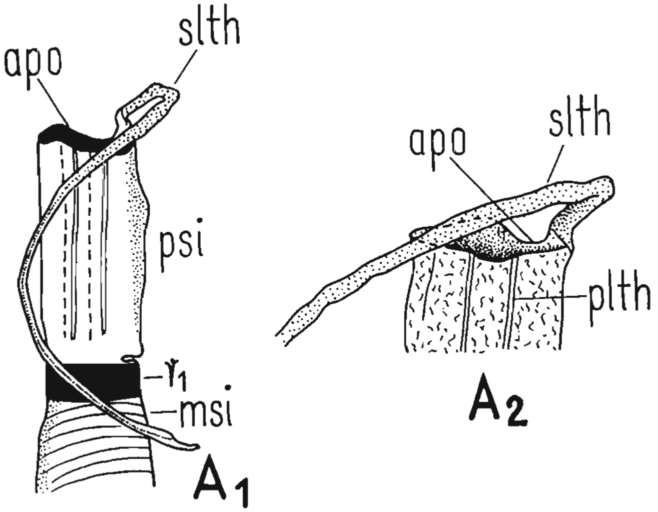
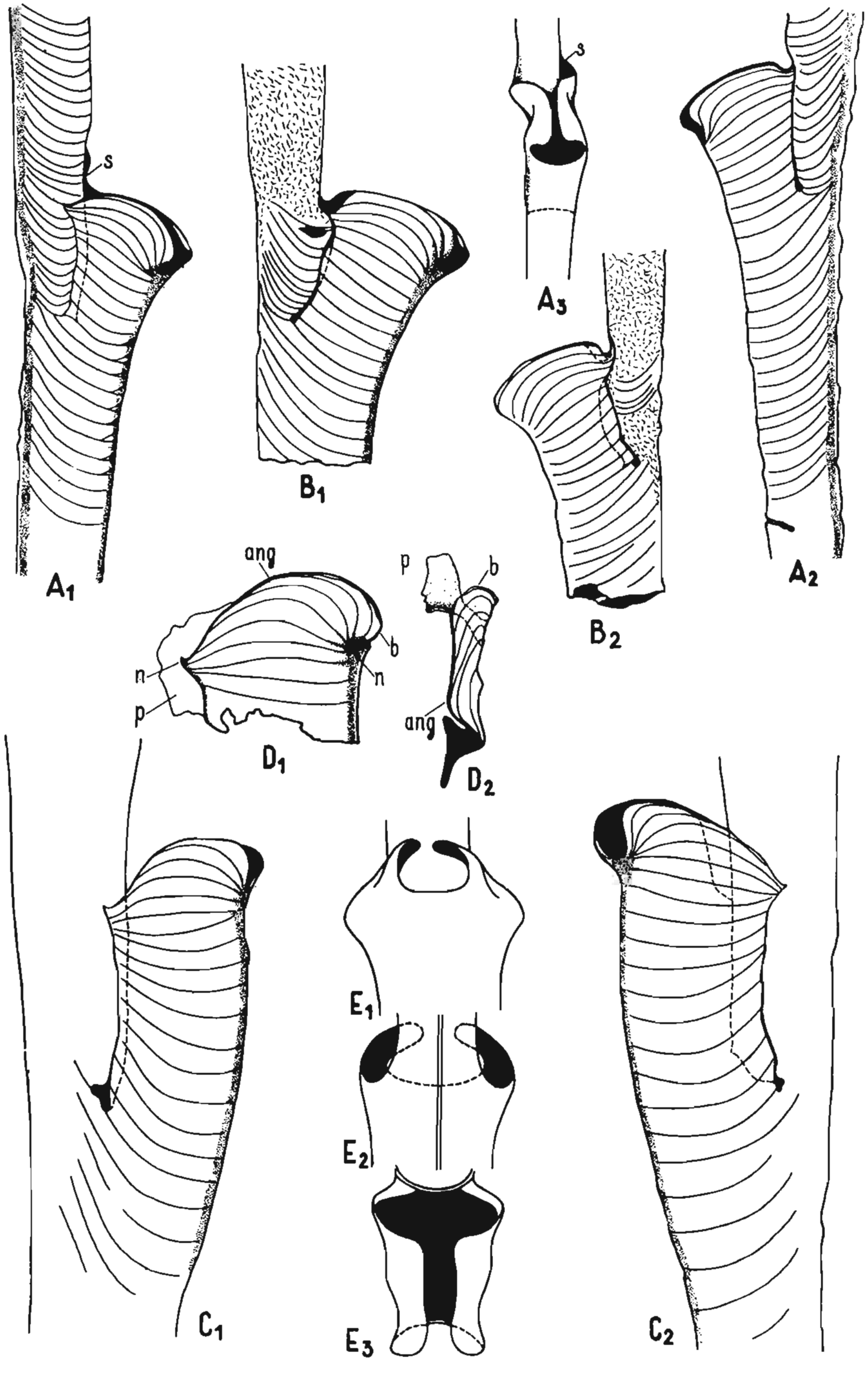


Fig. 5. — *Lobograptus simplex* Urbanek. Sicula with damaged prosicular apex and regenerative virgula (nema): A_1 apical part of sicula, ca. ×126; A_2 details of structure on broken margin of prosicula (S. 219, Lubin), ca. × 200,
apo apical opening, *msi* metasicula, *psi* prosicula, *plth* primary longitudinal thread, r_1 first sicular black ring, *slth* secondary longitudinal thread.

Plate XVI

Lobograptus simplex Urbanek. Structure of thecae. A_1-A_2 lateral views of a proximal theca with abnormally high suspension of left apertural lobe; A_3 top view of the same; B_1-B_2 lateral views of a proximal theca with normal shape of apertural lobes; C_1-C_2 lateral views of a more distal theca; D_1-D_2 lateral and top views of an isolated right apertural lobe showing details of its fusellar structure; E_1-E_3 ventral dorsal and top views of apertural part in more distal theca (S. 219, Lubin); ca. ×70.
ang angular bending of fuselli; *b* beaklike process of apertural lobe, *n* node, *p* fragment of damaged periderm, *s* highly suspended outgrowth of left apertural lobe.

PLATE XVI



presence of a distinct dorsal process ca. 0.05—0.16 mm long and of a strong virgella. The formation of virgella seems to be initiated at a considerable distance from the aperture of prosicula (Fig. D). The base of virgella situated on the ventral fusellar suture is produced by an alternate succession of fuselli whose thickness is locally increased (*tr.*). Dorsal process of metasicula, although distinct, is shorter than in *L. progenitor* n.sp. Lateral margins of aperture are situated in adult siculae some 0.28 mm from the anterior margin of an initial bud.

The first theca is slender, and gradually expanding towards its aperture. Its length, apertural lobes included, ranges from 1.75 to 1.80 mm, its width (*tr.*) — from 0.06 at the base of protheca (initial bud), to 0.19—0.23 at the apex of prosicula, and 0.25 mm at the aperture. Prothecal segment very strongly resembles the same part of the first theca in *L. progenitor* n.sp., and is approximately 1.5—1.54 mm long. Metathecal part occupies some 0.26 mm, the protheca takes 85% of total thecal length. Apex of sicula terminates at about 2/3 of the total length of the first theca. Aperture of metatheca is provided with paired and symmetric apertural lobes which in adult thecae consist of 3—4 fuselli.

The proximal part of the rhabdosome is, in all examined cases, incomplete and consists of small fragments only (two thecae). Bending of the dorsal line of these thecae suggests the presence of a dorsal curvature in the most proximal part of rhabdosome (Pl. VII, 2). Most probably it involves some 3—4 thecae, beginning with the second theca. Dorsal curvature of proximal part of rhabdosome is in contrast with its rather straight mode of growth in the majority of lobograptids.

Proximal thecae are slender and tubular with total length of some 1.58—1.81 mm, protheca being 1.42—1.55 mm and metatheca 0.16—0.30 mm long. Protheca takes 90—83% of total thecal length in proximal part of rhabdosome. Aperture of metatheca is provided with paired and symmetric lateral lobes, separated on the ventral side by a distinct apertural notch. Each lobe consists of some 6 fuselli, 2—4 lower ones being dorsally attached to the ventral wall of adjacent protheca and gathered into a node on the ventral side. The rest of the fuselli are disposed on top of this node and terminate freely at both ends. In some cases, the attached lower part is relatively high (Pl. XVI, Figs. A_1-A_2),

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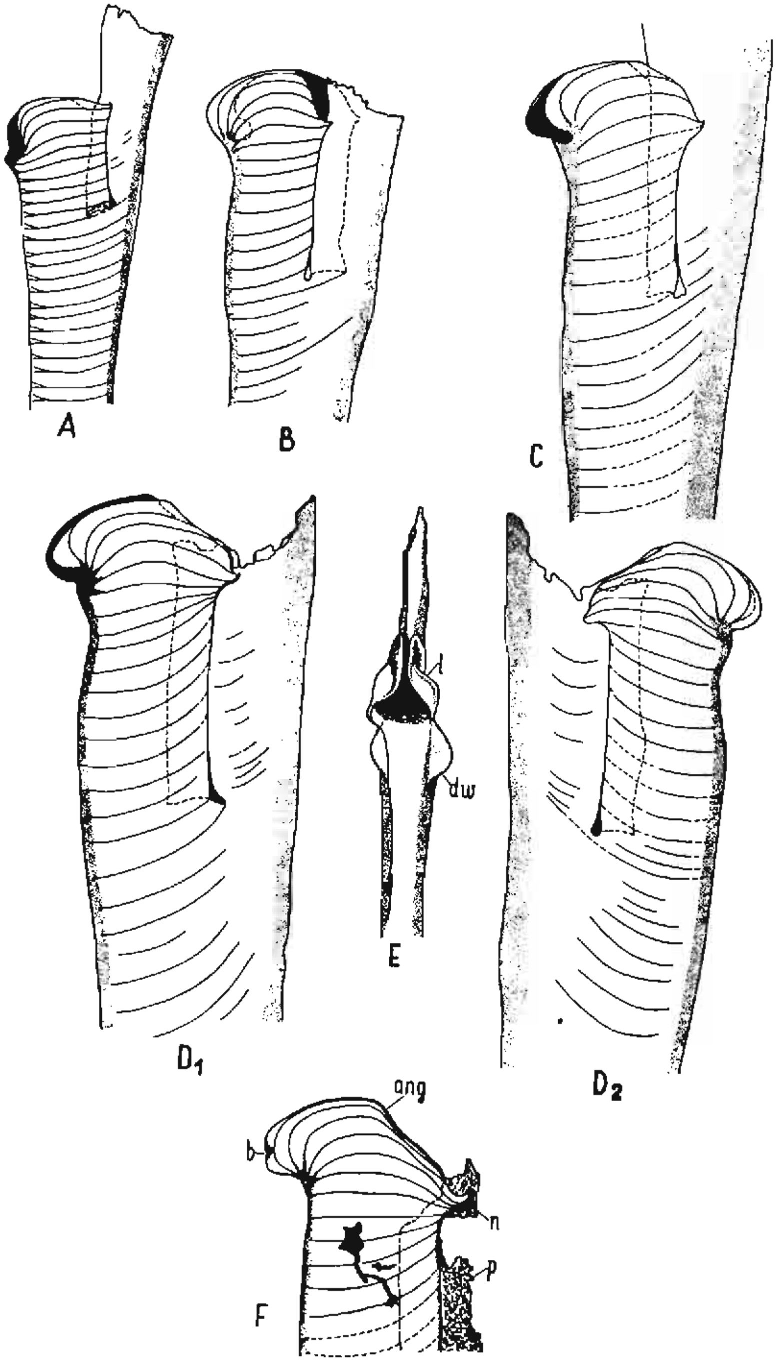
Plate XVII

Lobograptus simplex Urbanek. Structure of thecae in slightly flattened state of preservation. *A-B* lateral view of proximal thecae; *C* lateral view of medial theca; D_1-D_2 lateral views of a distal theca; *E* ventral view of a distal theca; *F* lateral view of an isolated left apertural lobe showing details of its fusellar structure (Mielnik, depth 1,017.9 m); ca. ×63.

ang angular bending of fuselli, *b* beaklike process of apertural lobe, *dw* deformed wall of theca, *l* apertural lobe, *n* node, *p* fragment of damaged periderm.

PLATE XVII



in other — rather low (Pl. XVII, Fig. B). Free margins of both lobes are separated by a distinct fissure (Pl. XVI, Fig. A_3). Some lobes display a slight and obviously accidental asymmetry. This is shown in Pl. XVI, Figs. A_1-A_3, depicting the left lobe with a higher point of dorsal attachment than the right one.

Distal thecae reach some 1.77—2.35 mm in length with the protheca 1.38—1.75 and metatheca 0.39—0.65 mm long. The protheca occupies 76—72% of total length in distal thecae. Their width ranges between 0.26—0.40 mm at the base of the protheca and 0.25—0.42 mm at the base of the metatheca. Approximately at the level of the free margin of interthecal septum, the ventral wall of distal thecae displays a slightly outlined bending (incipient geniculation) which is absent from more proximal thecae (Pl. XVI, Figs. C_1-C_2; Pl. XVII, Figs. D_1-D_2). The aperture of metatheca is provided in distal thecae with paired, symmetric, lateral apertural lobes, formed by some 6—7 fuselli. The height (*long.*) of apertural lobes in distal thecae amounts to 0.14—0.19 mm, the length — to about 0.35—0.45 mm. The 2—3 lowermost fuselli are dorsally attached to the ventral wall of adjacent prothecae, the remaining ones are shorter and terminate freely at the dorsal margin, being gathered into a node ventrally. The last 2—3 fuselli are incomplete, very short and limited to the ventral margin of the lobe where they form its beak-like process (*b*). This results in a characteristic subtriangular outline of the lobe, ventrally rounded, angularly bent in the middle where the last fuselli terminate forming an oblique margin in the dorsal part. The latter is formed by a gradual tapering of fuselli (Pl. XVI, Figs. D_1-D_2; Pl. XVII, Fig. F). The uncompressed, or very slightly compressed specimens from erratic boulders, have the upper margin of apertural lobes distinctly bent and partly overlapping the aperture (Pl. XVI, Fig. E_{1-3}). It seems likely that these conditions were also characteristic of the animal's life-time. In flattened specimens from the Mielnik core, the outline of apertural lobes is somewhat different, most probably due to the state of preservation, involving nearly complete lateral compression of apertural lobes (Pl. XVII, Figs. D_1-D_2; Figs. E-F). Due to straightening of the normally bent part, the upper margin of the lobe looks more angular than in specimens coming from erratic boulders. Apart from the feature mentioned above which occurs only as a result of some preservational changes, there are no greater differences between populations of *L. simplex* from the drift and core material (except for the population from S. 225, Rewal, described below, p. 404).

Stratigraphic range. — In the core of the Mielnik boring, *L. simplex* makes its first appearance at a depth of some 1,020.9—1,020.6, where a small fragment of its rhabdosome has been found. Between the depths of 1,020.6—1,019.9 m, *L. simplex* becomes more frequent and its remains consist of both distal and proximal parts of rhabdosome, including siculae. The peak in the quantitative development was attained between depths of 1,018.0—1,017.0 m where the species in question is very frequent and in some samples displays even a mass occurrence. At a depth of 1016.9—1016.6 m only few and rather uncertain fragments of *L. simplex* were found (comp. Pl. I). It seems, therefore safe to generalize that at least in its distribution in time *L. simplex* displays in the Mielnik core a sudden decrease after a short period of an abundant population. The upper limit of its stratigraphic range may not, however, be determined without some uncertainty. This is caused by morphological transients which occur between *L. simplex* and *L. scanicus parascanicus*, filling — at least in part — the morphological gap between both species (comp. p. 392). Taking into consideration the presence, at a depth of 1,016.9—1,016.6 m, of a lower zonal mutation of *L. scanicus parascanicus*, associated with typical *scanicus* siculae and, moreover, the absence of any reliable remains of *L. simplex* from the same horizon upwards, a depth of 1,015.9 m is accepted here as the upper limit of the vertical distribution of the latter species in the Mielnik core. The entire range of occurrence is limited, therefore, to a narrow band between 1,020.9—1,016.6 m in depth, i.e. to some 4.3 m of thickness.

In the Mielnik core *L. simplex* is associated with the following graptolite fauna: *Saetograptus chimaera* (Barrande), "*Barrandeograptus*" *operculatus* (Münch), *Monoclimacis micropoma micropoma* (Jaekel), *Pristiograptus dubius* (Suess), "*Pristiograptus*" *bohemicus* (Barrande), *L. progenitor* n.sp., and, in the upper part of this core, moreover, with *L. exspectatus* Urbanek and L. *scanicus parascanicus* (Kühne). Furthermore, in the lower region of its occurrence it is associated with *Colonograptus/Saetograptus* transients.

In the Baltic drift material, *L. simplex*, has been found in three boulders (S. 219, Lubin on Island Wolin; S.223, Zegrze; S. 225, Rewal). Boulder S. 219 contained a rich and well-preserved material of *L. simplex,* associated with: *Monoclimacis micropoma micropoma* (Jaekel) and *Pristiograptus dubius* (Suess). Boulder S. 223 contained few short fragments of rhabdosome of *L. simplex,* associated with: *Saetograptus chimaera* cf. *salveyi* (Hopk.), *Pristiograptus dubius* (Suess), and *Holoretiolites mancki* (Münch). Boulder S. 225, Rewal, in addition to a variety of *L. simplex* (see p. 392), yielded the following graptolite assemblage: *Holoretiolites* cf. *mancki* (Münch)., Hydrozoa and Scolecodonta.

Systematic position. — As indicated by the core and drift material, the morphology and stratigraphic range of the rhabdosome seems to support the opinion, that *L. simplex* constitutes a further development of *L. progenitor* n.sp., the latter being probably a forerunner of all other lobograptids. There is a number of remarkable structural characters, in which *L. simplex* is similar to *L. progenitor* n.sp. (structure and dimensions of sicula, presence of dorsal curvature in proximal part of rhabdosome, structure of prothecal segments and subapertural parts of metathecae in all thecae). The only significant difference consists in a degree of development of apertural apparatus. Compared with those in *L. progenitor* n.sp., apertural lobes in *L. simplex*' distal thecae consist of a much greater number of fuselli (at least twice as much) and instead of being small elevations of the margin, they represent prominent earlike lappets. Moreover, in *L. simplex*, apertural lobes are observed throughout the rhabdosome in contradistinction to *L. progenitor* n.sp. in which they are limited only to the distal part of rhabdosome. These differences in thecal characters between both successive members of *Lobograptus* may be explained by changes in the degree of expressivity and penetrance of corresponding genetic factors (see also p. 351).

The early appearance of *L. simplex* (in the upper part of the distribution range of *L. progenitor* n.sp. at a depth of 1,020.9 m), preceding the first appearance of all other lines of lobograptids (*L. scanicus parascanicus* at a depth of 1,016.9 m, *L. imitator* n.sp. at a depth of 986.9 m and *L. exspectatus* at a depth of 1,009.9 m), and the lack of specialized features in its structure (a low degree of development and a full symmetry of apertural apparatus) suggest that the species in question most probably occupies a central position in the family tree of lobograptids. *L. simplex* seems to represent a "node" from which individual lines of lobograptids may derive through a further development of lobes (as indicated by *L. exspectatus*), combined in other lines with the development of asymmetry (as indicated by *L. scanicus parascanicus* and *L. imitator* n.sp.). Especially close is the relationship of *L. simplex* to *L. scanicus parascanicus* (Kühne), and it is only a few changes such as a further gracilization of sicula, a certain increase in apertural lobes and a slight development of the asymmetry that are necessary for the transformation into the latter species. The lower zonal mutation of *L. scanicus parascanicus*, found in the Mielnik core between 1,016.9—1,005.9 m of depth and which is characterized by a slight asymmetry of apertural apparatus, combined with a "gracile" sicula, fills, at least in part, the morphological gap between both species.

Particulary noteworthy in this respect is a scanty assemblage of proximal thecae and siculae, obtained from erratic boulder S. 225, Rewal (Figs. 6, A-C). In its size and robust appearance (total length 1.40 mm, metasicula 0.85 mm long, aperture 0.26 mm in diameter) the sicula coincides more with *L. simplex* siculae. It differs, however, from the typical *simplex* siculae in its small apertural dorsal process which reaches only 0.06 mm in length and is twice as long as that in *L. scanicus parascanicus*, but three to two times shorter than that in the typical *L. simplex*. The first theca is longer than in *L. simplex* (1.99 m)

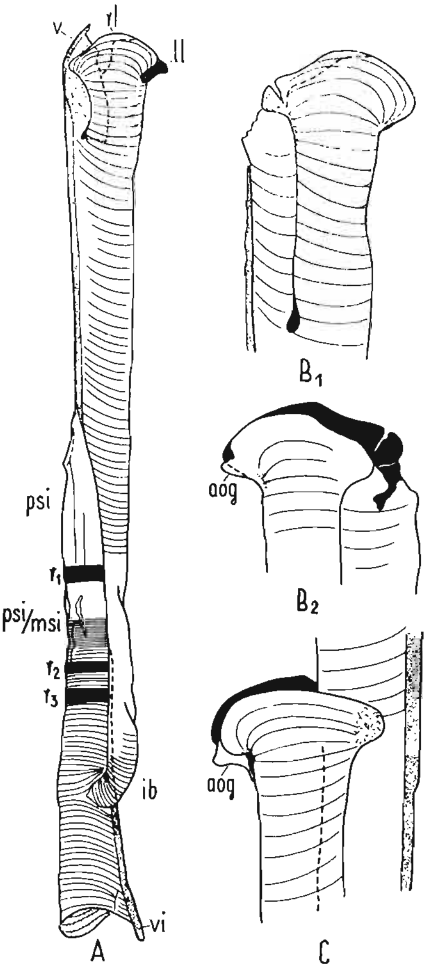


Fig. 6. *Lobograptus* cf. *simplex* Urbanek, showing transient characters to *L. scanicus parascanicus*: *A* sicula and first theca in reverse view, B_1-B_2 medial theca in reverse and obverse view, *C* obverse aspect of an adjacent theca (S. 225, Rewal), *A* ca. × 53, *B*-*C* ca. × 68.
aog abnormal outgrowth on the left lobe, *ib* initial bud, *ll* left apertural lobe, *psi* prosicula, *psi/msi* boundary of pro- and metasicula, r_1-r_3 successive sicular rings, *rl* right apertural lobe, *v* virgula, *vi* virgella.

and, in its proportions (a free part above the apex of prosicula — 0.90 mm long), is similar rather to that in *L. scanicus parascanicus*. It is also more slender, reaching only 0.20 mm in diameter at the apex of prosicula. Most striking is, however, the structure of apertural apparatus in proximal thecae. It consists of two lobes, rather large as compared with a true *L. simplex* and displaying a very small degree of asymmetry, the right lobe being somewhat larger than the left (Fig. 6, A). In spite of an incipient character of this asymmetry, it is invariably observed in all thecae (Figs. 6, B-C). Such form may be considered a transient one to *L. scanicus parascanicus*. Description of the population of *L. scanicus parascanicus* (lower zonal form) which occurs at a depth of 1,016.9 m in the Mielnik core, is given on p. 432.

Lobograptus exspectatus exspectatus Urbanek, 1960

(Figs. 7—8; Pls. XVIII—XX)

1958. *Lobograptus parascanicus* (Kühne), A. Urbanek, Monograptidae..., Figs. 43—44, pp. 74—76.

1960. *Lobograptus exspectatus* Urbanek; A. Urbanek, An attempt..., Pl. 2, Figs. 1 a-b, 3,4; Text-figs. 13B, 14B, pp. 213—214.

Material. — Numerous proximal and distal fragments of rhabdosomes, flattened or partly flattened, and rare siculae etched from the Mielnik boring core samples. In the Baltic drift material recorded in 5 boulders (see p. 416), the boulder S. 218, Ustka, being the richest. Erratic boulder material well-preserved, but strongly "carbonized". Examination of specimens needs strong bleaching. Complete rhabdosomes unknown.

Description. — Sicula rather long and wide, gradually expanding towards the aperture, provided with a distinct dorsal apertural process, In all examined specimens, black rings on sicula are slightly expressed or absent. The total length of sicula ranges between 1.46—1.61 mm.

Prosicula reaches a length of 0.54—0.59 mm and a width (*tr.*) of some 0.13 mm (on its boundary with metasicula). The apex of prosicula reaches approximately as far as the lower margin of the first metatheca. The periderm of prosicula, in all examined specimens, is strongly damaged and wrinkled, a few (1—3) longitudinal threads being the only visible details. No traces of black rings are displayed by the prosicula.

Metasicula is rather long (0.91 to 1.02 mm). It widens gradually from 0.13 mm on the boundary with prosicula, through some 0.20 mm at the level of the primary notch, to ca. 0.21—0.28 mm at the aperture of metasicula. In all examined specimens, both those from the erratic boulders and from the Mielnik bore hole, metasicula is devoid of black rings, except for the poorly developed and rather narrow r_1, situated right on the boundary of prosicula and metasicula and which is noted in some siculae (e.g. a sample from a depth of 1,000.9—1,000.6 m in Mielnik bore hole). The "ringless" condition seems to be, therefore, prevailing in this species. The structure of the primary notch region indicates that initial bud was developed according to the normal monograptid pattern (Fig. 7, *pn*). The aperture of adult metasicula is elaborated and provided with a strong and wide shovellike dorsal apertural process (Fig. 7, *dp*) reaching some 0.08—0.14 mm in length. By the presence of the dorsal process the aperture of metasicula is provided with distinct lateral incisions. Virgella is usually strong.

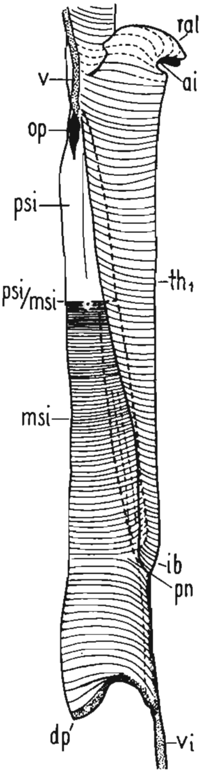


Fig. 7. — *Lobograptus exspectatus exspectatus* Urbanek. Structure of sicula and the first theca (slightly diagrammatically). (Mielnik, depth 1,009.9—1.009.6 m), ca. ×50. *ai* apertural incision, *dp* dorsal process of metasicular aperture, *ib* initial bud, *msi* metasicula, *op* secondary opening in the apical part of prosicula, *pn* primary notch, *psi* prosicula, *psi/msi* boundary between pro- and metasicula, *ral* right apertural lobe, *v* virgula, *vi* virgella.

The first theca is rather short and comparatively wide, reaching only some 0.20 mm above the apex of prosicula. The free part of the theca, stretching beyond the sicula, is therefore very short as compared with other species of lobograptids. The total length of the first theca ranges from 1.03 to 1.42 mm, the prothecal part being some 0.96—1.35 mm and the metathecal 0.07—0.10 mm long. The prothecal part occupies, therefore, about 93% of thecal length. The first theca starts at some 0.29—0.38 mm from the lateral margins of the aperture of metasicula. The metathecal part of the first theca is provided with paired lateral apertural lobes. Each lobe ventrally terminates in a beak-like part provided with a slightly oblique dorsal margin (Fig. 7). Below the ventral termination, the ventral apertural notch forms two lateral embayments, in form of corresponding apertural incisions (*ai*). All specimens are difficult for bleaching, and in the present writer's material there are no satisfactorily transparent preparations of the first theca. The fusellar structure and the number of fuselli cannot be, therefore, accurately determined. Both lobes seem, however, to consist of an identical number of fuselli (about 6—8), being also, in practice, identical in size.

The degree of primary overlap of apertural lobes in the first theca may be recognized only on unflattened or slightly flattened specimens. They show that the upper margins of apertural lobes are strongly incurved over the aperture, separated by a narrow fissure and touching or even slightly overlapping each other. Thus, apertural lobes form a sort of a roof over the aperture of the first theca. No stable pattern of overlapping of apertural lobes is, however, displayed by the examined specimens. In some cases, the right lobe is overlapped by the left, in others — the other way around. Moreover, it is possible, at least in some cases, that this overlapping of apertural lobes may be caused by a certain compression of specimens, being therefore rather a preservational than primary feature.

The apertural apparatus in *L. exspectatus* may thus be considered bilaterally symmetric, and the observed elements of asymmetry (some overlapping of one lobe by the other, small differences in size of lobes) seem to be random. The outer surfaces of the apertural lobes, as examined in unflattened specimens, are slightly concave in the medial part and convex (projecting) on the margins.

Proximal thecae (Pl. XVIII, Figs. A-C; Pl. XIX, Figs. A-C) are tubular and about 1.25—1.65 mm in total length, with the prothecal part ca. 1.17—1.25 mm, and metathecal 0.08—0.45 mm long. The prothecal part occupies therefore 90—93% of total thecal length. The width of proximal thecae is about 0.11—0.30 mm at the base of protheca and 0.15—0.27 mm at the base of metatheca. In most proximal thecae the ventral wall is completely straight (Pl. XVIII, Fig. A). In more centrally placed thecae it is slightly convex and forms, just below the lower

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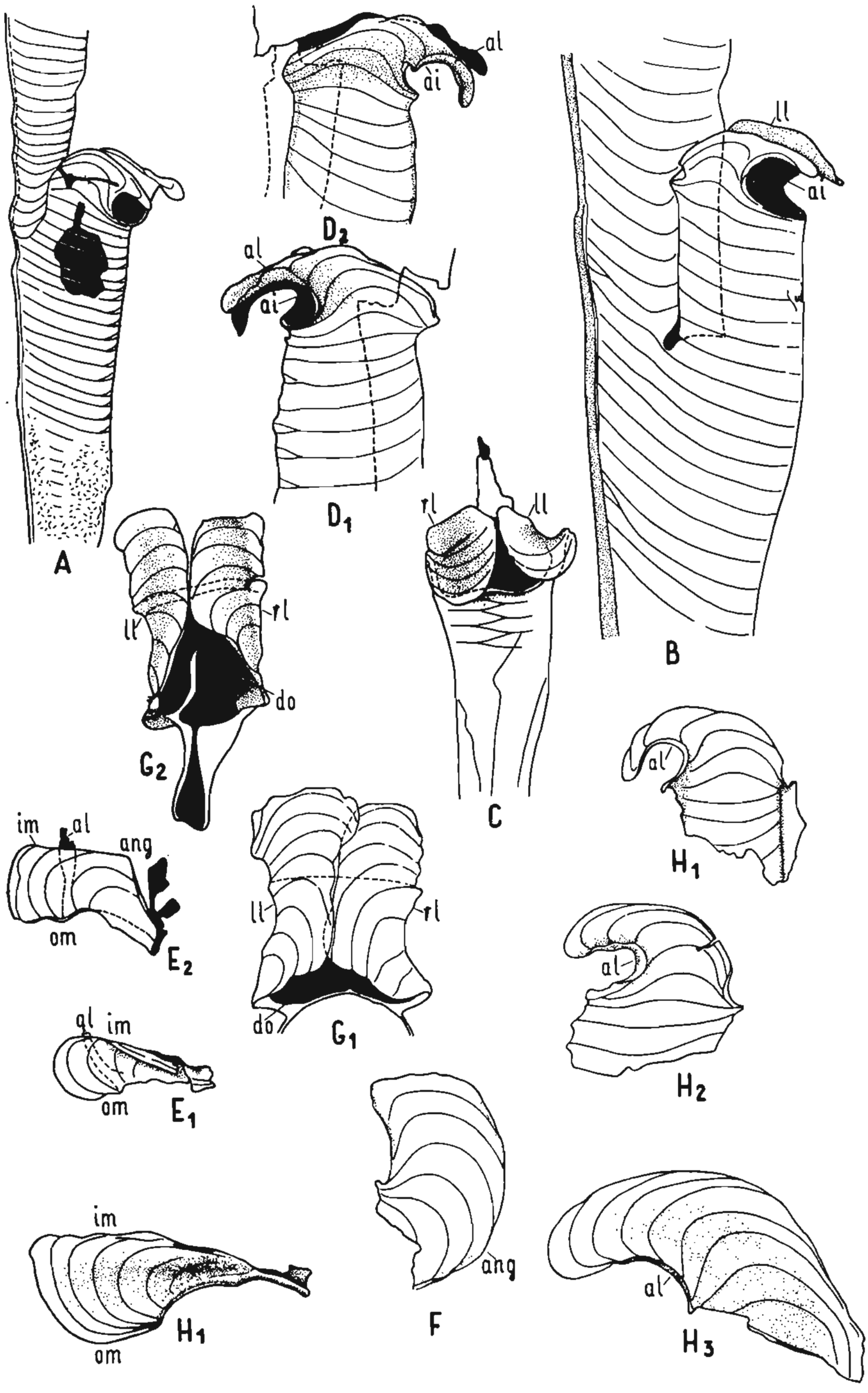
Plate XVIII

Lobograptus exspectatus exspectatus Urbanek. Structure of thecae and details of structure of apertural apparatus. *A* upper part of a proximal theca in ventro-lateral view; *B* upper part of a more central theca in lateral view; *C* upper part of a proximal theca in ventral view; D_1-D_2 apertural part of more distal theca in obverse and reverse aspects; E_1-E_2 isolated left apertural lobes from most proximal and more distal theca in top view; *F* isolated left apertural lobe seen in top view and somewhat laterally to show its fusellar structure; G_1-G_2 top views on complete apertural apparatus; H_1-H_3 isolated left apertural lobes in lateral view (H_1 also in top view) in most proximal and more distal thecae (S. 218, Ustka); ca. × 63.

ai apertural incision, *al* extroverted apertural lip, *ang* angular bending of fuselli, *do* dorsal opening, *im* inner (paraxial) margin of the apertural lobe, *ll* left apertural lobe, *om* outer (adaxial) margin of the apertural lobe, *rl* right apertural lobe.

PLATE XVIII


al
ai
D2
ll
al
al
ai
D1
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margin of the interthecal septum — a slightly marked geniculation (Pl. XVIII, Fig. B).

The metathecal part of proximal thecae is provided with paired lateral apertural lobes strongly incurved over the aperture and roofing the apertural opening of the theca. Each lobe forms a beaklike ventral termination, with rounded or blunt, nearly straight margin (Pl. XVIII, Figs. E_1, E_2, F), slightly incurved downwards (Figs. C, H_1, H_2). The upper margin of each lobe is straight and the dorsal margin oblique. Aperture forms a distinct ventral notch, provided with two lateral apertural incisions, rather deeply incised into the base of each lobe (Fig. B, *ai*). Aperture also opens dorsally through the triangular notch situated between both apertural lobes and formed as a result of an oblique position of their dorsal margins. The ventral margin of the aperture is thickened and forms a kind of selvage. It is also prolonged laterally into extroverted lateral margins of the lateral lobe, forming there an apertural rim (Figs. H_1-H_2,*al*). The number of fuselli making up each lobe in proximal thecae may be estimated at 6 or 7. Some 3—4 more basally situated fuselli are strongly arcuate and gathered ventrally into an indistinct node, but terminating freely in the dorsal margin (Fig. F). The remaining fuselli terminate freely in both margins of the lobe. The third or fourth fusellus ends angularly which results in a characteristic curvature of the free margin (Figs. E_2, F, *ang*) of the lobe, situated between a straight upper (inner) margin and an oblique dorsal one.

The size of apertural lobes in the same theca is usually somewhat different, sometimes the left and, sometimes, the right lobe being somewhat larger. The outline of the lobes in the same apertural apparatus may also slightly vary. The incurved parts of both lobes may be separated by a more or less narrow fissure, or lobes may touch each other, even displaying some overlap of the margins. This is, however, not a stable relation between apertural lobes and it is even in adjacent thecae that, sometimes, the left lobe is overlapped by the right and, sometimes, the right lobe by the left one. This is, therefore, not a definite asymmetry, observed in the size and arrangements of apertural lobes and in spite of small random differences, the apertural apparatus seems to be bilaterally symmetric. Moreover, due to a partial compression of specimens, it is very difficult to distinguish the primary from the secondary overlap of lobes. This overlap of lobes may be, at least in part, rather preservational than primary in character. The outer surface of

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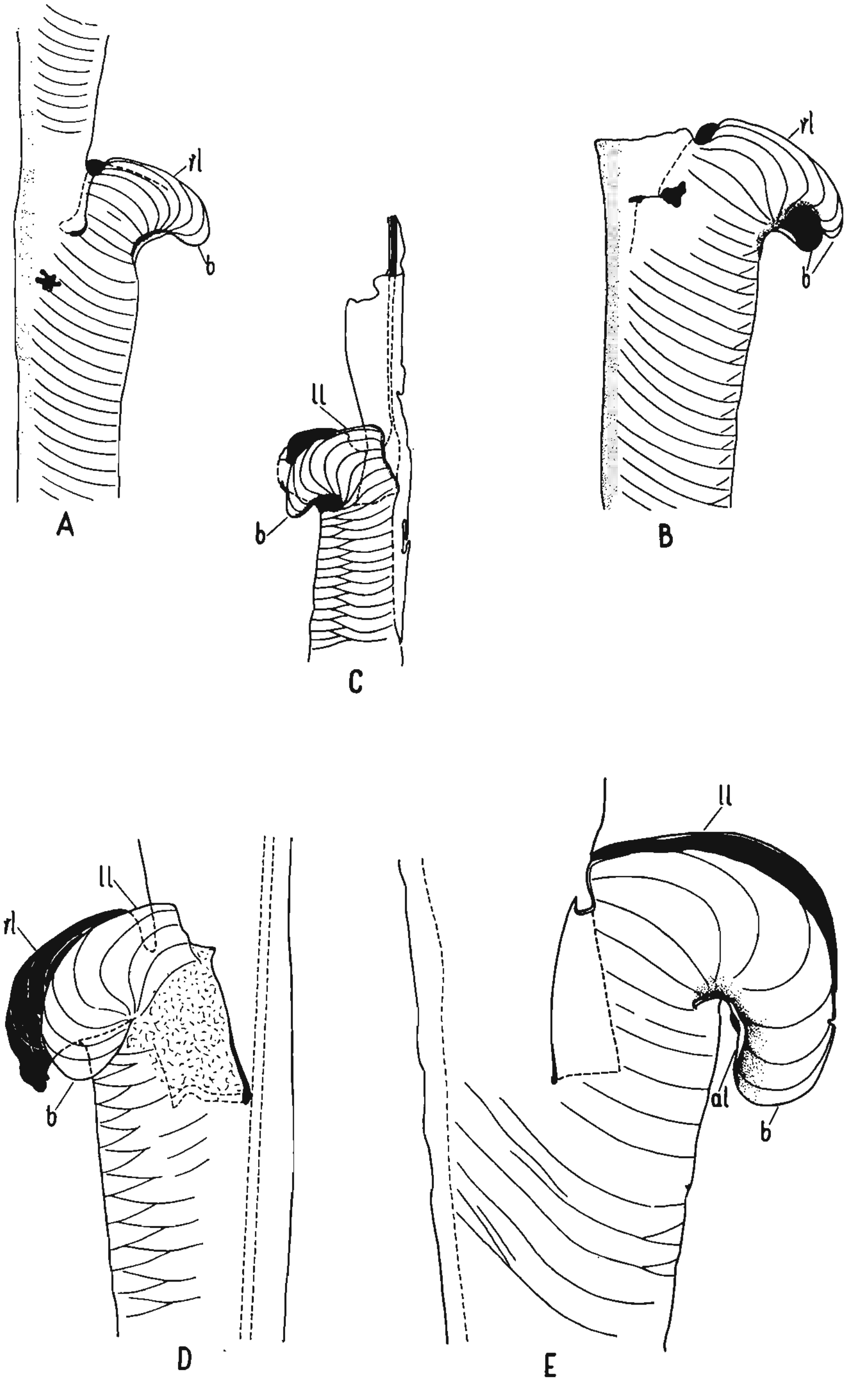
Plate XIX

Lobograptus exspectatus exspectatus Urbanek. Lateral views of upper parts of proximal (*A-C*) and distal (*D-E*) thecae to show its fusellar structure. *A, B, E* reverse aspect; *C, D* obverse aspect (Mielnik, depth 1000.9—1000.6 m); ca. ×63.

al apertural lip, *b* beaklike termination of the lobe, *ll* left lobe, *rl* right lobe.

PLATE XIX



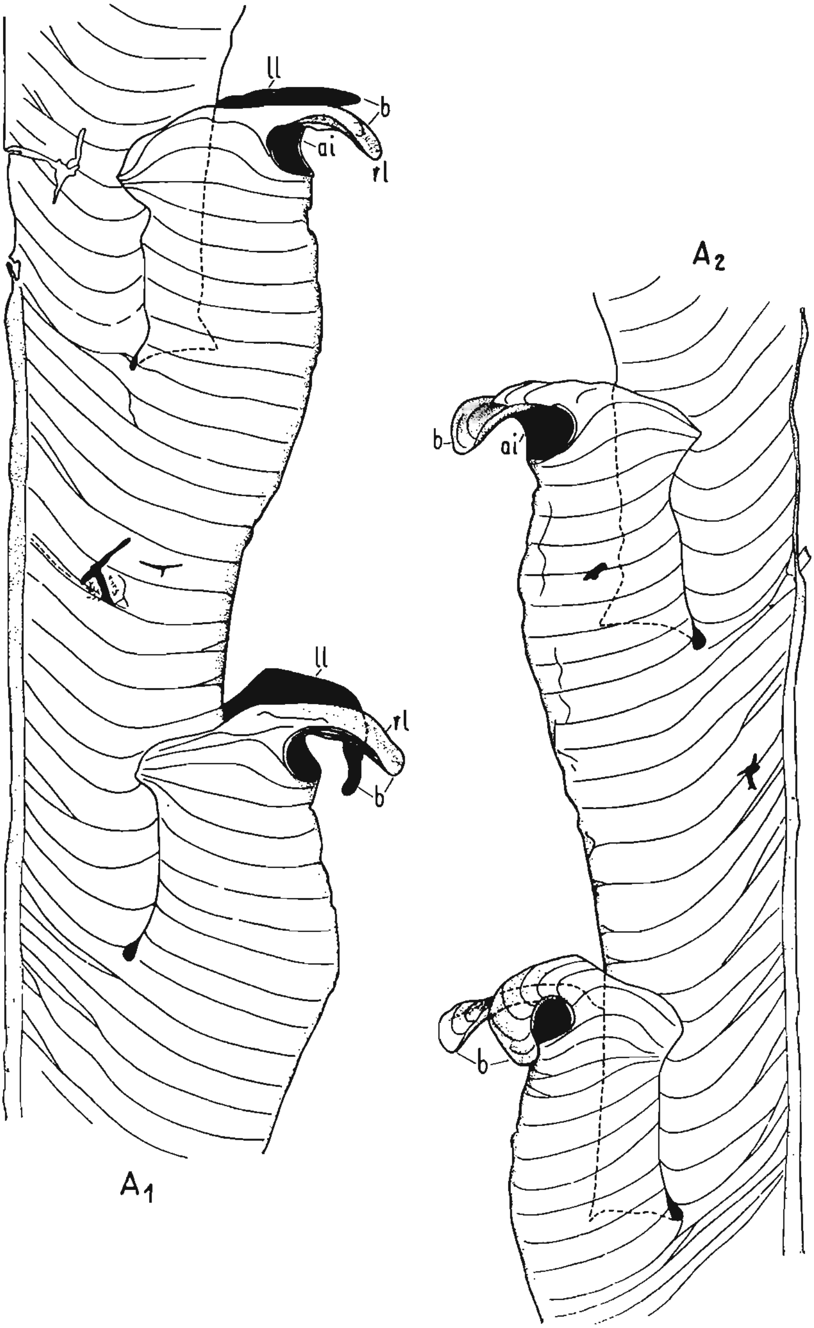
each lobe is, in its central part, somewhat depressed with the outer and inner margins slightly protruding upwards (Pl. XVIII, Figs. H_1, H_3).

Distal thecae, shown completely in Pl. XX, Fig. A, are about 1.70—2.10 mm long, with prothecal parts some 1.23—1.58 mm and a metathecal part about 0.40—0.67 mm in length. The prothecal part occupies, therefore, 68—80% of total thecal length. Thecae are 0.39—0.62 mm wide (*tr.*) at the base of protheca reaching a width of 0.30—0.37 mm at metatheca. The presence of a gently but distinctly marked geniculation of the ventral thecal wall is characteristic of distally placed thecae of *L. exspectatus* (comp. Pl. XX).

Apertural borders of metatheca terminate laterally in two apertural lobes, displaying a tonguelike or rounded triangular outline. They are, therefore, relatively more narrow than apertural lobes in more proximal thecae (comp. Pl. XVIII, Figs. D_1-D_2, H_3). Each lobe forms a broad and strong ventral termination, producing a beaklike process (Pl. XVIII, Fig. D_{1-2}, Fig. H_3; Pl. XX, Fig. A_{1-2}, *b*). The free (inner) border of lobes is oblique dorsally and, after a gentle angular bending, becomes almost straight and rounded at the ventral end of the lobe. The outer margin, provided with a more or less narrow, extroverted apertural lip (particularly well-developed in a specimen shown in Pl. XVIII, Fig. D, *al*), forms a distinct apertural incision, forming an embayment of the ventral apertural notch (*ai*). Each lobe is strongly incurved over the aperture, thus forming a kind of an apertural roof. The inner margins of the lobes, viewed from the top, may be separated by a more or less distinct fissure, or may touch and even slightly overlap each other. Like in the more proximal thecae, however, no definite asymmetry is noted in the arrangement of apertural lobes and in the size differences and, therefore, the overlapping patterns seem to be random. In spite of these minor differences the apertural apparatuses in more distal thecae may, however, be considered bilaterally symmetrical (Pl. XVIII, Figs. G_1-G_2).

The upper surface of each apertural lobe is somewhat depressed in the medial part with margins slightly protruding (Pl. XVIII, Figs. D, H_3). When laterally viewed, the apertural lobe is somewhat depressed and groovelike. Beaklike ventral processes are disposed horizontally, or slightly incurved downwards, thus being almost clawed appearance. This seems to be a very characteristic feature, especially of more distal thecae in *L. exspectatus* (Pl. XVIII, Fig. D; Pl. XX, Fig. A). Owing to a certain degree of concavity of the surface in apertural lobes, their fusellar structure may be examined only on single lobes, separated from thecae by the needle preparation and properly oriented prior to drawing (Pl. XVIII, Fig. H_3), or due to their state of preservation on thecae with strongly flattened apertural lobes (Pl. XIX, Figs. D, E). Each apertural

PLATE XX



Lobograptus exspectatus exspectatus Urbanek. Structure of distal theca. A_1-A_2 complete distal theca in reverse and obverse views (S. 218, Ustka), ca. ×63.

ai apertural incision, *b* beaklike termination of the lobe, *ll* left apertural lobe, *rl* right apertural lobe.

lobe in a distal theca consist of some 8—9 fuselli which are more or less arched and superimposed one upon another. Ventral node absent, or indistinct and gathering ventral ends of only 3 lowermost fuselli. The remaining fuselli end freely on both margins of the lobe. Preadult shape of lobes in distal thecae is shown in Pl. XIX, Fig. D, representing the apertural apparatus of a young theca. Adult distal thecae are provided with longer and usually incurved ventral processes (Pl. XVIII, Fig. D; Pl. XIX, Fig. E; Pl. XX, Fig. A).

Prothecal parts in distal (Pl. XX, Fig. A_{1-2}; Pl. XIX, Fig. E) and more proximal thecae (Pl. XVIII, Fig. B) display the presence of numerous short and wedgelike fuselli, situated along the dorsal (virgular) margin of a theca. They are intercalated between normal, longer fuselli which, touching each other alternately, form a ventral zigzag suture. The occurrence of intercalary fuselli, although by no means common, is noted also in other lobograptids, e.g. *L. progenitor* n.sp.

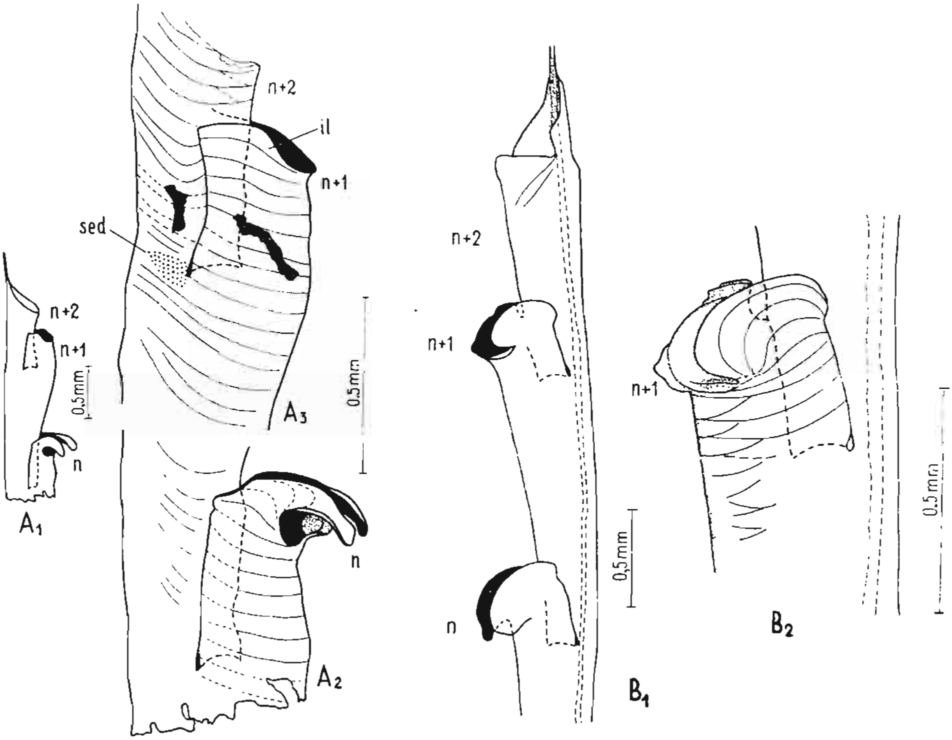


Fig. 8. — *Lobograptus exspectatus exspectatus* Urbanek. Growth pattern of rhabdosome: A_1 termination of growing tip of rhabdosome, showing an adult (n) and younger theca ($n+1$) with incipient prothecal part of theca ($n+2$), A_2-A_3 upper parts of thecae from the same specimen enlarged, B_1 another termination of a growing tip, B_2 enlarged apertural part of young theca $n+1$ from the same specimen (A — S. 218, Ustka; B — Mielnik, depth 1,000.9—1,000.6 m).

il incipient apertural lobe, $n - n+2$ successive thecae, *sed* grains of sediment attached to the periderm, *v* virgula.

Growth pattern of rhabdosome. Specimens presented in Fig. 8, A-B show fragments of growing tips of rhabdosome in two successive growth stages, the earlier stage being represented by specimen A_1-A_3 and a more advanced stage by specimen B_1-B_2. The specimen in Fig. 8, A_1 consists of a metathecal part of theca *n*, provided with a complete and adult apertural apparatus (details shown in Fig. 8, A_2), an adjacent and more distally placed theca *n+1* with its apertural apparatus in a very early formation stage of apertural lobes (details shown in Fig. 8, A_3) and a growing basal part of the next theca *n+2*. The specimen shows the following succession of events that occur on the growing tip of rhabdosome: a given theca (e.g. theca *n*) reaches the adult shape of its apertural apparatus simultaneously with the growth of protheca and the subapertural part of the metathecal segment of the next theca. The formation of the apertural apparatus, marked by the first fusellus of apertural lobes (comp. Fig. 8, A_3), coincides with the early growth stage of the prothecal part of the next theca which does not exceed the length of some 0·60 mm. The formation rate of apertural lobes seems to be, therefore, rather low as compared with the growth rate of the entire subapertural part of the theca, the rate being taken as proportional to the length of the structure formed.

Taking roughly theca *n+2* as being nearly equal to a half of the length of the subapertural part of the theca (0·60 mm : 1·40 mm respectively), and the number of fuselli, making up this subapertural part, as being on the average 14, we arrive at a proportion of some 8 fuselli, formed in the apertural apparatus, to some 12—14 fuselli, formed simultaneously in the subapertural part of the next theca.

The specimen shown in Figs. 8, B_1-B_2 represent a somewhat more advanced growth stage of theca *n+1* which corresponds to an adequately more advanced growth stage of the subapertural part of the next theca (*n+2*). The most proximally situated theca *n* is fully grown and its apertural apparatus has an adult shape. Theca *n+1* has a juvenile shape of apertural lobes (details shown in Fig. 8, B_2), being most probably still not completely adult (preadult). The lack of a distinct ventral termination of the lobes and a small number of fuselli making them (4), which is in contrast with the shape and number of fuselli in adult thecae, are a remarkable feature of this theca. Theca *n+1* is, therefore, in a growth stage intermediate between that, represented by theca *n+1* in Fig. 8, A_3 and a fully grown stage. This four-fusellar development stage of apertural lobes of theca *n+1* coincides with the growth stage of theca *n+2* which corresponds to its length of about 1·2 mm, i.e. twice as long as theca *n+2* in specimen Fig. 8, A_3, which in turn corresponds to the one-fusselar growth stage of lobes in theca *n+1* [18].

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[18] These data are comparable because the length of the subapertural part of theca *n+1* is, in both specimens, nearly identical (about 1·40 mm).

A smaller number of preadult thecae, observed at a given time on the growing tip of rhabdosome, is a remarkable feature of the rhabdosome growth pattern in *L. exspectatus* as compared with that in *L. scanicus parascanicus* (comp. p. 429). This suggests a rather rapid decrease in the growth activity gradient towards the distal end of the colony, that is conditions similar to those, known for saetograptids (comp. also considerations on p. 344).

Stratigraphic range.—The first doubtless remains of *L. exspectatus* have been found in the Mielnik core at a depth of 1,009•9—1,009•6 m. However, below, at a depth of 1,015•9 m, some proximal fragments of rhabdosome were encountered which also may (although with some uncertainty) be referred to the species in question. They seem to display a smaller degree of elaboration of apertural lobes (smaller size, especially that of the beaklike ventral prolongation of the lobes). This sample is, however, too small to allow one for drawing reliable conclusions as to the nature of these small differences which may as well be ascribed to the young growth stage of the thecae under study. The early appearance of a more primitive lower zonal mutation with a smaller degree of elaboration of apertural lobes also cannot be precluded. Starting from a population, recorded at a depth of 1,009•9 m, *L. exspectatus* is represented by the type form, marked by morphological features, described above. This form shows a rather long occurrence range, making its last appearance at a depth of 940•0 m. The total thickness of strata, occupied by *L. exspectatus*, is, therefore, not less than some 69•9 m (accepting a range of 1,009•9—940•0 m as the total range of its occurrence).

In the lowermost horizons of the occurrence of *L. exspectatus*, it is accompanied by the following assemblage: *Lobograptus scanicus parascanicus* (Kühne), uncertain remains of *L.* cf. *simplex* Urbanek, *L. scanicus amphirostris* n. subsp., "*Pristiograptus*" *bohemicus* (Barrande), *Pristiograptus dubius* (Suess), *Saetograptus chimaera* Urbanek, *Monoclimacis micropoma micropoma* (Jaekel), and retiolitids: *Plectograptus macilentus* (Törnquist), *Holoretiolites erraticus* Eisenack, *H. mancki* (Münch). In the highermost horizon, the associated assemblage is different and consists of: *Lobograptus cirrifer* n.sp., *Cucullograptus hemiaversus* Urbanek, *Pristiograptus dubius* (Suess), *P. dubius tumescens* (Wood), "*Pristiograptus*" *bohemicus* (Barrande), *Saetograptus fritschi* (Perner).

In the fauna from Baltic drift material, *L. exspectatus* has been found in 5 boulders, associated with the following graptolite assemblages. Boulders: S. 58, Jarosławiec — *Lobograptus scanicus amphirostris* n. subsp.; S. 134, Gdynia-Orłowo—*Monoclimacis haupti* (Kühne), *Pristiograptus dubius* (Suess), *Saetograptus chimaera* cf. *cervicornis* Urbanek; S. 140, Władysławowo — *Pristiograptus* sp.; S. 149, Jarosławiec — *Monoclimacis micro-*

poma micropoma (Jaekel), *Saetograptus chimaera cervicornis* (Urbanek), *Holoretiolites* sp.; S. 218, Ustka — *Neodiversograptus beklemishevi* Urbanek, *Monoclimacis micropoma nannopoma* (Jaeger), *M. haupti* (Kühne), *Saetograptus chimaera cervicornis* Urbanek, *Pristiograptus* cf. *dubius* (Suess).

These assemblages indicate horizons which fit into the stratigraphic range of *L. exspectatus* in the Mielnik core. My previous opinion (Urbanek, 1960 p. 234) that its stratigraphic occurrence may also include the uppermost part of the *nilssoni* zone, now seems to be unfounded.

Systematic position. — The relatively early appearance of *L. exspectatus* (only 7·30 m above last occurrence of *L. simplex)* and its structure, especially that of the apertural apparatus, seem to indicate its close relationship to the latter species. The stable symmetry of apertural lobes, combined, however, with a further enlargement of both apertural lobes, may be regarded as a direct prolongation of the development of the "stem line" of lobograptids (*L. progenitor* n.sp. — *L. simplex*). This is indicated by the great resemblance between a young, preadult structure of apertural lobes in *L. exspectatus*, as shown in Fig. 8, B_2, and the structure of adult apertural lobes in *L. simplex*, as figured in Pl. XVI, Figs. C-D. The origin of these lobes in the former species may, therefore, be ascribed to the addition of only few novelties, mainly some enlargement of lobes and formation of their ventral beaklike process. The decrease in the dorsal curvature of the proximal part of rhabdosome and almost complete disappearance of black rings from the sicula — necessary to convert *L. simplex* into primitive form of *L. exspectatus* — indicate, on the other hand, that the latter species initiated a new and separate lineage, with *L. exspectatus bicornis* n. subsp. as its climax and the extremest representative (comp. p. 372). This lineage is called here the *exspectatus-bicornis* lineage. A progressive tendency to a further elaboration of the apertural apparatus (enlargement of apertural lobes, tendency to their partial coiling), combined with its persistent bilateral symmetry, is the most remarkable feature of the evolution of this lineage. The latter feature displays a distinct independence of *exspectatus-bicornis* lineage from all other cucullograptid trends in which a certain stage of the elaboration of apertural apparatus is invariably connected with the development of its asymmetry. From this reason, the *exspectatus-bicornis* lineage occupies a central position in the family tree of cucullograptids.

Lobograptus exspectatus bicornis n. subsp.

(Fig. 9, A_1-A_3)

Type specimen (holotype): Fig. 9, A_1-A_3.

Type stratum: Greenish-blue mudstones and marls in the core of the Mielnik deep-boring between 952·9—942·3 m of depth (*hemiaversus* zone, upper part of Mielnik Beds).

Derivation of the name: *bicornis* — Lat. *bi* = two, twice; *cornis* = horned, i.e. provided with two strongly incurved ventral terminations of apertural lobes, projecting laterally like hornlike outgrowths.

Diagnosis. — *L. exspectatus* with strongly incurved and projecting laterally beaklike process.

Material. — Scanty and rather incomplete remains from the Mielnik bore-hole, containing 3 fragments of rhabdosome with thecae from its medial (central) part and, moreover, a few associated, incomplete remains of more proximal thecae. Specimens are partly unflattened and partly slightly flattened. After bleaching, fusellar structure not easily discernible.

Description. — Preserved medial (central) thecae are about 1·55 mm long, at the base of protheca 0·09–0·15 mm and at the metathecal part 0·13 mm wide. Prothecal part measures about 1·10 mm in length and the metathecal one — some 0·45 mm, the prothecal part occupies, therefore, about 70% of total length.

Metatheca terminates in two laterally placed apertural lobes which rather closely resemble the apertural apparatus of a true *L. exspectatus.*

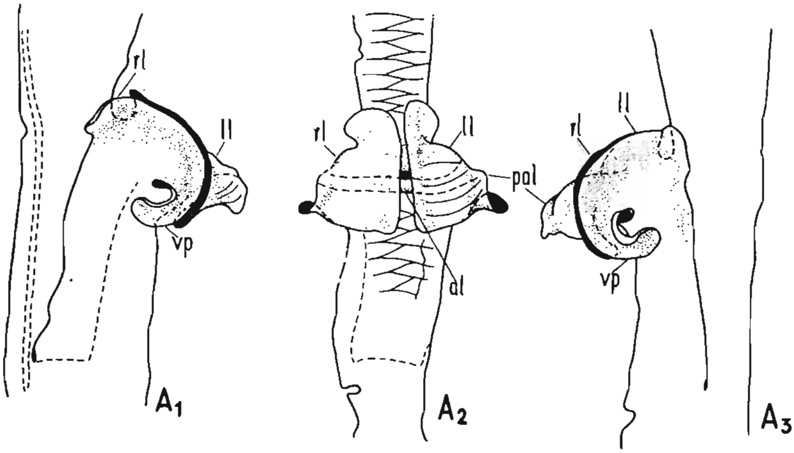

Fig. 9. — *Lobograptus exspectatus bicornis* n.subsp. A_1-A_3 upper part of a medial (central) theca in reverse, obverse and ventral views (Mielnik, depth 942,5—942.3 m), ca. × 63.
al apertural lip, *ll* left apertural lobe, *pal* prolongation of the apertural lip, *rl* right apertural lobe, *vp* ventral process of apertural lobes.

Ventrally, however, both lobes end with a longer and broader ventral process which, moreover, is very strongly incurved and also projects somewhat laterally (Fig. 9, A_1-A_3, *vp*). The ventral margin of the lobe ends bluntly. The apertural margin ventrally forms a broad, extroverted apertural lip (A_2,*al*) which on the lower margin of ventral processes, is prolonged in the form of a more or less narrow extroverted list (A_2-A_3, *pal*), projecting laterally and somewhat upwards. The upper (inner) margins of the lobes are slightly rounded, the dorsal margin is almost straight and rectangularly inclined towards the former (comp. A_1, A_3). The outer surface of the lobes is distinctly depressed (concave) in the center and framed by margins which slightly project upwards. Both lobes are almost identical in size and shape, the apertural apparatus being, therefore, bilaterally symmetric. Both apertural lobes are strongly incurved over the aperture, thus forming a kind of an apertural roof above it. In specimens, examined in a ventral (A_2) or top view, one may observe, however, that both apertural lobes do not touch each other with their inner margins but are separated by a distinct fissure.

Owing to a rather strong concavity of the outer walls of apertural lobes, their fusselar structure is not discernible. Probably, it closely resembles the fusellar structure of lobes in *L. exspectatus exspectatus.*

The available material does not include any true distal thecae. More proximal thecae, associated in the sample from a depth of 942•5—942•3 m, with medial (central) thecae, described above, may be also, although with some uncertainty, refered to *L. exspectatus bicornis* n. subsp. They very closely resemble the proximal thecae in true *L. exspectatus.* In most proximal thecae the aperture is provided with two lateral apertural lobes, incurved over the aperture and having their inner margins separated by a wide fissure. The apertural apparatus is bilaterally symmetric. Each lobe consists of some 5—6 fuselli, provided with a slightly rounded inner margin, straight dorsal and almost straight ventral margin, the latter having a slightly marked, incipient ventral process.

The ventral margin of the aperture forms a narrow apertural lip. If these thecae really belong to the subspecies in question, they indicate that the proximal thecae of *L. exspectatus bicornis* n.subsp. differ very little from those in *L. exspectatus exspectatus.* More pronounced differences (the presence of long and strongly incurved ventral processes on apertural lobes, having prominent margins) are marked in medial (central) and, probably, distal parts of rhabdosome. This suggests a rather distal phylastogenetic introduction of characters responsible for morphological differences between both subspecies.

Stratigraphic range. — *L. exspectatus bicornis* n.subsp. has been found in the Mielnik core at depths of 952•9—952•6 m and 942•5—942•3 m in samples discontinuously occurring over a layer of some 10•50 m in thickness. This species is limited to the uppermost part of the vertical distribution range occupied by *L. exspectatus exspectatus.* The graptolite association, recorded in the lower horizon consisted of *Cuc. hemiaversus* Urbanek and, in higher horizon, *L. exspectatus exspectatus* Urbanek, *Pristiograptus dubius* (Suess), *P. dubius tumescens* (Wood) and "*P.*" *bohemicus* (Barrande).

Systematic position. — *L. exspectatus bicornis* n. subsp. may be considered a further development of the true *L. exspectatus*. It also makes up more extreme form of the latter species, produced by a strong incurvation of apertural lobes, projecting laterally in the form of two hornlike outgrowths. These protruding parts of apertural lobes present a certain analogy to similar structures (rostral processes in *L. cirrifer* n.sp. and in *Cuc. aversus rostratus*, or a protruding apertural lip in *L. invertus* n.sp. and *L. scanicus amphirostris* n.subsp.) in other cucullograptids. This may indicate the existence, among the Cucullograptinae, of a general trend to the formation of similar superstructures in phylogenetically more advanced forms (comp. p. 373). For systematic position — see also p. 372.

Lobograptus scanicus parascanicus (Kühne, 1955)

(Pls. XXI—XXIV; Pl. XLVII, Fig. 1)

1883. *Monograptus scanicus* Tullberg; S.A. Tullberg, Scanes graptoliter..., pp. 26—27, Pl. 2, Figs. 40?, 42?.

1955. *Monograptus parascanicus* Kühne; W. G. Kühne, Unterludlow-Graptolithen..., pp. 392—395, Figs. 15, 16.

1958. *Lobograptus scanicus* (Tullberg); A. Urbanek Monograptidae..., pp. 72—74 (partim), Figs. 41, 42; Pl. 2, Fig. 5; non Pl. 2, Fig. 6, non *Lobograptus parascanicus* (Kühne); pp. 74—76, Figs. 43—44.

1960. *Lobograptus scanicus parascanicus* (Kühne); A. Urbanek, An attempt..., p. 177 (mentioned), Fig. 13, C.

Material. — Many hundreds of specimens (fragments of rhabdosomes) including numerous and well-preserved siculae in different growth stages, proximal and distal thecae, etched from the Baltic drift material (erratic boulders: S. 16, Łebcz; S. 32, Gdańsk-Wrzeszcz; S. 36, Jarosławiec; S. 37, Island Wolin; S. 137, Ustka; S. 174, Lubin; S. 181, Czarnogłowy; S. 185, Rewal; S. 228, Jarosławiec). In boulder S. 181, the species in question occurs in abundance (comp. Pl. XLVI, Figs. 1—2), being also very frequent in S. 32 and S. 137. The material, obtained from the Mielnik bore-core (at a depth of 1,016·9—978·6 m) is also very rich, but rather poorly preserved (flattened, compressed or otherwise deformed), siculae occurring less frequently than in the drift samples. The specimens from the erratics and bore core may be easily bleached. A detailed study of a minute structure of thecae and their development is possible by the combination of these specimens. All stages of astogeny are represented, but the majority of fragments are rather small and complete rhabdosomes are unknown.

Because of the uncertainty which of its three recently recognized members may correspond to the true *Monograptus scanicus scanicus* Tullberg, the concept of particular subspecies and the use of correct nomenclatorally names meet some difficulties with regard to the members of the *scanicus* line of evolution. These difficulties are primarily connected with the fact, that the original material of *Monograptus scanicus*, described in Tullberg's monograph (1883, pp. 26—27, Pl. 2, Figs. 38—44) is not available in his collection, housed at Sveriges Geologiska Undersökning in Stockholm. Unfortunately, according to the information obtained from Swedish palaeontologists, the figured specimens from "Cardiolaskiffern vid Marianelund" (Scania, the vicinities of Löberöd) were most probably destroyed by this eminent scientist himself during his insanity period.

Actually, Tullberg's collection contains some number of specimens, labelled by him as *Monograptus scanicus* with indication of a locality as "Shale near Church in Ask" (Scania, the vicinities of Röstanga). The specimens examined are, however, in a rather poor state of preservation, excluding any exact comparison with the etched material (comp. Urbanek, 1960, p. 218). The attempt to solve the problem by collecting topotypes from the "Cardiola Shale" locality in Marianelund is complicated by the fact that this locality is part of a longer section in the neighbourhood of Röverekulan and comprises a number of different horizons. There are, however, no closer indications where the Tullberg's originals were collected. Moreover, specimens, collected by the present author during his excursions (in June, 1960) with Dr. F. Brotzen and Mr. R. Skoglund to the Röverekulan section display a rather poor state of preservation, excluding the possibility of a reliable comparison with the etched material.

No accurate knowledge can also be gained from the examination of Tullberg's drawings (Pl. 2, Figs. 38—44) which however, show that the original material of *M. scanicus* most probably represents a mixture of different species and subspecies.[19] Figs. 38, 39 and 43 are not distinct enough to allow one for a comparison; Figs. 40, 42 and 44 probably represent *L. scanicus scanicus* and *L. scanicus parascanicus*, Fig. 41 may be a distal fragment of *Cuc. pazdroi*. Neither of these forms were indicated by Tullberg as the type specimen of *M. scanicus*. Přibyl's (1948, p. 34) information that Fig. 38 on Pl. 2 in the 1883 Tullberg's work represents the holotype is, therefore, incorrect.

Taking into consideration the fact that the shale material is, in general, unsuitable for detecting minor morphological differences in the structure of thecae, the lack of original material of *M. scanicus* Tullberg and the uselessness of topotypes for solving nomenclatoral problems, the present author supports his earlier suggestion (comp. Urbanek 1960, p. 218). The suggestion was to use the name of *L. scanicus scanicus* (Tullberg) to denote the forms subspecifically identical with that which, on the basis of the material etched from North German erratic boulders was described

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[19] The same is indicated by the fact that a specimen from Tullberg's collection, housed in Lund (Sweden), and labelled as a distal end of *M. scanicus* (from the Röfvarekulan locality) is in fact a *Cucullograptus pazdroi*.

by Bulman (1953) as *Monograptus scanicus* Tullberg. *Monograptus parascanicus* Kühne (Kühne, 1955) is considered here only a subspecies of *L. scanicus* (comp. Urbanek, 1960). Morphological differences between both forms are evaluated as occurring at the subspecific level, mainly because of its rather "quantitative" character and the presence of morphological transients, filling the gap between them (*L. scanicus amphirostris* n. subsp.).

The "*scanicus* lineage", as it is understood here, consists, therefore, of the following three subspecies: *Lobograptus scanicus parascanicus* (Kühne) — *L. scanicus amphirostris* n.subsp. — *L. scanicus scanicus* (Tullberg) sensu Bulman. Moreover it has recently been recognized that *L. scanicus parascanicus* occurs in two varieties which differ from each other mainly quantitatively, i. e. in the degree of development of apertural lobes and in their asymmetry. These infrasubspecific varieties are classified here as lower and higher zonal forms of *L. scanicus parascanicus.*

It is beyond any doubt that the higher zonal form corresponds to the true *L. scanicus parascanicus* as described by Kühne (1955). The concept of a lower zonal form is introduced here for a number of populations, occurring at the lower part of the stratigraphic range of the subspecies in question which, in the Mielnik core, correspond to a depth of 1,016•9——1,005•9 m. All available material is rather scanty and consists of small fragments of rhabdosome and isolated thecae, displaying a rather smaller degree of asymmetry and associated with siculae whose apertural parts are more expanded than those in the higher zonal form (comp. also p. 435).

Description. — Sicula (Pl. XXI; Figs. G, H, I_3; J_1; Pl. XXII, Figs. A, F) straight, very slender and rather short 0•94—1•20 mm). It is tubular and almost of the same width throughout the metasicular part.

Prosicula ranging from 0•46 to 0•60 mm in length in 10 measured specimens. The presence of thin longitudinal threads (ribs), varying in number (1—3 in examined specimens), is the only detectable structure detail in the prosicula. Young prosiculae are devoid of black rings (Pl. XXI, Figs. A, B) which are, however, developed in all examined specimens in

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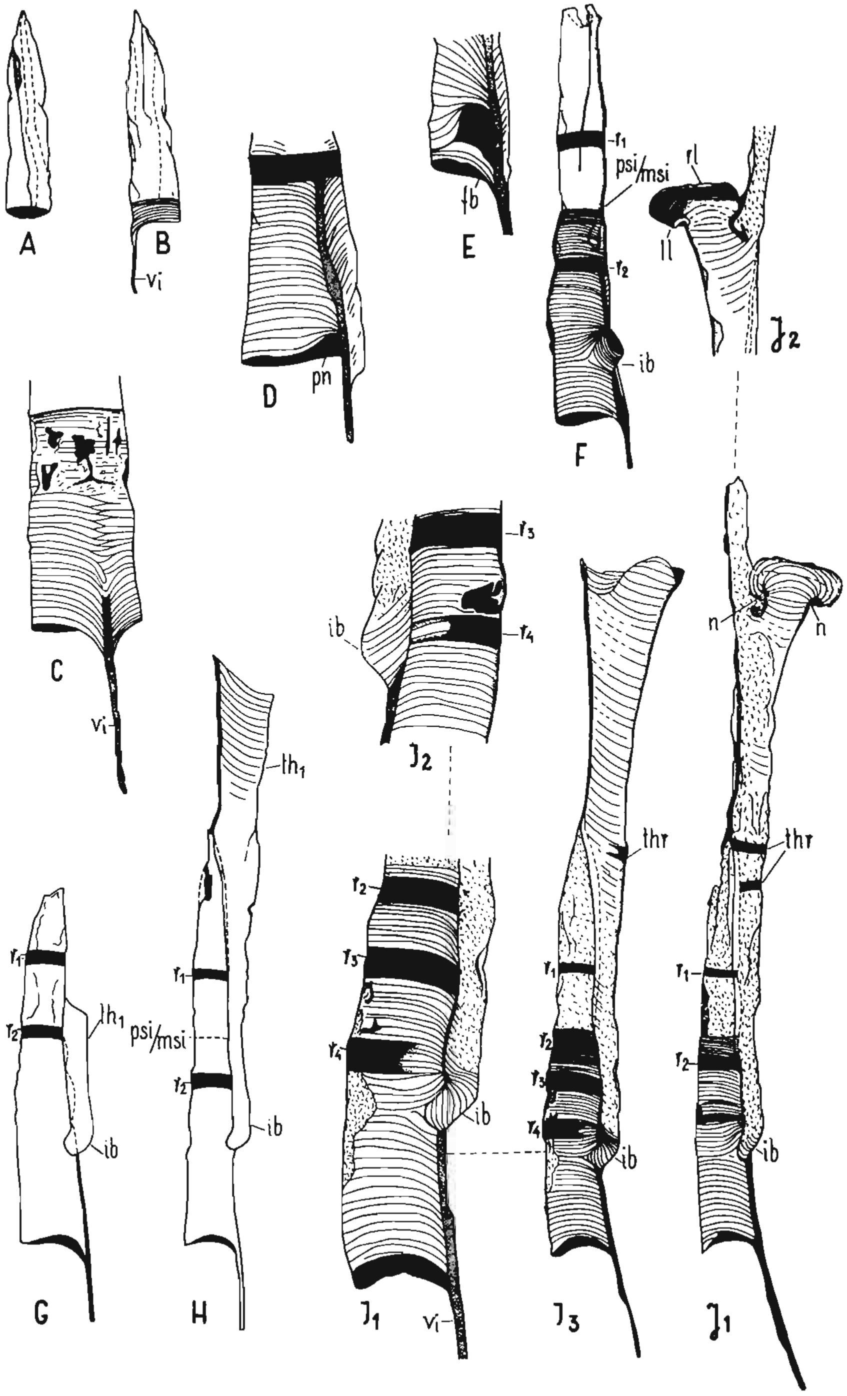
Plate XXI

Lobograptus scanicus parascanicus (Kühne). Development and structure of sicula and 1st theca in higher zonal form (drift material). *A* prosicula, *B* young metasicula with incipient virgella, *C* details of origin of virgella, *D* early stage in formation of primary notch (early sinus stage), *E* late stage in formation of initial notch (lacuna stage), *F* advanced metasicula with incipient initial bud, *G* sicula with initial bud in advanced growth stage, *H* sicula with nearly complete prothecal part of first theca, I_{1-2} details of fusellar structure of metasicula and base of initial bud from reverse and obverse side, I_3 complete reverse view of same specimen showing apertural lobes of the first theca in early growth stage, J_1 adult sicula and first theca from reverse side, J_2 obverse view of apertural fragment of the first theca (S. 181, Czarnogłowy); *A*, *B*, *G*, *H*, I_3, J_1 ca. × 50; *C*-*E* I_1-I_2 ca. × 100; *F* ca. × 70.

fb fusellar bar closing the primary notch, *ib* initial bud, *ll* left apertural lobe, *n* node, *pn* primary notch, *psi*/*msi* boundary between pro- and metasicula, r_1-r_4 successive sicular rings, *rl* right apertural lobe, th_1 first theca, *thr* thecal rings, *vi* virgella.

PLATE XXI


A
B
vi
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r1
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F
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C
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r1
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n
thr
r1
r2
ib

more advanced growth stages of the sicula (Pl. XXI, Figs. F-H, I_3, J_1) and situated at a certain distance from the aperture of the prosicula (r_1). It is only in one case that this first black ring is observed on the boundary of both parts of the sicula (Pl. XXII, Fig. A). Its position on the prosicula seems, therefore, to be a stable and fixed feature. The width of the prosicula at the aperture measures approx. 0•10—0•12 mm.

Metasicula is 0•47—0•65 mm long and, in measured adult siculae, showing only a very slight expansion towards the aperture. It attains some 0•11—0•15 mm of width (*tr.*) at the level of the initial bud, and 0•13——0.16—0.20—0.25 mm in the apertural part. Metasicula has 1—3 black rings, situated in different positions (Pl. XXI, Figs. F-H, I_3, J_1; Pl. XXII, Figs. A_1, F). In some cases, the last black ring is incomplete (r_4 in Pl. XXI, Fig. I). The formation of virgella seems to start at various distances from the beginning of the metasicula. Its early formation is shown in specimen, figured in Pl. XXI, Fig. B, and a much later formation in Fig. C. In latter case the distance of the base of virgella from the aperture of prosicula is more than 5 times as much as in the former. The formation of the initial bud takes place according to the normal monograptid pattern, through the “sinus” (open primary notch) and “lacuna” (closed primary notch) stages (Pl. XXI, Figs. D-E).

The apertural border in adult metasicula is almost straight and displaying a very slight elaboration of its dorsal process which, in some cases, is very slightly expressed. If present at all, the dorsal apertural process does not exceed 0•04 mm in length in the lower zonal siculae. Lateral borders of the aperture in adult siculae are situated some 0•13—0•25 mm from the anterior margin of the initial bud. Apertural border is only slightly thickened.

The first theca is slender, tubular and, beyond the apex of prosicula, has an almost stable diameter without any distinct expansion towards the aperture. Its length ranges from 1•53 mm to 1•60 mm, its width — from 0•05 mm at the base of protheca (initial bud), to 0•11—0•13 mm at the apex of prosicula and same width at the aperture. The first fuselli of the initial bud in the form of short strips are disposed along the right corner of the primary notch. Later fuselli gradually extend along the entire mar-

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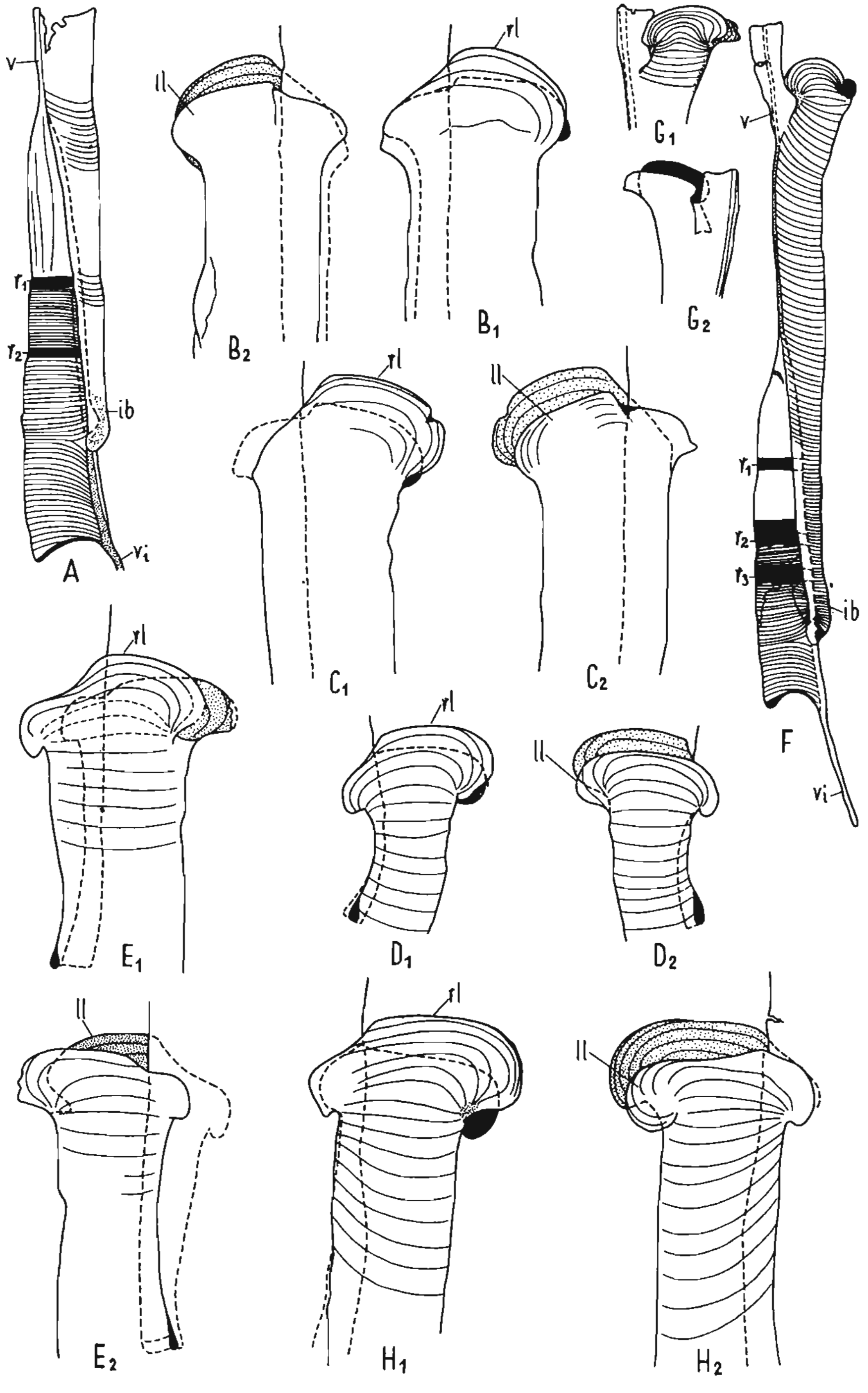
Plate XXII

Lobograptus scanicus parascanicus (Kühne). Sicula and structure of thecae in lower (*A-E*) and higher zonal form (*F-H*). *A* sicula with damaged first theca; B_1-B_2 medial theca with small degree of asymmetry in reverse and obverse aspects; C_1-C_2, D_1-D_2, E_1-E_2 medial, proximal and distal thecae with greater degree of asymmetry in reverse and obverse aspects; *F* sicula with complete first theca in reverse aspects; G_1-G_2 upper part of the first theca in two aspects; H_1-H_2 distal theca in reverse and obverse aspects (Mielnik, *A-E* depth 1015.9—1015.6 m; *F* depth 993.9—993.6 m; *G* depth 996.6 m; *H* depth 1000.9 m).

ib initial bud, *ll* left apertural lobe, r_1-r_3 successive black rings of sicula, *rl* right apertural lobe, *v* virgula, *vi* virgella.

PLATE XXII


v
r_1
r_2
ib
v_i
A
ll
B_2
rl
B_1
G_1
G_2
v
rl
ll
C_1
C_2
r_1
r_2
r_3
ib
F
v_i
rl
E_1
rl
ll
D_1
D_2
ll
E_2
rl
H_1
ll
H_2

gin of the primary notch and, forming an alternate arrangement, produce a zigzag suture (Pl. XXI, Figs. I_1, I_2). The fuselli are obliquely arranged over the entire length of the protheca, changing in the metathecal part into more rectangularly disposed ones (Figs. I_3, J_1). Successive growth stages of the first theca are shown in Figs. G, H, I_3, J_1.

The prothecal part of the first theca reaches a length of some 1·47—1·52 mm. The presence of black bands, situated on the wall of the protheca, was noted in some cases (Pl. XXI, Figs. I_3, J_1). They resemble the sicular rings and, when first recognized (Urbanek, 1954, 1958) they were called "thecal rings". The number and position of the thecal rings are variable, some of them being incomplete, some completely closed. Like the sicular rings, the thecal rings in *L. scanicus parascanicus* are most probably internal thickenings of the wall, due to the secondary deposition of the peridermal substance (Urbanek, 1958, p. 78, internal position of thecal rings, established for "*Pristiograptus*" *bohemicus*).

The metathecal part of the first theca measures some 0·06—0·08 mm in length, the prothecal part occupies therefore about 95% of thecal length. The aperture of the first theca is provided with two lateral and distinctly asymmetric lobes, the right (reverse) being larger than the left one. The right lobe, transversely elliptic in outline, with a length (*tr.*) of about 0·20—0·24 mm and a height (*long*) of about 0·08 mm, is produced by the addition of some 8—9 fuselli, gathered ventrally and dorsally into the nodes. The ventral and dorsal terminations of the lobe form a free beaklike prolongation, the upper margin slightly overlapping the left lobe (Pl. XXI, Fig. J_2; Pl. XXII, Figs. G_1, G_2). The left lobe is distinctly smaller than the right one, being some 0·03—0·04 mm shorter (*tr.*) and some 0·03 mm narrower (*long.*).

The outer surface of both lobes is slightly convex. Most probably, the left lobe consists only of some 6—7 fuselli, the exact number is, however, difficult to recognize owing to a certain preservational deformation of the lobe which occurs in the majority of specimens. An early formation stage of apertural lobes is figured in Pl. XXI, Fig. I_3 which shows that both lobes start their development as symmetric structures, produced on lateral margins of the aperture by addition of a few, arched fuselli. The elaboration of asymmetry occurs in later growth stages through a differentiated growth rate of lobes. In the examined specimens, both lobes touch each other with their upper margins, this circumstance may, how-

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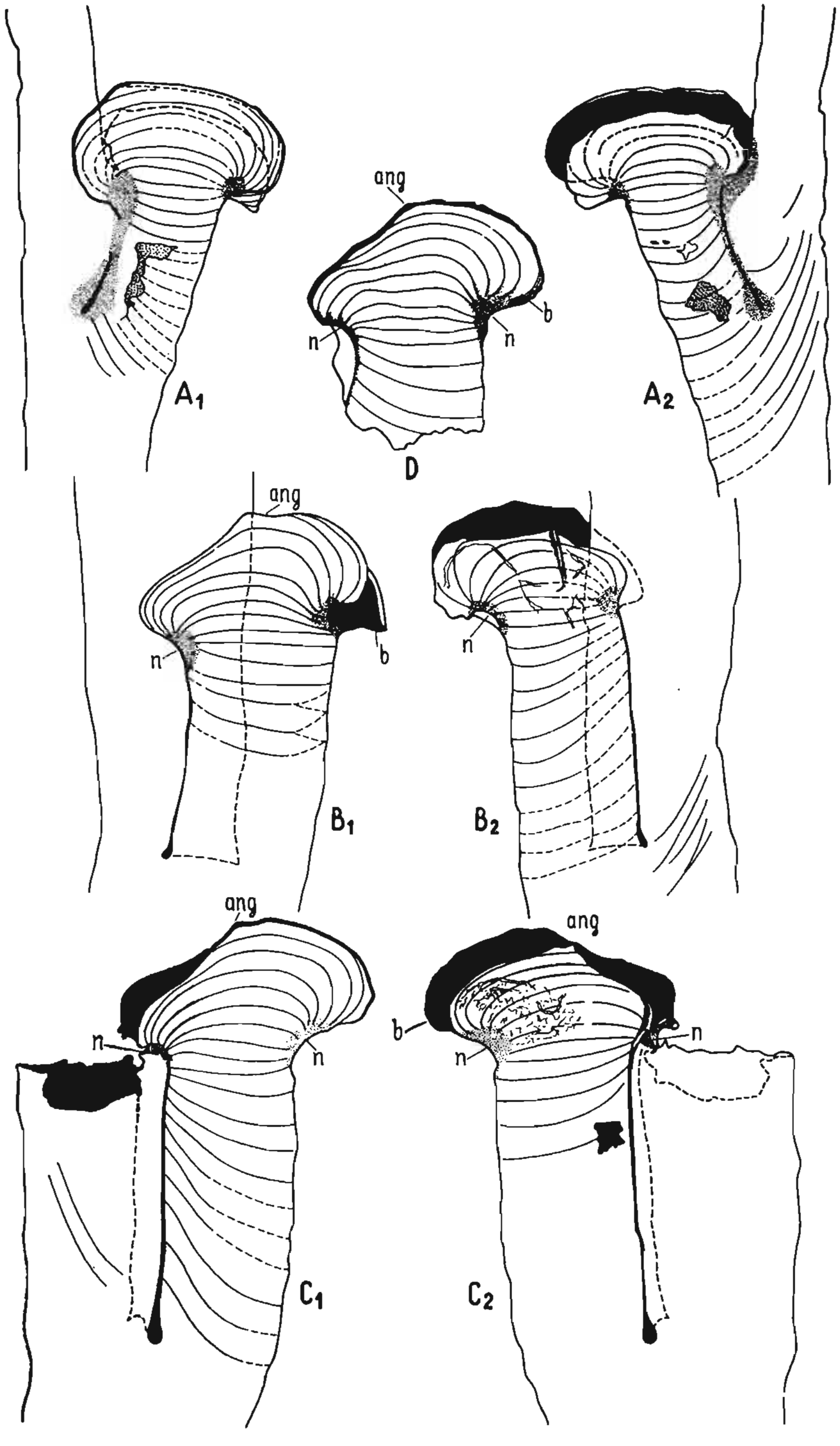
Plate XXIII

Lobograptus scanicus parascanicus (Kühne). Structure of thecae in higher zonal form (drift material). A_{1-2} lateral views of a proximal theca; B_{1-2} lateral views of a medial theca; C_{1-2} lateral views of a distal theca; *D* lateral view of an isolated right apertural lobe in distal theca showing details of its fusellar structure (S. 181, Czarnogłowy); ca. × 63.

ang angular bending of fuselli, *b* beaklike process of apertural lobe, *n* node.

PLATE XXIII



ever, be secondary and result from some deformation. Most probably, in the living animal, both margins were separated by a narrow fissure.

Proximal thecae (Pl. XXIII, Figs. A_1-A_2) are narrow, straight tubes with very small overlap gradually widening towards the aperture. A total length of proximal thecae amounts in the measured specimens from erratic boulder S. 181, Czarnogłowy, to 1·90—2·33 mm and in the measured specimens from the population of a higher zonal form in the Mielnik core, to 2·12—2·54 mm.

The prothecal part is 0·05—0·25 mm wide at the base. In proximal thecae, for the population in S. 181, is the metathecal part 0·08—0·30 and for the specimens in higher zonal populations at Mielnik 0·17—0·60 mm long. The width of the metatheca is 0·10—0·17 mm in the former and 0·15—0·22 mm in the latter case. In proximal thecae the prothecal part occupies about 96—87⁰/₀ of a total length.

In proximal thecae the metathecal part is inclined towards the longitudinal axis of theca at an angle of some 20—30°. The metathecal aperture is provided with a pair of lateral lobes. The right lobe is distinctly larger that the left one, i.e. about 0·03—0·05 mm longer (*tr.*) and about 0·05—0·08 mm higher (*long.*). The right lobe is oval or semicircular in outline and consists of some 8 complete, curved fuselli, gathered into ventral and dorsal nodes. It is only one, marginal fusellus (9th) that is incomplete and occupies about $^2/_3$ of the margin, beginning at the ventral node and terminating at the distal margin of the lobe and, therefore, it does not reach the dorsal node of the lobe. Its termination produces a slight angular bending on the margin (Pl. XXIII, Fig. A_1). The upper incurved margin of the lobe slightly overlaps the left lobe. In proximal thecae the left lobe consists of a smaller number of fuselli. Some 5 of them are complete, slightly arched and gathered into ventral and dorsal nodes, some 3 very short and present only on the ventral margin of the lobe, producing there a distinct beaklike process (Fig. A_2) which is better expressed than that on the opposite lobe. The outer surface of the lobe is only slightly convex, flat or even concave, the lobe itself being somewhat incurved over the aperture.

In more distal thecae, their total length reaches some 2·05—2·52 mm, the metathecal part being 0·55—0·85 mm long and the prothecal part occupying about 74—73 per cent of the total length of a theca. The width of thecae at the base of protheca is 0·23—0·50 mm and in the metathecal part — 0·22—0·30 mm. The ventral wall of most distal thecae displays a slight convexity, thus forming an incipient geniculation of the theca, especially well discernible at the level of the metathecal base (Pl. XXIII, Figs. C_1-C_2). This geniculation is indistinguishable on more proximal thecae which still are straight tubes (Figs. B_1-B_2). Laterally the apertural border terminates in a pair of apertural lobes that display a distinct asymmetry. The right lobe, transversely shaped like a rough ellipse with a depressed dorsal margin, is markedly larger that the left lobe, i.e. 0•05—0•11 mm longer (*tr.*) and 0•04—0•08 mm wider (*long.*).

The right apertural lobe in distal thecae (Pl. XXIII, Figs. B_1, C_1, D) strongly resembles, in its outline, the apertural lobes in *L. simplex* but is distinctly larger. The main part of the lobe consists of some 5 complete and arched fuselli, gathered into a ventral and dorsal node. The remaining part is formed by 1—2 fuselli dorsally successively tapering, which results in the formation of an oblique dorsal margin of the lobe. One or two further fuselli form short strips, disposed at the ventral border of the lobe which following its sudden decrease, produce, more dorsally, a characteristic angular bending of the upper margin of the lobe (*ang*). A ventral beaklike process is simultaneously produced by these fuselli on the lobe.

The upper margin of the right lobe is incurved over the aperture and the smaller left lobe is, therefore, slightly overlapped by the larger right one. In unflattened specimens the free upper margins of both lobes do not touch each other and are separated by a narrow fissure. Most probably, they never touched each other in the lifetime of the animal. Through the ventral and dorsal apertural notch, bordered by both lobes, the aperture is widely open ventrally and dorsally.

Some 7—8 fuselli are involved in the formation of the left apertural lobe, 3 or 4 of them being complete and united into a ventral and dorsal node. The remaining fuselli are shorter and freely terminate dorsally, forming a short oblique border of the lobe. Following their rather sudden decrease the last one or two fuselli form an angularly protruding outgrowth on the margin of the lobe (Pl. XXIII, Figs. B_2, C_2; Pl. XXII, Fig. H_2). These fuselli also form a more or less distinct beaklike ventral process.

The outer surface of the right lobe is usually slightly convex, the left one being almost flat or even depressed. In a few cases the presence of some roughnesses was noted on the surface of the wall in the left lobe (Pl. XXIII, Figs. B_2, C_2). The nature of these structures is uncertain, some morbid affection of the soft tissues, caused e.g. by parasites seems, however, to be the most reliable explanation. The left lobe is incurved over the aperture and is overlapped by the right one.

Growth pattern of rhabdosome. — A fragment of a growing tip of rhabdosome was found in the rich material of *L. scanicus parascanicus*, etched from erratic boulder S. 181 (comp. Urbanek, 1960, p. 152, Fig. 8, b). It represents a series of 4 nearly complete terminal thecae of a rhabdosome with a growing tip damaged, beyond the fourth theca whose apertural lobes are in an early growth stage. Successive terminal thecae are in different growth stages, the two most proximal ones having completely developed and asymmetric apertural lobes, the third displaying an incomplete development of lobes with a small degree of their asymmetry (Pl. XXIV, Figs. A, B_1-B_3). The most interesting is the fourth theca, having apertural lobes in an incipient formation stage and being only small apertural elevation, separated ventrally by a shallow apertural notch. Each lobe consists of only 3 fuselli, both being of the same size and, therefore, symmetric (Fig. B_4).

In the growing tip this theca was followed by the next one whose apertural part is damaged. The observed picture may, however, be combined with and completed by another specimen, etched from erratic boulder S. 137. The latter consists of an apertural part of a theca, with apertural lobes in a growth stage, comparable with that in theca B_4 of the specimen, described above, and with a more distal theca which has only subapertural part of metatheca developed. This specimen terminates in a growing prothecal part of a still more distal theca of rhabdosome (Pl. XXIV, Figs. C, D_1-D_2). This specimen doubtlessly represents the termination of the growing tip of the rhabdosome. By combining both specimens, a complete picture of the growth pattern in *L. scanicus parascanicus* may be restored (Fig. E). The termination of a rhabdosome consists of a series of thecae in different growth stages. An early stage in the formation of apertural lobes of a given theca coincides with the growth of the next theca which forms its subapertural part, simultaneously with the formation of some 3 basal fuselli in apertural lobes of the preceding theca (Figs. C, D_1).

The formation of supraapertural part of a particular theca seems, therefore, to be delayed when compared with the growth rate ot its subapertural part. The formation of the subapertural part of a metatheca takes place simultaneously with the formation of a basal part of the protheca in the next theca (comp. Pl. XXIV, Fig. E).

The early development of apertural lobes is marked by the stage when both lobes are symmetric (up to 3 fuselli). The asymmetry starts to develop through differences in growth rate, probably at the stage when the left apertural lobe has 5 fuselli, and the right apertural lobe 6 fuselli (comp. conditions pictured in Pl. XXIV, Figs. B_3-B_4). The condition described here for a higher zonal form in *L. scanicus parascanicus*, seems to indicate a relatively rapid decrease in the growth activity gradient towards the distal end of the colony. This decrease is here, however, less rapid

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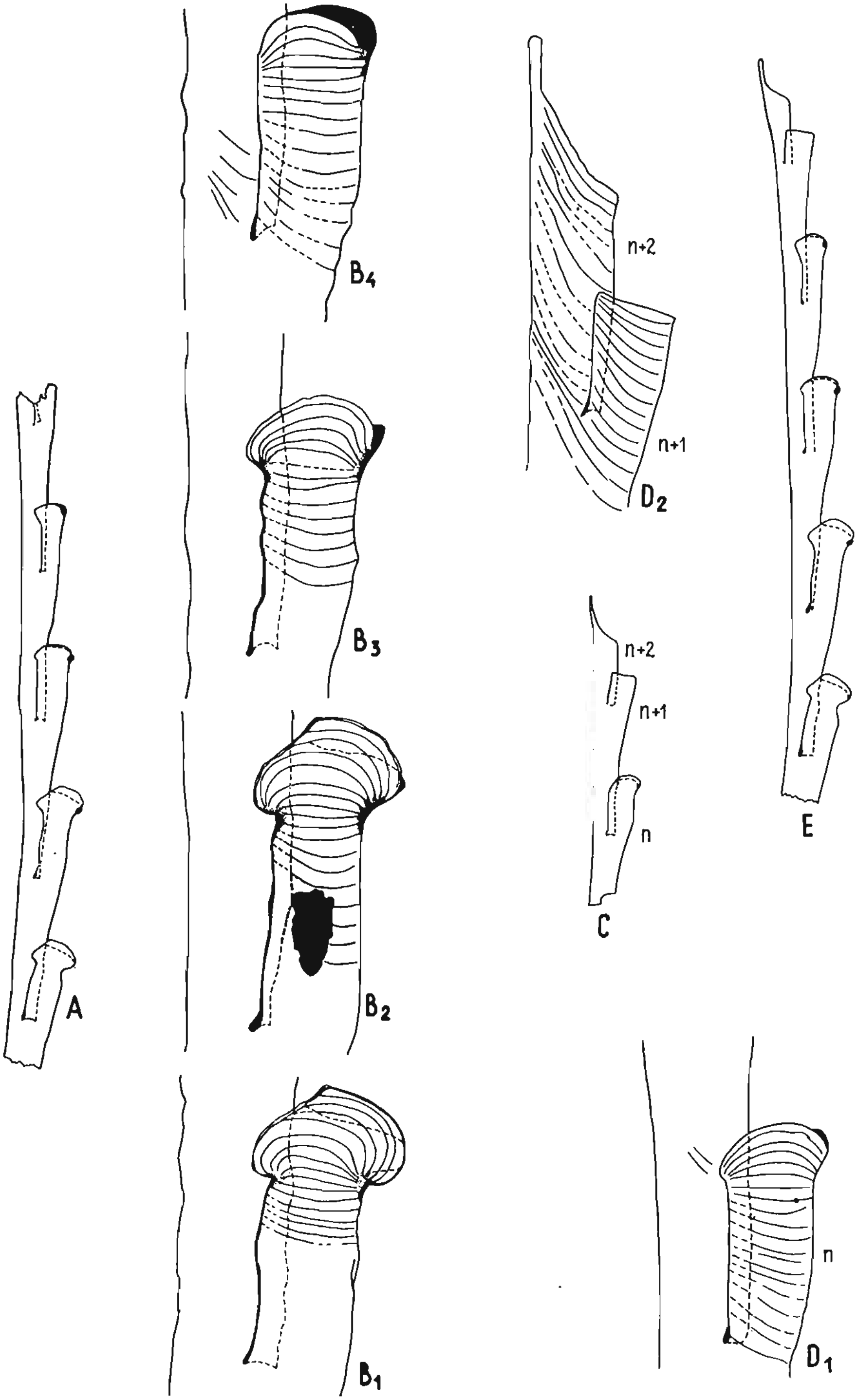
Plate XXIV

Lobograptus scanicus parascanicus (Kühne). Growth pattern of rhabdosome. *A* growing tip of a branch with damaged termination; *B_1-B_4* details of fusellar structure of metathecal parts in successive thecae on specimen figured *A*; *C* another termination of a growing tip of rhabdosome; *D_{1-2}* details of fusellar structure of metathecal parts in successive thecae on specimen figured *C*; *E* restored complete picture of growth relations on the tip of rhabdosome, based on specimens figured *A*. *C* (*A-B* S. 181, Czarnogłowy; *C* S. 137, Ustka); *A*, *C*, *E* ca. × 15; *B*, *D* ca. × 48.

PLATE XXIV



as compared, for instance, with saetograptids (e.g. *S. chimaera*) and *L. exspectatus exspectatus*, described below (comp. p. 344).

Regeneration of rhabdosome — see Urbanek, 1963, pp. 213—220, Text-pl. 15, Figs. A-F.

Stratigraphic range. — The first asymmetric thecae of the *parascanicus* type have been found in a sample from the Mielnik core at a depth of 1,016·9—1,016·6 m. This sample consists of scanty distal thecae with the *parascanicus* type of lobes and a distinct asymmetry as well as of proximal thecae with a slight asymmetry or almost complete symmetry. They are associated with siculae devoid of the preserved first thecae which in their size and proportions (total length 1·46 mm and diameter of aperture 0·22—0·28 mm) resemble rather the *L. simplex*, than *L. scanicus parascanicus* siculae. They have, however, a small apertural dorsal process, reaching only 0·05—0·06 mm in length. The simplest explanation of these conditions seems to be that the assemblage in question represents a mixed population which consists of a few fragments of both *L. simplex* (siculae, some proximal thecae) and *L. scanicus parascanicus* (distal thecae). The stratigraphic range of both species mentioned above seems, therefore, to display a small overlap.

Both proximal and distal thecae from the next sample (depth 1,015·9 m) are of the *parascanicus* type. Some of the distal thecae display, however, a rather small degree of asymmetry as compared with higher zonal forms, some other being "normally" asymmetrical. The associated siculae are in their appearance similar to the *parascanicus* ones, are rather gracile and shorter (total length 1·16—1.10 mm, length of metasicula 0·68—0·56 mm, length of apertural process 0·04 mm), but still more expanded at the aperture where they reach 0·25—0·20 mm in diameter. The last appearance of *L. scanicus parascanicus* with almost symmetric apertural lobes in distal thecae was noted at a depth of 1,005·9 m.

In order to comprise a number of populations mentioned above, the present writer is inclined to introduce the term of a "lower zonal form" of *L. scanicus parascanicus*. In the morphological aspect, the populations of the lower zonal form are marked by the presence of specimens, displaying a small degree of asymmetry, but associated with "gracile" *parascanicus* siculae which, in the present writer's opinion, may probably belong to the same rhabdosome as the thecae.

It is, however, very difficult to draw the morphological and stratigraphical boundary between the lower and higher zonal forms of *L. scanicus parascanicus*. According to available data, the last appearance of the population which contains almost symmetric thecae of the *parascanicus* type is recorded at a depth of some 1,005·9—1,005·6 m (comp. Pl. I). In the immediately overlying strata, at a depth of 1,005·6—1,002·9 m, the graptolite fauna becomes poor. Only few poorly preserved and uncertain fragments of lobograptids were etched from the thickness mentioned above. After its reappearance, however, in samples from a depth of 1,002·9—1,002·7 m, the scanty *L. scanicus parascanicus* populations contain no more thecae with only slight asymmetry as in lower zonal type and consist exclusively of distinctly asymmetrical thecae. A rather strongly developed beaklike process on the left lobe makes up another noteworthy feature of these forms. The depth 1,002·9 m is, therefore, suggested as a probable lower limit in the vertical distribution of the higher zonal form.

The first abundant occurrence of higher zonal form of *L. scanicus parascanicus* is noted at a depth of 1,000·9—1,000·5 m. The associated siculae are of the *parascanicus* type, the first thecae being rather short but with distinctly asymmetric apertural lobes.

The upper limit of the distribution range in the higher zonal form may be also determined only with some uncertainty. The sample from a depth of 978·9—978·6 m shows the horizon of the last appearance of the forms which doubtlessly are *L. scanicus parascanicus*. However, at a depth of 973·85—973·6 m some uncertain, strongly deformed thecae have been found which may still belong to the subspecies in question. Moreover, the upper limit of its occurrence is overshadowed by the presence of *L. imitator* n.sp. Short fragments of the rhabdosome and isolated thecae are, in both cases, similar to such an extent that they do not allow one to recognize their true nature.

The total thickness of the *L. scanicus parascanicus* distribution range may, therefore, be estimated at some 38·3 m and this range is contained between 1,016·9 and 978·6 m of depth in the Mielnik core. The subspecies under study displays, within this thickness, a discontinuous distribution and are absent from some samples, reappearing in the next ones.

In the Mielnik core, this is associated with the following graptolite assemblage: *Lobograptus scanicus scanicus* (Tullberg)*, *L. imitator* n.sp.*, *L. exspectatus exspectatus* Urbanek, *Cucullograptus pazdroi* Urbanek*, *Pristiograptus dubius* (Suess), "*Pristiograptus*" *bohemicus* (Barrande), *Saetograptus chimaera cervicornis* Urbanek, *Monoclimacis micropoma* cf. *micropoma* (Jaekel)**, *Holoretiolites erraticus* Eisenack, *H. mancki* (Münch), *H. simplex* Eisenack*, *Plectograptus macilentus* (Törnquist). (Single asterisk denotes graptolites, associated only with the higher zonal form; double asterisk denotes those, associated only with the lower zonal form).

L. scanicus parascanicus is a common species in the Baltic drift material and has been found in the following boulders: S. 16, Łebcz; S. 32, Gdańsk-Wrzeszcz; S. 36, Jarosławiec; S. 37, Island Wolin; S. 137, Ustka; S. 174, Lubin; S. 181, Czarnogłowy; S. 185, Rewal; S. 228, Jarosławiec. Especially noteworthy is erratic boulder S. 181 from Czarnogłowy (Western Pomerania) from which a very rich graptolite material has been etched out. *L. scanicus parascanicus* is predominating in a well-preserved association (only slightly flattened). A preserved part of this boulder is shown in Pl. XLVI, Fig. 1 (about half the size of the original erratic prior to etching). The boulder in question seems to be part of a larger erratic, probably being originally (*in situ*) a marly concretion in the Silurian shale or mudstone. Lithologically it is a strongly impure (marly), ashy-bluish limestone of the "Graptolithengestein" type (comp. Urbanek, 1963, p. 213).

In erratic boulders, the species in question is associated with a more or less complete assemblage which may include the following graptolites: *Cucullograptus pazdroi* Urbanek (frequent), *Saetograptus chimaera cervicornis* Urbanek (frequent), *S. chimaera* cf. *salveyi* (Hopk.) (rare), *S. chimaera* cf. *chimaera* (Barr.), *"Pristiograptus" bohemicus* (Barr.), *Pristiograptus dubius* (Suess), *Neodiversograptus beklemishevi* Urbanek, *Plectograptus macilentus* (Törnquist) (S. 32), *Holoretiolites* cf. *simplex* Eisenack (S. 137), *H. mancki* (Münch) (S. 137, S. 181), *H. erraticus* Eisenack (S. 16, S. 185, S. 228).

This assemblage coincides well with an association found in the Mielnik core material and indicates for a similar stratigraphic range.

Systematic position. — There is no doubt that the form, described above, is subspecifically identical with that, described by Kühne (1955) as *Monograptus parascanicus.* The size and structure of thecae are much the same in both cases, there is, however, some uncertainty as to the dimensions of the sicula. Kühne stated the length of sicula in his *M. parascanicus* to be very small (0·75 mm in his Table on p. 393 and 0·7 mm in the diagnosis on p. 395). This considerable difference in length of siculae in the specimens from the erratic boulders of the North German Plain (the vicinity of Berlin) and from Polish Lowland (the drift and bore-core materials) seems, however, to be only apparent. This opinion is based on measurements, made, at the present writer's request, by Dr L. Teller (Warsaw)[20] on specimens, indentified by Dr. H. Jaeger (Berlin) as *Monograptus scanicus parascanicus* and etched from boulders, collected at Hidensee and Spandau. They indicate the sicula 0·95—1·05 mm long in the former, and 1.1 mm in the latter case. This coincides well with the size of siculae in the present writer's material, their length being 1.07—1.15 mm in the drift material and some 0·94 mm in the bore core. The data, given by Kühne (1955) for the length of the sicula in his *M. parascanicus*, are probably misleading.

It seems to be quite safe to generalize that *L. scanicus parascanicus* represents only a further development of *L. simplex*. An especially close relationship of both species is suggested by the structure of thecae in which only few simple changes were enough to transform the latter into

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[20] During his visit to Berlin in 1961.

the former species (some enlargement of apertural lobes and elaboration of their asymmetry, gracilization and elongation of proximal thecae). The reduction of the dorsal curvature in its proximal part was the only necessary change in shape of the rhabdosome. Perhaps, some greater changes were necessary to transform the *simplex* siculae into the *parascanicus* siculae (a general "gracilization", i.e. a considerable shortening of the sicula — mostly metasicula — and, moreover, narrowing of the formerly expanded apertural part, combined with a simultaneous reduction of the dorsal process in the metasicula).

As far as the thecae are concerned, the morphological gap between *L. simplex* and *L. scanicus parascanicus* is filled, at least in part, by the presence of progressive forms of the former (*L. simplex* from S. 225 with a robust sicula but with a somewhat asymmetric thecae) and primitive forms of the latter species (lower zonal form with smaller asymmetry of thecae than in higher zonal form but associated with already gracile siculae). If the siculae, mentioned above, actually belong to the associated *parascanicus* thecae (which is, however, still uncertain), this may suggest that the transformation of the sicula was a more rapid change in the evolutionary line as compared with probably gradual changes in the thecal structure. The presence of *L. simplex* with a rather primitive, robust sicula but with an incipient asymmetry of thecae may suggest that the evolutionary changes started with the elaboration of the incipient asymmetry but hereafter were followed by a rather rapid reconstruction of the sicula, connected with a rather gradual enlargement of lobes and elaboration of its asymmetry. Such speculations are, however, based on still inadequate material, and should be approached with necessary caution.

On the other hand, *L. scanicus parascanicus* seems to be closely related to *L. scanicus amphirostris* n.subsp. which is probably a descendant of the former subspecies in a chain of closely linked *scanicus* subspecies.

L. scanicus amphirostris appears in a lower part of the stratigraphic range of *L. scanicus parascanicus* (the first appearance at a depth of 1,009.6—1,009.9 m) and is often associated with the latter (comp. p. 442). In size and proportions of sicula, both species are closely alike, but distinctly differing in structure and degree of asymmetry of apertural lobes in thecae. In *L. scanicus amphirostris* n.subsp. they are enlarged and provided on both sides with strongly developed, beaklike, ventral processes. The larger right lobe is strongly incurved over the aperture, displaying a greater overlap than that in *L. scanicus parascanicus*. *L. scanicus amphirostris* n.subsp. forms at least morphologically and stratigraphically, an intermediate link between *L. scanicus parascanicus* and *L. scanicus scanicus*. This enables one to place *L. scanicus parascanicus*, as the most primitive member of *scanicus* lineage, in the family tree of the Cucullograptinae (comp. also p. 370).

Lobograptus scanicus amphirostris n. subsp.

(Fig. 10; Pls. XXV—XXVI)

Type specimen (holotype): Fig. 10, A_1-A_2 (distal theca).

Paratype: Pl. XXV, Fig. D (proximal theca).

Type stratum: Greenish-blue mudstones and marls in the core of the Mielnik deep-boring between 1,009.9—959.6 m of depth (*parascanicus* and *invertus* zones, upper part of Mielnik Beds).

Derivation of the name: amphirostris — Gr. latinized *amphi* = on both sides, and Lat. *rostrum* = a beak, a prow of a ship; this refers to the presence of a beaklike process of both lobes in all thecae of the rhabdosome.

Diagnosis. — Lobograptid with a gracile sicula (approx. 1.10 mm long) and without a distinct dorsal process. The asymmetric apertural apparatus of thecae consists of a larger right lobe, provided with a beaklike ventral termination and an oblique dorsal margin; a smaller, left lobe also displays the presence of an incurved beaklike, ventral termination and a deep apertural incision at its base.

Material. — Numerous thecae and fragments of rhabdosome, including a few siculae with attached first theca were etched from the Mielnik boring samples, from a depths of 1,009.9—959.6 m. The richest population were obtained in the samples from depths of 959.9—959.7 m and 965.9—965.6 m. All specimens were strongly flattened and partly deformed with fusellar structure not always easily distinguishable. In the drift material, known so far, they were found only in erratic boulder S. 58, Jarosławiec.

Description.— Sicula (Pl. XXV, Figs. A, B) straight and rather short, measuring approx. 1.10 mm in length. The width of the sicula is almost uniform throughout its metasicular part.

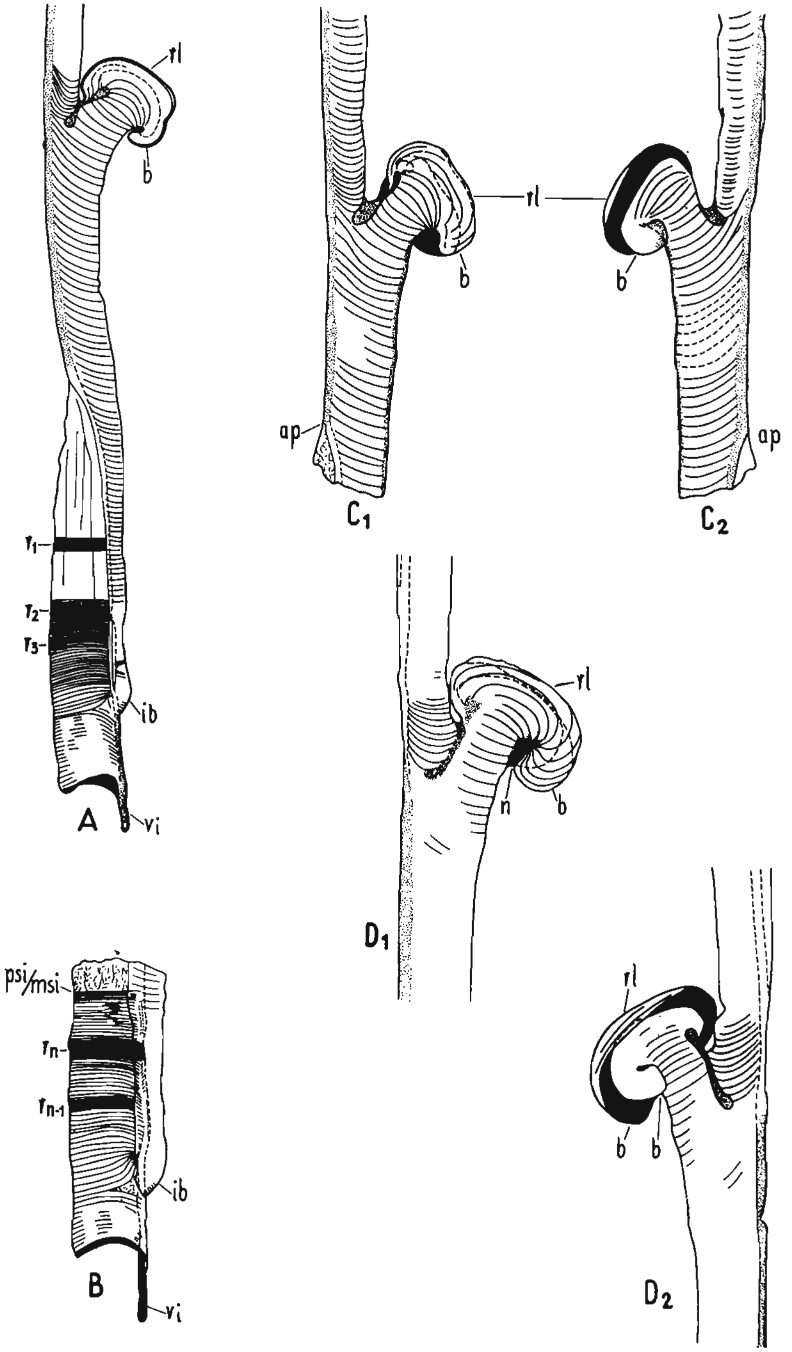
Prosicula ranging from 0.60 mm to 0.51 mm in lenght (in 2 measured specimens). In most specimens, the periderm is strongly wrinkled and partly damaged, so that the presence of some number (3—4) of longitudinal threads (ribs) is the only detectable detail. The prosicular parts of adult siculae are provided with a prosicular black ring (r_1, Pl. XXV, Fig. A) which is placed at a certain distance from the aperture of the prosicula (0.13—0.10 mm on measured specimens). The width of

Plate XXV

Lobograptus scanicus amphirostris n.subsp. Structure of sicula and proximal thecae. *A* sicula and first theca in reverse view; *B* metasicular part of a sicula in reverse aspect to show details of its fusellar structure; C_1-C_2 structure of upper part of first theca from reverse and obverse side; D_1-D_2 structure of upper part of a proximal theca (Mielnik, *A*, *B*, *D* depth 965.6—965.9 m; *C* depth 1,009.7—1,009.9 m); *A* ca. × 50, *B*-*D* ca. × 67.

ap apex prosiculae, *b* beaklike process of apertural lobe, *ib* initial bud, *n* node, *psi/msi* boundary between pro- and metasicula, *rl* right apertural lobe, r_1-r_3, r_n+r_{n+1} succesive sicular black rings, *vi* virgella.

PLATE XXV


rl
b
r1
r2
r3
ib
A
vi
psi/msi
rn
rn-1
ib
B
vi
rl
b
b
ap
ap
C1
C2
rl
n
b
D1
rl
b
b
D2

the prosicula at the aperture amounts to 0.30 mm. This rather great dimension may be in part due to very strong flattening of specimens.

Metasicula is 0.59—0.50 mm long (in 2 measured specimens) and is nearly identical in diameter over the entire length up to the aperture. It reaches some 0.30 mm at the level of the initial bud and the same width in the apertural part. In the examined specimens, the metasicula is provided with 2 black rings, the first of them being situated at a varying distance from the prosicula. In the specimen, figured in Pl. XXV, Fig. A, it is disposed nearly on the boundary with the prosicula, in the specimen, figured in Fig. B — at a greater distance from it. The last black ring is sometimes incomplete (Fig. A, r_3). The formation of the initial bud took place according to the normal monograptid pattern as indicated by the fusellar structure of the reverse side of metasicula (Fig. B). This shows the presence of a normal primary notch, closed by a series of fuselli, making up the adapertural part of metasicula. The apertural margin in adult siculae is nearly completely straight, displaying the presence of a very small dorsal elevation (a vestigial dorsal process) which does not exceed 0.02 mm in length. In the specimen, figured in Fig. B, the apertural margin is framed by a number of microfuselli, forming a kind of a slightly marked selvage.

The first theca is slender, tubular and, beyond the apex of the prosicula, has a nearly stable diameter of some 0.23—0.24 mm. It is about 1.80 mm long, its width ranges from 0.06 mm at the base of the protheca (initial bud) to 0.23 mm at the apex of prosicula and to some 0.30 mm at the aperture. The basal part of the initial bud has, in all examined specimens, a strongly wrinkled and damaged periderm with no fusellar structure discernible. The remaining part of the protheca consists of obliquely disposed fuselli. The prothecal part of the first theca reaches some 1.57 mm in length, with the free part (stretching above the apex of the prosicula) some 0.80 mm long. The metathecal part of the first theca is, in its distal half, isolated, being some 0.23 mm long. The aperture is provided with two lateral and distinctly asymmetric lobes, the right (reverse) being larger than the left one. Both lobes are, however, larger as compared with apertural lobes of the first theca in *L. scanicus parascanicus* (comp. Pl. XXV, Figs. A, C_1-C_2).

The ventral terminations of both lobes form a strong, beaklike prolongation or a kind of a rostral process (*b*). The right lobe, almost semicircular in outline some 0.25 mm in length (*tr.*) and 0.10 mm in height (*long.*) is formed by the addition of some 8—9 fuselli to the apertural margin. The latter are gathered dorsally into a dorsal node. Owing to the unsatisfactory state of preservation, the fusellar structure of the ventral termination of the lobe is less known. It seems, however, that, in general appearance, it should resemble the structure of this part in other proximal thecae (Pl. XXV, Fig. D_1). The free upper margin of the right lobe stretches distinctly beyond the margin of the left lobe and, being somewhat incurved over the aperture, it displays some overlap (Fig. C_2).

The left apertural lobe in the first theca is distinctly smaller but, following the unsatisfactory state of preservation, the number of its fuselli cannot be accurately established. Ventrally, the lobe terminates in a strongly developed beaklike prolongation which forms a rostral process similar to that on the right lobe. In some specimens, this rostral outgrowth is slightly twisted (Pl. XXV, Figs. C_2, *b*). This rostral process is larger than a corresponding structure in *L. scanicus parascanicus.*

Proximal thecae form long, slender and straight tubes, with a small degree of overlap (Pl. XXV, Figs. D_1-D_2). The total length of proximal thecae is 1.97 to 1.70 mm (in measured specimens). The prothecal part is very long (1.45—1.35 mm) and rather narrow, measuring 0.13—0.25 mm at the base, and 0.13—0.20 mm below the base of the metatheca. The metathecal part is some 0.25—0.62 mm long and 0.13—0.20 mm wide at the aperture. The prothecal part occupies in proximal thecae 85—68% of their total length. The metathecal part is inclined towards the longitudinal axis of the theca at an angle of some 20—30° and is adnate to the adjacent protheca.

Lateral apertural borders of thecae terminate on both sides with apertural lobes. The right lobe is distinctly larger than the left one, i.e. about 0.15—0.19 mm longer (*tr.*) and some 0.03—0.05 mm higher. The outline of the lobe is transversely elliptical. It consists of some 12 fuselli, the first 8 of them being complete and gathered into a ventral and a dorsal node, the remaining 4 form a shovellike ventral termination of the lobe, i.e. the rostral process. These fuselli terminate in a free margin of the lobe. The upper margin of the lobe is distinctly incurved over the aperture, strongly overlapping the left lobe (Pl. XXV, Fig. D_2). The left apertural lobe is distinctly smaller but provided with a strong beaklike ventral termination. The number of fuselli making up the left lobe is unknown since the specimens are poorly preserved. The outer aperture, more or less closed in the middle, is widely open dorsally and ventrally owing to the presence of a dorsal and ventral apertural notch (Fig. D_1, *n*). On the obverse side, the ventral apertural notch forms a narrow apertural incision, surrounded by the incurved ventral termination of the left lobe.

More distal thecae are shown in Fig. 10 and Pl. XXVI, Figs. A, B. They are wider (0.25—0.54 mm at the base of protheca and 0.25—0.30 mm at the base of metatheca), straight tubes with a greater overlap. The length of the prothecal part amounts to 1.46—1.10 mm and of the metathecal part — 1.00—0.56 mm; the prothecal part occupies therefore about 66—56% of total length of thecae. The metatheca is inclined at an angle of some 10° to the longitudinal axis of thecae and reaches some 0.25—0.30 mm in width at the aperture. The aperture of the theca is provided with two lateral apertural lobes with a great degree of asymmetry, the right one being larger. It is some 0.05—0.10 mm longer (*tr.*) and some 0.05—0.08 mm higher than the left lobe. In the most distal thecae, the outline of the right lobe is nearly subrectangular (Fig. 10, A_1; Pl. XXVI, Fig. B_1), in less distal ones it is roughly transversely elliptical (Pl. XXVI, Fig. A_1). The right lobe consists of some 10—13 fuselli, the first 7—8 being complete and gathered in a ventral and dorsal node. The remaining fuselli make up a ventral and distal termination of the lobe, forming a shovellike prolongation. The free upper margin of the right lobe is strongly incurved over the aperture and overlaps the left lobe (Fig. 10, A_2; Pl. XXVI, Fig. B_2). The

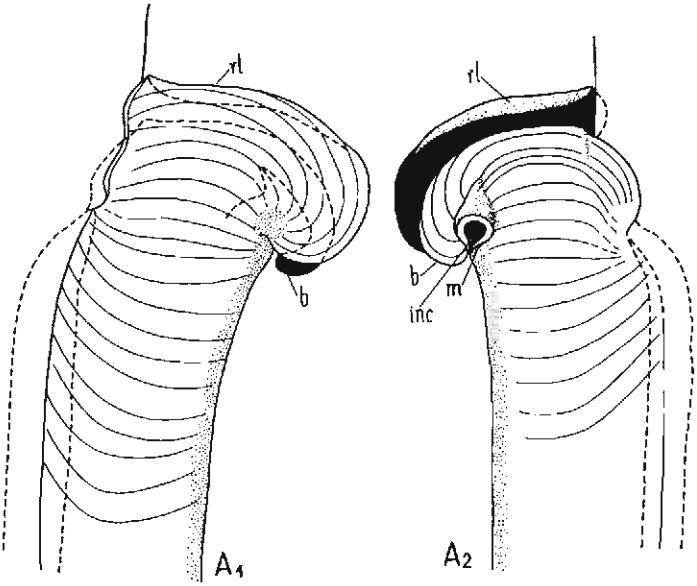


Fig. 10. — *Lobograptus scanicus amphirostris* n.subsp. Structure of apertural apparatus in a true distal theca: A_1 in reverse, A_2 in obverse aspects (Mielnik, depth 959.7—959.9 m), ca. × 67.

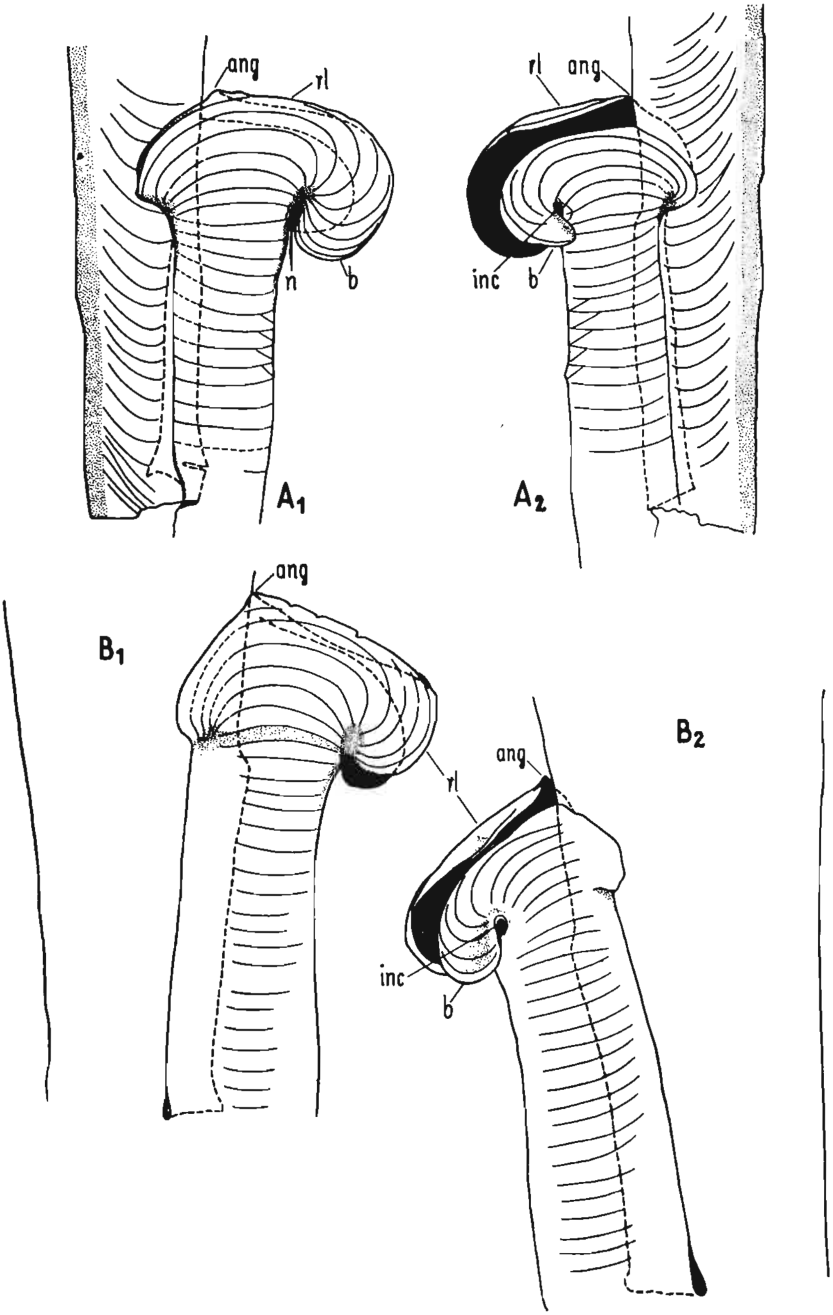
b beaklike process of apertural lobe, *inc* apertural incision in the left lobe, *m* extroverted margin of the left apertural lobe, *rl* right apertural lobe.

Plate XXVI

Lobograptus scanicus amphirostris n.subsp. Structure of more distal thecae. A_1-A_2 structure of metathecal part in a medial theca in reverse and obverse view; B_1-B_2 structure of metathecal part in a distal theca in reverse and obverse view (Mielnik, *A* depth 965.6—965.9, *B* depth 959.7—959.9 m); ca. × 67.

ang angular bending of free margin of apertural lobe, *b* beaklike process of apertural lobe, *inc* apertural incision in the left lobe, *n* node, *rl* right apertural lobe.

PLATE XXVI



fuselli making up the antero-ventral termination of the lobe end dorsally at a free margin which, tapering, forms an angular bending (*ang*, Pl. XXVI). The dorsal margin of the lobe is obliquely inclined towards the longitudinal axis of the theca (Pl. XXVI, Fig. A) with a tendency to a more parallel inclination in most distal thecae (Fig. 10, A_1; Pl. XXVI, Fig. B).

The left apertural lobe has an outline which generally is similar to that of the right lobe with the ventral termination proportionally more elongated and characteristically incurved or twisted (Pl. XXVI, Figs. A_2, B_2). While in the right lobe all fuselli are gathered ventrally into a node, here they converge rather to the free margin, framing the narrow incision of the ventral apertural notch (Fig. 10, A_2, *inc*; Pl. XXVI, Figs, A_2, B_2, *inc*.). The margin surrounding this incision seems to be extroverted in flattened specimens but, in the less compressed ones, it simply makes up a laterally protruding edge (Fig. 10, A_2, *m*).

Owing to the presence of the apertural incision mentioned above, on the obverse side of the aperture, the ventral termination of the left lobe is always free and never attached to the ventral wall. This is the chief difference in structure of thecae in *L. scanicus amphirostris* n.subsp. as compared with *L. scanicus scanicus* in which the termination of the left lobe is fused with the ventral wall of the theca (comp. Pl. XXVII, Figs. *C-D*). This incision occurs in the free ventral part of the left lobe and is a feature of all thecae of rhabdosome in *L. scanicus amphirostris* n.subsp., the most proximal excepted. In contrast, it is present even in the most distal of the examined thecae (comp. Fig. 10, A_2).

The left lobe consists of 8—11 fuselli, some 6—7 being complete, the remaining shorter and constituting only a ventral, beaklike prolongation of the lobe. The left lobe has an angular bending and an obliquely inclined dorsal margin, similar to those on the right lobe.

Stratigraphic range. — As compared with other members of the *scanicus* group, *L. scanicus amphirostris* n.subsp. appears rather early. Its first occurrence in the Mielnik boring has been recorded at a depth of 1,009.9—1,0009.55 m. In the samples from this depth it is represented by few distal and more medial fragments of the rhabdosome. From its first appearance upwards, the subspecies in question displays a discontinuous distribution, the next larger population being recognized in the samples from a depth of 963.9—962.5 m. After a successive disappearance, *L. scanicus amphirostris* reappears at a depth of 959.9—959.6 m, represented there once more by a rather rich population. The depth of 959.6 m may, however, be accepted as a horizon of its last appearance because no other surely stated representatives of *L. scanicus amphirostris* were found above it. The total thickness of strata, occupied by the distribution range of *L. scanicus amphirostris* amounts, therefore, to about 50.3 m, contained between 1,009.9—959.6 m of depth.

In the Mielnik core, *L. scanicus amphirostris* n.subsp. is commonly associated with the following graptolite assemblage: *Pristiograptus dubius* (Suess), "*Pristiograptus*" *bohemicus* (Barr.), *Saetograptus chimaera* (Barr.) *Holoretiolites mancki* (Münch), *H. erraticus* Eisenack, *Neodiversograptus beklemishevi* Urbanek, *Lobograptus imitator* n.sp., *L. exspectatus* Urbanek, *Cucullograptus pazdroi* Urbanek, and, in the upper part of its distribution range, with *Cuc. hemiaversus* Urbanek (see also distribution on Pl. I). The vertical range of *L. scanicus amphirostris* n.subsp. overlaps the range of *L. scanicus parascanicus* (partly) and *L. scanicus scanicus* (totally). The subspecies, mentioned above, are not, however, directly associated with *L. scanicus amphirostris*, except, may be, for the samples in which only proximal thecae were found and in which a true *scanicus* cannot be satisfactorily distinguished from an *amphirostris.*

In the Baltic drift material, *L. scanicus amphirostris* n. subsp. has been found only in erratic boulder S. 58, Jarosławiec, where it is accompanied by the following graptolite association: *L. exspectatus exspectatus* Urbanek, *Monoclimacis haupti* (Kühne), *Pristiograptus dubius* (Suess) and *Saetograptus chimaera* cf. *cervicornis* Urbanek.

Systematic position. — As it has already been stated (p. 370), *L. scanicus amphirostris* n. subsp. may be considered as a stratigraphically and morphologically intermediate form between *L. scanicus parascanicus* and *L. scanicus scanicus.* Stratigraphically, it appears later than the former subspecies (some 7.0 m. above its first appearance) but precedes the appearance of the latter (some 28.0 m below its first appearance). It is, however, more persistent than two other members of the *scanicus* group, surviving some 23.0 m above last occurrence of true *scanicus.* Morphologically it also fills the gap existing between two other members of the *scanicus* group, being truly intermediate in structure of thecae, especially so in size, outline and degree of asymmetry of apertural lobes. As compared with *L. scanicus parascanicus*, the latter are enlarged, showing also a greater overlap but are correspondingly smaller than those in *L. scanicus scanicus.* The most distal thecae of *L. scanicus amphirostris* n.subsp. (Fig. 10), very closely approach the distal thecae of *L. scanicus scanicus*, indicating that the distal introduction, subsequent development and spreading of only few new characters (changes in expressivity and penetrance of given morphogenetic factors), constituted the main evolutionary event resulting in the formation of the latter. The sicula of *L. scanicus amphirostris* n.subsp. strongly resembling that in the true *scanicus*, suggests that this sicula, being very stable in the entire *scanicus* group, was in practice not involved in the evolutionary changes.

Lobograptus scanicus scanicus (Tullberg, 1883) sensu Bulman, 1953

(Fig. 11—12; Pl. XXVII; Pl. XLVII, Fig. 2)

1883. *Monograptus scanicus* Tullberg; S. A. Tullberg, Skanes graptoliter........., pp. 26—27, Pl. 2, Fig. 44?, non Figs. 40, 42?.
1953. *Monograptus scanicus* Tullberg; O. M. B. Bulman, On the thecae of *M. scanicus*....., pp. 131—136, Figs. 1—2.
1955. *Monograptus scanicus* Tullberg; W. G. Kühne, Unterludlow-Graptolithen......., pp. 391—392, Fig. 14.
1958. *Lobograptus scanicus* (Tullberg); A. Urbanek, Monograptidae......., pp. 72—74 (partim), Pl. 2, Fig. 6, non Pl. 2, Fig. 5.
1960. *Lobograptus scanicus scanicus* (Tullberg); A. Urbanek, An attempt......, p. 177 (mentioned), Fig... 13, D.

Material. — Rather scanty fragments of rhabdosomes and isolated thecae were etched from the Mielnik core (at a depth of 988•9—982•6 m) but only one sicula associated with the true *scanicus* thecae has been found. All specimens are more or less flattened.

In the Baltic drift material, *L. scanicus* has been found so far only in boulders S. 128 — Władysławowo, S. 145 — Jarosławiec and S. 122 — Lubin. The best material was obtained from S. 128 (numerous fragments of rhabdosomes and thecae, almost unflattened, but lacking the siculae). Observations on minute details of structure are mostly based on specimens from Baltic erratic boulders.

Description. — Sicula[21] (Fig. 11) straight and rather short, measuring 1•07 mm in length, very similar in appearance to the sicula of *L. scanicus amphirostris* n.subsp. It keeps an almost uniform width throughout its metasicular part.

Prosicula measures about 0•55 mm in length. Like in other lobograptids, prosicula has a strongly wrinkled and damaged periderm. The presence of longitudinal threads whose exact number cannot be established (two or more?), is the only visible detail. In adult siculae, their prosicular part is provided with prosicular black ring (r_1, Fig. 11), which is situated approximately 0•13 mm above the aperture of prosicula. The width of prosicula at the aperture amounts to 0.15 mm.

Metasicula is 0•52 mm long and has an almost constant width, being some 0•15 mm wide at the level of the initial bud and some 0•16 mm in the apertural part. In examined specimen, it is only one sicular ring that is placed on metasicula some 0.06 mm from the boundary with prosicula (r_2, Fig. 11).

The structure of the primary notch region shows that the budding of the initial bud followed the normal monograptid pattern, i.e. through

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[21] The sicula attributed here to *L. scanicus scanicus* was found at a depth of 992.9—992.6 m, where it was associated with typical distal thecae. But it remains somewhat uncertain whether or not it belongs to the same species as the associated thecae.

the formation of open ("sinus" stage) and closed ("lacuna" stage) primary notch. The apertural border in the adult sicula is almost completely straight, with very slight, hardly visible dorsal prominence. There is no distinct thickening of the margin. Virgella is comparatively strong (*vi*, Fig. 11).

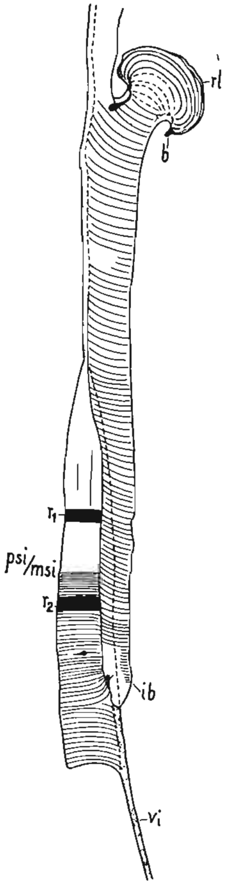

Fig. 11. — *Lobograptus scanicus scanicus* (Tullberg) sensu Bulman. Structure of sicula and the first theca (Mielnik, depth 992.9—992.6 m), ca. × 50.

b beaklike termination of the left lobe, *ib* initial bud, *psi/msi* boundary between pro- and metasicula, r_1-r_2 successive sicular rings, *rl* right apertural lobe, *vi* virgella

The first theca (Fig. 11) is a long (1,60 mm), slender tubule in which the prothecal part is 1·50 mm and the metathecal subapertural part — only 0·10 mm long. Protheca occupies, therefore, about 94% of subapertural part of the first theca. At the level of the apex of the prosicula the protheca reaches a width of 0.12 mm, being also 0.12 mm wide at the base of the metatheca. The entire protheca consists of obliquely disposed fuselli, the metatheca has, in its subapertural part, fuselli placed perpendicularly to its longitudinal axis. In the examined specimen, the entire metathecal part of the first theca is isolated which is in contrast with its adnate position in *L. scanicus parascanicus* and only a slightly isolated one in *L. scanicus amphirostris* n.subsp. The aperture of the theca is provided with lateral apertural lobes, displaying a distinct asymmetry. The larger right lobe [0·25 mm long (*tr.*) and 0·15 mm high (*long.*)] is almost semicircular in outline with ventral and dorsal shovellike terminations. Following the unsatisfactory state of preservation, the exact number of fuselli making up the right lobe cannot be estimated. Probably it consists of about 10 fuselli, some 7—8 being complete and gathered into nodes, the rest of them are shorter and form a ventral termination of the lobe. Unfortunately, the left lobe is strongly damaged (compressed) and its structure cannot be described. It is, however, provided with a distinct beaklike ventral prolongation.

Complete proximal thecae are rare in the material investigated. They form slender tubes with a total length of some 2·00—2·07 mm (as measured on specimens from sample S. 128) and 2·10—2·23 mm respectively (as measured on specimens from the Mielnik core). Their width amounts to 0·13—0·20 mm at the base of the protheca and to 0·16—0·20 mm at the base of the metatheca. The prothecal part is some 1·60—1·81 mm long, the metatheca being very short and measuring only some 0·30—0·40 mm. The prothecal part occupies therefore about 84—80% of their total length. The metatheca is inclined at an angle of some 30° to the long axis of rhabdosome. A certain degree of isolation of their subapertural parts (Pl. XXVII, Figs. A-B) is a remarkable feature of the proximal thecae. In this respect, there exists some difference between *L. scanicus parascanicus* and *L. scanicus amphirostris* n.subsp. whose metathecal parts are, in proximal thecae, almost adnate or only very slightly isolated. A certain degree of isolation of apertural parts in proximal thecae seems, therefore, to be a phylogenetically newly acquired character of *L. scanicus scanicus*.

The apertural margins terminate in proximal thecae with two lateral apertural lobes, the right one being distinctly larger, strongly elongated (*tr.*), angular-elliptical in outline, as well as some 0·30—0·43 mm long (*tr.*) and 0·18—0·20 mm high (*long.*). The long axis of the lobe is inclined at an angle of about 20° to the long axis of the theca. It is some 0·01—0·09 mm longer and 0·05—0·08 mm higher than the left lobe. The right lobe consists, in proximal thecae, of 10—12 fuselli, some 7—8 of them being complete, bent and gathered ventrally and dorsally into corresponding nodes. The rest of them are shorter, the latest 3—4 being limited to a shovellike, ventral termination and a rooflike dorsal pro-

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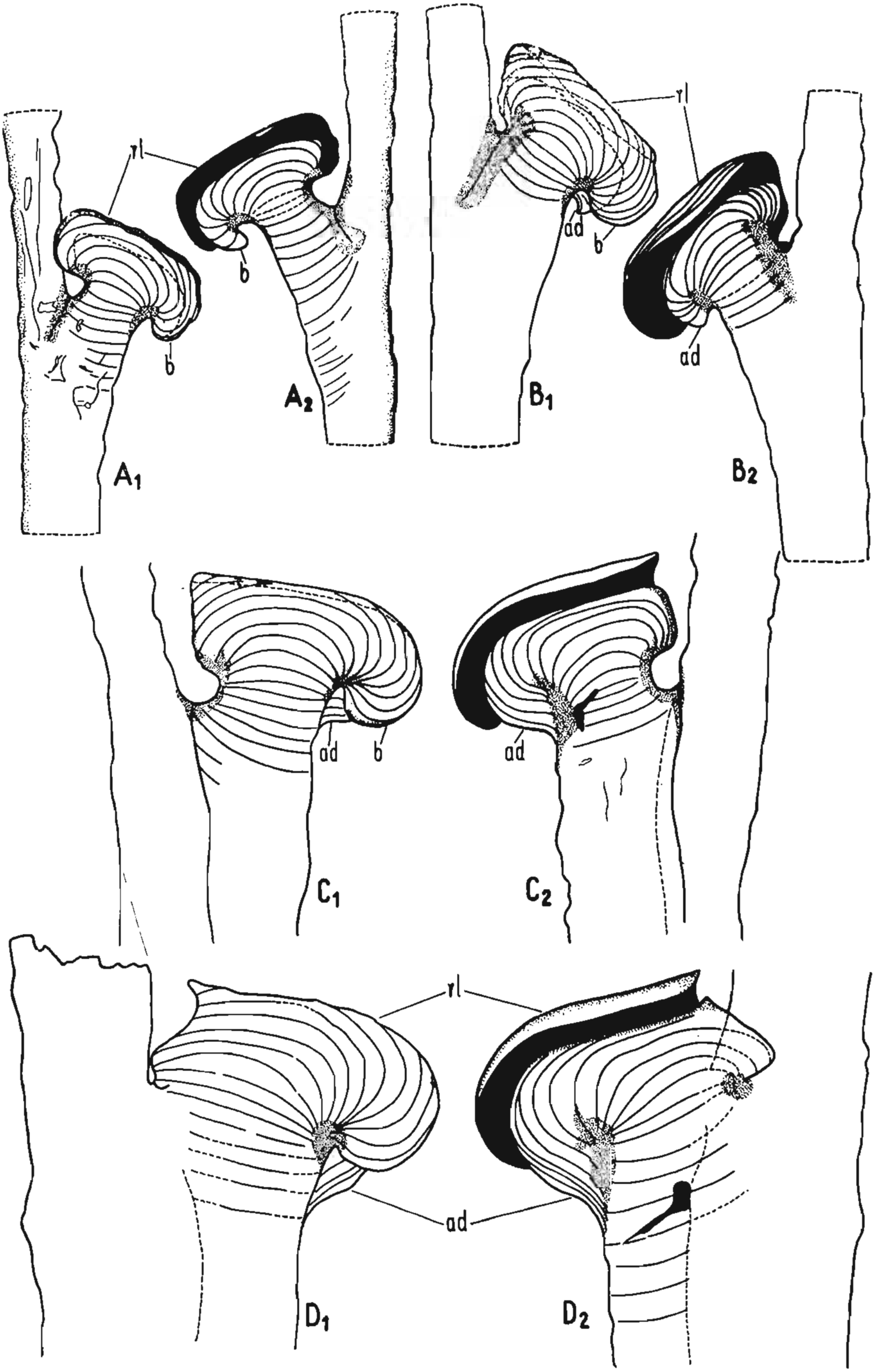
Plate XXVII

Lobograptus scanicus scanicus (Tullberg) sensu Bulman. Structure of thecae. A_1-A_2, B_1-B_2 upper parts of proximal thecae in reverse and obverse view; C_1-C_2 upper part of a more distal theca in reverse and obverse view; D_1-D_2 apertural part of a distal theca in reverse and obverse view (S. 128, Władysławowo); ca. × 63. *ad* adapertural plate, *b* beaklike termination of the apertural lobes, *rl* right apertural lobe.

PLATE XXVII



longation of the lobe (*b*, Pl. XXVII, Figs. A, B). The free, upper margin of the lobe is strongly incurved over the aperture, overlapping the smaller left lobe. In the top view, the left lobe is partly hidden beyond the overlapping upper margin of the right lobe, especially so in its more dorsal part. The degree of overlap seems to be greater than in any other subspecies of *L. scanicus*.

The left lobe is much smaller and contained inside the outline of the right lobe, the incurved beaklike ventral process excepted (Pl. XXVII, Figs. A_2, B_2). It consists of some 10 fuselli, 5—6 being complete and gathered into dorsal and ventral node. The rest of them are shorter and make up a dorsal and ventral termination of the left lobe. In the most proximal thecae, this ventral termination has the shape of a free beaklike process which is distinctly curved in and slightly protrudes beyond the limits of the right lobe (Fig. A_2). More distally situated proximal thecae show a tendency to the fusion of the process mentioned above with the ventral wall of metatheca (Fig. B_2). The ventral termination of the left lobe, attached by its inner margin to the thecal wall, is transformed into a structure for which the term "adapertural plate" was introduced to the present work. The presence, on the left lobe, of an adapertural plate, instead of a free beaklike termination, is a remarkable feature of thecae, the most proximal one excepted, in *L. scanicus scanicus*.

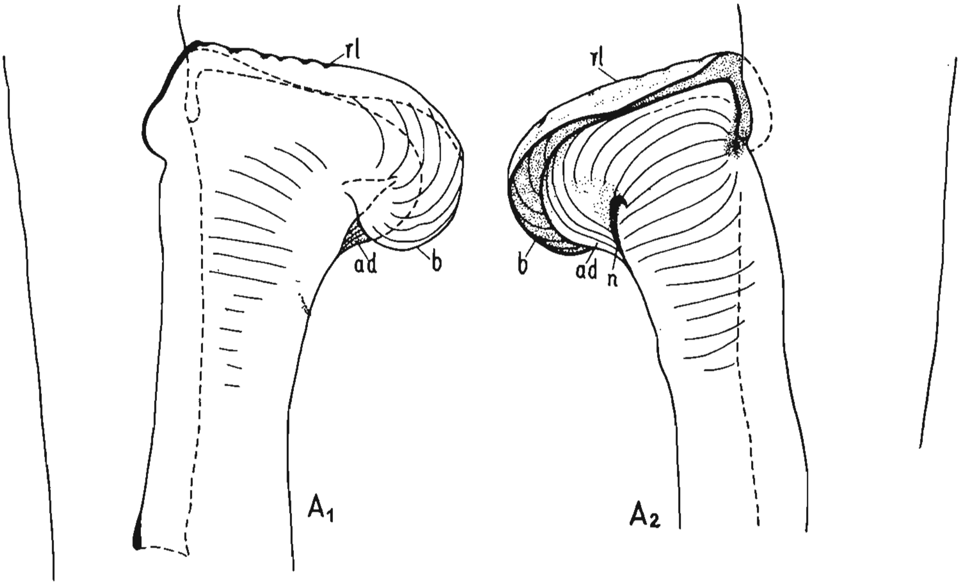


Fig. 12. — *Lobograptus scanicus scanicus* (Tullberg) sensu Bulman. Structure of the apertural part in a distal theca, in reverse (A_1) and obverse (A_2) aspects (Mielnik, depth 986.7—986.85 m), ca. × 63.
ad adapertural plate, *b* beaklike termination of the right apertural lobe, *n* ventral node, *rl* right apertural lobe.

The outer surface of the right lobe in proximal thecae is convex, being in the left one flat or in the middle part even slightly concave.

The more distal thecae are shown in Fig. 12 and Pl. XXVII, Figs. C, D. Their total length ranges between 2·02—2·60 mm. The prothecal part occupies some 1·22—1·83 mm and the metathecal one some 0·45—0·90 mm, the prothecal part occupies therefore 79—70% of their total length. The width at the base of the protheca is 0·30—0·36 mm and 0·24—0·25 mm at the base of metatheca. The ventral wall of theca is almost straight and at the level of the beginning of interthecal septum (comp. *L. scanicus parascanicus*) without any distinct geniculation. The metathecal part reaches some 0·22—0·27 mm in width at the aperture. In less distal but more medial (central) thecae, the subapertural part of metatheca is somewhat isolated Pl. XXVII, Fig. C). In more distal thecae, their metathecal part is adnate up to the base of the prothecal part of an adjacent theca (Fig. 12; Pl. XXVII, Fig. D).

The aperture is provided with lateral apertural lobes. The right one is larger, angularly elliptical and transversally elongated to the axis of the theca. It terminates ventrally in a free shovellike process, displaying the presence of an angularly bent and obliquely placed dorsal margin. In less distal thecae, this dorsal line is almost parallel to the long axis of the theca (Pl. XXVII, Fig. C), in more distal ones it is oblique to it (Fig. 12; Pl. XXVII, Fig. D). The free upper margin of the lobe is incurved over the aperture, strongly overlapping the left lobe which, in the top view, is almost entirely roofed, except for the most ventral part. The right lobe consists of some 12—13 fuselli, all of them gathered into a ventral node, in most specimens freely terminating in the dorsal border (Pl. XXVII, Figs. C_1, D_1). Some 4—5 last fuselli are short and constitute only a beaklike outgrowth on the lobe. In this case, the arrangement of fuselli is, therefore, different than that in more proximal thecae and resembling that in the most distal thecae of *L. scanicus amphirostris* n.subsp. (Figs. 10, A_1).

The left lobe is much smaller, being on the average 0·06 mm shorter (*tr.*) and some 0·05 mm narrower (*long.*) than the right one. It terminates angularly at the dorsal border, being provided at the ventral end with an adapertural plate. The latter is produced by the fusion of a number of fuselli (6—7) with the ventral wall of theca.

The lower part of the adapertural plate characteristically protrudes beyond the limits of the right lobe (Pl. XXVII, Figs. C_1, D_1). The fuselli that make up this plate terminate freely at the upper margin of the left lobe (Figs. C_2, D_2, *ad*). The rest of them (about 6) terminate, in part, freely at the dorsal margin in more distal thecae (comp. Fig. D_2), or are gathered into a dorsal node in less distal (central) thecae (comp. Fig. C_2). The arrangement of fuselli in the right and left lobe differs, therefore, considerably.

When describing the structure of distal thecae in *L. scanicus scanicus*, Bulman (1953) mentions that the left lobe "sometimes shows a tendency.... to fuse on the ventral side with the wall of theca" (p. 134). In the present writer's material, all distal thecae from the drift material, as well as from the boring are invariably provided with the adapertural plate mentioned above which has been formed by the fusion of the ventral termination of the left lobe with the thecal wall. Judging from Kühne's drawings (1955, Figs. 14, A-C, E), probably the same is in force for the population from boulders found in North German Plain.

The outer surface of the right lobe is, in the distal thecae, slightly convex, in the left one being flat or even slightly concave and with the dorsal border characteristically turned outwards to form a small elevation. The aperture, being roofed by the incurved margins of the right and, to a certain extent, also left lobe, is widely open ventrally, and dorsally through corresponding apertural notches.

Stratigraphic range. — In the Mielnik boring, *L. scanicus scanicus* occupies a rather narrow band about 6·30 m thick, between depths of 988·9 m and 982·6 m[22]. In its first appearance, in a sample from a depth of 988·9—988·6 m the remains of the subspecies in question are very scanty (sicula with first theca, fragment of distal thecae). It is rather uncommon throughout the entire range of its distribution and never occurs so abundantly as *L. scanicus parascanicus*. The most numerous specimens were found in a sample from a depth of 986.9—986.6 m.

In the Mielnik boring, *L. scanicus scanicus* is associated with: *L. imitator* n.sp., *L. scanicus parascanicus* (Kühne) (scanty and rather uncertain fragments), *L. exspectatus exspectatus* Urbanek, *Cucullograptus pazdroi* Urbanek, *Neodiversograptus beklemishevi* Urbanek, *Saetograptus chimaera cervicornis* Urbanek, *Pristiograptus dubius* (Suess), "*Pristiograptus*" *bohemicus* (Barrande), *Holoretiolites erraticus* Eisenack, *H. mancki* (Münch) and *Plectograptus macilentus* (Törnquist).

L. scanicus scanicus, being rather rare, has been met with the following erratic boulders: S. 128 — Władysławowo (predominating), S. 222 — Lubin and S. 145 — Jarosławiec. It occurs in these boulders together with the following association: *Cucullograptus pazdroi* Urbanek, *Saetograptus chimaera cervicornis* Urbanek, *Pristiograptus dubius* (Suess), *Holoretiolites mancki* (Münch) (very frequent) and *Holoretiolites* sp.

According to Kühne (1955), *L. scanicus scanicus* is frequent in the Berlin erratic boulders, even abundantly occurring in some of them.

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[22] Few uncertain fragments which may still belong to *L. scanicus scanicus* have been found in the sample from a depth of 981·75—981·9 m.

However, it seems safe to generalize that, as compared with other members of the *scanicus* group, the true *scanicus* is less frequent.

Systematic position. — When comparing *L. scanicus parascanicus* (Kühne) and *L. scanicus scanicus* (Tullberg) sensu Bulman, Kühne (1955) mentions: "Ich glaube anfangs, dass beide Arten durch morphologische Übergänge miteinander verbunden und tatsächlich zu einer Art gehörten. Der Vergleich adulter Theken erbrachte aber deutliche morphologische Verschiedenheiten und keine intermediären Formen" (p. 395). After the discovery of *L. scanicus amphirostris* n.subsp., the morphological gap between two forms, mentioned by Kühne, was, however, at least in part, filled. Recently the *scanicus* line seems to constitute an almost continuous chain of closely related varieties, ranked here as different subspecies of *L. scanicus* (Tullberg). Their subspecific rank is due to generally minor morphological differences, distinguishing particular members of this group and due to the fact that the extreme forms (*Lobograptus scanicus parascanicus*, *L. scanicus scanicus*) are connected by an intermediate one (*L. scanicus amphirostris* n.subsp.). *L. scanicus scanicus* as understood here seems to represent morphologically a most advanced representative of the *scanicus* line of evolution. Most propably it constitutes a further development of *L. scanicus amphirostris* n.subsp. as a result of a progressive enlargement of apertural lobes, transformation of the free beaklike termination of the left lobe in more distal theca into an apertural plate and elaboration of some degree of isolation in proximal thecae.

The structure of the sicula which is very similar to that in other members of the *scanicus* line and the presence of a free beaklike termination of the left lobe in the most proximal thecae approaching that in the thecae of *L. scanicus amphirostris* n. subsp., are the most indicative features for the ancestry of *L. scanicus scanicus*. The latter feature may indicate that the most characteristic traits in the thecal structure of the true *scanicus*, were involved through the distal introduction of a phylogenetically new character (comp. Urbanek, 1960). This complex of characters, introduced distally, comprise an enlargement of lobes and changes in their shape. The elaboration of a certain degree of isolation in proximal thecae with its gradual decrease towards the distal part of the rhabdosome seems to indicate, however, another trend, operating in this evolutionary line and displaying a proximal introduction of this new character in the course of phylogenetic changes of astogeny (comp. p. 347).

When compared with other members of the group, a rather small stratigraphic range of *L. scanicus scanicus* and its relative rarity, may indicate that it was adaptively a specialized form. This may also supply the explanation for its earlier extinction as compared with *L. scanicus* *amphirostris* n.subsp. and indicated by the succession, met with in the Mielnik boring. The latter subspecies precedes *L. scanicus scanicus* in its first appearance by some 28 m, continuing upwards from its last appearance for some 23,0 m. *L. scanicus scanicus*, although morphologically more advanced, seems to represent — in comparison with more primitive members of the group — a rather short-lived taxon.

Lobograptus imitator n.sp.

(Pl. XXVIII)

Type specimen (holotype): Pl. XXVIII, Fig. D (sicula damaged after drawing).

Paratype: Pl. XXVIII, Fig. H (medial theca).

Type stratum: Greenish-blue mudstones and marls in the core of the Mielnik deep-boring between 986.9—963.6 m of depth (upper part of *parascanicus* zone and *invertus* zone, upper part of Mielnik Beds).

Derivation of the name: Lat: *imitator* — as imitative of *L. scanicus parascanicus* in degree of development of the apertural lobes but representing a different trend in specialization.

Diagnosis. — *Lobograptus* with a gracile and rather short sicula (length, 1.08—1.18 mm) but provided with a distinct dorsal apertural process. Thecae provided with asymmetric apertural apparatus, the right lobe being distinctly larger. Degree of asymmetry of apertural lobes similar to that in *L. scanicus parascanicus*, the lobes being less transversely elongated and more rounded (ovate) in outline.

Remarks. — The concept of *L. imitator* n.sp. is, to some extent, uncertain. Morphologically, this concept is based above all on characters of siculae, preserved with the first thecae attached to them. These siculae are slender and short, like those in the *scanicus* group but invariably provided with a strong dorsal process. The first thecae are, in their general appearance, similar to those in *L. scanicus parascanicus* and showing a comparable degree of asymmetry of apertural lobes but, on the other hand, displaying certain small differences (longer free part of thecae which stretches beyond the sicula, apertural lobes without transversely elliptical outline but semicircular). Some proximal and more distal thecae associated with the siculae and first thecae, mentioned above, show similar morphological features and may, in the present writer's opinion, be attributed to the same species. They are more slender than thecae in *scanicus* group, but provided with apertural lobes showing a degree of asymmetry similar to that in *L. scanicus parascanicus*. In spite of the fact that the evidence for common assignment of siculae and associated thecae is not completely satisfactory, these thecae are described here as the thecae of *L. imitator* n.sp.

Material. — Numerous siculae with the first theca attached, proximal thecae or fragments of the proximal part of rhabdosome, etched from the Mielnik core at a depth of 986.9—963.6 m. True distal thecae unknown. Specimens strongly flattened but bleachable. From Baltic drift material unknown.

Description. — Sicula (Pl. XXVIII, Figs. A-D) of the gracile type, slender but provided, in the adult growth stage, with a distinct dorsal apertural process. The total length of sicula amounts to 1.08—1.18 mm.

Prosicula ranges from 0.48 mm to 0.51 mm in length (in 3 measured specimens). The periderm of prosicula, like those in other lobograptids described here, is partly damaged and wrinkled, so that the presence of a number (up to 5) of longitudinal threads, which converge at the apex of prosicula into a nema, is the only detectable structural detail. Prosicular parts of adult siculae are provided with a prosicular black ring (r_1), situated at a certain distance from the aperture of the prosicula (0.05—0.11 mm). In no observed case, this first black ring is situated just on the boundary with the metasicula[23]. At its aperture, the prosicula reaches a width of some 0.12—0.15 mm.

The metasicula measures some 0.60—0.67 mm in length, being almost uniformly wide, except for the apertural part proper which, due to the presence of a dorsal apertural process, is distinctly expanded. The metasicula reaches a width of some 0.16—0.17 mm at the level of the primary notch and some 0.18—0.20 mm at the aperture. Usually, it is provided with 1—2 metasicular black rings (r_2-r_3), the last (r_3) one being often incomplete (Pl. XXVIII, Figs. B, D).

The formation of the initial bud took place in the normal course of events, following the open primary notch stage (sinus stage) and the closed primary notch stage (lacuna stage), as shown by the structure of the initial bud region (Pl. XXVIII, Figs. A-D, *ib*). The aperture of an adult metasicula displays, besides the virgella, the presence of a distinct dorsal process which reaches a length of some 0.07—0.11 mm. In young siculae (Fig. A), this process is somewhat smaller than in the completely grown up siculae (Fig. B-D). The dorsal process is rounded, roughly obtriangular in outline and displays the presence of a slightly thickened margin formed by a number of very narrow fuselli (microfuselli) as shown in Figs. B, D. Lateral borders of the aperture are situated some 0.19—0.29 mm. from the anterior margin of the initial bud.

In its general appearance the sicula of *L. imitator* n.sp. combines the features of those of *L. simplex* and of the *scanicus* group of lobograptids. It is gracile (short and narrow) like the siculae of the latter

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[23] Except for a specimen, found in a sample at a depth of 982.4 m with a very indistinct black ring, situated just on the boundary of the prosicula and metasicula and provided moreover with incipient traces of another ring on metasicula. This somewhat aberrant sicula is associated with siculae "normally ringed".

group but provided with a distinct dorsal apertural process as in the former species. Moreover, it shows a remarkable resemblance to siculae of *L. invertus* n.sp. and *L. cirrifer* n.sp. (comp. p. 316).

The first theca is a rather long and narrow tubule whose aperture is disposed about 1.00 mm above the apex of the prosicula. The total length of the first theca ranges between 1.87 and 1.97 mm, its width is contained between about 0.10—0.13 mm at the apex of the prosicula and some 0.14 mm at the aperture. The metathecal part, some 0.10—0.14 mm in length, is inclined at an angle of 30° towards the longitudinal axis of the protheca. The length of the prothecal part amounts to 1.77—1.83 mm, the protheca occupying therefore about 93—95% of length of this theca.

The aperture of metatheca terminates in two lateral apertural lobes, the right being larger than the left (Pl. XXVIII, Figs. E_1-E_2). The right lobe, some 0.09—0.13 mm high, and 0.20 mm long, is rounded, almost semicircular in outline. The exact number of fuselli making up this lobe cannot be exactly stated, but probably it amounts to 7. They are gathered into two nodes without any distinct ventral process like those in the representatives of the *scanicus* group. The left lobe is 0.05—0.09 mm high (*long.*) and 0.19—0.20 mm long (*tr.*) showing a flat or concave external surface. The number of its fuselli may be estimated at 6—7. They are gathered into ventral and dorsal nodes. There is no trace of any elongated process on the ventral margin of the lobes. Both lobes are separated ventrally by a rather deep apertural notch.

Proximal thecae (Pl. XXVIII, Figs. F-H) are rather infrequent in the material described. They form very slender, rather long and narrow tubules with apertures, provided with small lateral apertural lobes. Their total length ranges from 1.78 mm to 1.85 mm in 2 measured specimens, whose prothecal part is 1.47—1.55 mm and the metathecal one some 0.31—0.30 mm long. The prothecal part occupies therefore about 82—84% of thecal length. The width of the proximal theca is, at the base of the protheca, about 0.13—0.16 mm, being the same to the metathecal part inclusively. Metathecal parts are inclined towards

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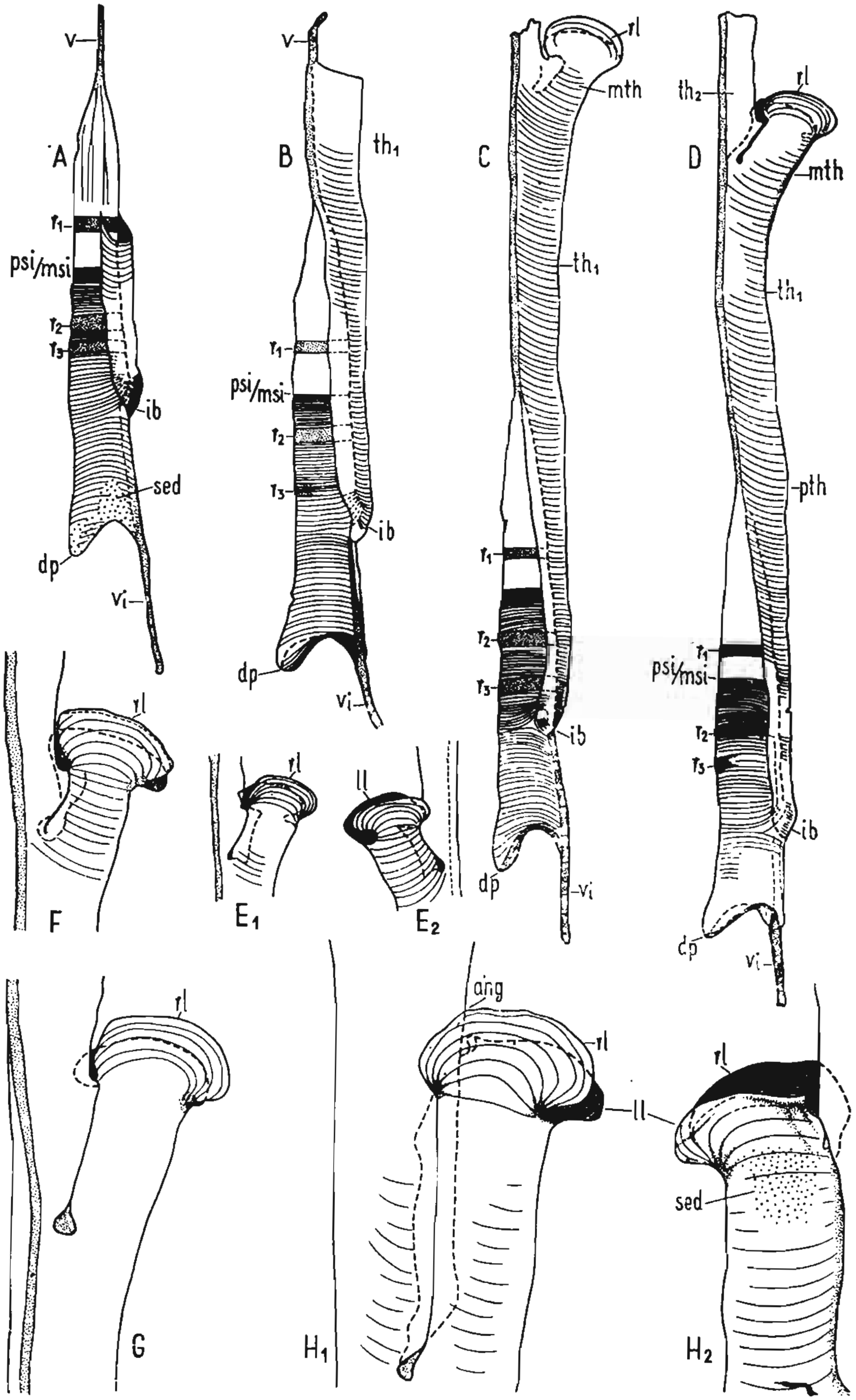
Plate XXVIII

Lobograptus imitator n.sp. Structure of sicula and thecae. *A* sicula with initial bud in advanced growth stage (reverse aspect); *B* sicula and first theca in more advanced growth stage; *C-D* siculae with complete first theca; E_1-E_2 details of structure of metatheca in specimen figured *D*, seen from reverse and obverse sides; *F-G* upper parts of proximal thecae in reverse view; H_1-H_2 upper part of a medial (central) theca in reverse and obverse aspects (Mielnik, *A-C*, *F-H* depth 974.9—974.5 m; *D-E* depth 980.9—980.75 m); *A-E* ca. × 50, *F-H* ca. × 63.

ang angular bending of upper margin in the right lobe, *dp* dorsal process of metasicula, *ib* initial bud, *ll* left apertural lobe, *mth* metatheca, *psi/msi* boundary between pro- and metasicula, *pth* protheca, r_1-r_3 successive sicular rings, *rl* right apertural lobe, *sed* grains of sediment attached to periderm, *v* virgula, *vi* virgella.

PLATE XXVIII



the axis of the protheca at an angle of 20—30°. The entire subapertural part of the metatheca is adnate to the adjacent protheca.

The metathecal aperture is provided with two lateral apertural lobes, the right lobe being distinctly larger. It is slightly ovate, almost semicircular in outline, with the dorsal line nearly straight, and the ventral termination rounded. The number of fuselli may be estimated at some 6—8. They are gathered ventrally into a corresponding node, ending partly free at the dorsal border (Pl. XXVIII, Figs. F-H). The ventral termination of the lobe is not well-developed but forms a short, broadly rounded process. The height (*long.*) of the right apertural lobe comes to 0.13—0.19 mm, its length (*tr.*) being 0.14—0.26 mm.

The left apertural lobe is distinctly smaller, and measuring respectively 0.07—0.10 mm in height (*long.*) and 0.12—0.22 mm in length (*tr.*). It has an outline very similar to that of the right lobe. Owing to a rather poor state of preservation of the majority of specimens, the number of fuselli may be only roughly estimated at, probably, some 6—7. The ventral termination of the left lobe is somewhat more elaborated than that in the right, protruding somewhat outside the opposite lobe but it never forms a distincly incurved beaklike process (Pl. XXVIII, Figs. F, H_2).

All specimens are strongly flattened and the degree of their primary overlap cannot be accurately established. In many specimens the right lobe has, however, a slightly incurved upper margin, the left being flat or even concave and slightly bent over the aperture. This suggests the presence of a certain degree of overlap probably comparable with that in the proximal thecae of *L. scanicus parascanicus.*

Perhaps, there is no true distal theca present in the material. The most distal theca which was found is, however, figured in Pl. XXVIII, Figs. H_1-H_2. The more distally placed thecae are straight tubes without a distinct geniculation at the base of the metatheca. The total length of distal thecae is 1.90—2.11 mm in 4 measured specimens, the prothecal part being 1.66—1.72 mm long, the metathecal respectively 0.45—0.58 mm. The prothecal part in distal thecae occupies therefore about 74—79% of their length. The width of the protheca amounts, at the base, to 0.16—0.26 mm, the width of the metatheca being some 0.17—0.26 mm. The aperture is provided with lateral apertural lobes, the right one being larger than the left. These lobes, showing a degree of asymmetry, comparable with that in *L. scanicus parascanicus*, are distinctly smaller than those in the latter species.

The right lobe is very characteristic in outline, broadly ovate, with dorsal line almost straight and ventrally rounded. It consists of some 7 fuselli, gathered into ventral and dorsal nodes. The lobe reaches some 0.20 mm in height (*long.*) and about 0.30—0.35 mm in length (*tr.*).

The left lobe has an outline generally similar to that in the right lobe, being, however, angularly cut at the dorsal margin (Pl. XXVIII, Fig. H_2). The number of fuselli, making up the lobe, may be estimated at about 7. The ventral termination of the lobe forms a beaklike process, protruding beyond the right lobe. This process consists of 2—3 short fuselli which end freely on upper margin of the lobe. The dorsal border of this lobe is, in its upper part, characteristically undulated, forming a kind of an incision (Fig. H_2). The left lobe is 0.17—0.15 mm in height (*long.*) and some 0.30—0.34 mm in length (*tr.*). On preserved but strongly flattened specimens, the degree of primary overlap of the apertural lobes cannot be reliably established. It seems, however, that the degree of overlap of lobes was probably somewhat smaller than in the distal thecae of *L. scanicus parascanicus.*

Stratigraphic range. — *L. imitator* n.sp. is known only from the Mielnik bore-hole where it makes its first appearance at a depth of 986.9—986.5 m. In samples from that depth, the remains of *L. imitator* n.sp. are very scanty and consist of few fragments of siculae and single thecae.

More abundant populations, including numerous siculae and thecae, have been found in samples from depths of 982.4—980.9 m and 967.9—967.5 m. These zones of a more common occurrence of the species in question are separated by a rather thick series of strata, showing only an occasional presence of *L. imitator* n.sp. (982.4—967.9 m).

The last appearance has been noted in a sample from a depth of 963.9—963.6 m. The total thickness of strata, occupied by the vertical distribution of *L. imitator* n.sp., may be estimated at about 23.3 m.

The species in question is never very common, being — throughout the range of its distribution — always overshadowed by the remaining graptolite assemblage. The latter consists mainly of the following species: *Pristiograptus dubius* (Suess), "*Pristiograptus*" *bohemicus* (Barrande), *Saetograptus chimaera cervicornis* Urbanek, *Cucullograptus pazdroi* Urbanek, *Lobograptus exspectatus exspectatus* Urbanek, *L. scanicus amphirostris* n.subsp. (mainly in the upper part of the zone of occurrence), *Neodiversograptus beklemishevi* Urbanek, *Holoretiolites erraticus* (Eisenack), *H. simplex* (Eisenack), *H. mancki* (Münch), *Plectograptus macilentus* (Törnquist). Since the distribution range overlaps that in *L. scanicus parascanicus*, *L. imitator* n.sp. may be also associated with the former. However, in the Mielnik bore-hole, they were never found together in one sample.

Systematic position. — The ancestry of *L. imitator* n.sp. is somewhat uncertain. In the presence of a gracile sicula, it is similar to specialized lobograptids of the *scanicus* line and, in the structure of thecae, it resembles to a great extent *L. scanicus parascanicus.* On the other hand, the sicula of *L. imitator* n.sp. is, however, provided with a distinct dorsal apertural process, similar to that in primitive "stem" lobograptids such, as *L. progenitor* n.sp. and *L. simplex*. This rather unusual combination of some primitive and progressive features in structure of sicula is also common to two other lobograptids, described beneath as *L. invertus* n.sp. and *L. cirrifer* n.sp. They appear later and may be considered probable descendants of *L. imitator* n.sp. *Lobograptus imitator* n.sp. is, therefore, understood here as a forerunner of the *invertus-cirrifer* lines of evolution. It is rather unspecialized in structure of apertural apparatus, representing their stage of development comparable with that in *L. scanicus parascanicus* in the *scanicus* line, but simultaneously foreshadowing in structure of sicula an independent trend (the *invertus-cirrifer* evolution trend). For morphological and stratigraphic reasons (comp. p. 371), the derivation of *L. invertus* n.sp. and *L. cirrifer* n.sp. from *L. imitator* n.sp. presents no difficulty. These close relationships show that *L. imitator* n.sp. cannot be included into the *scanicus* line but it represents a primitive stage in the evolution of a separate lineage. This stage paralleled, as far as the thecal characters are concerned, the *parascanicus* stage in the phylogeny of the *scanicus* group (comp. also p. 334).

The theoretical alternatives of the derivation of *L. imitator* n.sp. from other lobograptids are discussed in the chapter on phylogeny (p. 368).

Lobograptus invertus n.sp.

(Pls. XXIX—XXXI)

Type specimen (holotype): Pl. XXX, Fig. D (distal theca).

Partypes: Pl. XXIX, Fig. F (sicula with 1st theca): Pl. XXX, Fig. B (proximal theca).

Type stratum: Greenish-blue mudstones and marls in the core of the Mielnik deep-boring between 966.85—964.9 m of depth (*invertus* zone, upper part of Mielnik Beds).

Derivation of the name: Lat. *invertus* — inverted, as representing inversion in the position of the adapertural plate, formed on the right lobe and not on the left as in *L. scanicus scanicus*.

Diagnosis. — Lobograptid with gracile sicula (1.08—1.44 mm long) but provided with a distinct dorsal process. Asymmetric apertural apparatus of thecae consists of a larger right lobe, forming the dorsal and ventral adapertural plate by the fusion with thecal walls and a smaller left lobe, having a strongly incurved or twisted ventral termination. Metatheca in proximal part of rhabdosome completely, in distal partly isolated.

Material. — Numerous young and adult siculae with the first theca attached, proximal and distal thecae etched from the Mielnik core samples, mainly from depth of 966.85—965.9 m. Specimens are flattened or partly flattened, but easily bleachable and allow one to examine the development and fusellar structure. From Baltic drift material unrecorded.

Description. — Sicula (Pl. XXIX, Figs. D-F) straight, slender and rather short, provided with a distinct dorsal apertural process. Its total length ranges in 5 measured specimens between 1.08 and 1.14 mm.

Prosicula (Pl. XXIX, Figs. A-B) varies in 5 measured specimens, from 0.48 mm to 0.50 mm in length. In young developmental stages, prosicula is provided only with numerous (up to some 5—6) longitudinal threads (ribs) which are, however, devoid of a black ring (Fig. A). In more advanced growth stages of the sicula, its prosicular part is invariably provided with a prosicular black ring (r_1), situated 0.09—0.13 mm from the prosicular aperture. In no observed case this first sicular black ring is placed just on the boundary of both parts of sicula. The width of prosicula at the aperture measures approx. 0.12—0.14 mm.

Metasicula is 0.58—0.65 mm long in 4 measured adult siculae and has an almost completely uniform width throughout, except for the most adapertural part, where it is somewhat more expanded. It reaches a width of some 0.13—0.15 mm at the level of the initial bud and 0.18—0.22 mm in the apertural part. The youngest growth stage of metasicula with incipient virgella is shown in Pl. XXIX, Fig. A. Adult metasicula is provided with 1—2 black rings which probably appear gradually from the most apical (r_2) to the most apertural one (r_3), as suggested by a specimen, figured in, Fig. B, whose metasicular black ring (r_2) is still only slightly marked, which is in contrast with a heavy black prosicular ring (r_1). This seems to indicate that the formation of the second black ring (r_2) was started later than the formation of the first one (r_1), the former being, therefore, less advanced than the latter. In a specimen in Fig. C, showing a more advanced growth stage of the metasicula, r_2 is equally strongly marked as r_1. The series of specimens, figured as A, B, C, seem therefore to indicate an actual sequence of events.

The formation of virgella, as indicated by specimens in Pl. XXIX, Figs. A, C, seems to start rather early. The formation of the initial bud took place according to a normal monograptid pattern as indicated by the course of fuselli in the primary notch region. A specimen in Fig. B shows an advanced "lacuna" stage with a closed primary notch, and Fig. C — an advanced growth stage of the initial bud (*ib*). Further growth stages of the first theca and sicula are shown in Figs. D-F.

The aperture of the adult metasicula is provided with a distinct dorsal apertural process which comes to 0.05—0.09 mm in length (Pl. XXIX, Figs. D-F). This process is less distinctly marked in young (Fig. C) and entirely absent from still younger siculae (Fig. B). An adult shape of aperture is reached when the first growing theca reaches the level of the apex of prosicula (Fig. D), the aperture is also provided with a rather strong and long virgella. At the aperture, metasicula is slightly expanded transversely.

The first theca (Pl. XXIX, Figs. E-F) is tubular and slender with a total length ranging between 1.80—1.60 mm. The prothecal part occupies some 1.70—1.47 mm in length, the metathecal one 0.13—0.10 mm, the prothecal ratio being, therefore, 94—92%. Width of these thecae is about 0.10 mm at the apex of prosicula and 0.14—0.12 mm at the aperture of metatheca. The initial bud starts at a distance of 0.25—0.17 mm from the lateral margins of the aperture of metasicula. Owing to the rather poor state of preservation of specimens, the fusellar structure of periderm in the basal part of the first theca cannot be satisfactorily recognized. The metathecal part of the first theca is almost completely isolated, being inclined at an angle of 40° towards the longitudinal axis of the prothecal part. It terminates in two asymmetric lateral apertural lobes the right being distinctly larger than the left one (Figs. E-F_1-F_2). The right lobe has an almost circular outline and consists of 7—9 fuselli, some 5 of them being gathered into nodes, the rest being also complete but attached to the ventral and dorsal wall of metatheca. The right lobe forms, therefore, a ventral prolongation which consists of overhanging fuselli, fused with the ventral wall of metatheca and a similar dorsal prolongation (Fig. F_1). The right lobe reaches a length (*tr.*) of some 0.23—0.21 mm, and a height (*long.*) of some 0.13—0.12 mm.

The left lobe is distinctly smaller and it does not exceed a length (*tr.*) 0.21—0.20 mm, being 0.10—0.08 mm high (*long.*). It differs in shape being more transversely elongated than the right lobe and is provided with a free ventral termination. The latter forms a strong shovellike process, characteristically twisted dorsally (Pl. XXIX, Figs. F_2, *tp*). Following the unsatisfactory state of preservation, the fusellar structure of the left lobe cannot be examined.

Proximal thecae form long, slender tubes, provided with a characteristically elaborated apertural apparatus. Their total length varies from 2.35 mm to 2.05 mm, the prothecal part measuring 2.14—1.84 mm

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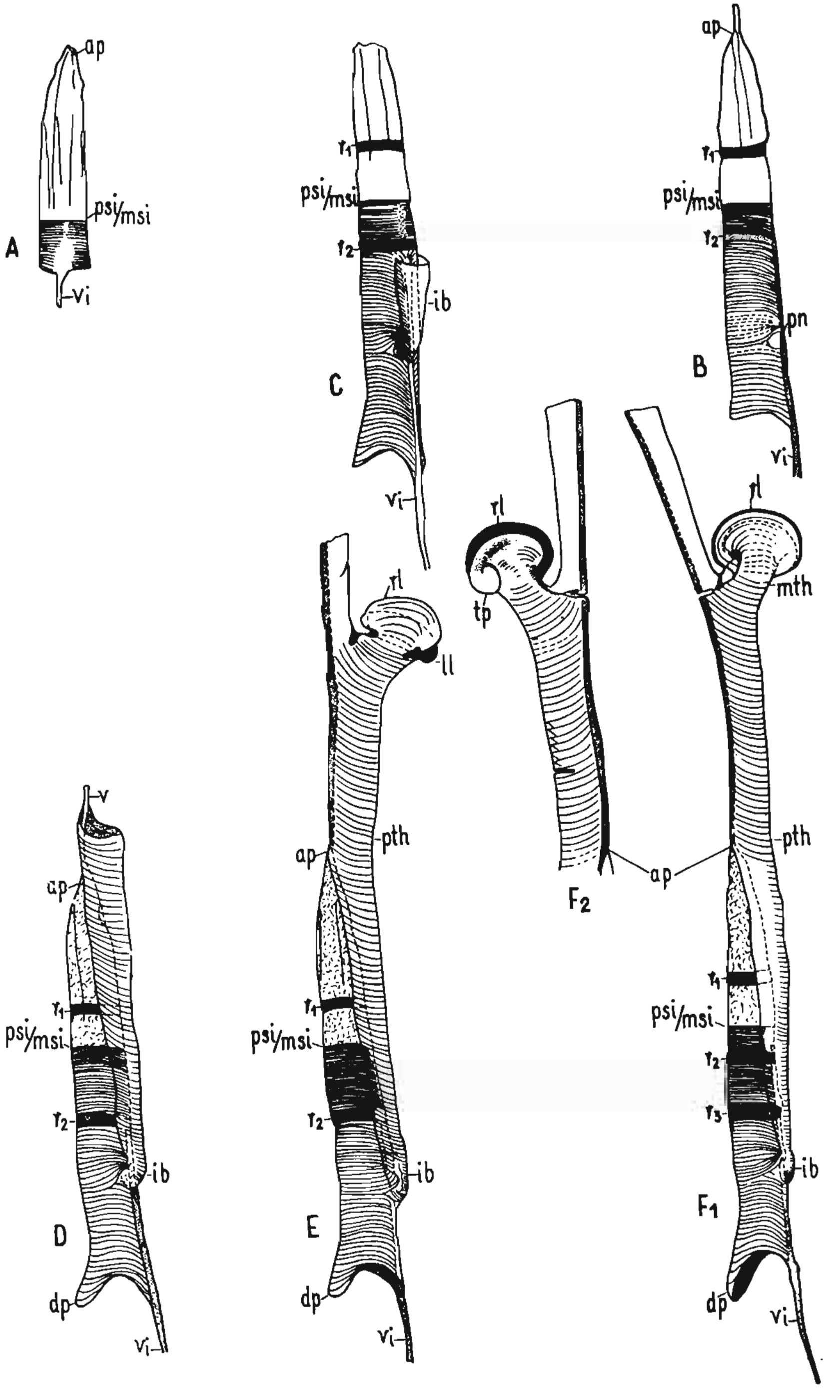
Plate XXIX

Lobograptus invertus n.sp. Development of sicula and the first theca. *A* young metasicula with prosicular segment preserved; *B* sicula with advanced growth stage of metasicula; *C* sicula with initial bud; *D* adult sicula with advanced growth stage of the first theca; *E* reverse aspect of an adult sicula with complete first theca showing rather short upper (free) part of theca; F_1 reverse aspect of another adult sicula with rather long upper (free) part; F_2 free part of the first theca of the same specimen in obverse aspect (Mielnik, *A*-*C*, *E* depth 965.9—965.45 m, D_1, *F*, 966.85—966.5 m); ca. × 50.

ap apex of prosicula, *dp* dorsal process of *msi*, *ib* initial bud, *ll* left lobe with metatheca, *mth* metatheca, *pn* primary notch, *psi*, *msi* boundary of prosicula and metasicula, *pth* protheca, r_1-r_3 successive black rings of sicula, *rl* right lobe, *tp* terminal process of the left lobe, *v* virgula, *vi* virgella.

PLATE XXIX


A
ap
psi/msi
vi
C
r1
psi/msi
r2
ib
vi
B
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r1
psi/msi
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rl
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E
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psi/msi
r2
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r3
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r1
psi/msi
r2
ib
dp
vi

and the metathecal one — 0.35—0.17 mm. The prothecal part occupies therefore about 91—93% of their length. The width of proximal thecae is, at their base, about 0.15—0.08 mm and, at the aperture of metatheca, 0.16—0.13 mm.

The metathecal part in most proximal thecae is isolated throughout, while in slightly more distally situated thecae, it is isolated over $^2/_3$ of its entire length. Metatheca is inclined at an angle of 20—30° towards the longitudinal axis of the theca.

The right lateral apertural lobe is larger than the left one and, in most proximal thecae, very closely resembles its structure, described above, for the first theca (Pl. XXX, Fig. A). It is almost circular in outline and the lobe forms two overhanging terminations, a ventral and a dorsal one. Each termination consists of some 3—4 fuselli, fused with the adjacent wall of theca and forms an adapertural plate. In proximal thecae, placed slightly more medially in the rhabdosome, the right lobe becomes still larger, having correspondingly larger ventral and dorsal adapertural plates (Fig. B, *ap*). All adapertural plates, almost identical in size, are formed by some 4—5 fuselli fused with the adjacent wall of metatheca. The rest of them (some 4—5) are gathered into two nodes, so that the number of fuselli making up the right lobe amounts, in proximal thecae, to 8—10. The right lobe in proximal thecae is about 0·39—0·23 mm long (*tr*). and about 0·25—0·14 mm high (*long*)..

The left apertural lobe in most proximal thecae (Pl. XXX, Fig. A_2) is similar to that described for the first theca. The lobe is provided with a ventral termination in the form of a beaklike process which is strongly incurved dorsalwards. In proximal thecae, situated more medially (Fig. B_2), the general outline of the lobe remains nearly the same, the ventral termination being, however, transformed into a broad, shovellike process, strongly incurved dorsally. Moreover, the margin of the ventral notch in the aperture of metatheca is provided with a distinctly extroverted apertural lip. The presence of this structure was established through the needle preparation after the removal of a part of the incurved ventral process (Pl. XXXI, Figs. B, C). The extroverted apertural lip sends, on its left side, an ascending ramus, running upwards along the apertural incision to the upper margin of the incurved ventral termination of the left lobe. This prolongation, becoming gradually narrower, forms

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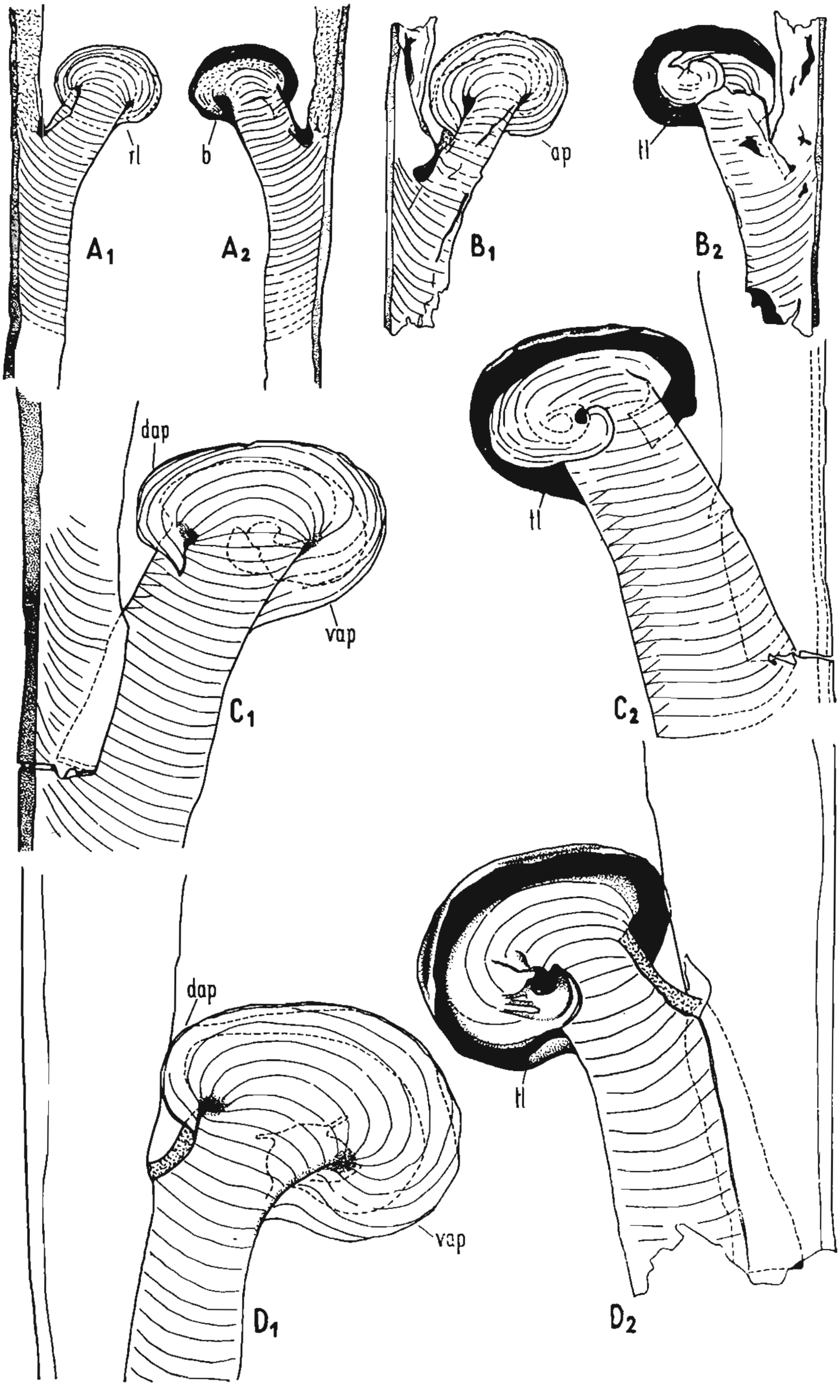
Plate XXX

Lobograptus invertus n.sp. Structure of thecae. A_1-A_2 most proximal theca in reverse and obverse aspect: B_1-B_2 proximal theca in reverse and obverse aspect; C_1-C_2 medial (central) theca in reverse and obverse aspect; D_1-D_2 distal theca in reverse and obverse aspect (Mielnik, *A*, *B*, *D* depth 966.85—966.5 m, *C* depth 965.90—965.45 m); ca. × 63.

ap adapertural plate, *b* beaklike process of the left lobe, *dap* dorsal adapertural plate, *rl* right lobe, *tl* incurved termination of the left lobe, *vap* ventral adapertural plate

PLATE XXX



a thickened rim on the upper margin of the free ventral termination of the lobe (Fig. C, *al*).

The terminal part of the ventral process on the left lobe is characteristically curved in and its lateral margin (*lm*) is also slightly thickened. This incurved part of the process mentioned above produces a laterally protruding semitubular outgrowth on the lobe. The isolated termination is shown in Pl. XXXI, Figs. D_1-D_3 in a ventral, dorsal, and ventrolateral view. Its relation to extroverted apertural lip (*al*) is shown by the trace of broken lines, indicating the apertural margin. Especially noteworthy is Fig. D_2 which shows that the outgrowth opens dorsally through a slitlike opening (*so*).

Probably as a result of their great fragility, specimens having complete distal thecae are not preserved in the material studied. Due to the combination of some specimens with preserved complementary parts of the theca, the estimation of its length was possible. It reaches about 2.60 mm with the metathecal part being 0.75 mm long. The prothecal part occupies about 70% of their complete length. The protheca is about 0·23 mm wide at the base and the metatheca reaches a width of about 0·25 mm at the aperture.

The metathecal part is inclined at an angle of 25—30° towards the long axis of protheca and is isolated only over about 1/2—1/3 of its length The isolated part of the metatheca forms a kind of a neck, provided a the free end with lateral apertural lobes.

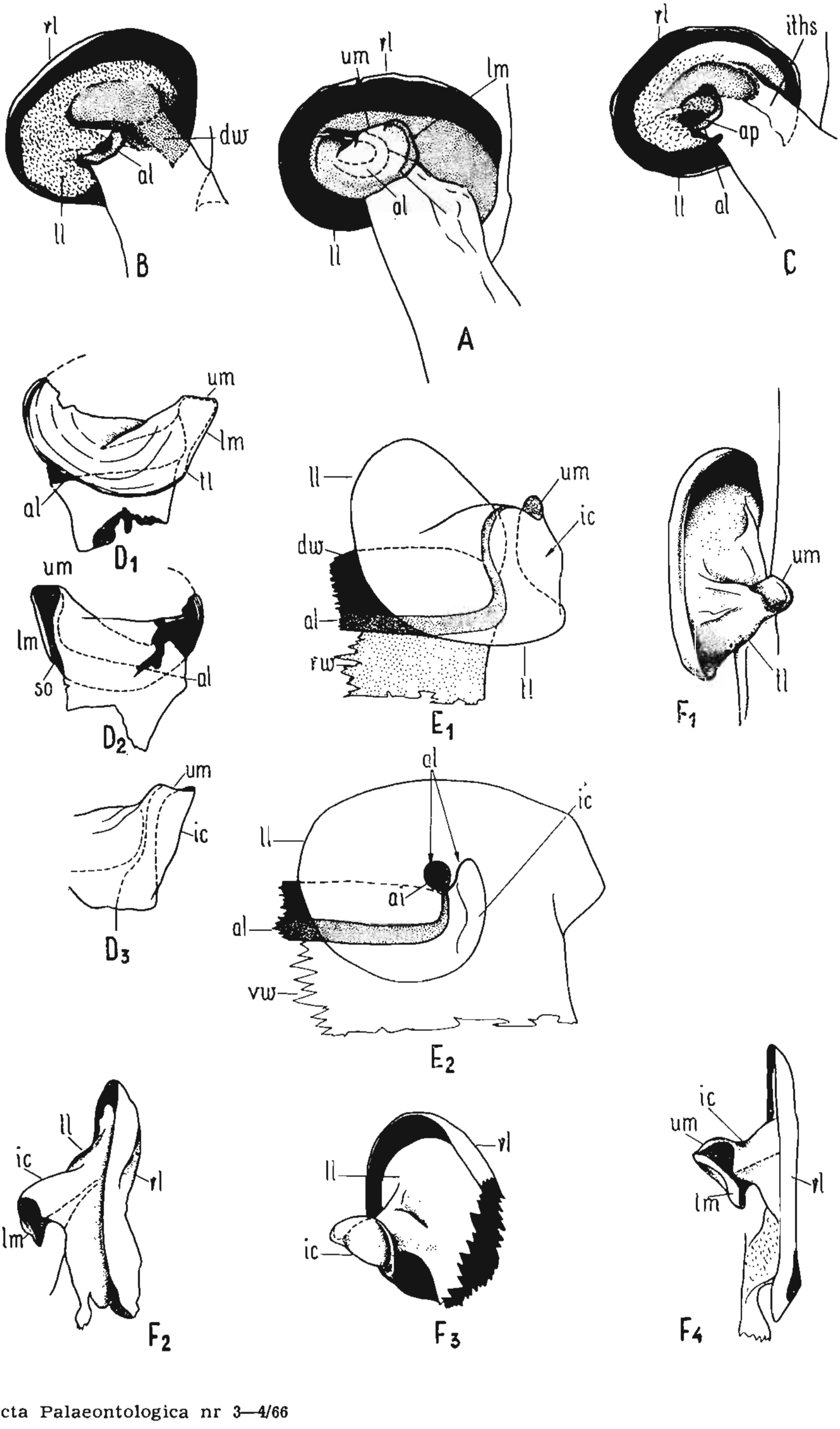
The larger, right, apertural lobe is more transversely elongated being ovate in outline owing to the asymmetry in size of the ventral and dorsal adapertural plates. Both plates are produced through the fusion of a number of fuselli with the wall of metatheca but the ventral adapertural plate is distinctly larger (Pl. XXX, Figs. C_1, D_1, *dap*, *vap*).

Plate XXXI

Lobograptus invertus n.sp. Structural details of apertural apparatus. *A* semitransparent specimen showing relation of the incurved termination of the left lobe to the extroverted ventral apertural lip (indicated by broken lines); *B* specimen with the incurved termination of the left lobe, partly removed by the needle preparation, to show the extroverted ventral apertural lip lying inside; *C* similar specimen showing the prolongation of the ventral apertural lip on the upper margin of the incurved termination of the left lobe; D_1-D_3 isolated termination of the left apertural lobe with attached fragment of apertural border seen from ventral (D_1). dorsal (D_2) and ventro-lateral side (D_3); E_1-E_2 diagrammatical restoration of the structural relations around the incurved termination of the left apertural lobe as seen from the ventral side (E_1), and from the ventral and the top (E_2); F_1-F_4 details of the structure of the incurved termination of the left lobe in ventral view (F_1), in the top view and somewhat dorsally (F_2), in lateral (obverse) view (F_3). and in the true top view (F_4) (Mielnik, *A-D*, *F* depth 968.85—966.5 m); *A*, *D* ca. × 107; *B*, *C*, *F* ca. × 64.

al ventral apertural lip, *ap* aperture of theca, *dw* dorsal wall of the metatheca, *ic* incurved part of the termination of the left lobe, *ll* left lobe, *lm* lateral margin of the incurved termination of the left lobe, *rl* right lobe, *so* slit-like opening at the end of ventral process, *tl* termination of the left apertural lobe, *um* upper margin of incurved termination of the left lobe, *vw* ventral wall of the metatheca.

PLATE XXXI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F1
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um
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F4

Some 5 fuselli form the central part of the lobe gathered into nodes. The remaining fuselli are complete or shorter, and produce both terminations of the lobe in the form of adapertural plates. The larger ventral adapertural plate is made up by some 6—7 fuselli, attached to the ventral wall of the metatheca. This structure strikingly resembles the adapertural plate, formed by a similar fusion of the terminal part of the opposite, left lobe in *L. scanicus scanicus* (comp. p. 449). The smaller, dorsal adapertural plate consists of some 3—4 fuselli which, on the dorsal side, fuse with the wall of metatheca. The right apertural lobe is some 0·46 mm in length (*tr.*) and 0·30 mm in height (*long.*).

The left apertural lobe is less circular, transversely more elongated and angularly bent at the dorsal margin (Pl. XXX, Figs. C_2, D_2). From the ventral side, the lobe is deeply incised through an embayment of the ventral apertural notch and terminates in a strongly incurved (Fig. C_2) or even slightly coiled (Fig. D_2) ventral terminal process (*tl*).

The left lobe ventrally ends, therefore, freely in contrast with the conditions stated for *L. scanicus scanicus* in which it forms an adapertural plate, attached to the ventral wall of metatheca. Owing to this inversion in the structural modifications of the ventral termination of the lobe, the specific name "*invertus*" was introduced for the species in question.

The ventral apertural notch is bordered by an extroverted apertural lip (*al*) which, as in more proximal thecae, sends an ascending ramus, running around the apertural incision in the left lobe (*ai*) to the upper margin of the incurved ventral process of the left lobe (*um*). These rather complex relations are shown diagrammatically in Pl. XXXI, Figs. E_1-E_2. The incurved part of the ventral process forms a laterally protruding, semitubular outgrowth on the left lobe which is shown in different positions in Figs. F_1-F_4. It is open dorsally through a slit, visible in Figs. F_2, F_4. Internally, this slit communicates with the ventral apertural notch and its derivative — the apertural incision. The lateral margin of the incurved part of the lobe is slightly thickened and forms a rim (*lm*).

In connection with rather strong flattening of the specimens, the estimation of a true degree of overlap in apertural lobes is difficult. This is especially true with regard to more proximal thecae which never show the presence of the incurved upper margin of the lobe, overhanging the aperture. In more distal thecae, as those, shown in Pl. XXX, Figs. C, D, the upper margin of the right lobe is distinctly curved in — which indicates a rather considerable overlap of the left lobe. Most probably, the lack of overlap in proximal thecae is a preservational feature, depending on the flattening of the specimens. It seems likely, therefore, that primarily they displayed some degree of overlapping.

The outer wall of the right lobe is always more convex than that in the left lobe. In the latter, the outer wall is nearly flat or even slightly concave. The aperture, covered in distal thecae by the incurved upper margin of the right lobe, opens through a ventral and dorsal apertural notch. The former is provided with a characteristic embayment — the apertural incision entering the left lobe. In the presence of apertural incision *L. imitator* n.sp. resembles *L. scanicus amphirostris* n.subsp. (comp. p. 442).

Stratigraphic range. — In the Mielnik bore-hole, *L. invertus* n.sp. has been found in a narrow band between the depth of 966·85 m and 964·9 m, thus occupying a bed some 2 m in thickness only.

In the graptolite sequence, *L. invertus* n.sp. makes its first appearance about 20 m above that of *L. imitator* n.sp., but 25·85 m below the lower limit of the occurrence of *L. cirrifer* n.sp. It occupies, therefore, an intermediate stratigraphic position. The richest populations were etched from samples from depths between 966·85—965·9 m. They contain siculae, numerous thecae and fragments of rhabdosome. In the Mielnik core, *L. invertus* n.sp. is associated with the following graptolite assemblage: *Lobograptus exspectatus exspectatus* Urbanek, *Neodiversograptus beklemishevi* Urbanek, *Saetograptus chimaera cervicornis* Urbanek, *S. chimaera* cf. *chimaera* (Barrande), *Pristiograptus dubius* (Suess), *P. dubius tumescens* (Wood), "*P.*" *bohemicus* (Barrande) and *Holoretiolites mancki* (Münch). Moreover, some hydrozoans and scolecodonts are contained in the etched assemblages. *L. invertus* n.sp. from the Baltic drift material is unknown till now.

Systematic position. — In the structure of the apertural apparatus of thecae, *L. invertus* n.sp. displays certain resemblances to *L. scanicus amphirostris* n.subsp. (structure of the left lobes) and to *L. scanicus scanicus* (the right lobe of *L. invertus* n.sp. being similar to the left lobe of the latter). The structure of sicula is, however, quite different in the species under study and a direct derivation of *L. invertus* n.sp. from the *scanicus* line seems to be rather hardly likely.

In contrast, it is easy to derive *L. invertus* n.sp. directly from *L. imitator* n.sp. The structure of sicula in *L. invertus* n.sp. is foreshadowed by the sicula of *L. imitator* n.sp. and the specialized thecae of the former species may be derived from the thecae of the latter on the basis of a few changes in their structure. The necessary changes are above all: the enlargement of the right lobe, connected with the formation of its adapertural plates and the enlargement of the ventral process of the left lobe, connected with its incurvation and the formation of apertural incision, provided with an extroverted apertural lip. Both morphological and stratigraphical data suggest the relationship of the two species mentioned above in the following sequence: 1) *L. imitator* n.sp., 2) *L. invertus* n.sp.

The morphological similarites to the representatives of the *scanicus* line discussed above seem, therefore, to result only from the parallelism in the evolution of thecal characters in cucullograptids. For more details— see also the chapter on phylogeny (p. 371).

Lobograptus cirrifer n. sp.

(Fig. 12; Pls. XXXII—XXXIV; Pl. XLVII, Fig. 3)

Type specimen (holotype): Pl. XXXIV, Fig. C (distal theca).

Paratypes: Pl. XXXIII, Fig. B (medial theca), Fig. D (distal theca).

Type stratum: Greenish-blue mudstones and marls in the core of the Mielnik deep-boring between 941.0—939.25 m of dept (upper part of *hemiaversus* zone, upper part of Mielnik Beds).

Derivation of the name: cirrifer, Lat. *cirri* = tendrils, curls, *fero, ferre* = to bear; as bearing long tendrillike rostral processes on apertural lobes.

Diagnosis. — A lobograptid with a gracile and rather short sicula (1.18—1.34 mm long), provided with a strong and somewhat incurved dorsal apertural process. Thecae with asymmetric apertural apparatus, the right lobe being pronouncedly larger. Both lobes virtually provided with a rostral process which may vary in form from a small outgrowth (protuberance) to a long tendrillike and curved process. In rhabdosome, this process also displays a distalward increase in size.

Material. — Numerous proximal and medial fragments of rhabdosome and single thecae, including sicula, etched from the Mielnik core from a depth of 941.0—939.25 m. Specimens are partly flattened, but are bleachable. True distal thecae unknown. In the Baltic drift material not recorded.

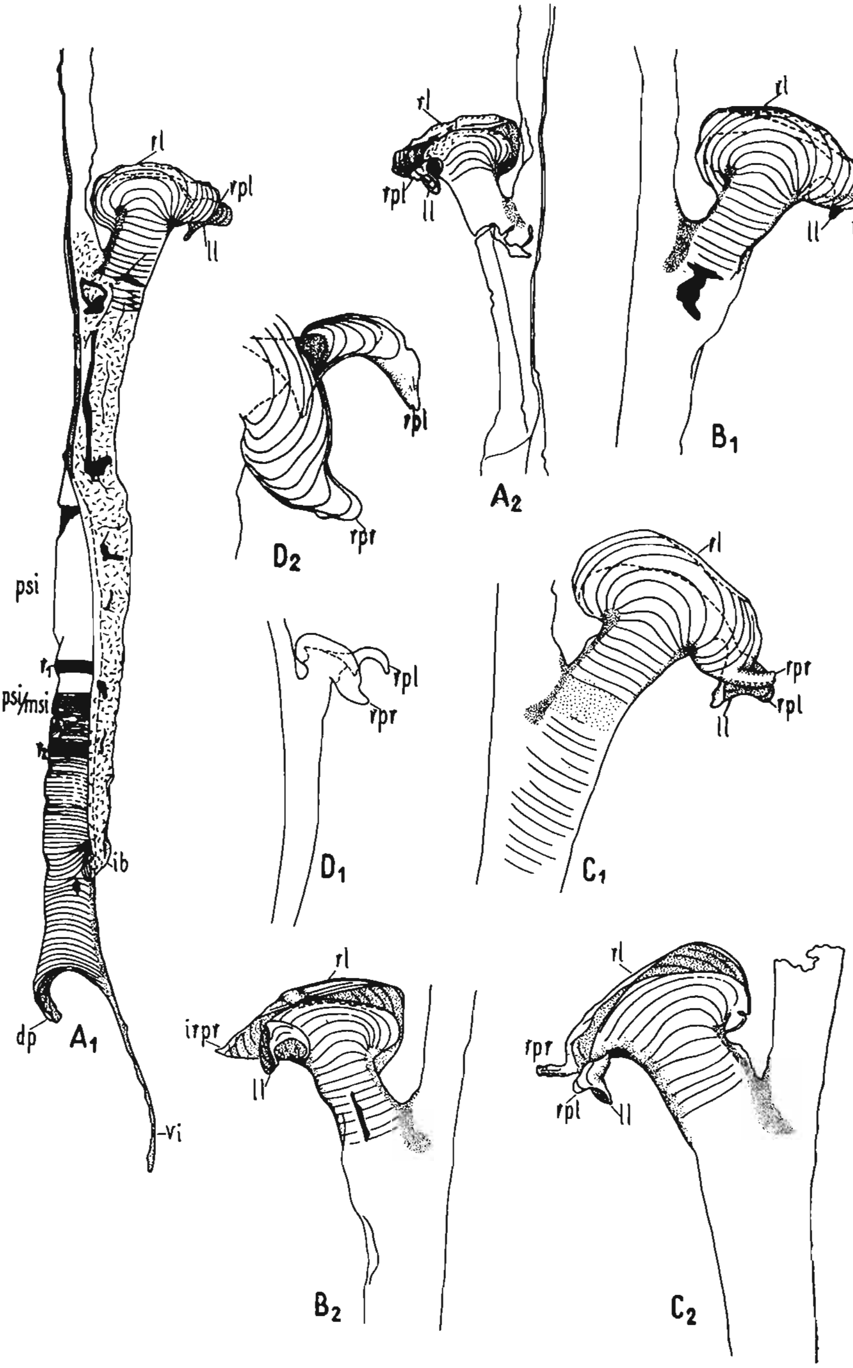
Description. — Sicula rather short and slender, almost uniform in width, except for a somewhat expanded apertural part, provided with a distinct and slightly incurved dorsal apertural process. A total length of sicula ranges between 1.18—1.34 mm (Pl. XXXII, Fig. A_1).

Prosicula is rather long, reaching 0.55—0.58 mm. The periderm is, in the majority of specimens, strongly damaged, so that the presence of longitudinal threads was hardly discernible. The prosicular part in adult

Plate XXXII

Lobograptus cirrifer n.sp. Structure of sicula and details of structure in proximal thecae. *A* sicula and first theca in reverse aspect (A_1) and free part of same theca in obverse aspect (A_2); *B* upper part of a proximal theca in reverse (B_1) and obverse (B_2) aspects; *C* another proximal theca probably from more central (medial) part of rhabdosome in reverse (C_1) and obverse (C_2) aspects; D_1 general appearance of a proximal theca (reverse aspect) with well developed rostral processes on apertural lobes; D_2 details of fusellar structure of rostral processes of same specimen (Mielnik, depth 940.0—940.25 m); *A* ca. × 50, *B-C* ca. × 63, D_1 ca. × 27, D_2 ca. × 100. *dp* dorsal process of metasicula, *ib* initial bud, *irpr* initial rostral process of right lobe, *ll* left lobe, *psi* prosicula, *psi/msi* boundary between pro- and metasicula, *rl* right lobe, *rpl* rostral process on left lobe, *rpr* rostral process on right lobe, r_1-r_2 successive sicular rings.

PLATE XXXII


rl
rpl
ll
psi
r1
psi/msi
r2
ib
dp
A1
vi
rl
rpl
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A2
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rpl
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irpr
B1
rpl
rpr
D2
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rpr
D1
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rpr
rpl
ll
C1
rl
irpr
ll
B2
rl
rpr
rpl
ll
C2

siculae may be provided with 1 or even 2 sicular black rings (!), situated at a variable distance from the boundary with metasicula. In the case when only one prosicular black ring was present, it was situated rather close (0.04 mm) to that boundary; in the case when two of them were present, the first (r_1) was situated 0.10 mm and the second (r_2) 0.05 mm from the aperture of the prosicula. In one observed case, the prosicula was devoid of any black ring, despite the fact that it doubtlessly belonged to an adult sicula, provided with a metasicular black ring.

Metasicula is rather long, measuring from 0.63 to 0.76 mm. It has a nearly uniform width throughout, except for the apertural part where it is somewhat expanded, being 0.14 mm wide at the level of the initial bud and 0.18—0.25 mm at the aperture. In all examined specimens the metasicular part is invariably provided with a black ring. The structure of the primary notch region indicates that the development of the initial bud took place according to the normal monograptid pattern (Pl. XXXII, Fig. A_1). The aperture of metasicula is elaborated and provided with a strong and usually somewhat incurved, shovellike dorsal process, which reaches 0.12—0.20 mm in length. The preserved fragment of virgella may be also rather long up to some 0.50 mm.

The structure of thecae in *L. cirrifer* n.sp., in particular that of apertural apparatus, displays, in the material under study, a distinct variability. These conditions are shown in Pl. XXXIII for a "less advanced form" (morphotype A), occupying a somewhat lower horizon (depths of 941.0—940.25 m) and in Pl. XXXIV for a "more advanced form" (morphotype B), occupying a somewhat higher horizon (a depth of 939.25 m). They differ in a more or less extreme expression of morphological characters concerning the apertural part of theca. These differences may depend on growth stages of the thecae investigated, the less advanced forms being in this case simply younger, and the more advanced forms correspondingly older. Certain facts may indicate, however, that this is not the case, and most probably these differences exhibit rather a process of zonal evolution in *L. cirrifer* n.sp., in the case of Mielnik boring condensed in reduced thickness of strata.

The latter suggestion is corroborated by the fact that the less advanced forms from the lower horizon are never associated with more ex-

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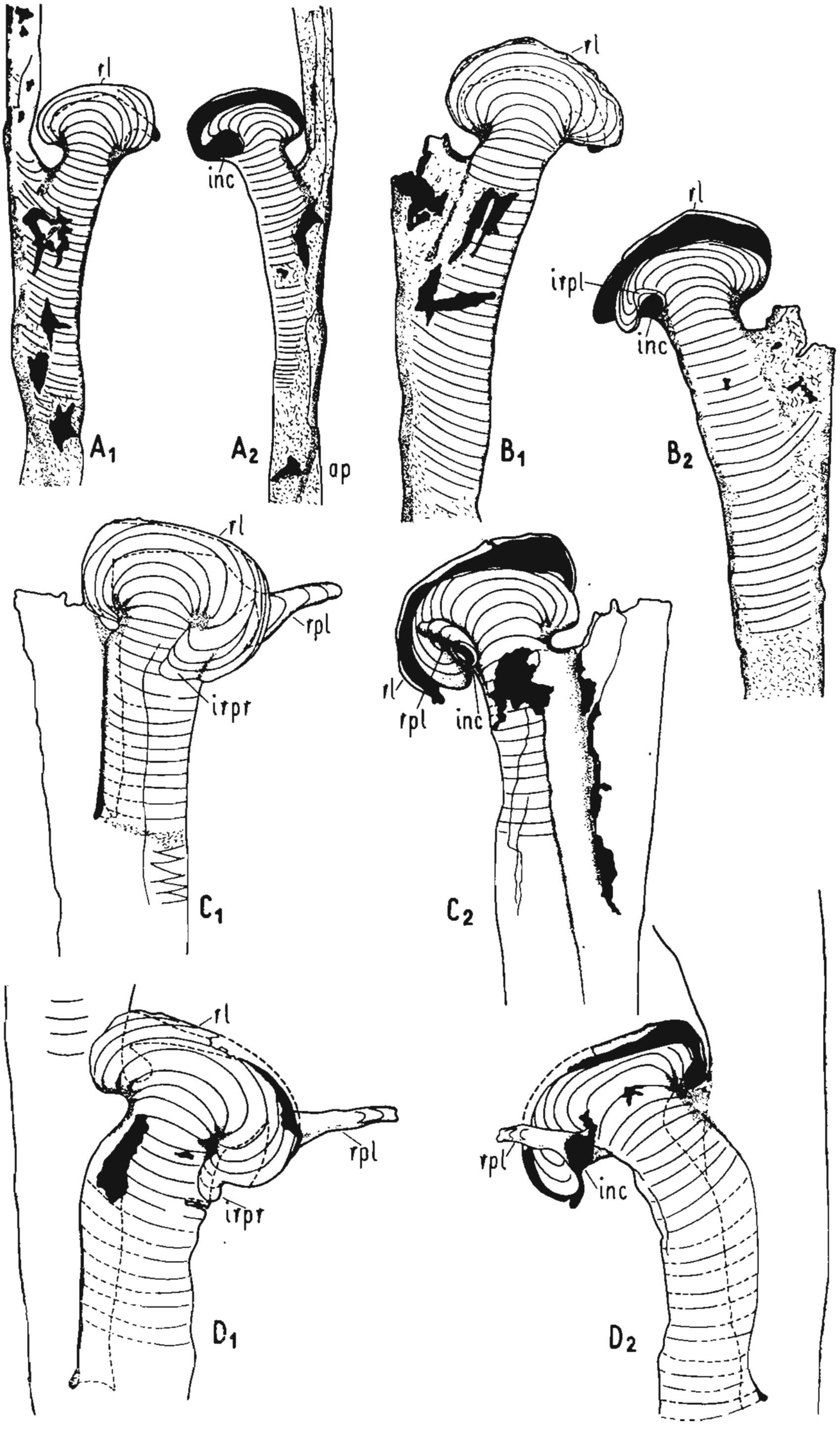
Plate XXXIII

Lobograptus cirrifer n.sp. Structure of thecae in a less advanced form. *A* free part of the first theca in reverse (A_1) and obverse (A_2) aspects; *B* upper part of a proximal theca in reverse (B_1) and obverse (B_2) aspects; *C-D* upper parts of more distal thecae in reverse (C_1, D_1) and obverse (C_2, D_2) aspects (Mielnik, depth approx. 941.2—940.5 m); ca. × 66.

ap apex of prosicula, *inc* apertural incision in the left lobe, *irpl* incipient rostral process on left lobe, *irpr* incipient rostral process on right lobe, *ll* left lobe, *rl* right lobe, *rpl* rostral process on left lobe.

PLATE XXXIII



treme thecal types. However, the fact of rather small differences in depths between the less advanced "lower zonal" form and more advanced "higher zonal" form does not enable one formally to distinguish these forms as true zonal fossils and they are described below simply as "less" and "more advanced" forms of *L. cirrifer* n.sp. The stratigraphic sequence of both morphological forms mentioned above agrees with the supposed trend in phylogeny, however, both show certain overlap at depth 940.25—940.0 m.

The first theca, being a slender tube of a total length of 1.74—1.87 mm, starts, in an adult sicula, some 0.29—0.30 mm from the lateral margin of the aperture. The metathecal part of the first theca reaches a length of some 0.27—0.35 mm (including apertural lobes), the mere subapertural segment of it being 0.15—0.20 mm long. The prothecal part of th_1 measures 1.60—1.39 mm, the protheca occupies therefore about 90—88% of their length. Metatheca is inclined towards the main axis of theca at an angle of 20—30°. The aperture of metatheca is provided with two lateral asymmetric apertural lobes, the right lobe being larger than the left. In less advanced forms (Pl. XXXIII, Fig. A_1), the right apertural lobe has an only slightly transversely elongated outline, consists of some 6 complete fuselli gathered into nodes and some 2 additional fuselli, forming an incipient ventral termination of the lobe.

The left lobe is smaller and provided with a distinct apertural incision on its ventral margin. This margin, surrounding the incision (Pl. XXXIII, Fig A_2), forms a slightly extroverted lip. The left lobe consists of some 7 fuselli, only 4 being complete. The remaining fuselli make up the beaklike ventral process of the lobe. The incurved upper margin of the right lobe displays a certain degree of overlap of apertural lobes.

In more advanced forms (Pl. XXXIV, Fig. A) the right lobe is somewhat more transversely elongated and consists of some 10 fuselli, some 6 being complete and gathered into nodes and some 4 making the ventral and dorsal terminations of the lobe. The dorsal termination forms an adapertural plate, fused with the dorsal wall of metatheca and the ventral one forms a free, beaklike process. This latter is provided, at its base on the ventral wall, with a thin outgrowth passing into a rostral spine. The specimen, figured in Fig. A, probably represents

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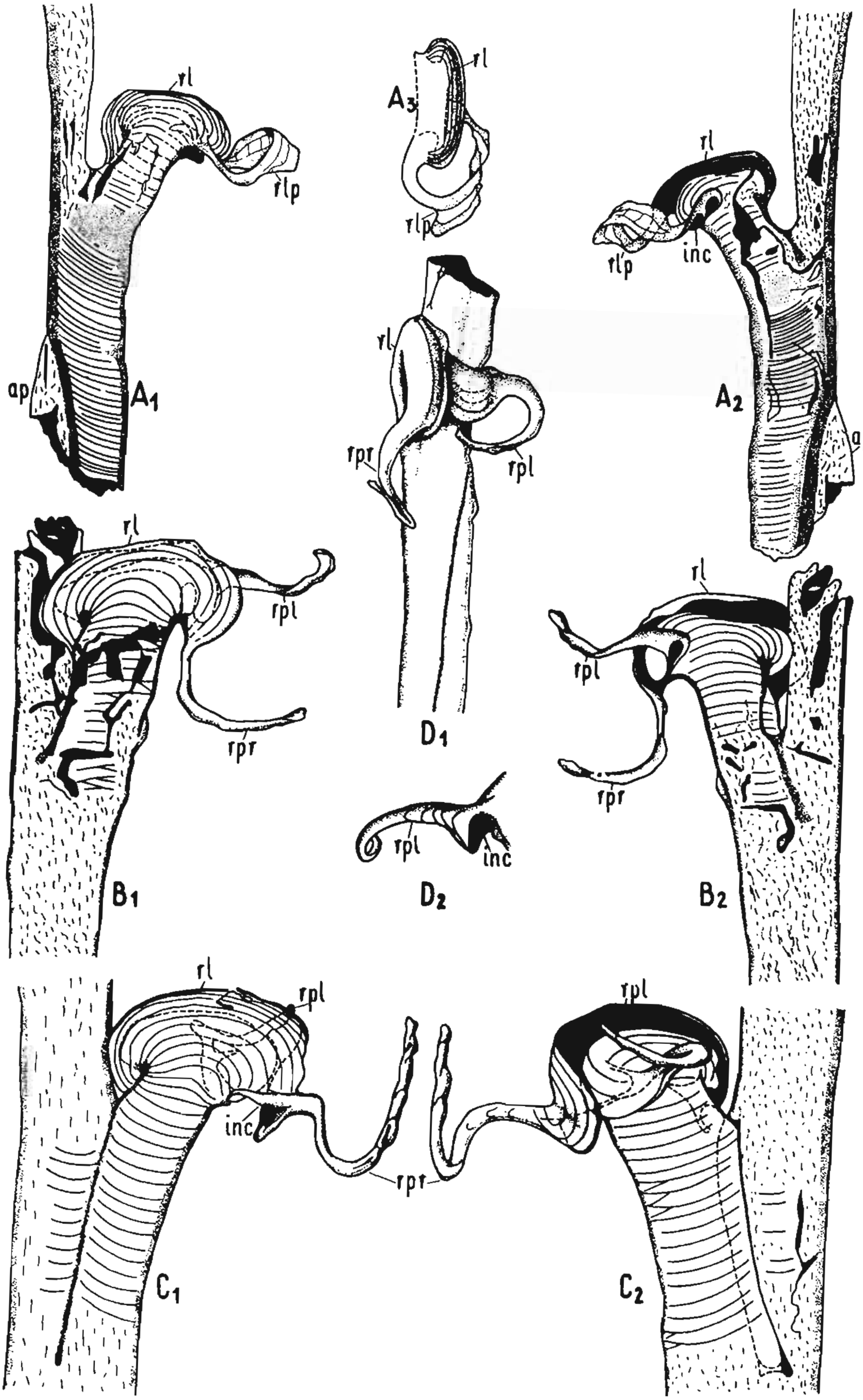
Plate XXXIV

Lobograptus cirrifer n.sp. Structure of thecae in a more advanced form. *A* free part of the first theca in reverse (A_1), obverse (A_2) aspects and in the top view (A_3); *B* upper part of a proximal theca in reverse (B_1) and obverse (B_2) aspects; *C* upper part of a more distal theca in reverse (C_1) and obverse (C_2) aspects; *D* upper part of a proximal theca in ventral view (D_1) and rostral process on left lobe from obverse side (same specimen) (Mielnik, depth approx. 939.25 m); ca. × 67, *rl* rostral loop formed owing to the fusion of both rostral processes. Further explanations — as in Pls. XXXII and XXXIII.

PLATE XXXIV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A2
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B1
rpl
inc
D2
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rpl
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B2
rl
rpl
inc
rpr
C1
rpl
C2

an extreme case of the development of rostral spines on the right and left lobe, these being, on their free ends, fused with a rather broad lamella, thus forming a rostral loop (Fig. A_3). The central lamella on the rostral loop shows traces of fusellar structure, visible in the form of growth lines. The fusion of both lobes may be considered as a rather teratological phenomenon, connected, in this case, with a generally high degree of elaboration of the rostral processes.

The left apertural lobe is rather unsatisfactorily preserved and the number of fuselli it consists of cannot be determined. The lobe is provided with a ventral termination in the form of a ventral beaklike process and with a distinct ventral apertural incision. The lateral and upper margin of this incision are framed by an extroverted lip which stretches ventrally and passes into a long rostral process (Pl. XXXIV, Fig. A_2). The length (*tr.*) of the right lobe varies between 0.24—0.30 mm, its height (*long.*) — 0.12—0.14 mm, the length of the left lobe being 0.22—0.23 mm, their height respectively about 0.10 mm.

The first theca, figured in Pl. XXXII, Figs. A_1-A_2, represents a morphological stage intermediate between the less and the more advanced forms described above. The transversely elongated outline of the right lobe provided with a dorsal adapertural plate and a rather high horizon of its occurrence (at depth of 940.0 m) suggest rather its conspecificity with a more advanced form of *L. cirrifer* n.sp. In comparison with young growth stages of other proximal thecae it seems probable that this is a preadult growth stage of the first theca of a more advanced type. The right lobe, strikingly similar to that in a more advanced form, is provided with a distinct dorsal adapertural plate and shovellike ventral process. It lacks, however, any trace of rostral process. The lobe consists of some 5 complete fuselli, 5—6 other ones forming the ventral process of the lobe, and some 3 fuselli making up the dorsal adapertural plate, fused with the dorsal wall of metatheca. The upper margin of the lobe is distinctly incurved over the aperture of theca. The left lobe is provided with a long and slightly bent ventral process and a distinctly outlined ventral apertural incision (Fig. A_2). The margin of the incision forms a narrow extroverted lip, extended ventrally and passing into a short, probably incipient (growing) rostral spine (*rpl*). This suggests that the formation of a rostral spine on the right lobe is delayed as compared with its formation on the left lobe.

Proximal thecae form rather long (about 1.70 mm) and slender tubes, 0.07—0.16 mm wide at the base of protheca and 0.13—0.16 mm at the aperture of metatheca. The length of metatheca is 0.22—0.44 mm, the prothecal part occupies, therefore, about 70—86% of their length. The length (*tr.*) of apertural lobes amounts to 0.35—0.45 mm in the right lobe, and 0.20—0.32 mm in the left one. Their height (*long.*) is 0.12—

0.14 mm for the former and 0.10 mm for the latter. The metatheca is inclined at an angle of 30°.

In the proximal thecae of the less advanced form (Pl. XXXIII, Figs. B_1-B_2), the metatheca is only slightly isolated (over some 1/4 of its length) and provided with lateral apertural lobes, displaying distinct asymmetry.

The right, larger lobe is ovate in outline and consists of some 8—9 fuselli, forming a distinct ventral beaklike process, characteristically pointed at the end. This pointed ventral termination of the right lobe may suggest only a certain tendency to form a rostral outgrowth.

The left lobe resembles a much the same lobe, described above for the first theca in a less extreme form. The apertural incision is framed by an extroverted lip whose upper margin extends, however, and passes into a triangular outgrowth. This outgrowth is doubtlessly the onset of a corresponding rostral process (Pl. XXXIII, Fig. B_2, *irpl.*).

The metathecal part of proximal thecae in a more advanced form shows a more pronounced isolation, involving about 1/2 of its length (Pl. XXXIV, Figs. B_1-B_2). The right lobe is transversely elliptical in outline and provided with a beaklike ventral process and a dorsal adapertural plate (Fig. B_1). The lobe consists of about 9 fuselli, some 5 of them complete and some 4 producing the ventral and dorsal prolongations of the lobe. The ventroproximal termination passes into a long and narrow, arched rostral process (*rpr*). In some cases, this rostral process is slightly spirally incurved as seen in ventral view in Fig. D_1. The observation of specimens shows that the inner surface of the rostral process is somewhat concave, thus forming a groovelike structure. The uper margin of the right lobe is incurved over the aperture, overlapping the left lobe.

The left lobe is provided with a distinct shovellike ventral process and a deep apertural incision, framed by an extroverted apertural lip. This lip is extended into a rostral spine, showing a strong curvature and some tendency to spiral coiling along its axis (Pl. XXXIV, Figs. B_2, D_1-D_2). The preserved parts of the rostral process may suggest that the left rostral process was somewhat shorter than the right one.

The specimens, shown in Pl. XXXII, Figs. B-D, are interpreted here as younger growth stages of proximal thecae in advanced form. Theca in Figs. B_1-B_2 was, in all likelihood, the most proximally situated one.

The right lobe is provided with a dorsal adapertural plate and the ventral process — with a small outgrowth, forming a pointed termination which is most probably an early stage in the formation of the rostral process (Pl. XXXII, Fig. B_1, *irpr*). The left apertural lobe is provided with a shovellike ventral process and an apertural incision, framed by an extroverted apertural lip, having a pointed triangular outgrowth which, when compared with the same structure on the opposite lobe, also represents an early, but somewhat more advanced stage. The theca figured C_1-C_2 in same Plate, was probably slightly more centrally placed in the rhabdosome. Its right lobe terminates ventrally in a short, blunt and somewhat incurved rostral process in the early growth stage (Fig. C_1, *rpr*). The left lobe shows the presence of a bluntly triangular outgrowth similar in size, also an early growth stage of a corresponding rostral process (Fig. C_2, *rpl*). The specimen, shown on the same Plate as Figs. D_1-D_2, displays details of structure of a proximal theca in an advanced growth stage of the rostral processes. That on the right lobe forms a short blunt outgrowth on the ventral process, consists of three short (*long.*) but rather wide (*tr.*) and arched fuselli which are an incipient rostral spine (Fig. D_2, *rpr*). The left rostral spine is distinctly longer, slightly incurved and rests on the extroverted margin of an apertural lip. It consists of some 7 easily discernible arched fuselli which are so thickened at the end that the growth lines on it can no longer be noted (Fig. D_2, *rpl*).

An analysis of a series of thecae, described above, may indicate that the growth relations between rostral spines on the right and left lobe in proximal thecae still show a delayed formation of the right rostral spine (comp. Pl. XXXII, Figs. B, D). This closely resembles the conditions, stated before for the growth relations of rostral spines in the first theca of more extreme forms (comp. Fig. A). Moreover, the comparison of the theca in Fig. B, probably more proximally situated in the rhabdosome, with the theca in Fig. C, probably more centrally situated, suggests a certain decrease in differences, expressed in time of the onset of both rostral spines. The size of rostral processes is, in this case, almost the same, both of them being in an early growth stage. This may indicate a certain shifting in the growth relations of both rostral spines, distalwards in the rhabdosome, towards a nearly simultaneous beginning of their formation in more distal thecae. The material is, however, not complete enough for a safe elucidation of the growth relations and to prove that we actually have to do with a change in astogeny from a heterochronous to isochronous onset of structure mentioned above.

The specimen in Pl. XXXIV, Fig. D_1 represents a ventral view of proximal thecae in a more advanced form of *L. cirrifer* n.sp. Both rostral processes, characteristically incurved and stretching out and down, resemble "mammoth tusks". A single left rostral process of the same specimen, seen from the left (obverse) side, is figured in the same Plate, Fig. D_2. At the base of this rostral process, its fusellar structure is still discernible, the spine proper (*rpl*) being mounted on the extroverted apertural lip, bordering the apertural incision (*inc.*)

Judging from the comparison with other lobograptids, none of the isolated fragments include true distal thecae. However, the most distal of the etched thecae are shown in Pl. XXXIII, Figs. C, D — for a less advanced form, and in Pl. XXXIV, Fig. C — for a more advanced form.

More distally situated thecae in less advanced forms are nearly completely adnate to the adjacent protheca, or have very short isolated parts. The length of thecae amounts to 1.76—1.90 mm, the metathecal part being 0.55—0.77 mm long and the prothecal part respectively 1.35—0.99 mm. The prothecal part occupies in these thecae about 70—56% of their length. The width of protheca amounts, at its base, to 0.14—0.28 mm and, at the aperture of metatheca, it reaches 0.22—0.23 mm. The length (*tr.*) of the right apertural lobe is 0.36—0.39 mm, of the left — 0.32—0.34 mm, the height (*long*) being respectively 0.19—0.20 mm and 0.15—0.16 mm. The metatheca is inclined towards the main axis of theca at an angle of 20°.

The right apertural lobe is transversely elongated with the upper margin distinctly incurved over the aperture. The ventral terminations of the lobe are extended into a strong and slightly incurved beaklike process. The latter terminates in a short, triangular outgrowth (Pl. XXXIII, Fig. C_1), or with a short, blunt process (Fig. D_1). Both structures represent an incipient form of a rostral process. The right lobe consists of about 8—11 fuselli, some 5—7 of them being gathered into nodes and the remaining ones constituting the ventral and dorsal terminations of the lobe.

The left apertural lobe is provided with a broad, shovellike ventral process whose lower margin frames a deep apertural incision (Pl. XXXIII, Figs. C_2, D_2, *inc*). The margin of the apertural incision forms an extroverted lip which in turn is prolonged into a strong and relatively broad rostral spine (*rpl*). Figure C_2 shows the fusellar structure of this rostral process which consists of some 3 obtriangular fuselli disposed each over another. The microstructure of these rostral processes resemble, therefore, that observed on proximal thecae in a more extreme form of *L. cirrifer* n.sp. A strong difference in size of rostral processes, the right one being much shorter than the left one, is therefore a remarkable feature of the distal thecae in less extreme forms.

The distally placed thecae in a more advanced form still display a certain degree of isolation of the most distal parts of their metathecal segments, involving however only about 1/4 of a total length of the metatheca (Pl. XXXIV, Fig. C). The right apertural lobe is roughly transverse-elliptical in outline and has a distinct and broad, free ventral process, as well as a short dorsal adapertural plate. Some 9 long and arched fuselli make up the central part of the lobe and its dorsal prolongation, while 3—4 shorter fuselli constitute its ventral prolongation. The lower margin of this ventral process is slightly incised, provided with a thickened apertural rim and in turn prolonged into a long and characteristically incurved rostral process (Fig. C_1, *inc*, *rpr*).

The left lobe is much smaller and has a distinct ventral process, laterally prolonged into a strong and incurved rostral process. The latter seems to be primarily shorter than the right one.

The minute details in structure of rostral processes are obscured by its thickening. The semitransparent terminal parts of the processes, as seen in Pl. XXXIV, Fig. C, suggest that the rostral processes consist throughout of short, wedge-shaped fuselli, disposed along the spine. The primary shape of the rostral processes cannot be easily established.

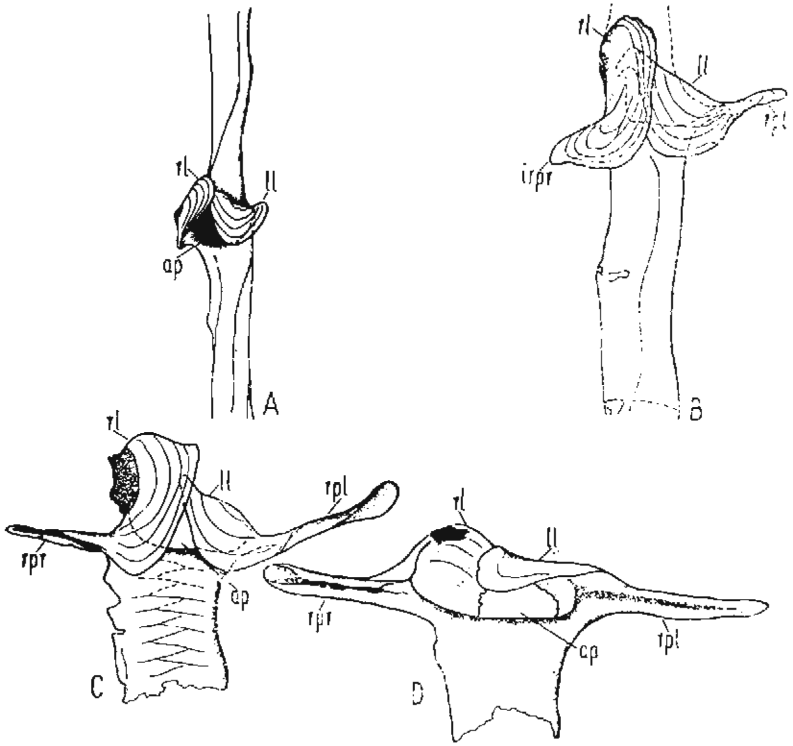


Fig. 13. — *Lobograptus cirrifer* n.sp. Ventral view of apertural apparatus in a proximal (*A*), medial (central) (*B*) and more distally placed thecae (*C*, *D*) (Mielnik, depth 940.0 m), ca. × 67.

ap apertural opening, *irpr* incipient rostral process of the right lobe, *ll* left apertural lobe, *rl* right apertural lobe, *rpl* rostral process of the left apertural lobe, *rpr* rostral process of the right apertural lobe.

They have the appearance of thickened (dark) and flat rods. Most probably, this is however only a preservational feature, related to a certain degree of flattening of the rostral spine margin, primarily slightly protruding. Certain facts indicate that primarily rostral processes are grooved in shape like those in more proximal thecae.

The ventral apertural notch is provided with an extroverted apertural lip, connected with the bases of both rostral apertural processes.

In the right rostral process, the prolongation of this apertural lip forms a somewhat projected margin, framing the central, slightly concave surface of the process, rimmed from the other side by a similarly projecting margin, made up by the prolongation of the margin of the free ventral process. In the left rostral process, this extroverted apertural lip continues into the spine itself, forming there, like on the right side, a protruding margin.

Ventral views of apertural apparatus in proximal and distal thecae are shown on Fig. 13, A-D.

Stratigraphic range. — *L. cirrifer* n.sp. is geologically the youngest representative of *Lobograptus* known so far. At present it is known only from the Mielnik bore-core where it occupies a very narrow band between depths of 941.0—939.25 m. It appears 25.85 m above the level of the first appearance of *L. invertus* n.sp. and 45.9 m above the level of the first appearance of *L. imitator* n.sp. and is separated from the level of their last occurrence by 23.9 m and 22.6 m of thickness respectively.

Populations consisting of morphologically less advanced forms (comp. p. 470) have been etched out from a sample, limited to a depth of 941.0—940.25 m. Their graptolite association consists of *L. exspectatus* cf. *exspectatus* Urbanek, *Saetograptus fritschi* cf. *fritschi* (Perner), *Linograptinae* sp. indet., *Pristiograptus dubius* (Suess) and "*P.*" *bohemicus* (Barrande).

A population with more advanced morphological features was obtained from a sample, collected at a depth of 939.25 m. The association consists of *Saetograptus fritschi* cf. *fritschi* (Perner), *Pristiograptus dubius* (Suess), *P. dubius tumescens* (Wood) and a few uncertain fragments of *Lobograptus exspectatus* cf. *exspectatus* Urbanek.

The stratigraphic distribution of both morphological forms of *L. cirrifer* n.sp. may suggest that they reflect a certain zonal evolution of this species. The occurrence of more advanced form is, however, separated only by 1 m of thickness from the last representatives of a less advanced form. This produces a difficulty in considering these forms as independent zonal indicators.

Systematic position. — The shape of sicula (gracile but with a strong dorsal process) may be considered a "token" which marks *L. cirrifer* n.sp. as a member of a common group, also comprising *L. imitator* n.sp. and *L. invertus* n.sp. As compared with *L. imitator* n.sp., the species in question displays a great degree of specialization in structure of apertural apparatus of thecae, which moreover is different from the trend represented by *L. invertus* n.sp. Both *L. invertus* n.sp. which appears somewhat earlier and *L. cirrifer* n.sp. which appears later may, therefore, be considered a derivative of *L. imitator* n.sp. which precedes them stratigraphically and, at the same time, is morphologically less specialized.

On the other hand, proximal thecae of *L. cirrifer* n.sp., which are less affected by secondary phylogenetic novelties than the distal ones, are only slightly different from the same thecae in *L. invertus* n.sp. This is especially true for the first theca in a less advanced form of the former species (Pl. XXXIII, Figs. A_1-A_2) which, in many respects, resembles the same theca in *L. invertus* n.sp. (Pl. XXX, Figs. A_1-A_2) (outline of apertural lobes, incipient adapertural plates in the right lobe and a strongly developed ventral beaklike termination on the left lobe, in both cases provided with a deep ventral incision). This resemblance in structure of most proximal thecae may suggest that, for a certain time, both species mentioned above constituted a common phylogenetic line which later on (above the structural stage, represented by *L. imitator* n.sp.) split into two, independent lineages. This suggestion remains, however, purely hypothetical because such a form, more advanced than *L. imitator* n.sp. (a greater degree of isolation of the metathecal part, a stronger elaboration of the ventral process) but, in distal thecae, less specialized than *L. invertus* n.sp. (intermediate between *L. imitator* n.sp. and *L. cirrifer* n.sp.), has not been recorded. Nevertheless, the presence of a number of intermediate populations between *L. imitator* n.sp. and a true *L. invertus* n.sp. seems quite likely and a divergence in directions of evolution, represented by *L. invertus* n.sp. and *L. cirrifer* n.sp. may be considered as starting to operate at this stage of phylogeny. For the sake of simplicity, however, both lineages are shown in phylogenetic tables as separated immediately above the *L. imitator* n.sp. (comp. Pls. VIII and IX).

Genus *Cucullograptus* Urbanek, 1954

Cucullograptus hemiaversus Urbanek, 1960

(Figs. 14—16;; Pls. XXXV—XXXVI; Pl. XLVII, Fig. 4)

1960. *Cucullograptus hemiaversus* Urbanek; A. Urbanek An attempt....., pp. 215—216, Pl. 2, Figs. 2 a-b; Text-figs. 2A, 6, 13E, 14C.

Holotype: Refigured partly in Pl. XXXVI, Figs. B_1-B_2, to show details of structure.

Material. — Numerous fragments of rhabdosome, proximal (without siculae) and distal thecae etched from the Mielnik core at a depth of 959.9—938.0 m. They are strongly flattened and, in part, deformed but bleachable. A score or so of single thecae or short rhabdosome fragments and two siculae without the first theca have also been obtained from erratic boulder S. 200, Rewal (comp. Urbanek, 1960, p. 215). Specimens from the drift material are well-preserved and only slightly compressed. They have been used for the study of minute structures.

Description. — In the material available, no siculae of *Cuc. hemiaversus* attached to rhabdosome fragments have been recorded. However, the siculae associated with thecae and rhabdosome fragments of *Cuc. hemiaversus* in the boulder S. 200, Rewal, are almost certainly conspecific (Fig. 14, A-B). The description of siculae is, therefore, based on these two specimens. Sicula is rather short, about 1.00—1.08 mm in length, and slender with a maximum width reaching about 0.16 mm. Owing to its uniform width the sicula is almost cylindrical. The aperture of an adult sicula is almost straight with only very slightly marked dorsal apertural elevation.

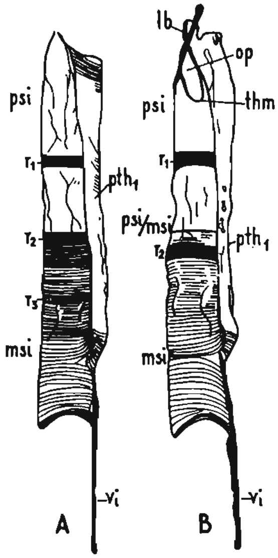


Fig. 14. — ***Cucullograptus hemiaversus*** **Urbanek. Structure of sicula: *A* almost complete sicula with prothecal part of the first theca, *B* sicula with damaged apex and first theca broken off (S. 200, Rewal), ca. × 50.**

msi metasicula, *lb* regenerative longitudinal bands of prosicula, *psi/msi* boundary between pro- and metasicula, pth_1 prothecal part of the first theca, r_1-r_3 successive black rings of sicula, *thm* thickened margin of the apical opening of prosicula, *vi* virgella.

Judging from two preserved specimens, the adult prosicula is provided with a black ring (r_1) situated approximately in its centre (Fig. 14, A-B, r_1). The length of the prosicula, estimated on the basis of these specimens, slightly damaged at the apex, amounts to about 0.55—0.58 mm. The specimen, figured on Fig. 14, B, displays some traces of a probably primary damage at the apex of the prosicula similar to that observed in other monograptids (comp. Urbanek, 1953, p. 102 of the French summary).

The primary nature of the destruction of periderm in the apical part of prosicula is marked by the presence of thickened margins of the peridermal membrane (*thm*), rimming the opening which was formed as a result of destruction. This seems to indicate certain "healing" or reconstruction processes which took place during the animal's lifetime. The presence of broad longitudinal bands (Fig. 14, B, *lb*), much broader than the primary longitudinal threads of prosicula, may also indicate a regenerative nature of these apical structures. They resemble the secondary longitudinal bands, probably formed owing to the regeneration in other monograptids (comp. Urbanek, 1958, pp. 38—39).

Conditions in specimen, shown in Fig. 14, B, may be most probably described as a result of the formation of two regenerative bands, the ventral one serving as a true "Ersatznema", the dorsal one being an independent, additional rod ("double nema").

The second black ring (r_2) is placed just on the boundary of pro- and metasicula (Fig. 14, A) or slightly below and situated on the metasicula proper (B).

Metasicula is about 0.50—0.45 mm long, with a uniform width of some 0.11—0.16 mm and without an adapertural expansion. The metasicula is therefore almost cylindrical in shape, provided with a simple aperture and showing only a slight dorsal elevation instead of a dorsal process. It is provided with a black ring (r_2), situated close to the boundary with prosicula, or with one ring (r_2) disposed just on this boundary plus a slightly marked additional ring (r_3) approximately in the middle of the metasicula.

The presence of a primary notch indicates that the development of the initial bud followed the normal monograptid pattern. The first theca starts some 0.12—0.15 mm from the lateral border of the aperture of metasicula. No complete first theca is known and preserved fragments comprise only initial parts of its prothecal segment (Fig. 14, A, B, pth_1).

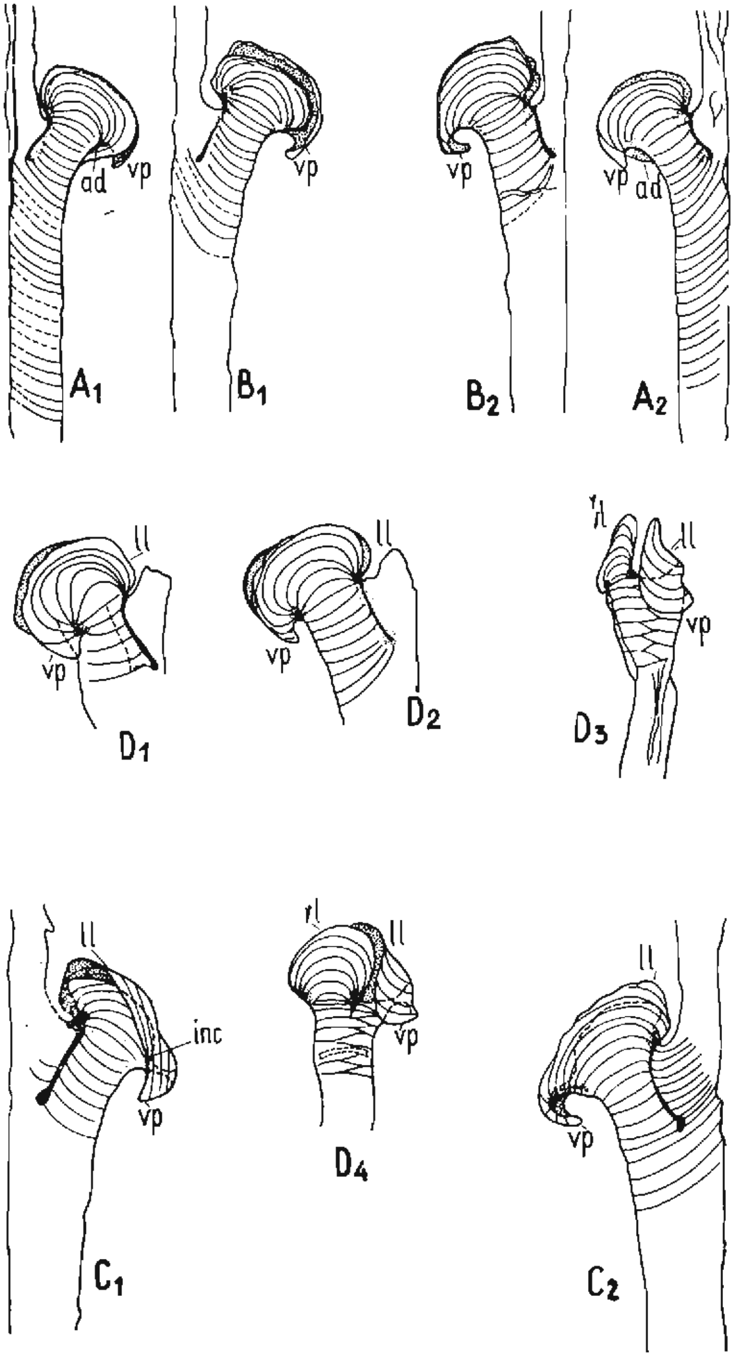
Proximal thecae (Pl. XXXV, Figs. A-D; Pl. XXXVI, Fig. A) are slender tubes provided with elaborated apertural apparatuses. Their total length ranges within limits of 2.37—2.20 mm, the prothecal part being some 2.13—1.96 mm long, the metathecal some 0.24—0.10 mm respectively. The prothecal part occupies about 66—69$^0/_0$ of total length of these thecae. The width of proximal thecae is 0.13—0.09 mm at the base of protheca and 0.17—0.12 mm at the base of metatheca. Metatheca in proximal thecae is inclined towards the main axis at an angle of

Plate XXXV

Cucullograptus hemiaversus Urbanek. Structure of proximal thecae. *A*-*C* upper parts of proximal thecae arranged successively from most to less proximal and seen in reverse (*1*) and obverse (*2*) aspects; *D* metathecal part of a proximal theca in lateroventral (D_1), lateral (obverse) (D_2) ventral (D_3) and ventrolateral (reverse (D_4) aspects (S. 200, Rewal); ca. × 63.

ad adapertural plate of the right lobe, *inc* incision seen in right through transparent lef apertural lobe, *ll* left apertural lobe, *rl* right apertural lobe, *vp* ventral process of the lef lobe.

PLATE XXXV


ad
vp
A1
vp
B1
vp
B2
vp
ad
A2
ll
vp
D1
ll
vp
D2
rl
ll
vp
D3
ll
inc
vp
C1
rl
ll
vp
D4
ll
vp
C2

25—30°. The ventral wall in proximal thecae is completely straight, without any traces of geniculation.

The metathecal part in most proximal thecae (Pl. XXXV, Figs. A_1-A_2) is provided with two lateral apertural lobes almost identical in size. The right lobe is almost semicircular in outline and consists of some 6 fuselli dorsally gathered into a dorsal node and ventrally forming an adapertural plate (A_1, *ad*), formed by the last two fuselli which are attached to the ventral wall of metatheca instead of being gathered into a ventral node.

The outer surface of the right lobe is nearly flat. The left lobe is, in contrast, distinctly convex and terminates ventrally in a short ventral process (Pl. XXXV, Fig. A_1-A_2, *vp*). The lobe consists of some 6—7 fuselli. The details of the structure of this lobe in another proximal theca is shown in Figs. D_1-D_4. As compared with the right, the base of the left lobe forms a distinct lateral geniculation resulting in a convex shape of the left lobe (Figs. D_1, D_3-D_4). The ventral process is formed by one or two very short wedge-shaped fuselli.

Fuselli of the left lobe are gathered dorsally into a dorsal node and ventrally they converge towards the anteroventral margin except for an incomplete fusellus of the ventral process which is superimposed on the lobe (Pl. XXXV, Figs. D_1-D_2). It may be found, by the examination of specimens in ventral view, that the ventral process hangs downwards without overlapping the opposite lobe (Fig. D_3-D_4).

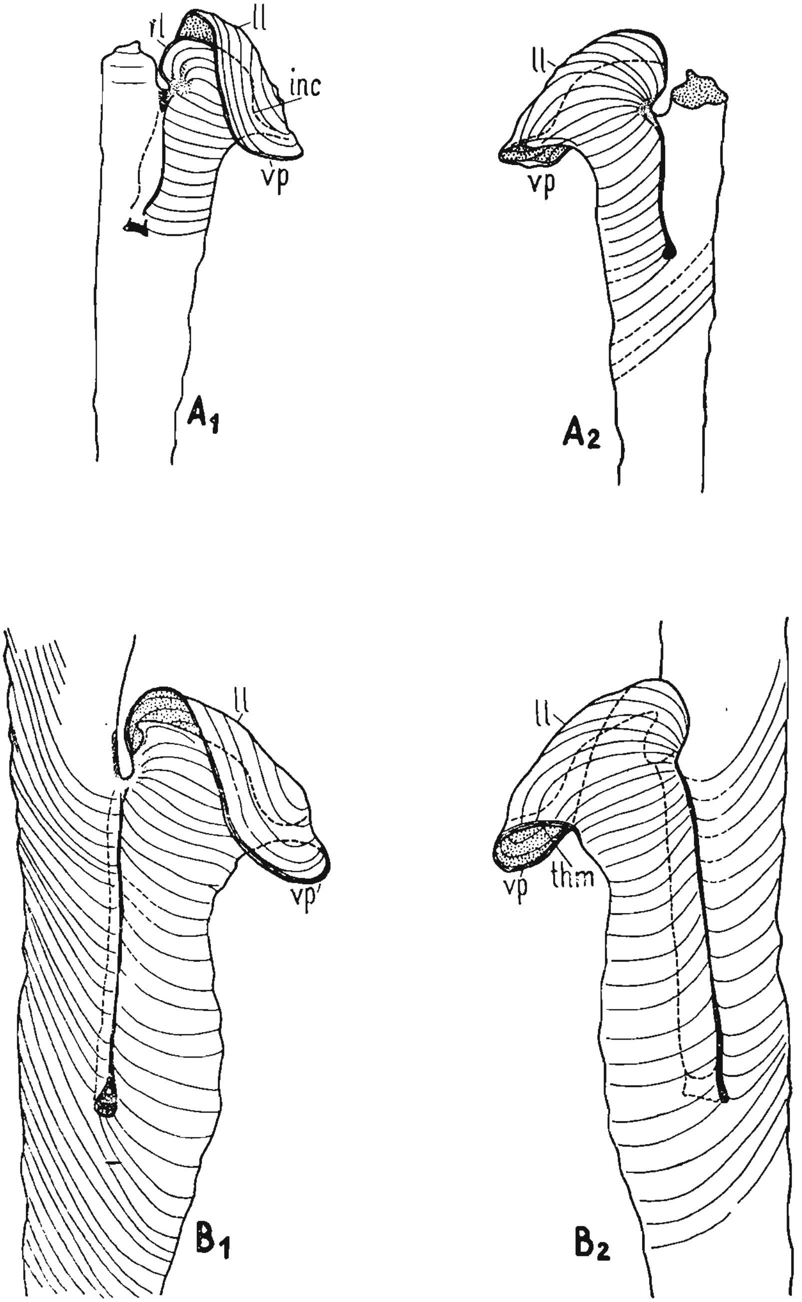
Judging from the specimens observed, the size of both apertural lobes is nearly the same, the left lobe is, however, slightly ventrally shifted in relation to the right lobe (comp. especially Pl. XXXV, Figs. A_2, D_2).

In proximal thecae, disposed somewhat more centrally in the rhabdosome (Pl. XXXV, Figs. B_1, B_2), the degree of asymmetry of apertural lobes slightly increases. The upper margin of the left lobe distinctly extends above the right lobe and its shovellike ventral process is stronger and more incurved. The right lobe is devoid of the ventral adapertural plate and ends freely (Fig. B_1). The outline of this lobe which consists of some 5—6 fuselli is semicircular with still complete ventral and upper margins. The left lobe is distinctly incurved over the aperture and consists of 7—8 fuselli. The ventral process of the latter shows the tendency to a slight overlap of the ventral margin of the right lobe

Plate XXXVI

Cucullograptus hemiaversus Urbanek. Structure of more distal thecae. *A* upper part of a medial (central) theca in reverse (*1*) and obverse (*2*) aspects; *B* upper part of a distal theca in reverse (*1*) and obverse (*2*) aspects (S. 200, Rewal); ca. × 63. *inc* incision seen in right through transparent left apertural lobe, *ll* left apertural lobe, *rl* right apertural lobe, *vp* ventral process of the left lobe, *thm* thickened margin of the left apertural lobe.

PLATE XXXVI



(Fig. B_1). Metatheca in medial thecae is inclined towards the main axis at an angle of 15—20°.

Thecae, shown in Pl. XXXV, Figs. C_1-C_2 and Pl. XXXVI, Figs. A_1-A_2, are placed still more distally. They preserve the general appearance of proximal thecae, expressed by their slenderness and by the presence of a straight ventral wall but display a distinct asymmetry of the apertural apparatuses. The latter feature is manifested by the hypertrophy of the left lobe which is incurved over the right one and overlaps it ventrally over some 2/3 of its length (*tr.*). The overlapping portion of the left theca is formed mostly by a strongly incurved ventral process (*vp*) and, in part, by an incurved upper margin of the lobe. The hypertrophied left lobe consists of some 9—10 fuselli which are dorsally partly gathered into a node and partly terminate freely at the border of the left lobe. On the ventral margin, the majority of fuselli converge towards the anteroventral border of the lobe. Only the fuselli, making up the ventral process, end freely.

The outline of the right lobe in these thecae distinctly differs from that in thecae placed more proximally, i.e. in the overlapped ventral part of the lobe (covered by the opposite apertural lobe), the free margin is provided with a shallow incision (comp. Pl. XXXV, Figs. C_1-C_2; Pl. XXXVI, Figs. A_1-A_2, *inc*, where the trace of the boundary of the right lobe is indicated by zigzag lines). The formation of this incision seems to be connected with a certain degree of the development of asymmetry of apertural apparatus and most probably is closely correlated with a degree of overlap of apertural lobes. The greater the degree of overlap in the hypertrophied left lobe, the more notched is the margin of the right lobe.

In Fig. 15, the structure of apertural apparatus in most proximal thecae with a smaller degree of asymmetry and without the overlap of lobes (A_1-A_2) are compared with those in proximal thecae which are more centrally placed in the rhabdosome and display a relatively greater asymmetry, as well as a certain degree of overlap of the lobes (C_1-C_4). In the former case, the margin of the right lobe is still entire, the outline of the lobe being almost semicircular (Fig. 15, A_1). In the latter case in which the degree of overlap is greater (reaches approximately the stage, represented by a similar theca in Pl. XXXVI, Fig. B), the right lobe has a distinct apertural incision (*ai*), situated ventrally on the lobe. It is especially well seen on the specimen in Fig. 15, C_1 in which the overlapping left lobe has been removed with a needle (C_3, C_4). The incised margin of the right lobe shows the presence of a slightly extroverted apertural lip (*al*), formed by an attenuated periderm, incurved upon the wall of the lobe. A certain light may be shed on the significance of this peculiar structure by the comparison with similar structures, found in apertural apparatuses of other monograptids (comp. Urbanek, 1960, pp. 187—193).

The notched appearance of the right lobe is most probably connected with the overlapping position of the opposite lobe. In some sense, the apertural incision in the right apertural lobe produces more space for the left lobe which is hypertrophied and strongly incurved over the ventral part of the aperture (overlapping). This apertural incision may be compared with "notched" apertural processes, described in *Saetograptus chimaera cervicornis* Urbanek in which the posterior margin is usually serrated by a number of small incisions (Urbanek,

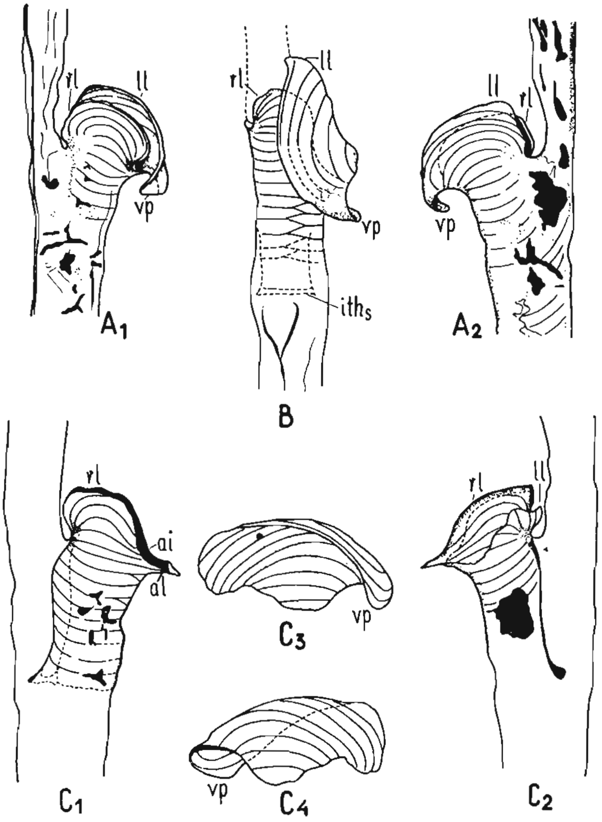


Fig. 15. — *Cucullograptus hemiaversus* Urbanek. Structural details of apertural apparatus: A_1-A_2 upper part of a proximal theca seen in reverse and obverse aspects and showing complete right apertural lobe with only small overlap by the left one, *B* ventral view of proximal theca with greater degree of overlap of the right apertural lobe by the left one, *C* upper part of theca with left apertural lobe removed by the needle preparation to show the internal structure of apertural apparatus, C_1 in reverse aspect, C_2 in obverse aspect, C_3-C_4 isolated left apertural lobe in reverse and obverse aspects (S. 200, Rewal), ca. × 63.

ai apertural incision in the left lobe, *al* extroverted apertural lip in the right apertural lobe, *iths* internal thecal septum, *ll* left apertural lobe, *rl* right apertural lobe, *vp* ventral process of the left apertural lobe.

1960, pp. 188—190, Fig. 17). The formation of these incisions were ascribed by Urbanek to a partial reduction of the peridermal membrane, due to an inhibition of the peridermal growth. It seems also doubtless that the formation of an apertural incision in the right apertural lobe in *Cuc. hemiaversus* is an expression of an early stage of reduction of this lobe. This conclusion is supported by such facts as more advanced reduction stages of this lobe, manifested by more distal thecae of *Cuc. hemiaversus* and a yet more vestigial nature of this lobe in the representatives of *Cuc. aversus* group described below (comp. p. 492 and p. 506).

The presence of a slightly extroverted apertural lip on the margin of a partly reduced right lobe is most probably also a vestigial structure which may be compared with the tubular folding of the anterior margin of apertural processes in the *Saetograptus chimaera* group, formed in its representatives by an attenuated peridermal membrane (Urbanek, 1960, p. 189).

For a probable origin of such incurved or slightly rolled apertural lip — see discussion on p. 506, in which a similar but much more extreme structure in *Cuc. aversus rostratus* is dealt with.

The most distal thecae of *Cuc. hemiaversus* are shown in Fig. 16, A_1-A_2 and in Pl. XXXVI, Figs. B_1-B_2. The total length of these thecae reaches some 2.36—2.11 mm, the prothecal part being some 1.58—1.40 mm long and the metathecal 0.95—0.70 mm long. The prothecal part occupies in these thecae about 59—60% of their total length.

A steady increase in the length of the metathecal portion is a remarkable feature of astogeny in *Cuc. hemiaversus*, illustrated by a series of thecae, shown in Pls. XXXV and XXXVI. Metatheca is inclined towards the main axis at an angle of 8—10°.

The width at the base of protheca is 0.36—0.23 mm and at the base of metatheca some 0.28—0.20 mm. The presence of a distinct geniculation of the ventral wall, situated at the boundary of protheca and metatheca is a feature of the distal thecae, the more proximal thecae being completely straight.

The apertural apparatus displays a distinct asymmetry, expressed by the hypertrophy of the left lobe which is strongly incurved over the aperture and overlaps the right lobe over $^2/_3$ of its length (*tr.*). The left lobe is made up of some 8 fuselli which dorsally and ventrally converge into the lower margin of the lobe (Fig. 16, A_2 and Pl. XXXVI, B_2). The anteroventral margin towards which fuselli converge is slightly thickened (Pl. XXXVI, Fig. B_2).

The right apertural lobe which consists of some 4 fuselli is deeply incised ventrally, being flat or even slightly incurved over the aperture and rather narrow as compared with a relative size of the same lobe in more proximal thecae. The ventral part of the right lobe is covered by the left lobe, and only dorsal 1/3 of its length (*tr.*) is exposed in a lateral view. In a ventral view, however, the entire right lobe is covered by the left one. In this connection, it is difficult to establish safely the presence of apertural lip on the former, but this is indicated by a dark marginal band, observable on transparent specimens.

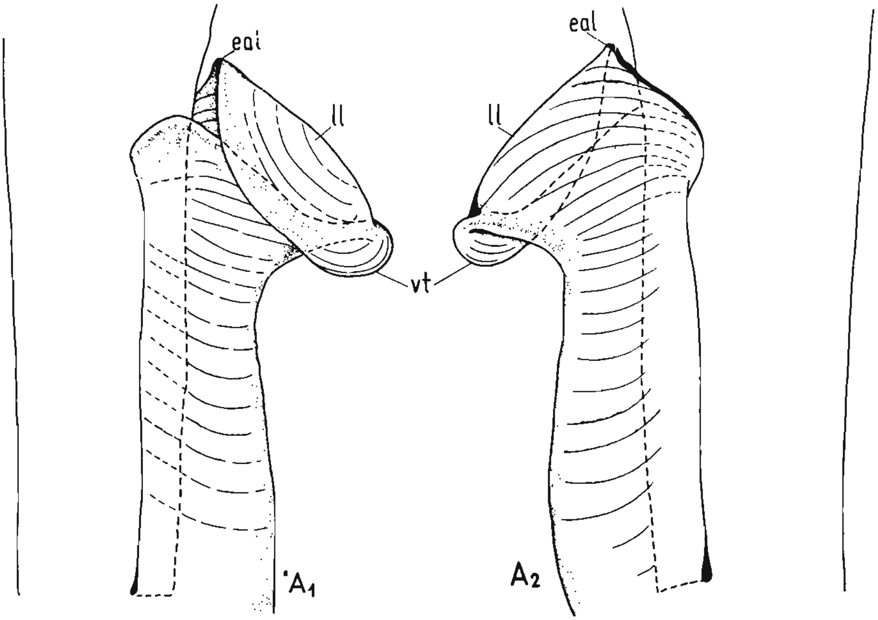


Fig. 16. — *Cucullograptus hemiaversus* Urbanek. Metathecal part of a most distal theca from reverse (A_1) and obverse (A_2) sides (Mielnik, depth 952.9—952.6 m), ca. × 63.

eal eaves of the left apertural lobe, *ll* left apertural lobe, *vt* ventral termination of the left apertural lobe.

The most distal theca is shown in Fig. 16, A_1-A_2. In spite of a steady tendency to the reduction of the right lobe, in the course of astogeny of *Cuc. hemiaversus*, this lobe is still present in most distal thecae. This may indicate that the stage of a full reduction of the lobe, or its transformation into an apertural lip, i.e. a vestigial form of the right apertural lobe in *Cuc. aversus* group, has not, in *Cuc. hemiaversus*, been reached so far. However, in most distal thecae, this lobe was transformed into a narrow (*long.*) list, almost entirely covered by the left lobe (a specimen, shown in Fig. 16, A_1-A_2, seems to be secondarily deformed and the primary overlap of apertural lobes was probably greater). This narrow list, provided with a shallow ventral incision, represents the reduced stage of the right apertural lobe of distal thecae.

Stratigraphic range. — In the Mielnik core, the first appearance of *Cucullograptus hemiaversus* has been recorded at a depth of 959·9—959·5 m where its scanty remains were associated with a rather rich population of *Lobograptus scanicus amphirostris* n. subsp. Above this level *Cuc. hemiaversus* becomes more common and continues up to a depth of some 950·0 m, although displaying any mass occurrence. Through this interval, it is associated with *L. exspectatus exspectatus* Urbanek, *L. exspectatus bicornis* n.sp., *Neodiversograptus beklemishevi* Urbanek, *Plectograptus* sp., *Holoretiolites mancki* (Münch), *Pristiograptus dubius* (Suess) and with uncertain fragments of *Monoclimacis haupti* (Kühne). Between the levels of 950.0 and 938.5 m, the graptolite fauna becomes poor, and *Cuc. hemiaversus* temporarily disappears. After the reappearance it occurs once more in samples,. from depths of 938·5—938·0 m, associated with *Saetograptus fritschi* cf. *fritschi* (Perner), *Pristiograptus tumescens* (Wood) and *Cuc. aversus* cf. *aversus* (Eisenack). Moreover, *Pristiograptus dubius* (Suess) and *"Pristiograptus" bohemicus* (Barrande) continue almost throughout the range of its distribution and are commonly associated with *Cuc. hemiaversus*. A depth of 938·0 m is accepted here as the upper limit of distribution of *Cuc. hemiaversus* in the Mielnik core.

In the Baltic drift material, the species in question has been found only in erratic boulder S. 200 (Rewal) in which it is associated with *Pristiograptus dubius* (Suess) and *Saetograptus chimaera* (Barrande), probably with its subspecies, *cervicornis* Urbanek and *salveyi* Hopkinson (comp. Urbanek, 1960, p. 215). This assemblage may indicate its derivation rather from the lower part of the distribution range of *Cuc. hemiaversus* as found in the Mielnik sequence.

Systematic position. — The earlier opinion "that this species belongs to the same evolutionary trend as *Cucullograptus aversus* (Eisenack), but that it represents a lower morphological stage expressed only in partial reduction of the right lobe and smaller hypertrophy and overlap of the left lobe" (Urbanek, 1960, p 216) seems to be now supported by a more complete knowledge of the species in question.

It seems certain that *Cuc. hemiaversus* is the most primitive of all known members of a lineage which, according to our present knowledge, consists of the following links: *Cuc. hemiaversus* Urbanek — *Cuc. aversus aversus* (Eisenack) — *Cuc. aversus rostratus* Urbanek. It is also a species which combines certain characters of the *aversus* lineage with more primitive features inherited from the "stem", symmetric cucullograptids.

Morphologically, these transient features are seen in astogeny of the thecal characters of *Cuc. hemiaversus*. The occurrence of proximal thecae with a very small degree of asymmetry and a complete right apertural lobe and of distal thecae with a distinct asymmetry of the apertural apparatus and a "notched" right lobe, prove that the species under study is biform in character. This biformism results probably from a distal introduction of a new character, responsible for the development of asymmetry of apertural apparatuses in thecae. This newly introduced character shows an incomplete expressivity and penetrance, resulting in a regular proximal decrease in asymmetry.

The distal introduction of this novelty is suggested by the fact that the greatest degree of expressivity of this new character is noted at the distal end of rhabdosome and from this it decreases towards the proximal end. The low degree of expressivity of this phylogenetic novelty is observed when compared with that in more advanced members of the same lineage (*Cuc. aversus aversus* (Eisenack), *Cuc. aversus rostratus* Urbanek) displaying a greater asymmetry and overlap of apertural lobes, connected with an almost complete reduction of the right lobe.

The incomplete penetrance of the introduced character is seen by the comparison with *Cuc. aversus aversus* (Eisenack) in which all thecae throughout the rhabdosomes are completely asymmetric. The biformism of thecae in *Cuc. hemiaversus* is, therefore, most probably connected with a low degree of expressivity of a phylogenetically new character, introduced distally and simultaneously displaying an incomplete penetrance (Urbanek, 1960, p. 194).

In connection with the interpretation, suggested above, a probable ancestor of *Cuc. hemiaversus* may be looked for in uniform cucullograptids with thecae showing completely symmetric apertural lobes. This indicates a common ancestry with the "stem lobograptid", i.e. *Lobograptus simplex* Urbanek. The latter meets a majority of requirements that are necessary for such an ancestral form, but "morphological differences between *Lobograptus simplex* and *Cucullograptus hemiaversus* are stronger than those occurring in the other members of that lineage. It is not out of question that new forms will be discovered in future which will fill up a certain discontinuity between these two species" (Urbanek, 1960, p. 180). This opinion is now supported by certain new stratigraphic and morphological data. A rather wide gap in their stratigraphic distribution in the Mielnik core (some 56 m of strata, separating the last appearance of *L. simplex* from the first appearance of *Cuc. hemiaversus*!) speaks for the presence of at least one still unknown intermediate form between *L. simplex* and *Cuc. hemiaversus*. The morphological data also speak in favour of such a hypothesis.

Particularly noteworthy is the structure of apertural lobes in the most proximal thecae of *Cuc. hemiaversus* which are the least modified thecae in the rhabdosome and, to a certain extent, indicate the degree of their development in a supposed ancestral form. Judging from the structure of the right lobe which was probably little affected by secondary modifications (Pl. XXXV, Figs. A_1, B_1, D_3, D_4), this immediate ancestor of the *hemiaversus-aversus* lineage reached a slightly higher degree of elaboration (the presence and enlargement of the adapertural plate) of lobes than that, represented by *L. simplex* (comp. Pl. XV, Fig. 1; Pl. XVI, Figs. A-B). In addition, this form most probably has already lost the traces of the primary dorsal curvature in the proximal part of rhabdosome and, to a certain degree, gracilized its sicula. Through such a hypothetical intermediate form the *aversus* lineage was probably linked with the "stem lobograptids", forming the following succession: *Lobograptus simplex* — unknown transient form — *Cucullograptus hemiaversus*. On the other hand, the latter species seems to be directly related to *Cuc. aversus aversus* (Eisenack) which probably emerged from *hemiaversus* populations by a further development of asymmetry in apertural apparatus, manifested by its greater expressivity and a complete penetrance (comp. p. 351). In its stratigraphic appearance and distribution in the Mielnik core, *Cuc. hemiaversus* precedes the representatives of a somewhat uncertain and more primitive *Cuc. aversus* cf. *aversus* (Eisenack) and a more progressive *Cuc. aversus rostratus* Urbanek (comp. also discussion on p. 517).

Cucullograptus aversus cf. *aversus* (Eisenack, 1942)

(Fig. 17)

Material. — Scanty fragments of proximal and medial thecae from the Mielnik deep-boring, found at a depth of 940.5—924.6 m, with their periderm well-preserved. Specimens unflattened or only slightly flattened. Siculae and distal thecae unknown.

Description. — The specimens preserved are fragmentary and, therefore, the length of thecae cannot be estimated, although at the base of protheca they are 0.06—0.08 mm wide and reach 0.10—0.16 mm in the metathecal part. The length of metatheca amounts to about 0·10—0·20 mm.

The metathecal part is inclined towards the main axis of theca at an angle of 10—20°, being completely adnate up to the base of the prothecal part in an adjacent theca and provided with an apertural apparatus. The latter consists of a hypertrophied left apertural lobe (0.23—0.35 mm long), strongly incurved over the aperture of theca. In more proximal thecae (Fig. 17, A-B) the left apertural lobe covers the aperture from the top only, the lateral side of the apertural margin being exposed and the apertural lip visible beneath the lobe (*al*). The presence of a complete apertural lip on the reverse apertural margin indicates that the form in question reached the *aversus* stage of the degree of elaboration of the apertural apparatus. In other proximal thecae, the apertural lip is hidden beneath a slightly more overlapping left apertural lobe and visible through it on transparent, bleached specimens (Fig. 17, C-F, marked by broken lines).

The left apertural lobe is disposed almost right on the apertural opening, never distinctly domed as in *Cuc. aversus rostratus.* In this respect, the shape of the lobe resembles rather the left apertural lobes in *Cuc. aversus aversus*, as figured by Eisenack (1942, Pl. 3, Figs. 1, 2, 8).

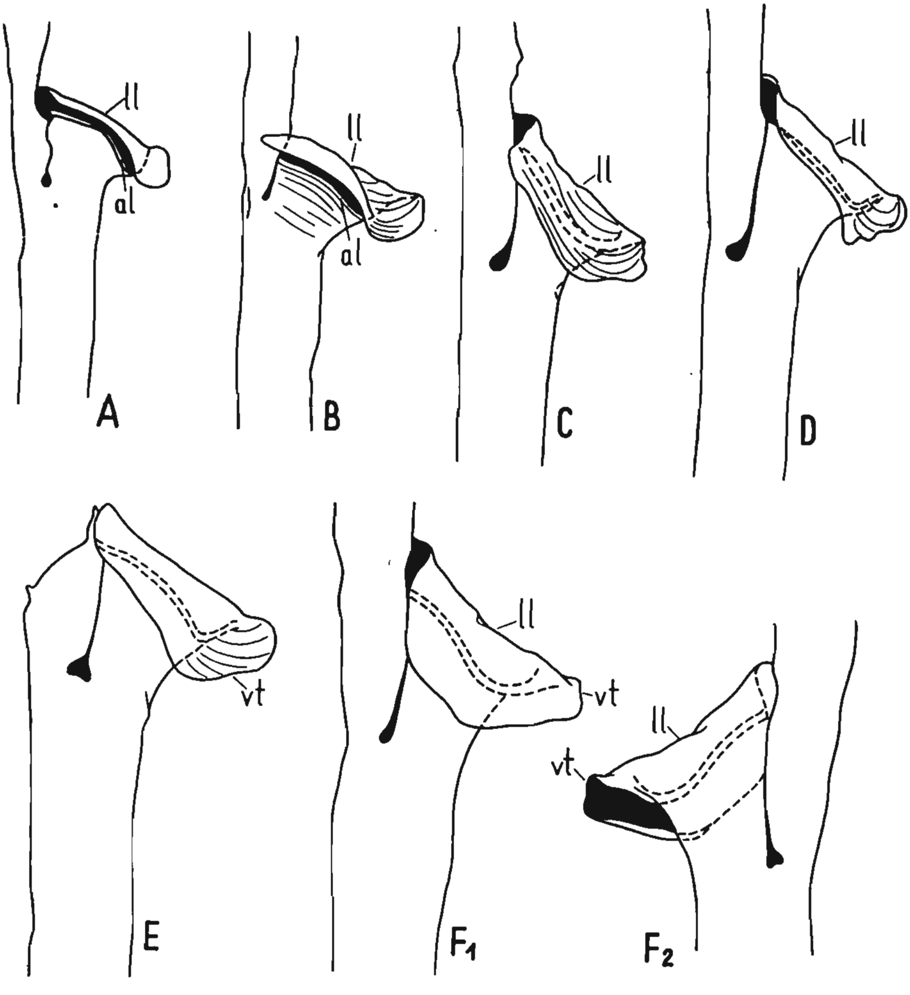


Fig. 17. —*Cucullograptus aversus* cf. *aversus* (Eisenack). Structure of proximal thecae: *A*-F_1 in reverse view, F_2 in obverse view (Mielnik, depth 925.1 m), ca. × 63. *al* apertural lip, *ll* left apertural lobe, *vt* ventral termination of the left lobe.

The dorsal line of the lobe is almost straight, the ventral forms a blunt and wide, rounded outgrowth. This is simply the ventral part of the lobe itself and not an incipient rostral process. The lower margin of this ventral termination is only slightly turned up (Fig. 17, F_2), thus forming a gular process at its very incipient stage of development. The latter character occurs only in thecae more medially placed and this incurved margin is absent at all from the most proximal ones (A-B).

Stratigraphic range. — The distribution range of *Cuc. aversus* cf. *aversus* in the Mielnik core (940.5—924.6 m) overlaps with an upper limit of the vertical distribution of *Cuc. hemiaversus* and with a lower limit of the distribution of *Cuc. aversus rostratus.* In a sample found at a depth of 938·5—938·2 m, the form in question is associated with the former species, and in a sample from a depth of 925.1—924.6 m — with the latter subspecies. It suggests a largely intermediate stratigraphic position between the zone of occurrence of *Cuc. hemiaversus* and that of *Cuc. aversus rostratus. Cuc. aversus* cf. *aversus* appears just below the base of the *leintwardinensis* zone (some 4 m below) and continues through it or reaches somewhat higher. Other associated graptolites are: *Saetograptus leintwardinensis* (Hopkinson), *S. fritschi* (Perner), *Lobograptus cirrifer* n.sp., *Pristiograptus dubius tumescens* (Wood), *P. dubius* (Suess) and "*P.*" *bohemicus* (Barrande).

Systematic position. — The elucidation of the systematic position of incomplete remains, described above, may be attained first of all by comparing them with *Cuc. aversus aversus* (Eisenack, 1942). They resemble Eisenack's form in the following two respects: 1) a transformation of the right apertural lobe into an apertural lip, 2) an absence of the rostral process.

In the latter character they differ from *Cuc. aversus rostratus*, in which thecae of a comparable size are already provided with incipient rostral process (comp. Fig. 17, E-F, and Pl. XXXVIII, Fig. D-F). Despite the lack of more distal thecae in *Cuc. aversus* cf. *aversus*, it seems rather safe to generalize that this form, as a true *Cuc. aversus aversus*, was devoid of rostral processes on the left apertural lobe. On the other hand, some minor details distinguish our *Cuc. aversus* cf. *aversus* from Eisenack's type-form. These are: 1) a lack of some isolation of the terminal part of metathecae, observable in proximal and distal thecae of *Cuc. aversus aversus* (comp. Eisenack, 1942, Pl. 2, Figs. 1, 2, 8, and Eisenack's note on p. 34), and in a contrasting adnate position of metatheca, 2) a slight degree of overlap of the left apertural lobe which, in most proximal thecae, does not entirely cover the aperture. The latter character resembles rather the conditions, described by Kühne for proximal thecae in his *Monograptus aversus* cf. *aversus* Eisenack (1955, p. 391, Fig.13, B, D) than the conditions, existing in a true *aversus* in which the incurvature of the lobe seems to be stronger.

Following the scarcity of the material obtained, it is very difficult to evaluate these differences. It seems, however, most important that our *Cuc. aversus* cf. *aversus* is earlier and more primitive subspecies than *Cuc. aversus rostratus* and has its apertural apparatus in about the same stage of elaboration as in the typical *Cuc. aversus aversus* of Eisenack. Some minor differences in shape of lobes may probably be ranked as infrasubspecific and possibly depending on some zonal or geographic differences.

Cucullograptus aversus rostratus Urbanek, 1960
(Figs. 18—24; Pls. XXXVII—XLII; Pl. XLVII, Figs. 5—10)

1954. *Monograptus aversus* Eisenack; A. Urbanek, Observations..., pp. 297—300, Figs. 9—12.
1958. *Cucullograptus aversus* (Eisenack); A. Urbanek, Monograptidae..., pp. 70—72, Figs. 36—39.
1960. *Cucullograptus aversus rostratus* Urbanek; A. Urbanek, An attempt..., pp. 216—218, Pl. 3, Figs. 1—5; Text-figs. 13G, 14D, 21 A-C.

Material. — Numerous fragments of rhabdosome, including siculae, proximal and distal parts have been etched from samples, taken from the Mielnik boring (a depth of 934.7—920.8 m). Best-preserved, unflattened specimens were obtained from a sample taken at a depth of 924.4—924.1 m. Known also from erratic boulders S. 121, Jarosławiec and S. 205, Ustka. Material obtained from both sources enable one to analyse a minute structure of thecae and their development.

Description. — Sicula almost straight, short (0.80—1.08 mm in length), slender and, following its stable width (Pl. XXXVII, Figs. G-H, K-N), nearly tubular.

Prosicula is some 0.49—0.60 mm long and at the aperture some 0.10—0.12 mm wide. Young prosicula (Pl. XXXVII, Figs. A-C) is devoid of any black ring and provided only with longitudinal threads (up to 6 in number) which converge apically into a nema (Fig. I). Helical line (spiral thread), probably due to the poor preservation stage, indistinguishable. Moreover, adult prosicula is provided with a black ring (r_1), situated approximately in the middle of a prosicular segment, 0.15—0.20 mm from the boundary with metasicula (Figs. D-N). The black ring is, however, still lacking in the early metasicular stage (Figs. B-C), appearing only during its later growth stages (comp. Figs. D). Its formation seems to be, therefore, somewhat delayed.

Metasicula is rather short, about 0.30—0.48 mm in length and with an almost uniform width of some 0.13—0.14 mm throughout its length. Usually, it is provided with a black ring (r_2) which is often situated right on the boundary of pro- and metasicula (Pl. XXXVII, Figs. D-L), sometimes being, however, separated from it by a number of fuselli (Figs. M-N). In some cases, metasicula is provided with two such rings (r_2, r_3; Pl. XXXVII, Fig. N), or is completely devoid of the black ring (r_1 being only present on prosicula). Figure 18 shows successive stages in the development of metasicula. Virgella may be formed rather early as indicated by Fig. 18, A, C, or delayed in formation as indicated by a specimen in Fig. 18, B.

Young metasicula is still devoid of black rings whose formation took place during later growth stages. Advanced metasicula in the "lacuna

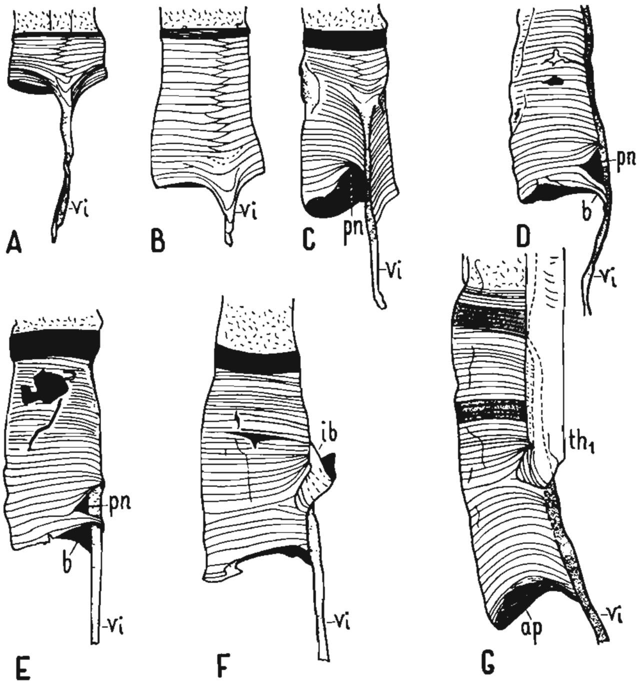


Fig. 18. — *Cucullograptus aversus rostratus* Urbanek. Details of fusellar structure of metasicula: *A-B* early stages in formation of virgella showing lower or higher position of its onsets, *C* stage of open primary notch (sinus stage), *D-E* stage of closed primary notch (lacuna stage) in ventrolateral (*D*) and lateral views (*E*), *F* an early stage in formation of initial bud, *G* adult metasicula and basal part of the first theca (the same specimen as Fig. *N* on Pl. XXXVII) (Mielnik, *A*, *B*, *D-G* depth 925.1—924.8 m; *C* depth 921.5—921.0 m), ca. × 85.

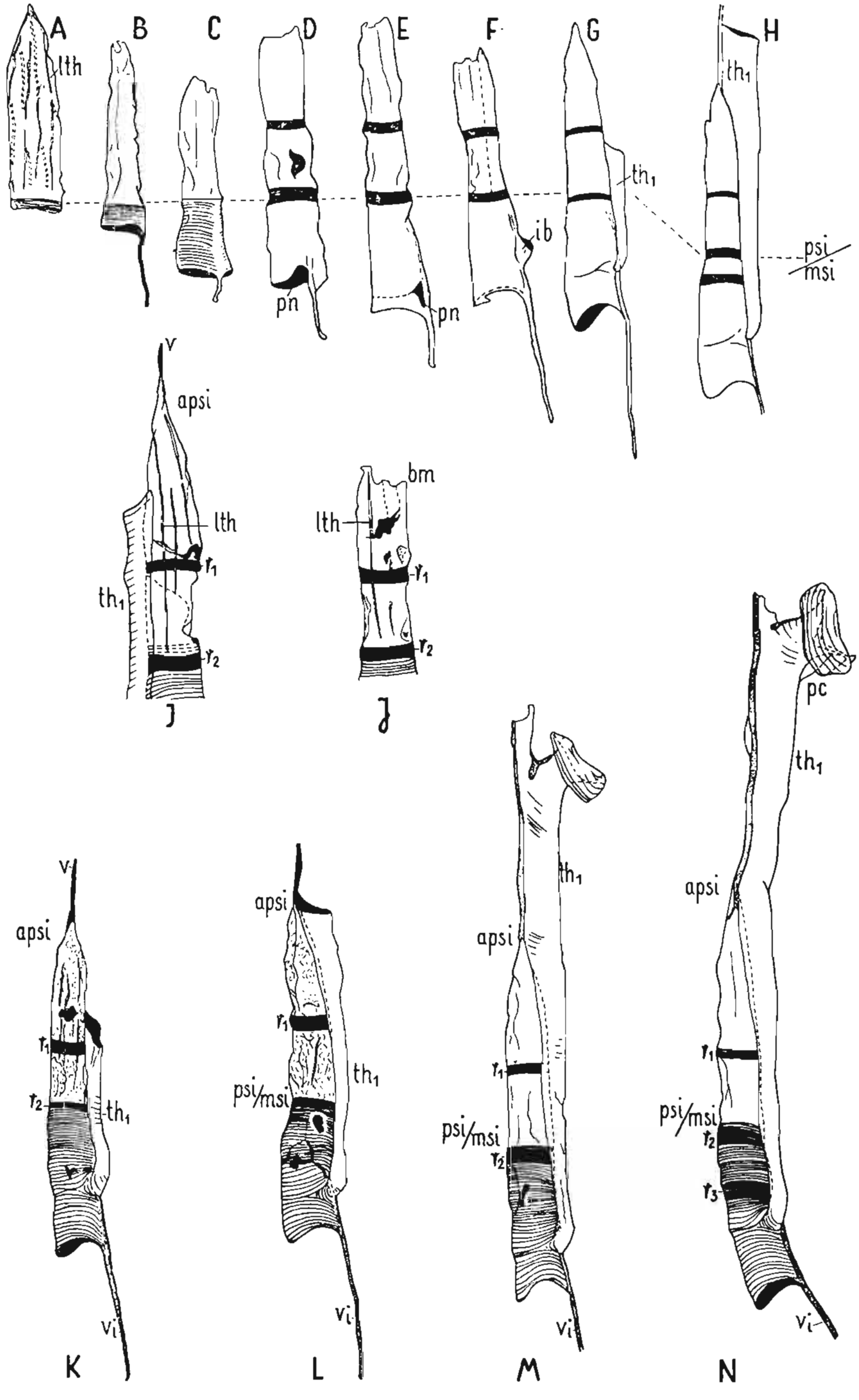
ap aperture of metasicula, *b* fusellar bar closing the primary notch, *ib* initial bud, *pn* primary notch, *vi* virgella.

Plate XXXVII

Cucullograptus aversus rostratus Urbanek. Development and structure of sicula and first theca. *A-G* successive growth stages of sicula from early to adult metasicula stage (*B-G* seen from reverse side); *H* adult sicula with advanced growth stage of the first theca; *I-J* prosicular segments showing arrangement and position of longitudinal threads and black rings; *K-L* structure of siculae with early (*K*) and more advanced (*L*) growth stage of the first theca; *M-N* siculae with complete first thecae showing short (*M*) and longer (*N*) free part of the first theca (Mielnik, *A-C*, *E*, *I*, *K-N* depth 925.1—924.8 m; *D*, *F-H*, *J* depth 921.5—921.0 m); *A-H*, *K-N* ca. × 50;; *I-J* ca. ×63.

apsi apex of prosicula, *bm* secondarily broken margin of prosicula, *lth* longitudinal threads. of prosicula, *psi/msi* boundary between pro- and metasicula, *pn* primary notch, *pc* pectoral crest of theca, r_1-r_3 successive black rings of sicula, *v* virgula, *vi* virgella.

PLATE XXXVII



stage" (open primary notch) may, however, have both the first (prosicular) and second black rings (r_1+r_2) (comp. Fig. 18, C, and Pl. XXXVII, Fig. D).

The formation of the initial bud proceeds according to the usual monograptid pattern, following the "open notch stage" (Fig. 18, C, and Pl. XXXVII, Fig. D), and "closed notch stage" (sinus stage), visible in Fig. 18, D-E and Pl. XXXVII, Fig.E. The lower border of the initial bud is situated some 0.07—0.17 mm from the lateral margin of the aperture in the adult metasicula. There is no adapertural expansion of the width of theca, the metasicula being of same width throughout. The aperture of the adult metasicula is almost straight, with only a small dorsal elevation or a slight dorsal lip which does not exceed 0.03—0.06 mm in length (*long.*). Virgella is usually thin and long, extending well beyond the aperture of metasicula. The ratio of length in the prosicular and metasicular parts is a remarkable feature of sicula in *Cuc. aversus rostratus*. It ranges from 1.83 to 1.25 mm and, as compared with the prosicular one, indicates a distinct shortening of the metasicular segment of sicula. The part of the metasicular portion in a total length of sicula decreases to some 44.4—35.4 per cent. These conditions markedly differ from those, described previously for primitive cucullograptids (e.g. *L. simplex*; comp. Table 3, p. 316). A probable comparative-anatomical significance of this reduction in the size of metasicula is discussed in the general part (pp. 316—320) of this monograph.

The first theca starts some 0.06—0.28 mm from the prosicular aperture. The origin of the initial bud is typically monograptid and the first fusellar strips of this theca are disposed in the outer corner of the primary notch (Fig. 18, F-G and Pl. XXXVII, F). Further growth stages of the first theca are shown in Pl. XXXVII, Figs. G, L, M, and those of the fully grown thecae — in Figs. M-N. The length of the first theca varies considerably from some 1.54 to 1.29 mm (comp. Figs. M, N). The first theca may be less (Fig. M) or more (Fig. N) elongated. This is especially true for a free part of the theca, stretching above the apex of sicula. In the former case, this free part is only 0.50 mm long, in

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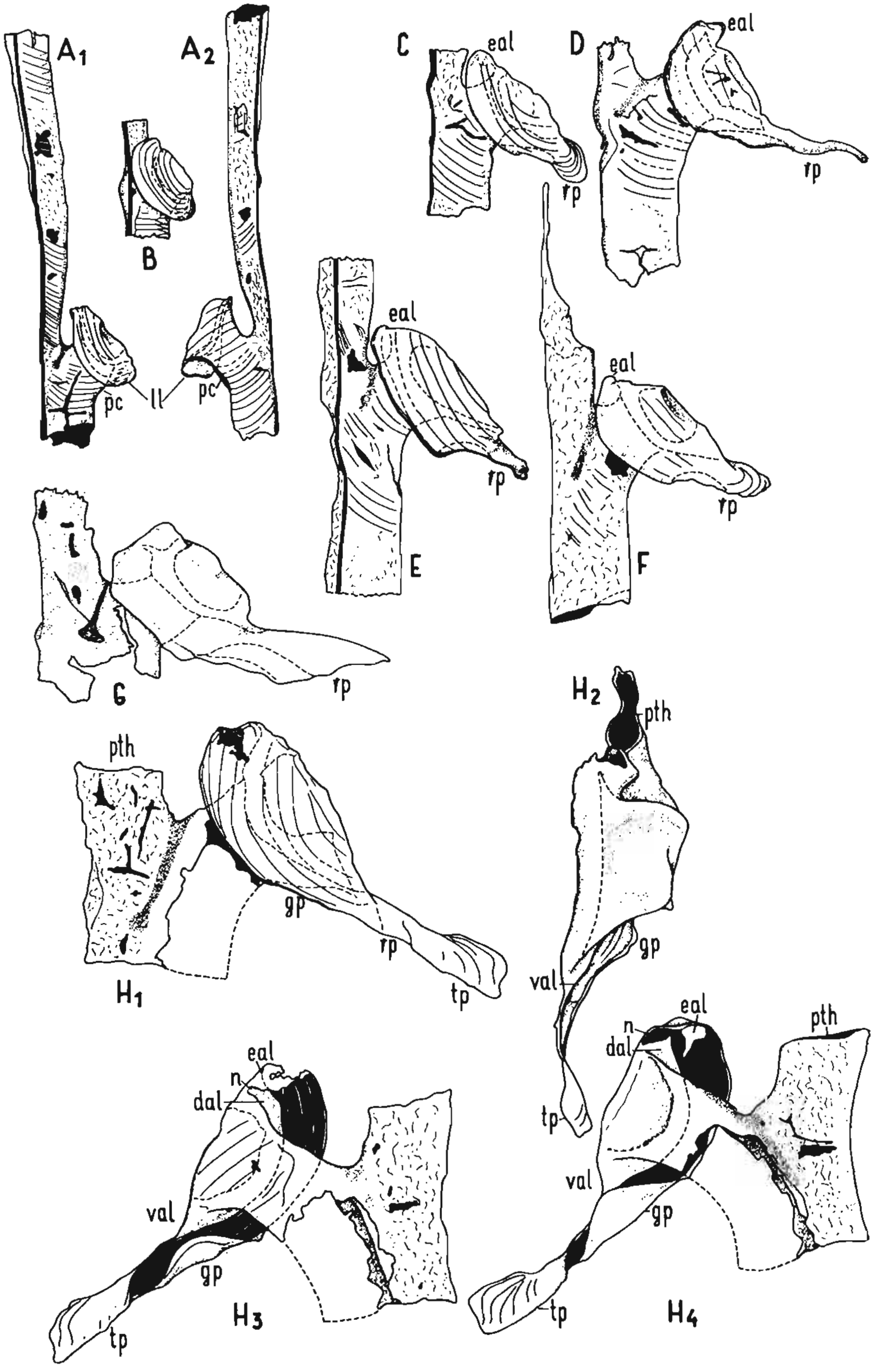
Plate XXXVIII

Cucullograptus aversus rostratus Urbanek. Structure of thecae in specimens from erratic boulders S. 205 representing lower stage in morphological differentation, A_1-A_2 fragment of a proximal theca in reverse (A_1) and obverse(A_2) views; *B* metathecal part of another proximal theca in lateroventral view; *C*-*F* series of proximal thecae arranged successively and seen in reverse aspect; *G* metathecal part of a more distal theca in reverse aspect; H_1-H_4 metathecal part of a distal theca with rostral process showing slight spiral coiling, in reverse (H_1), obverse (H_3, H_4) aspects and in the top view (H_2). S. 205, Ustka); ca. × 66.

dal dorsal prolongation of the apertural lip, *eal* dorsal eaves of the apertural lobe, *gp* gular plate, *ll* left apertural lobe, *n* notch separating the eaves from the main lobe, *pc* pectoral crest, *pth* prothecal part of an adjacent theca, *rp* rostral process of the left lobe, *tp* shovellike termination of the process, *val* ventral prolongation of the apertural lip.

PLATE XXXVIII



the latter — it reaches some 0.80 mm in length. The metathecal part is very short (0.10—0.15 mm), slightly isolated, inclined at an angle of some 60° and provided with a strongly elaborated and asymmetric apertural apparatus. This is formed by a strongly hypertrophied left apertural lobe, incurved over the aperture and covering it completely (Pl. XXXVIII, Fig. A; Pl. XXXIX, Fig. A). The number of fuselli, making up the left apertural lobe, may be estimated at 8—9, the 2 most marginal ones being only very narrow strips. The ventral termination of the lobe (*vt*) forms an incurved (to the left and downwards) process, while its dorsal termination is a slightly marked extension, an incipient eaves of the left lobe. The latter is about 0.20—0.28 mm long (*tr.*) and 0.08—0.14 mm high.

The internal apertural opening is situated inside the lobe and provided, over its entire right margin, with an extroverted apertural lip. This is visible through a bleached and, therefore, transparent left apertural lobe (indicated by broken lines) and may be exposed after the removal, by a needle, of the left apertural lobe (Pl. XLII, B_1, *al*). This extroverted apertural lip, ventrally and dorsally connected with and covered by the left apertural lobe, seems to represent a vestigial right apertural lobe, reduced and transformed into a narrow extroverted margin (comp. p. 506).

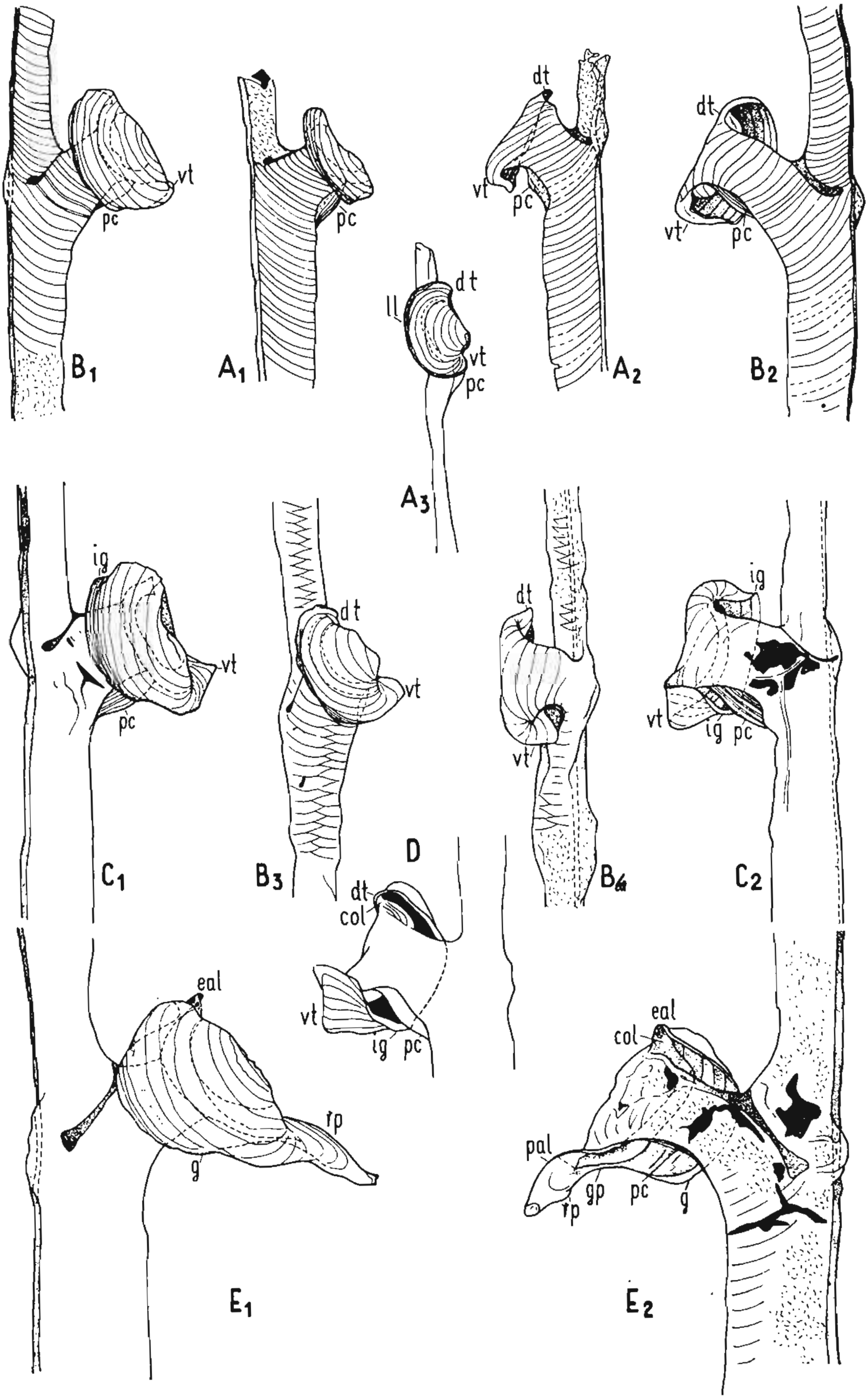
A pectoral crest, found in some populations of *Cuc. aversus rostratus* is a remarkable structural feature of the ventral wall of metatheca in the first and in a number of successive proximal thecae. It is a peculiar spindlelike, peridermal plate, fused with the ventral wall of metatheca (Pl. XXXVII, Fig. N; Pl. XXXVIII, Figs. A_1-A_2; Pl. XXXIX, Figs. A_1-A_2, *pc*), but shifted asymmetrically to the obverse side (Pl. XXXIX, Fig. A_3, *pc*). This pectoral crest extends from the apertural lip throughout the metathecal portion of the ventral wall and consists of a few, very fine peridermal strips which resemble the microfuselli (Pl. XXXIX, Figs. A, C).

Plate XXXIX

Cucullograptus aversus rostratus Urbanek. Structure of thecae in specimens from a lower zonal population from deep-boring Mielnik. A_1-A_3 upper part of a first theca in reverse (A_1), obverse (A_2), and ventral (A_3) aspects; B_1-B_4 upper part of a proximal theca in reverse (B_1), obverse (B_2), lateroventral (ventrally and somewhat from reverse side) (B_3) and in full ventral (B_4) views; C_1-C_2 upper part of proximal theca slightly more distally placed, in reverse (C_1) and obverse (C_2) aspects; *D* another theca similar to *C* in obverse aspect; E_1-E_2 more distal theca in reverse (E_1) and obverse (E_2) aspects (same specimen as Figure 21,C *in* Urbanek, 1960). Mielnik, depth 925.1—924.8 m); ca. ×63.

col columellar junction of the apertural lip with the left apertural lobe, *dt* dorsal termination of the lobe, *eal* dorsal eaves of the left apertural lobe, *g* gorget, *gp* gular process, *ig* incipient gorget, *ll* left apertural lobe, *pal* ventral prolongation of the apertural lip, *pc* pectoral crest, *rp* rostral process of the left lobe, *vt* ventral termination of the left apertural lobe.

PLATE XXXIX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When present, the pectoral crest is developed most completely in proximal thecae and it decreases in size in more distal ones, being there merely a narrow, vestigial strip (comp. Pl. XXXIX, Fig. E and Pl. XLI, Fig. D), or even absent at all — as in a specimen shown in Pl. XLI, Fig. C. This astogenetic behaviour of the pectoral crest is suggestive of a character, being, in the course of phylogenetic changes of astogeny, introduced proximally to the *aversus* lineage. The pectoral crest seems to be (among cucullograptids) an almost unique example of a thecal character which was, as a phylogenetic novelty, introduced proximally to the rhabdosome (comp. also p. 347).

The presence of the pectoral crest on ventral walls in more proximal thecae is, however, by no means a stable character of *Cuc. aversus rostratus*. It shows a remarkable expressivity and penetrance variation, most probably connected with a certain zonal influence. In the population from erratic boulder S. 121 (Jarosławiec), there are no indication of the presence of the pectoral crest which seems to be entirely absent (it was not mentioned, therefore, in earlier papers by Urbanek, 1954, 1958). In the population from erratic boulder S. 205 (Ustka), the pectoral crest is only slightly expressed in most proximal thecae (Pl. XXXVIII, Figs. A_1-A_2) but seems to be entirely absent from more distal thecae of the same population (Figs. C-H). It is only in exceptional cases that the pectoral crest is more completely developed (comp. Fig. 19, *pc*) and such higher elaboration of it seems to be associated with a somewhat teratologically formed ventral termination of the left lobe. The latter is transformed on the specimen in question into a strongly incurved and closed tubular structure (*vt*).

In contrast, the pectoral crest is well-developed in populations from the Mielnik deep-boring where the prevailing majority of specimens show a well-expressed pectoral crest in proximal thecae and an incipient, narrow pectoral strip in distal ones. The absence of pectoral crest from the Mielnik populations is rare and probably accidental (Pl. XXXVII, Fig. M). These conditions speak for a higher expressivity and penetrance of the character in question. This may indicate a phylogenetically more advanced stage of the Mielnik populations as compared with that from erratic boulder S. 121 (Jarosławiec) and S. 205 (Ustka). Moreover, with regard to expressivity and penetrance of pec-

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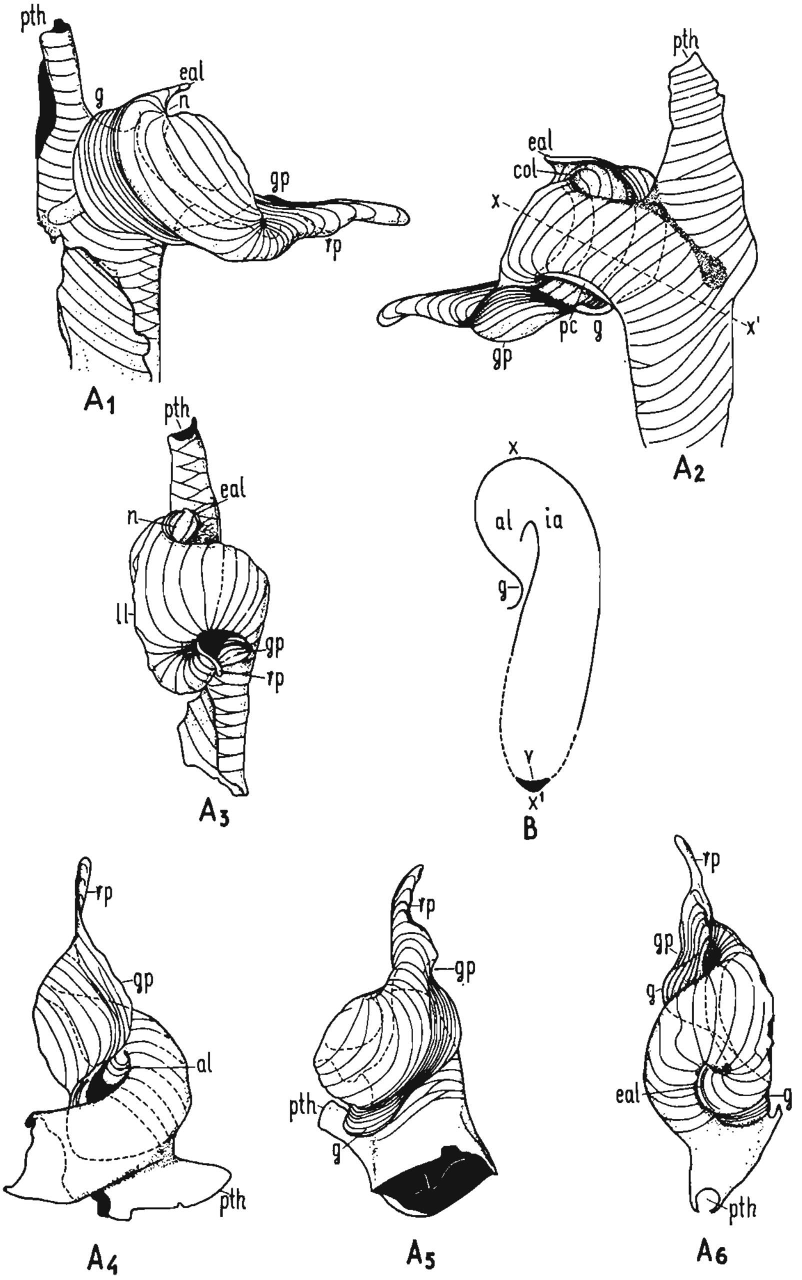
Plate XL

Cucullograptus aversus rostratus Urbanek. Details of structures of apertural apparatus in distal theca. A_1-A_6 upper part of same theca in reverse (A_1), obverse (A_2), ventral (A_3), from below (A_4), in lateroventral (A_5) and in the top (A_6) views; *B* diagrammatical cross section through line x-x′ on Fig. A_1 (Mielnik, depth 925.1—924.8 m); ca. ×70.

al apertural lip, *eal* eaves of the left apertural lobe, *g* gorget, *gp* gular process, *ia* internal aperture, *n* notch separating the dorsal eaves, *pc* pectoral crest, *pth* prothecal part of adjacent theca, *rp* rostral process of the left lobe, *v* virgula.

PLATE XL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toral crest, the latter is intermediate between S. 121 and the Mielnik populations.

Proximal thecae are rather long (1.45—1.51 mm) and slender tubes, gradually widening distally (0.06—0.11 mm in width at the base of protheca and 0.09—0.19 mm at the base of metatheca), with a straight ventral wall. The prothecal part is 1.22—1.33 mm long, the metathecal — 0.15—0.23 mm and the prothecal part occupies therefore about 73—90% of thecal length.

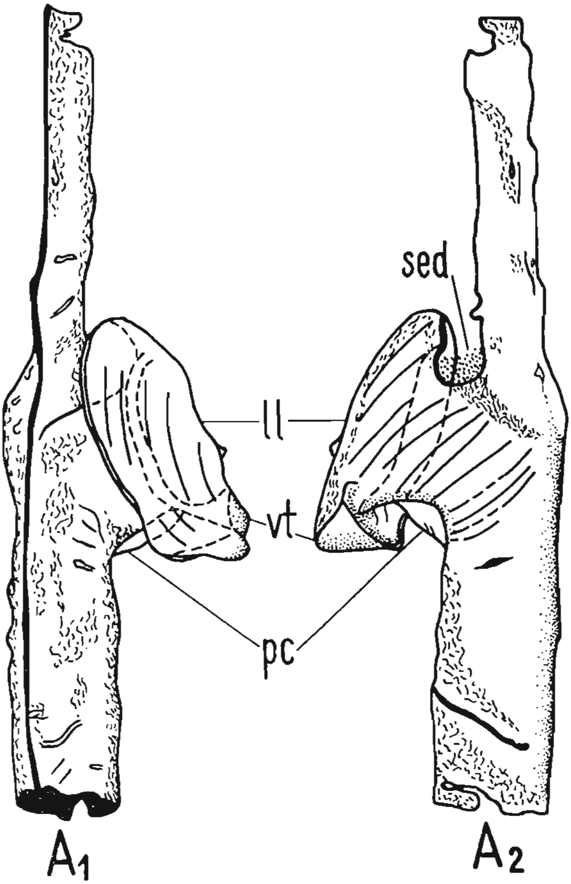


Fig. 19. — *Cucullograptus aversus rostratus* (Eisenack). Upper part of a proximal theca from drift material showing an excessive form of the ventral termination (*vt*) of the left lobe (*ll*) and the presence of a pectoral crest (*pc*) (S. 205, Ustka), ca. × 126; *sed* grains of sediment attached to the periderm.

The metathecal part is somewhat isolated and inclined at an angle of some 40° in adnate part and 55—70° in isolated part towards the main axis of theca. The isolated part of the metatheca involves 1/2—1/3 of its length. Metatheca terminates in the apertural apparatus which consists of hypertrophied left apertural lobe, strongly incurved over and overlapping the aperture. This lobe consists of some 8—10 fuselli which are archedly bent, the last 2 being rather short and forming a free ventral termination of the apertural lobe. In most proximal thecae, the latter forms a blunt and slightly incurved process as in specimens from erratic boulder S. 205 Pl. XXXVIII, Fig. C) or strongly incurved and folded outgrowth whose inner margin is fused with the ventral border of the left lobe proper as in specimens from the Mielnik core (Pl. XXXIX, Figs. B_1-B_2, C_1-C_2; Pl. XLI, Figs. B_1-B_2, *vt*). The left lobe in proximal thecae attains a length (*tr.*) of some 0.28—0.30 mm with the rostral process 0.05—0.06 mm long.

In proximal thecae more medially (centrally) placed in the rhabdosome, this ventral termination of the left apertural lobe is prolonged into a short rostral process (Pl. XXXVIII, Figs. E-F) or may occasionally form even a spinelike outgrowth (Fig. D). This rostral process in proximal thecae is in incipient stage of elaboration but shows a steady distalward increase in size (comp. Pl. VII, Fig. 11). Its structure, more completely developed in distal thecae, will be described in this connection later on.

The dorsal termination of the left apertural lobe forms free, flat or slightly domed eaves, extending beyond the aperture (Pl. XXXVIII, Figs. C-F; Pl. XXXIX, Figs. B_3-B_4, C_2; Pl. XLI, Figs. B_1-B_2, *dt*, *eal*). The obverse margin of the apertural eaves is joined with the apertural lip and the fuselli converge in this point, serving therefore as a kind of a node (Pl. XXXIX, Figs. B_3-B_4, D).

The main part of the left apertural lobe forms a distinctly domed, globular structure, covering the apertural opening of the theca. The lower margin of the lobe along the reverse side may be as simple as in specimens from erratic boulders S. 121 and S. 205, or may form a narrow band, a kind of a collar made up of very fine fusellar strips, resembling the microfusellar tissue (Pl. XXXIX, Figs. C_1-C_2; Pl. XLI, Figs. B_1-B_2, *ig*). This structural addition, present in specimens from the Mielnik core, is doubtlessly an incipient stage of another peculiar structure, i.e. the gorget which is more fully developed in distal thecae and will be described in this connection later on.

Inside the domed left apertural lobe, there is an apertural lip whose structure is shown in Pl. XLII, Figs. B_1-B_2 and in Fig. 20 A, C, where the overlapping left lobe has been removed by the needle or was destroyed naturally.

The apertural lip extends throughout the reverse side of the apertural border and represents a distinctly extroverted margin, hanging down and forming a tubular structure. The apertural lip is also easily seen through the bleached (transparent) left apertural lobe, as a rather wide and dark band, framing the margin of the apertural opening (marked by broken lines in Pl. XXXVIII and XXXIX). The dark colour of this structure may be, in part, a result of the condensation of narrow, fusellar strips (comp. p. 511) and, in part, of the deposition of the same secondary peridermal substance on the attenuated periderm of the apertural lip.

The apertural lip ventrally forms a prolongation, fused with the upper margin of the ventral termination of the left apertural lobe (Fig. 20, A-B, *pal*) and dorsally, after surrounding the apertural opening, it sends an ascending ramus (B, *aal*) which, through short columellar junction, is fused with the dorsal part of the left apertural lobe (B, A_2, *col*). Both terminations of the apertural lip serve also as the points (nodi) in which the fuselli of the left apertural lobe converge. This is clearly visible in ventral view of these lobes (Pl. XXXIX, Figs. A_3, B_4).

The strongly extroverted apertural lip in *Cuc. aversus rostratus* is doubtlessly a vestigial form of the right apertural lobe, being a more advanced stage of its rudimentation as compared with that in *Cuc. hemiaversus* (comp. p. 488). The entire right lobe is transformed here into the apertural lip, doubtlessly in connection with a more advanced hypertrophy and overlap of the opposite lobe. Such an apertural lip may be compared with an incipient apertural lip in *Cuc. hemiaversus* and with a folded anterior margin of apertural processes in *Saetograptus chimaera* (comp. Urbanek, 1960, p. 189). In all these cases, the formation of folded margins of periderm seems to be closely linked with a certain degree of its reduction.

The transformation of the internal right lobe into the extroverted margin in *Cuc. aversus rostratus* results in extending the space inside the apertural apparatus. Folding and hanging down of the margin may, at least in part, be ascribed to the attenuation of the periderm, the peridermal wall being too thin "to stay upwards".

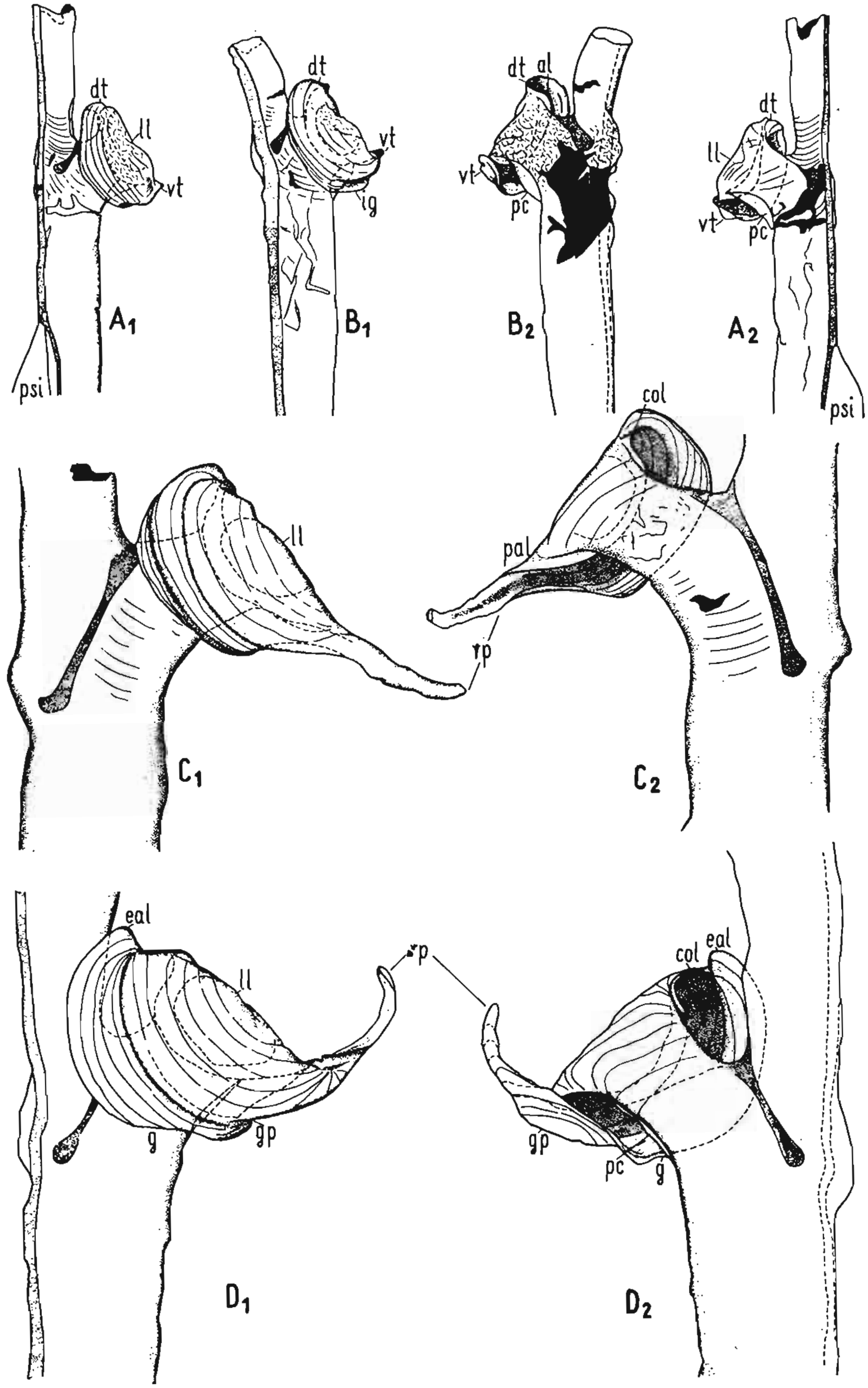
Distal thecae reach a total length of some 1.88—1.95 mm, with the prothecal portion 1.40—1.33 mm and metathecal 0.60—0.50 mm long. The protheca occupies, therefore, about 69—71% of thecal length. The width of distal thecae is at the base 0.30—0.25 mm, reaching the same figures in metathecal parts. The ventral wall of distal thecae is gently genicular and, at the boundary of pro- and metathecal part, slightly swollen (Pl. VII, Fig. 11).

Plate XLI

Cucullograptus aversus rostratus Urbanek. Structure of thecae in specimens from a higher zonal population from deep-boring Mielnik. A_1-A_2 upper part of a first theca in reverse (A_1) and obverse (A_2) aspects; B_1-B_2 upper part of a proximal theca in reverse (B_1) and obverse (B_2) aspects; C_1-C_2 upper part of a distal theca in reverse (B_1) and obverse (B_2) aspects; D_1-D_2 still more distally placed theca in reverse (D_1) and obverse (D_2) aspects (Mielnik, depth 921.5—921.0 m); ca. ×63.

pst prosicula; for remaining explanations-see Pl. XXXIX.

PLATE XLI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Metatheca is isolated over about 1/2 of its length and inclined at an angle of 40° in adnate, to 70—80° in isolated part to the main axis of theca. It is provided with a complex apertural apparatus which consists of a hypertrophied and strongly overlapping left apertural lobe and of different structural superadditions, connected with it (Pl. XXXVIII, Figs. G-H; Pl. XXXIX, Fig. E).

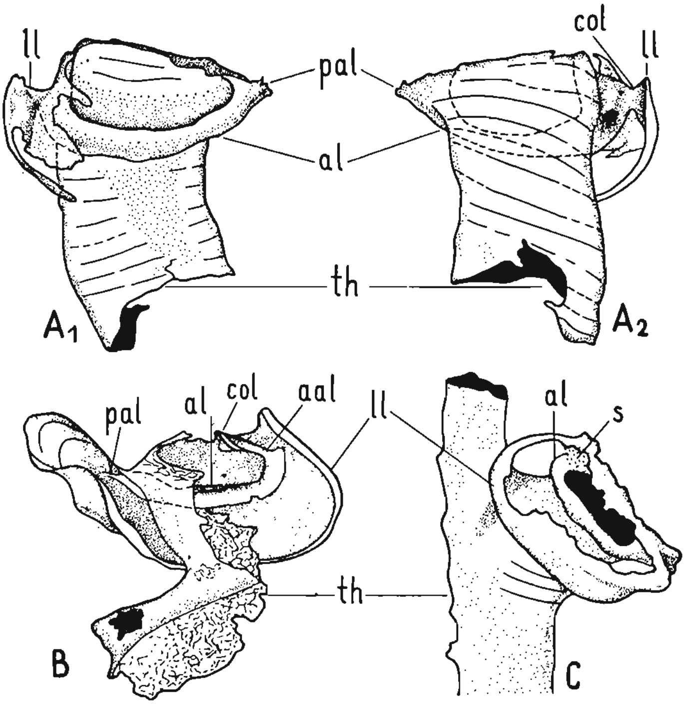

Fig. 20. — *Cucullograptus aversus rostratus* Urbanek. Internal structure of apertural apparatus: A_1-A_2 apertural part of a theca with left apertural lobe almost completely removed to expose the internal aperture, seen in reverse (A_1) and in obverse (A_2) aspects, *B* apertural lip exposed through the natural destruction of domed part of periderm in the left apertural lobe, *C* internal aperture visible through secondary (accidental) opening formed on the reverse side of the left apertural lobe (S. 205, Ustka), ca. × 100.

aal ascending ramus of apertural lip, *al* apertural lip, *col* columellar junction of the left apertural lobe with the apertural lip, *ll* left apertural lobe, *pal* ventral prolongation of the apertural lip, *s* grains of sediment, thecal walls.

In the most advanced stage of morphological development, reached by populations from the Mielnik core (Pl. XL), this apparatus consists of: 1) a strongly convex, globular, main part of the left apertural lobe, producing, through a strong incurvation over the aperture, a helmet-like structure; 2) a dorsal termination of the lobe, forming the apertural eaves; 3) a ventral termination of the lobe and its derivatives; 4) a gorget.

The main part of the left apertural lobe consists of some 9—11 fuselli, slightly arched and converging to the ventral and dorsal nodes. These are also the points of junction of the lobe itself and the apertural lip (comp. p. 506). The dorsal termination of the left lobe forms apertural eaves, i.e. a subtriangular outgrowth of the lobe, formed by the addition of some 3—4 short, wedge-shaped fuselli to the border of the lobe proper (Pl. XL, Figs. A_1-A_3, A_6, *eal*). The apertural eaves may be flat or slightly convex and rooflike (Pl. XXXIX, Fig. E; Pl. XXXVIII, Figs. H_3-H_4). It is separated from the globular body of the main lobe by a more or less incised notch (Pl. XXXVIII, Figs. H_3-H_4; Pl. XL, Figs. A_1, A_3, *n*).

The ventral prolongation of the lobe forms a semitubular outgrowth which is convex on the reverse and open on the obverse side, terminating in a rostral process (*rp*). The initial part of this structure is produced by arched fuselli, gathered into a ventral node, or fused with the ventral margin of the main portion of the lobe. The lower margin of this part forms, on the obverse side, a distinct shovellike lip, incurved upwards and surrounding the ventral termination ventrally and laterally. It is called here a gular process (Fig. 21, A_1; Pl. XXXVIII, Figs. H_3-H_4; Pl. XXXIX, Figs. E_1-E_2; Pl. XL, Figs. A_2-A_4; Pl. XLI, Figs. C, D, *gp*).

The gular process is formed by a ventral incurvation of some portion of the main lobe itself, forming beneath a shovellike lip and by an additional marginal part which is a prolongation of the gorget (Pl. XL, Fig. A_4, *gp*). As the gorget proper, this marginal part consists of narrow fusellar strips, while the main part of the gular process is produced by normal fuselli.

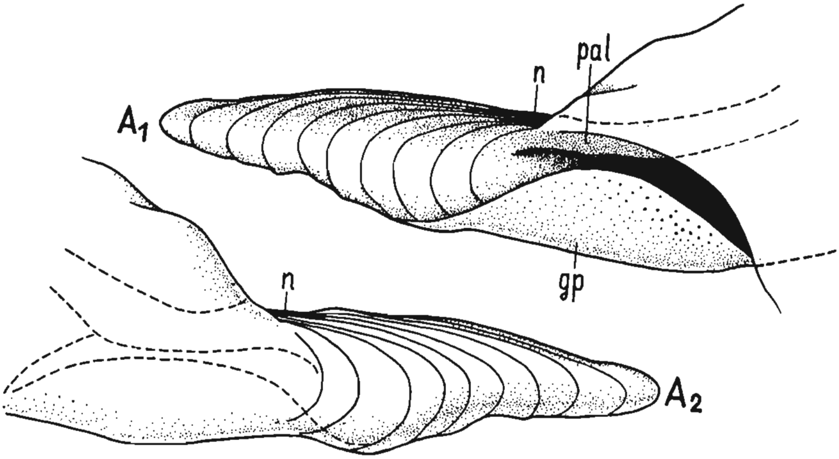

Fig. 21. —*Cucullograptus aversus rostratus* Urbanek. Fusellar structure of the rostral process, seen in obverse (A_1) and reverse (A_2) aspects (Mielnik, depth 921.5—921.0 m), ca. ×150.
gp gular process, *n* fusellar node, *pal* ventral prolongation of apertural lip.

The initial part of the ventral prolongation of the lobe terminates in a free rostral process which forms a rough spoonlike structure, slightly convex on the reverse, but concave and open on the obverse side (Fig. 21, A_1-A_2). This free portion consists of 4—9 short fuselli, strongly arched and superimposed on each other. The outline of this rostral process is strongly variable (Fig. 22). In addition to almost straight rostral processes (A, F) there are also rostral processes with a different degree of curvature (C_1-C_2, D, E_1-E_2) which are rather broad and blunt (B, C_1-C_2, D) or, in some cases, rather spined (E_1, F). These shape differences seem to be random in nature, but it is a distinct general trend to a distalward elongation of the rostral processes (comp. Pl. VII, Fig. 11). The left lobe in distal thecae, some 0.50—0.45 mm in length (*tr.*), is provided with a 0.35—0.25 mm long rostral spine.

A tendency to some spiral coiling along the long axis is a remarkable

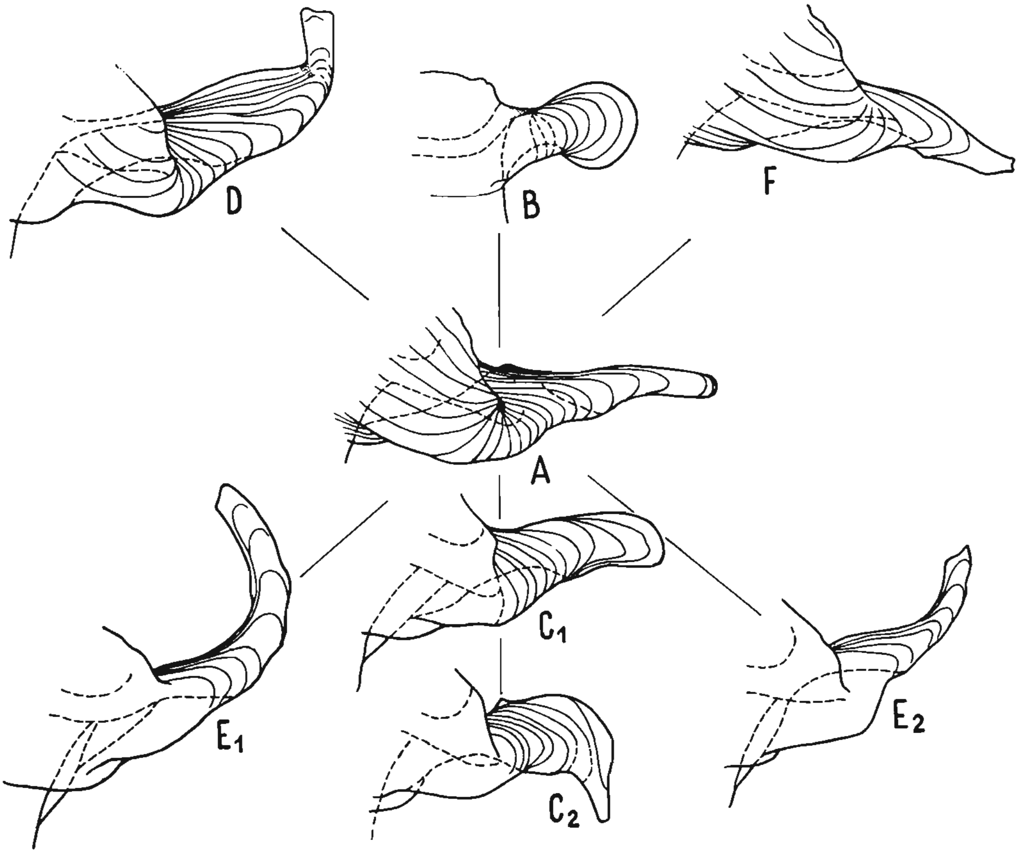

Fig. 22. — *Cucullograptus aversus rostratus* Urbanek. Selected morphotypes of rostral processes in attempt to show their variation range: *A* a morphologically average (central) straight type, *B* shovellike type found in proximal thecae, C_1-C_2 downwards incurved broad type, *D*, E_1-E_2 upwards incurved spinose and broad (*D*) type, *F* almost straight and spinose type (*A*, *C*-*F* — Mielnik, depth 925.1—924.8 m; *B* — *S*. 121. Jarosławiec); *A*, *C*-*F* ca. × 110, *B* ca. × 150.

feature of the free portion of the rostral process. This may be marked only slightly (Pl. XL, Fig. A_4), or more distinctly (Pl. XLI, Fig. D_1; Pl. XXXVIII, Figs. H_2-H_4). In certain cases, this free portion is, however, straight in practice (Pl. XLII, Fig. C).

The gorget, a collarlike prolongation of the lower margin of its main portion is a peculiar addition to the left lobe (Pl. XXXIX, Figs. E_1-E_2; Pl. XL, Figs. A_1-A_2, A_5, *g*). In adult distal thecae, the gorget represents a rather broad belt, situated close to the thecal wall on the reverse side. It is separated from the thecal wall only by a narrow fissure (comp. Pl. XL, Fig. B, *g*). Ventrally, the gorget is characteristically twisted and continues as a marginal member of the gular process (Pl. XL, Figs. A_1-A_3; comp. also p. 509). The gorget consists of numerous narrow fusellar strips which resemble the microfusellar tissue, being however intermediate in their width between the normal thecal fuselli and the true microfusellar periderm. In certain cases, there is a rather gradual passage from normal fuselli of the main part of the apertural lobe to narrow strips of the gorget proper (Pl. XLII, Figs. A_1-A_3) or even the gorget may consist of almost normal fuselli (Pl. XLI, Fig. D). The usually observed decrease of width of fuselli may indicate a gradual decrease in secretionary effectiveness of the zooid itself, related with its aging.

This rather complex picture of the structure of the left apertural lobe and its derivatives presents the peculiarity of morphologically most advanced populations from the Mielnik core. Specimens, etched from erratic boulders S. 121 and S. 205 present much simpler picture, showing apertural lobes which consist only of: 1) a main domed part, 2) a dorsal eaveslike prolongation, 3) a ventral prolongation and its derivatives (gular process and rostral process). There is no gorget (Pl. XXXVIII, Figs. G-H) and, consequently, the gular process, although well-developed, also consists only of the normal fusellar part, without the marginal addition. It seems probable that, like in other respects (comp. p. 518), also with regard to the development of apertural apparatus, the populations from the Mielnik core represent a phylogenetically more advanced stage than those in specimens, etched from erratic boulders S. 121 and S. 205. It is especially the gorget that seems to represent a phylogenetic novelty, acquired later than other structural elements of this apparatus.

Inside the domed, main part of the left apertural lobe, there is the apertural lip, forming an extroverted margin on the reverse side of the thecal wall (Pl. XL, Fig. B *al*). It is visible through the bleached periderm and marked by broken lines in Pl. XXXVIII, Figs. G-H; Pl. XXXIX, Fig. E; Pl. XL, Fig. A. The apertural lip, isolated by the needle preparation and strongly bleached, is shown in Pl. XLII, Figs. C_1-C_2. It shows the microstructure of the lip which consists of narrow fusellar strips, resembling the microfuselli and considerably narrower than the normal fuselli from the left apertural lobe and from the thecal wall (Fig. D). The width (*long.*) of the apertural lip in distal thecae comes to 0.05—0.06 mm.

This apertural lip forms a ventral prolongation, extending beyond the ventral apertural margin proper and attached to the inner surface of the left apertural lobe (Pl. XXXVIII, Figs. H_3-H_4, *val*; Pl. XXXIX, Fig. E_2; Pl. XLII, Fig. C_2, *val*). This place of fusion between the left apertural lobe and the apertural lip plays the role of a ventral node towards which the fuselli converge.

Dorsally, the apertural lip ends with an angular border, provided with more or less well-marked columellar outgrowth, fused to the inner surface of the left lobe just beneath the inner incision of the apertural eaves (Pl. XL, Fig. A_2; Pl. XLI, Figs. C_2, D_2, *col*). As seen from the reverse side, the left apertural lobe seems to be supported by this columellar outgrowth (Pl. XL, Fig. A_1; Pl. XLI, Figs. C_1-D_1; indicated by the trace of broken lines). This point of junction of the apertural lip and the left apertural lobe also plays the role of a dorsal node towards which fuselli converge dorsally.

The space relations inside the apertural apparatus in *Cuc. aversus rostratus* are shown in Pl. XL, Fig. B which is an optical cross section along the x-x' line on specimen, figured in the same Plate, Figs. A_1-A_6. The internal apertural opening (*ia*) in distal thecae is completely covered with a hypertrophied left apertural lobe, with the gorget (*g*) moved near — to the reverse side of thecal wall. The internal cavity of the aperture communicate with the outer space only through ventral and dorsal apertural notches (Pl. XL, Figs. A_2-A_3) and through a narrow slit between the gorget and the thecal wall(Fig. B).

Growth pattern of rhabdosome. Specimens shown in Fig. 23, A-C, show thecae growing from the proximal part of rhabdosome, Especially interesting is a fragment of the proximal part of rhabdosome, shown in Fig. 23, A_1-A_3. It consists of an adult theca *n*, with a fully developed

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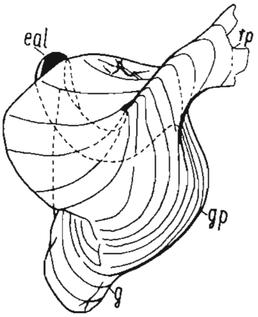
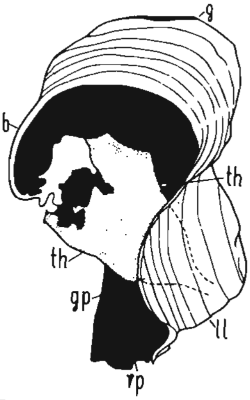
Plate XLII

Cucullograptus aversus rostratus Urbanek. Fusellar structure of apertural lobes. A_1-A_3 isolated left apertural lobe of a distal theca seen from below and ventrally (A_1), from below in order to show the gorget (A_2) and in lateral (reverse) view (A_3); B_1-B_2 apertural part of a proximal theca with the left lobe removed by a needle, in lateral (reverse) (B_1) and in reverse and from below (B_2) views; C_1-C_2 strongly bleached and isolated apertural lip of a medial theca, in reverse (C_1) and obverse (C_2) aspects; *D* lines indicating the relation of width of fuselli in left apertural lobe, subapertural part of metatheca and in apertural lip in same (medial) theca (in downwards order) (Mielnik, depth 925.1—924.8 m); *A-C* ca. ×100, *D* ca. ×63. *al* extroverted apertural lip, *db* dorsal border of the left apertural lobe, *dt* dorsal termination of the apertural lip, *g* gorget, *gp* gular process, *lb* lower border of apertural lip, *ll* left lobe, *pc* pectoral crest, *pth* prothecal part of an adjacent theca, *rp* rostral process, *th* thecal wall, *ub* upper border of apertural lip, *vt* ventral termination of the apertural lip.

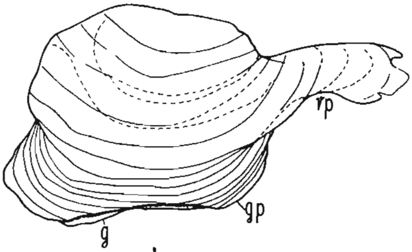
PLATE XLII



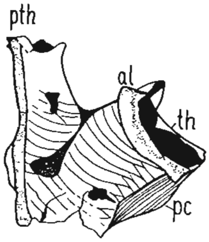
A₁



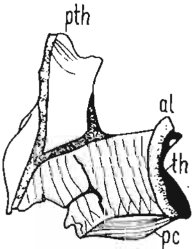
A₂



A₃

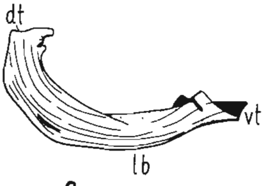


B₁

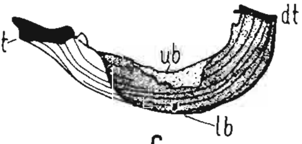


B₂

D



C₁



C₂

apertural apparatus, a younger, still growing theca *n+1* and a growing, incipient prothecal part of theca *n+2*. The specimen shows that the development of the left apertural lobe of a given theca occurs simultaneously with the formation of the basal part of the next theca. From

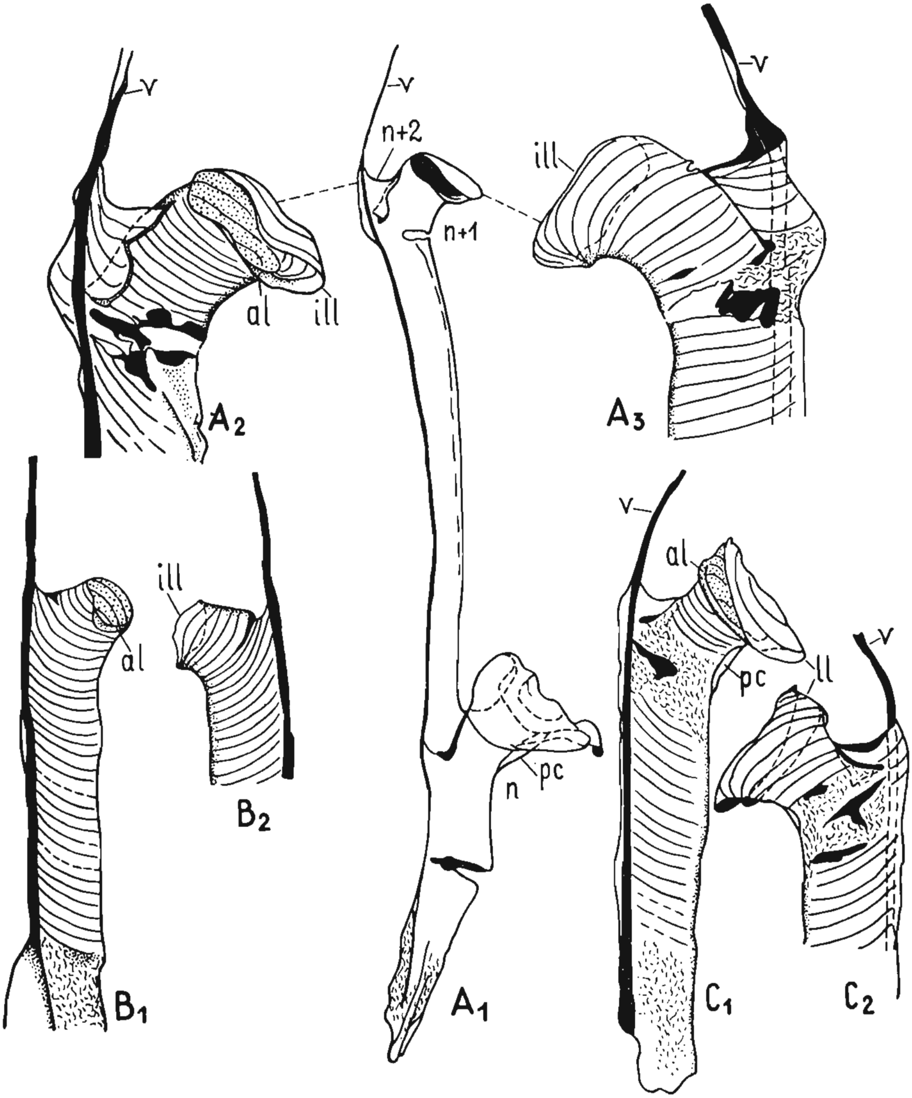


Fig. 23. — *Cucullograptus aversus rostratus* Urbanek. Growth pattern of rhabdosome: A_1 growing tip of a branch showing an adult theca (*n*) and a premature terminal (*n*+**1**) with a growing prothecal part of the next theca (*n*+2), A_2-A_3 enlarged apertural part of theca *n +1* from reverse (A_2) and obverse (A_3) sides, B_1-B_2 growing apertural apparatus of the first theca in reverse (B_1) and obverse (B_2) aspects, C_1-C_2 upper part of a young proximal theca with incomplete left apertural lobe in reverse (C_1) and obverse (C_2) aspects (Mielnik, depth 925.1—924.8 m), A_1 ca. x 42; A_2-A_3 *B*, *C* ca. × 120;

al apertural lip, *ill* incipient left apertural lobe, *ll* left apertural lobe, *n*—*n*+*2* successive thecae, *pc* pectoral crest, *v* virgula.

the very beginning, the apertural apparatus is asymmetric, the apertural lip being, however, initially extroverted only in the more ventral part of the margin (A_2-A_3, *al*).

A slightly more advanced stage in the development of a proximal theca is represented by Fig. 23, C_1-C_2. While on theca *n+1* (A) the apertural lip is incomplete and forms only a kind of a ventral incision, it is completely extroverted over the margin of theca in a specimen shown in Fig. 23, C_1-C_2. Folding of the apertural margin develops, therefore, gradually progressing from the ventral to the dorsal end. In the latter theca, the left lobe is correspondingly enlarged and the pectoral crest (*pc*) is already present. The last mentioned structure is developed simultaneously with later growth stages of the left apertural lobe. The same is indicated by specimen in Fig. 23, A_1, where adult theca *n* is provided with a well-marked pectoral crest (*pc*), while the younger theca *n+1* still lacks it.

Specimens in Fig. 23 A, C show that the formation of the left apertural lobe occurs simultaneously with the growth of the initial part of the next protheca and is probably completed much before the next theca reaches its metathecal stage. This may indicate that in *Cuc. aversus rostratus* only two or even one preadult theca was present at the growing tip of rhabdosome. These conditions resemble rather those, known in *Lobograptus exspectatus* than in *L. scanicus parascanicus* (comp. p. 344).

Fig. 23, B_1-B_2 show the first theca with a growing apertural apparatus which consists of an incipient left lobe (*ill*) and an incipient apertural lip (*al*) forming a shallow ventral incision as a result of an incomplete extroversion of the apertural margin. This development stage precedes the formation of the second theca which is still entirely lacking.

Structure of interthecal septa. The structure of the interthecal septum in a proximal theca is shown on a septum, bleached and isolated by the needle preparation (Fig. 24, A). The lower margin is, as usually, strongly thickened (*thm*) and connected with an annular thickening which frames the prothecal opening of the preceding theca (*ath*). The fusellar structure shows no intercalary fuselli which, however, occur in interthecal septa of more distal thecae. The dorsal zigzag suture is, however, somewhat irregular as compared with the ventral one.

The structure of interthecal septa in distal thecae is shown on specimens in Fig. 24, B-C, strongly bleached and isolated by the use of the needle. The lower, thickened margin (*thm*) is connected with lower thickenings to form an annular thickening, framing the prothecal opening of an earlier theca (*ath*). The fusellar structure displays the presence of a dorsal suture with a number of intercalated, fine or wedge-shaped fuselli (*if*). The appearance of intercalated fuselli distinguish the structure of interthecal septa in more distal thecae from that in more proximal ones.

Stratigraphic range. — In the Mielnik core, *Cuc. aversus rostratus* has been recorded at a depth between 934.7—920.8 m. In the lowermost place of appearance, the subspecies in question is represented by proximal and medial thecae, displaying already a slightly marked rostral prominence and a pectoral crest (a depth of 934.7—934.4 m). It seems, therefore, that it appears at Mielnik as a morphologically already advanced form, without being preceded by one of more primitive forms, known from the Baltic drift material (comp. p. 502). Somewhat higher, *Cuc. aversus rostratus* still occurs in a mixed population, accompanied by a less advanced form, described previously as *Cuc. aversus* cf. *aversus* (a depth of 925.1—924.6 m). This common occurrence of both forms in a single assemblage indicates a certain overlap in their stratigraphic range (see also Pl. I). It is, however, only slightly higher (a depth of 924.4—924.1 m) that *Cuc. aversus rostratus* occurs in abundance, from that level upwards being the only surviving cucullograptid. The last appearance of the subspecies under study is marked by a scanty assemblage from

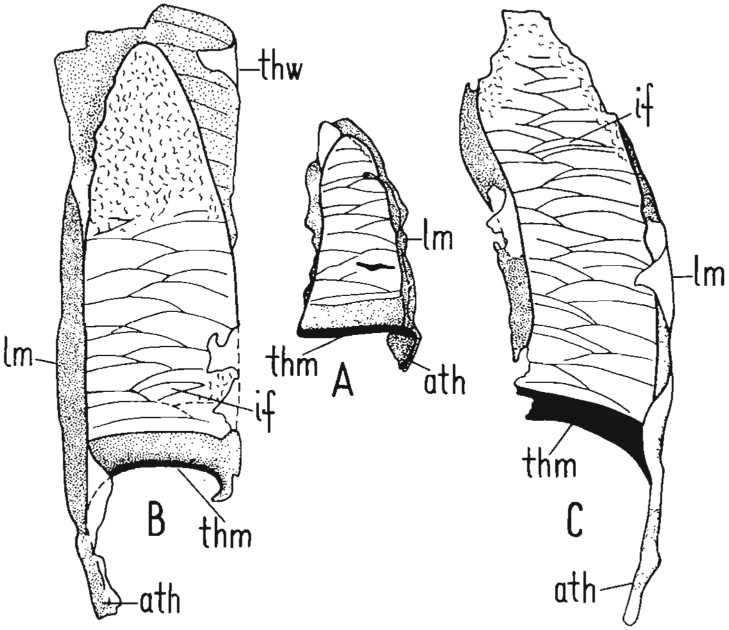


Fig. 24. — *Cucullograptus aversus rostratus* Urbanek. Fusellar structure of interthecal septa: *A* in proximal theca, *B-C* in distal thecae (Mielnik, depth: *A* — 925.0—924.8 m, *B-C* — 921.1—924.8 m), ca. × 100;
ath annular thickening surrounding the prothecal opening, *if* intercalary fuselli, *lm* lateral margin of interthecal septum, *thm* thickened lower margin of interthecal septum, *thw* lateral thecal wall.

a sample, taken at a depth of 921.1—920.8 m.In the lower part of its distribution in the Mielnik core, *Cuculograptus aversus rostratus* is associated with *Saetograptus leintwardinensis* (Hopkinson) (but curiously enough, never found directly in the same sample), *Monoclimacis haupti* (Kühne), *Pristiograptus dubius* (Suess), *P. dubius* cf. *tumescens* (Wood) and "*P.*" *bohemicus* (Barrande). Because of the disappearance of *S. leintwardinensis*, from a depth of some 934.0 m, the association becomes poorer. This seems to indicate that, in its vertical distribution, *rostratus* surpasses the top of *leintwardinensis* zone by some 13 m, being geologically the youngest member of the Cucullograptinae. According to the succession, met with at Mielnik, *Cuc. aversus rostratus* is confined to the *leintwardinensis* zone and to the strata, immediately overlying it.

The stratigraphic position of erratic boulders, yielding this subspecies, is less certain. Kühne's *Monograptus* cf. *aversus*[24] from his boulder No. 13, Spandau, has been found "mit *M. dubius*, *M. scanicus* (nur eine Th.) und *M. haupti*" (1955, p. 398).

Judging from the absence of more complete association of the *scanicus* zone and the presence of *M. haupti*, Kühne arrived at the conclusion that his boulder was derived from a horizon younger than the *scanicus* zone, might be even the Middle Ludlovian of age. This opinion was, in part, correct and a probable horizon of that and similar forms may be situated in the *leintwardinensis* zone, or at the top of the underlying beds. This conclusion seems to be valid also for *Cuc. aversus rostratus* from our erratic boulders S. 121, Jarosławiec (without any graptolite association) and S. 205, Ustka (associated with *Pristiograptus dubius* (Suess) and *Monoclimacis* cf. *haupti* (Kühne). More primitive morphological characters of specimens from those erratic boulders suggest rather their somewhat lower stratigraphic position than that, occupied by the more advanced Mielnik population of *Cuc. aversus rostratus* (see also p. 518).

Systematic position. — *Cuc. aversus rostratus* may be considered a further development of *Cuc. aversus aversus* and it represents the terminal, most advanced link in the *Cuc. hemiaversus* — *Cuc. aversus* lineage. The presence of some morphologically intermediate forms, filling the gap between *Cuc. aversus aversus*, as described by Eisenack (1942), and the most advanced *Cuc. aversus rostratus* populations from the Mielnik deep-boring, suggests a rather gradual passage from the former to the latter subspecies.

All morphological differences observed between these populations may be most probably ranked as being the infrasubspecific. Nevertheless, they indicate directional changes from a probably more primitive to more advanced phylogenetic stage.

The lower, structural stage in the evolution of the *rostratus* line is

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[24] Most probably, belongs to *Cuc. aversus rostratus*; comp. p. 518.

represented primarily by populations from the Baltic erratic boulders. The populations from boulder S. 121 (Jarosławiec) seems to be the most primitive, being, in thecal structure, the only difference from true *aversus* the presence of a distinct rostral process in medial and more distal thecae (comp. also Urbanek, 1954, pp. 82—83; 1958, pp. 70—71). About the same stage is probably represented by a specimen, described by Kühne from his boulder No. 13, Spandau, which also displays the presence of a rostral process in more distal thecae and other minor differences from true *Cuc. aversus* of Eisenack (Kühne, 1955, p. 391).

The presence of a broad and rather short, shovellike rostral process is a remarkable feature of both forms mentioned above (comp. Kühne, 1955, Figs. 13-A, C, G-H; Urbanek, 1958, Figs. 36—39). This type of rostral process, shown also diagrammatically in Fig. 22, B, may probably be considered a primitive form of the rostral process of the left lobe. Its longer, narrower, or even pointed forms most probably evolved somewhat later. The initial evolution stage of the *rostratus* line was connected with the formation of a rostral process alone, but already provided with a gular process (the latter being inherited from the true *aversus*, comp. p. 336), and the rostral process being probably blunt.

A somewhat more advanced stage in the evolution of the *rostratus* line is represented by a population from erratic boulder S. 205, Ustka (comp. Pl. XXXVIII). This is indicated by some modifications in the rostral process, which may be more elongated or even sharply pointed, and by the presence of a pectoral crest in the most proximal thecae. The latter was entirely absent from the lower structural stage of evolution and represents here a phylogenetic novelty, acquired by most proximal thecae.

The third structural stage is represented by populations from the Mielnik core. Besides elaborations, present in the previous stage, it shows a new addition — the gorget. The pectoral crest is also better developed and spread over the medial and, in part, even distal thecae. There is, however, no distinct morphological difference between the *Cuc. aversus rostratus* populations from the lower and the higher part of its distribution zone in the core (comp. Pls. XXXIX, XLI) and the forms from Mielnik seem to represent about the same structural stage. Nevertheless, the presence immediately beneath *Cuc. aversus* cf. *aversus* suggests that the course of evolutionary events had to approach the picture, described above, and that the *Cuc. aversus rostratus* from Mielnik is more advanced than the forms, known from the Baltic drift material. Despite some uncertainty in the determination of the stratigraphic position of these boulders, this may also suggest that they were derived from a horizon slightly lower than the zone, occupied by the advanced populations of *Cuc. aversus rostratus* in the Mielnik core.

Cucullograptus pazdroi Urbanek, 1954

(Figs. 25—27; Pl. XLIII-XLV)

1938. *Monograptus* sp.; O. M. B. Bulman, Graptolithina...., p. 31, Fig. 20, c.
1954. *Cucullograptus pazdroi* Urbanek; A. Urbanek, Some observations............, pp. 292—297, Figs. 1—8.
1955. *Monograptus eunebeni* Kühne; W. G. Kühne, Unterludlow-Graptolithen.........., pp. 386—389, Figs. 11—12.
1958. *Cucullograptus pazdroi* Urbanek; A. Urbanek, Monograptidae........., pp. 62—70, Figs. 32—35; Pl. 4, Fig. 4; Text-pls. 4—6.
1960. *Cucullograptus pazdroi* Urbanek; A. Urbanek, An attempt........., p. 177 (mentioned), Fig. 13, H.

Remark to synonymy: *Pomatograptus becki* Jaekel is probably conspecific with *Cuc. pazdroi*; O. Jaekel, Über das Alter........, 1889, pp. 683—684, Pl. 29, Figs. 7—9 (comp. Kühne, 1955; Urbanek, 1958). See also a nomenclatorial remark in the present work, p. 532.

Material. — Numerous specimens from the Baltic drift material (especially boulders: S. 32 — Gdańsk-Wrzeszcz, S. 181 — Czarnogłowy) and from the Mielnik core. Drift material well-preserved, mostly unflattened, while that from the core mostly strongly flattened and badly deformed. From both sources, there are no complete specimens with proximal and distal parts of rhabdosome, joined together. Siculae very rare.

Description. — Sicula short, reaching a total length of 0.95—0.85 mm[25], with very slight ventral curvature in the metasicular part and a simple, straight apertural border. In all examined specimens, no black rings of sicula are discernible (Fig. 25, A-B). Prosicula is about 0.43—0.45 mm long and provided with very thin longitudinal threads. At the aperture it reaches some 0.12 mm in width (A-B, *psi*). The apex of prosicula reaches about half-way the length of the first theca.

Metasicula is 0.46—0.52 mm long and ventrally slightly incurved. It reaches a width of 0.12—0.13 mm at the level of the primary notch and 0.12—0.14 mm at the aperture, being almost tubular throughout. In all examined specimens, there are no black rings on metasicula.

The formation of the initial bud was normally monograptid in character, as indicated by the structure of the primary notch region (Fig. 25, *A-B*). The anterior margin of the initial bud is situated some 0.16—0.21 mm from the aperture of metasicula. The later has almost straight margins, without any distinct dorsal elevation (dorsal elevation is 0.03 mm long). Virgella stretches beyond the aperture of metasicula which is normal in size and shape (A-B, *vi*).

The first theca is a slender tube which reaches some 1.33—1.15 mm in length, 1.23—1.05 mm being occupied by the prothecal and only 0.10 mm by the metathecal part. The metathecal part is almost completely

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[25] Sicula, described by Urbanek (1955) measured 1.05 mm; Kühne noted: "Sicula ist weniger als 1 mm lang" (1955, p. 388).

adnate, only the apertural lobes are freely stretching above the aperture of theca[26]. The upper part of metatheca is, however, strongly transversely expanded. Metatheca terminates in an apertural apparatus which in most cases is badly damaged. Only the specimens, figured by Urbanek, 1958, p. 65, Fig. 34, and, to a certain extent, also the specimen shown here in Fig. 25, A, may supply some evidence for its structure. It consists

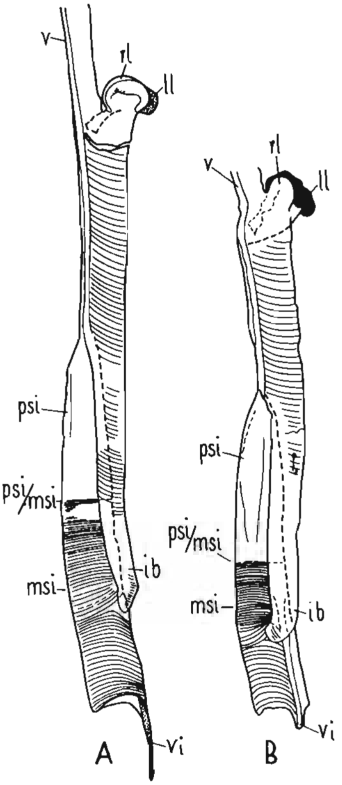

Fig. 25. — *Cucullograptus pazdroi* Urbanek. Structure of sicula and the first theca, visible on strongly flattened specimens:, *A* specimen seen from reverse side, *B* specimen seen in reverse aspect and somewhat ventrally (Mielnik, depth 977.9—977.5 m), ca. × 50.

ib initial bud, *ll* left apertural lobe, *msi* metasicula, *psi* prosicula, *psi/msi* boundary between pro- and metasicula, *rl* right apertural lobe, *v* virgula, *vi* virgella.

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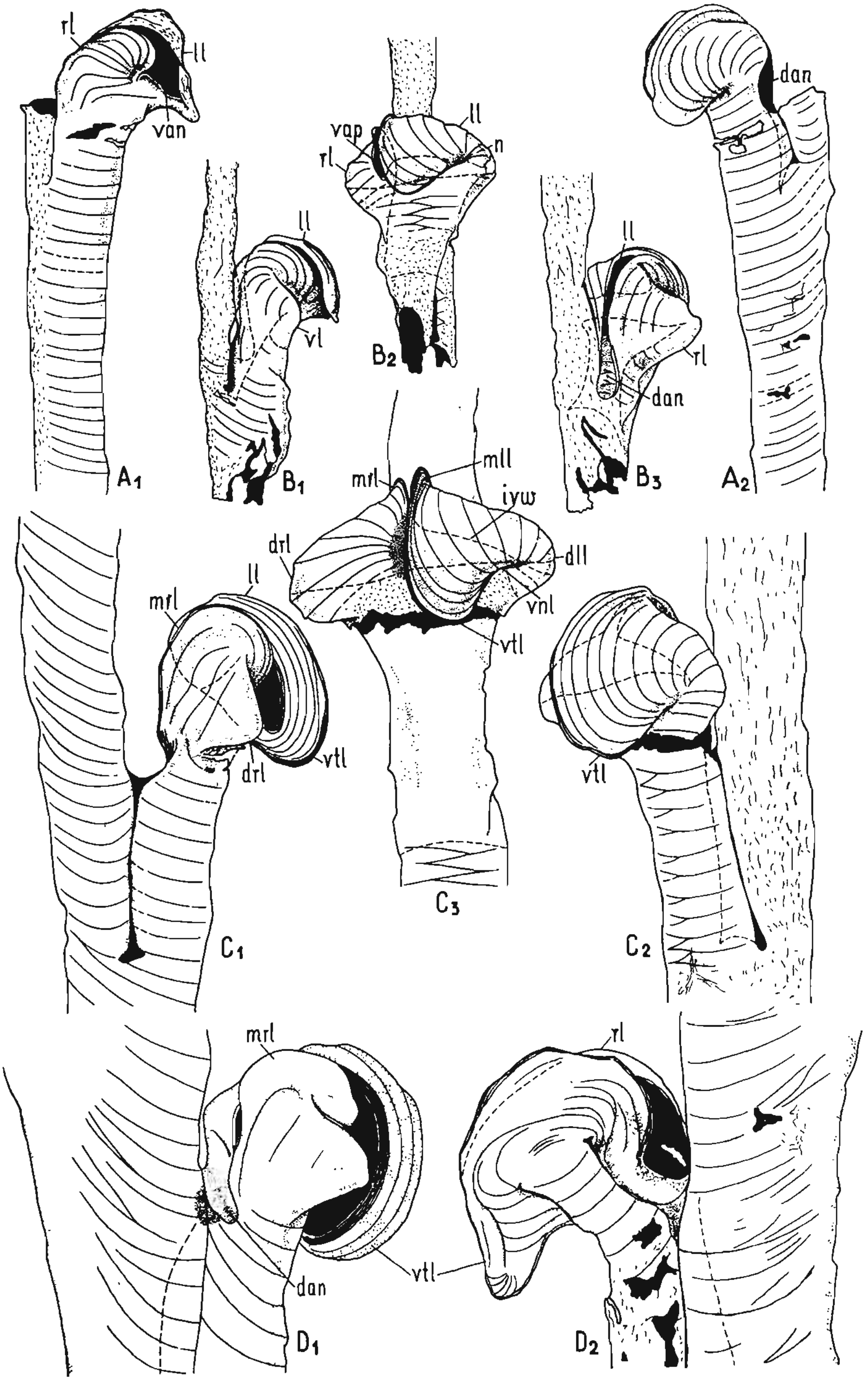
[26] Kühne described and figured a specimen of the first theca with a strongly isolated distal part, up to 40 per cent of its length (1955, p. 388, Figs. 11, A). This character seems to be accidental and was not repeated in the material described here. It also strongly differs from a degree of isolation, found in other proximal thecae (comp. p. 522).

Plate XLIII

Cucullograptus pazdroi Urbanek. Structure of thecae. A_1-A_2 upper part of a proximal theca in reverse (A_1) and obverse (A_2) views; B_1-B_3 upper part of a proximal theca in reverse (B_1), ventral view (B_2) and in dorsal and reverse aspects (B_3); C_1-C_3 upper part of a medial theca in reverse (C_1), obverse (C_2) and ventral (C_3) aspects; D_1-D_2 apertural apparatus of a distal theca in reverse (D_1) and obverse (D_2) aspects (S. 181, Czarnogłowy); ca. ×63.

dan dorsal apertural notch, *dll* domed part of the left lobe, *drl* domed part of the right lobe, *ll* left apertural lobe, *mll* marginal part of the left apertural lobe, *mrl* marginal part of the right apertural lobe, *rl* right apertural lobe, *vap* ventral apertural notch, *vnl* ventral node of the left apertural lobe, *vtl* ventral termination of the left apertural lobe.

PLATE XLIII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of two apertural lobes, the left being larger and provided with a distinct ventral shovellike termination, the right smaller, rounded in outline and lacking the elongated ventral termination. Both lobes are strongly convex and composed of domed hoodlike parts, directed sidewards, and of a marginal part forming a kind of a brim over the free margin of the lobe. The internal apertural opening forms a transversely elongated slit, and the apexes of the domed parts of both apertural lobes are directed laterally.

Proximal thecae are slender tubes some 2.2—2.0 mm long, with the prothecal part 1.67—1.06 mm and metathecal 0.94—0.53 mm long. The prothecal part occupies, therefore, about 71—76% of total thecal length. They are 0.13—0.23 mm wide at the base and 0.22—0.17 mm (dorsoventrally) in the metathecal part. Some part ($^{1}/_{4}$ to $^{1}/_{3}$) of subapertural metatheca is isolated and forms a kind of a short neck which terminates in a supraapertural part. Metatheca is inclined to the main axis at an angle of 10—20° in adnate part and 15—30° in isolated part. The upper part of the neck is transversely strongly expanded (in the right-left direction), reaching some 0.32—0.30 mm. It consists of two apertural lobes, forming a complex apertural apparatus of theca (Pl. XLIII, Figs. A-B). The right apertural lobe (*rl*) is smaller and in its outline resembles a hood. It consists of a strongly convex, hoodlike, domed part and a flat marginal part, forming a kind of a brim on the free margin of the right lobe. This marginal part is placed almost perpendicularly to the domed part of the right lobe, forming ventrally a small, rounded termination. Prolonged dorsally, it forms there a deep incision, i.e. the dorsal apertural notch (Pl. XLIII, Figs. B_1-B_3, *dan*). The right apertural lobe is made up by some 8—9 fuselli, showing a peculiar arrangement, found also in distal thecae and, in this connection, described later on (comp. p. 524).

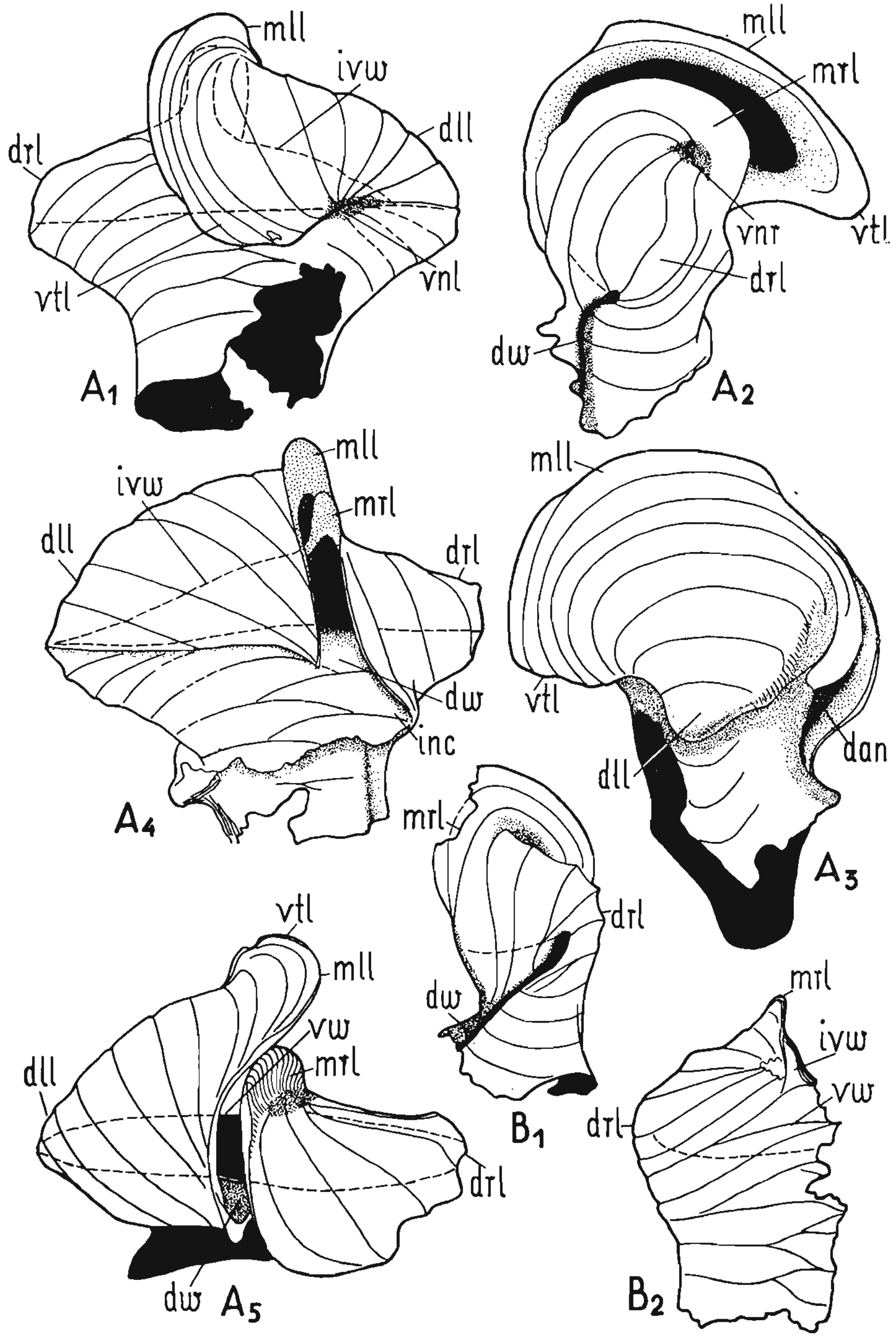
The left apertural lobe is distinctly larger and forms a domed, hoodlike part, stretched transversely and provided, on its free margin, with a marginal part in the form of a brim. The ventral free termination of the lobe forms a broad, rounded outgrowth, fastened, through a node (*n*), to the ventral wall of metatheca. On the dorsal side, the left lobe is fused with the dorsal wall of metatheca. The lobe consists of some 10 fuselli, showing a peculiar arrangement, described in detail in connection with distal thecae (comp. p. 526).

Plate XLIV

Cucullograptus pazdroi Urbanek. Details of fusellar structure of apertural lobes. A_1-A_5 isolated apertural part of theca, in ventral (A_1), reverse (A_2), obverse (A_3), dorsal (A_4) and top (A_5) views; B_1-B_2 isolated right apertural lobe, seen from dorsal side and somewhat laterally (B_1) and from ventral side (B_2) (S. 181, Czarnogłowy); A_1-A_5 ca. ×100; B_1-B_2 ca. ×75.

dw dorsal wall of apertural slit and dorsal wall of theca, *vnr* ventral node of the right apertural lobe; further explanations as in Pl. XLIII.

PLATE XLIV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The apertural slit is stretched transversely and almost entirely covered by apertural lobes, thus producing the internal aperture. Its ventral margin is formed by the ventral wall of the right lobe itself and by its prolongation which produces an obliquely lowering septum, situated inside the left apertural lobe. The dorsal margin of the internal apertural slit is made up by the dorsal wall of metatheca and by the left lobe with its prolongation which, in the form of an internal septum, penetrates inside the right apertural lobe. These, rather complex structures are presented in Pl. XLIII, Figs. B_1-B_3 where the course of internal apertural margins, visible in transparent specimens, are shown by broken lines. The details of the internal structure of the apertural apparatus are described further in connection with distal thecae (comp. p. 528).

The distal thecae are 2.54—2.34 mm in length, with the prothecal about 1.54—1.44 mm and the metathecal part about 1.10—0.86 mm long. The prothecal part occupies about 56—57% of their length. Thecae are 0.40—0.27 mm wide at the base and some 0.20 mm in the metathecal part. Ventral margin in most distal thecae is provided with a gently geniculate curvature.

The upper 1/3 of the subapertural part of metatheca is isolated in the form of a neck, inclined to the main axis of theca at an angle of 50°. In its upper part where it measures 0.55—0.60 mm in the right-left direction, this isolated neck is strongly expanded transversely. The apertural part is provided with a complex apertural apparatus which consists of two apertural lobes (Pl. XLIII, Figs. C, D).

The right apertural lobe is distinctly smaller than the left and has the form of a hood, provided with a globular, helmetlike and strongly convex part and a marginal part, forming a kind of brim (Pl. XLIII, Figs. C_1, D_1, *drl*, *mrl*). The globular part is composed of a number of fuselli (about 7) which, on the ventral side, extend in continuation of the fusellar system of the subapertural part of metatheca, being however slightly obliquely inclined as compared with lower fuselli of metatheca (Pl. XLIV, Fig. B_2, *drl*). The fusellar system of the metatheca proper is passing gradually into the fuselli of the right apertural lobe, showing one or two intermediate fuselli which make up the basal part of the lobe. Each fusellus of the lobe proper starts from the ventral node and, framing the apertural slit, terminates dorsally in the lateral margin of the dorsal wall of theca (Pl. XLIV, Fig. B_1). Lower fuselli terminate in the ventral margin of the dorsal wall of an isolated part of metatheca (neck), while higher fuselli overlap this wall and terminate in its dorsal margin (Fig. A_2, *drl*). The latter are slightly arched as compared with almost straight lower fuselli of the right lobe. The marginal part of the lobe consists of two additional fuselli which

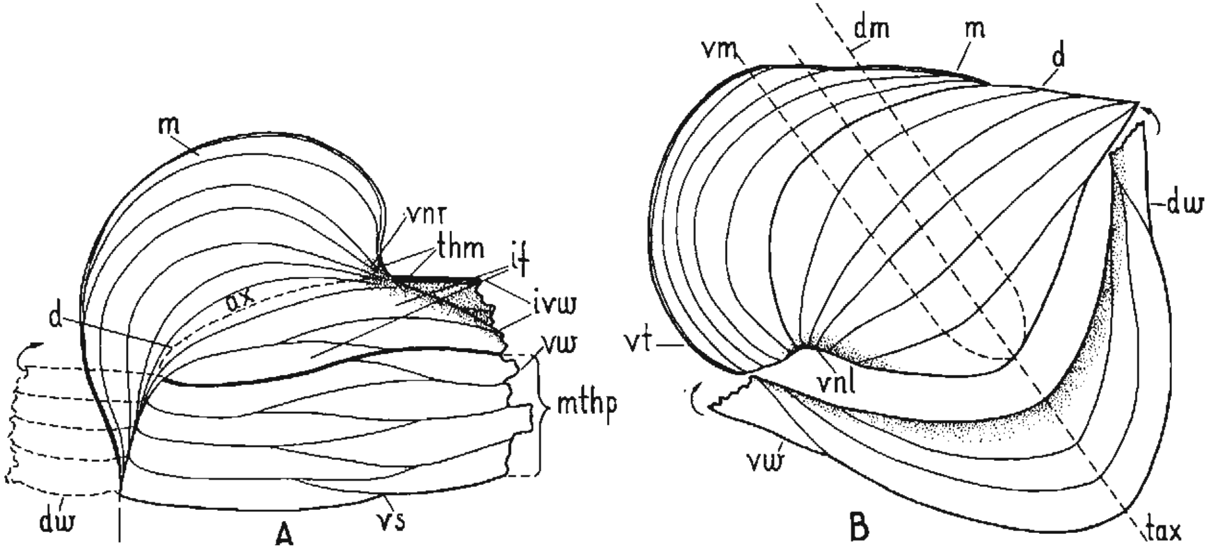


Fig. 26. — *Cucullograptus pazdroi* Urbanek. Diagram of the fusellar structure in apertural lobes. Arrows indicate directions in folding of the periderm. *A* fusellar diagram of the right lobe, *B* fusellar diagram of the left lobe and adjacent subapertural part of metatheca;

ax axial line along which the right lobe is domed, *d* domed part of the lobe, *dm* dorsal margin of the apertural slit shown by broken lines in its relation to the lobe, *dw* dorsal wall of subapertural part of metatheca, *if* intercalary fuselli, *ivw* internal ventral wall *m* marginal part of the lobe, *mthp* metathecal part, *vnl* ventral node of the left lobe, *nr* ventral node of the right lobe, *tax* transversal axis of the internal apertural slit, *vm* ventral margin of apertural slit shown by broken lines in relation to the lobe, *vs* ventral zigzag suture, *vt* ventral termination of the left apertural lobe, *vw* ventral wall of subapertural part of metatheca.

terminate freely on ventral and dorsal sides at a certain distance from the base of the lobe itself (Fig. B_1, *mrl*). The margin of the dorsal wall of the lobe frames a deep incision which communicates with a narrow space between the right lobe and the internal part of the dorsal wall (Fig. A_4, *inc*). A slightly simplified picture of the fusellar structure of the right lobe is shown in Fig. 26, A, in projection on a flat surface to visualize the arrangement of fuselli and the relation of fusellar systems of domed and marginal parts. This diagram is based on a combination of pictures shown on Pl. XLIV, Figs. A_2, B_1-B_2. It differs largely from an earlier reconstruction of fusellar structure of this lobe (suggested by Urbanek, 1958, Fig. 35, A, pp. 64 and 68) which, in many respects, was still incorrect, as indicated by recent investigations of rich and especially well-preserved thecae from erratic boulder S. 181, Czarnogłowy.

The ventral wall of the isolated part of metatheca (neck), underlying the apertural apparatus, consists normally of two series of fuselli, the right being prolonged to the right apertural lobe and the left gradually passing to the left apertural lobe. An additional structure is superimposed on this normal ventral thecal wall, forming an internal ventral wall inside the left lobe. It forms a kind of septum with oblique upper margin, leftwards gradually decreasing in height (Fig. 26, A, *ivw*; Pl. XLIII, Fig. C_3; Pl. XLIV, Figs. A_1, A_4-A_5).

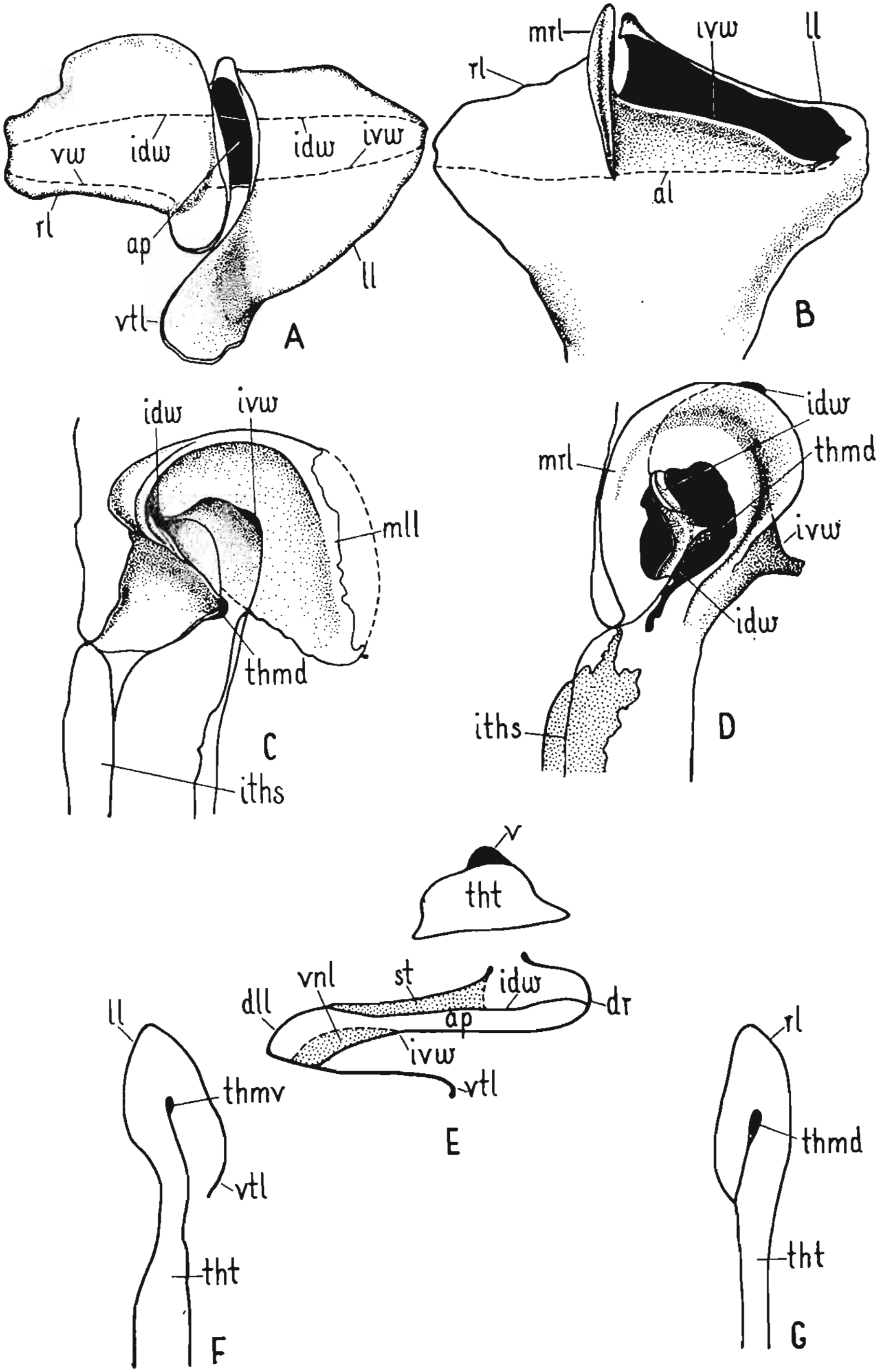
The left apertural lobe is much larger than the right, being composed of a strongly convex, hoodlike part, and a well developed marginal part, forming a wide brim on the free margin of the lobe (Pl. XLIII, Figs. C_2-C_3, D_1-D_2). The globular, domed part of the lobe consists of some 6—7 fuselli which are disposed successively on the lateral margin of the subapertural part of metatheca. They constitute a genicularly convex part of the lobe, each fusellus being fused, on the ventral and dorsal sides, with the margin of the thecal wall, or just below it

Plate XLV

Cucullograptus pazdroi Urbanek. Internal structure of apertural apparatus. *A* apertural slit (broken lines), visible through apertural lobes in the top view of a transparent specimen; *B* internal prolongation of the ventral wall inside the left lobe, visible after removing of the ventral part of the left lobe by the needle; *C* internal cavity of the left apertural lobe, visible in longitudinally sectioned specimen; *D* interior of the right apertural lobe, visible through opening in domed part of the right apertural lobe; *E* transversal microtome section through the apertural apparatus; *F* longitudinal microtome section through left apertural lobe and thecal tube; *G* longitudinal microtome section through the right apertural lobe and thecal tube. (*A*-*D* S. 181, Czarnogłowy; *E*-*G* S. 32 Gdańsk-Wrzeszcz); ca. ×100.

al level of internal aperture, *ap* internal apertural opening, *dll*, *drl* domed part of left and right lobe, *idw* internal part of the dorsal wall, *iths* interthecal septum, *ivw* internal part of the ventral wall, *ll* left apertural lobe, *mll* marginal part of the left lobe, *mrl* marginal part of the right lobe, *rl* right apertural lobe, *st* spongelike peridermal tissue filling the space between left lobe and internal dorsal wall, *thmd* thickened margin of the dorsal wall, *thmv* thickened margin of the ventral wall, *tht* thecal tube, *v* virgula, *vni* ventral node of the left apertural lobe, *vtl* ventral termination of the left lobe.

PLATE XLV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G

(Pl. XLIV, Figs. A_1, A_4, *dll*). The first fusellus has a wedge-shaped form, is short and situated horizontally. The rest of them are arched and cover the apertural slit. The last ones converge ventrally forming a ventral node (Pl. XLIV, Figs. A_1, *vnl*, A_3).

The marginal part of the left lobe is formed by a number (usually 3—4) of additional fuselli disposed along the free margin of the lobe and forming there a kind of a brim. It is placed almost perpendicularly to the surface of the left apertural lobe, except for the ventral termination of the lobe where the marginal fuselli constitute a direct prolongation of the domed part (Pl. XLIII, Fig. C_3; Pl. XLIV, Figs. A_1-A_5, *mll*). This ventral termination in the form of a broad shovellike outgrowth of the lobe proper stretches far beyond the ventral border of the right apertural lobe (Pl. XLIII, Figs. C_1-C_3, D_1-D_2; Pl. XLIV, Figs. A_2, A_5, *vtl*).

The diagrammatical picture of fusellar structure of the left apertural lobe is shown in Fig. 26, B. This is in complete conformity with an earlier reconstruction of its structure (shown by Urbanek, 1958, Fig. 35, B, pp. 64 and 68).

The internal structure of apertural apparatus is shown in Pl. XLV. The transversely elongated apertural slit is situated inside the apertural lobes. Their mutual relations are visible in the top view in Fig. A. The margins of the internal apertural slit are formed by the margins of thecal walls, but the relation of thecal walls to apertural lobes requires certain additional comments. The ventral margin of the thecal wall gradually passes on the right side into the right apertural lobe, forming on the left side an internal septum obliquely inclined to the left side (Pl. XLV, Figs. B, C, *ivw*).

Since the fuselli of the left lobe are connected with the dorsal thecal wall somewhat below its free margin (Pl. XLV, Fig. C, *idw*), the margin of the dorsal thecal wall also produces a lower internal wall inside the left apertural lobe. This wall also prolongs inside the right apertural lobe as an internal septum because the fuselli of the lobe are fused to both sides of the lateral margin of the wall. The internal part of the dorsal thecal wall serves, inside the right lobe, as a columella, supporting the entire fusellar structure (Fig. D, *idw*). The margins of internal thecal walls are more or less thickened.

This picture of the internal structure of the apertural apparatus, based on transparent specimens and needle preparations, was confirmed also by microtome sections (Pl. XLV, Figs. E-G). The transverse section of the apertural apparatus (Fig. E) reveals the presence of the internal dorsal wall inside both lobes and of the ventral wall inside the left apertural lobe. The right apertural lobe passes ventrally into the thecal wall. The ventral node of the left apertural lobe forms a distinct peridermal thickening (*vnl*) and between the dorsal thecal wall and the left lobe there is a membranaceous, or spongelike filling of unknown nature (probably, secondary internal deposit, *st*). The longitudinal cross section through the left lobe (Fig. F) shows the presence of an internal ventral wall inside the lobe, provided with a strongly thickened margin (*thmv*). A similar section through the right apertural lobe reveals the presence of an internal dorsal wall with a thickened margin (*thmd*) and a continuous ventral surface, passing gradually into the thecal wall.

A transversely elongated apertural slit, a peculiar feature of the apertural apparatus in *Cuc. pazdroi*, is clearly revealed by the microtome section (Pl. XLV, Fig. E, *ap*).

Growth pattern of rhabdosome. — Curiously enough, no growing point of rhabdosome has been found in the rich material of *Cuc. pazdroi*. A certain information on growth relations on the tip of rhabdosome may, however, be gained from the late Gerhard Holm's unpublished plates (which are housed in Riksmuseum, Paleozoologiska Avd., Stockholm), kindly set at my disposal by Dr. Harry Mutvei and Dr. V. Janusson, the keepers of the collection. In one of these plates, Holm figured doubtlessly a growing theca of *Cuc. pazdroi* (Nos. 28—30), showing a slitlike aperture provided, at lateral sides, with two earlike elevations being an incipient stage in the development of apertural lobes. These elevations, judging from Holm's figures, reproduced here (Fig. 27, A$_1$-A$_3$), were initially identical in size and the elaboration of their asymmetry has been achieved in later growth stages. In addition to the growing apertural apparatus of theca *n*, the growing end consists also of a short, initial prothecal part of the next theca ($n+1$), provided with a short virgula. The original specimen has not been found by the pre-

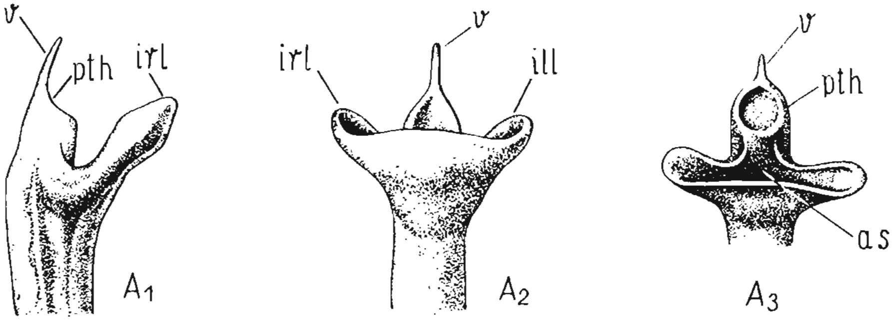

Fig. 27 — *Cucullograptus pazdroi* Urbanek. Growing end of rhabdosome showing the incomplete aperture of theca *n*, and lowermost part of the next theca: A_1 from reverse (right) side, A_2 in ventral view, A_3 from the top (from unpublished plates of Gerhard Holm, Naturhistoriska Riksmuseet, Paleozool. Avd., Stockholm, after permission of Prof. E. Stensiö and Prof. E. Jarvik, origin: Baltic drift, locality unknown);

as apertural slit, *ill* incipient left apertural lobe, *irl* incipient right apertural lobe, *pth* prothecal part of the next theca, *v* virgula.

sent writer in Holm's collection and, therefore, the structure of apertural apparatus in lower theca (*n-1*) is unknown, although it has been stated in Holm's handnote, put below this figure that "specimen has two apertures and belongs to lowermost part" (translated kindly by Dr. V. Jaanusson, 1960). The formation rate of the apertural apparatus, as compared with that of the next thecal tube, cannot be, therefore, established merely on the basis of Holm's figure. However, it seems most probable that the formation of the apertural apparatus in a given theca of *Cuc. pazdroi* has been completed before the growth of the next theca reached the metathecal stage, resembling, therefore, the conditions described in this respect for *L. exspectatus* and *Cuc. aversus.*

Stratigraphic range. — In the Mielnik boring, *Cuc. pazdroi* has been found at a depth between 1,002.5—974.9 m. Above this higher limit, the occurrence of short, poorly preserved remains which perhaps may belong to the species in question, have been stated in a sample from a depth of 970.9—971.0 m. The total thickness of the strata, occupied by *Cuc. pazdroi*, does not exceed 31.5 m. In the lower part of its distribution range, this species is commonly associated with *Lobograptus scanicus parascanicus* (a higher zonal form), *L. scanicus amphirostris* n.subsp., *L. exspectatus exspectatus* Urbanek, *Pristiograptus dubius* (Suess), *Neodiversograptus beklemishevi* Urbanek, *Saetograptus chimaera cervicornis* Urbanek, *Holoretiolites erraticus* Eisenack, *H. mancki* (Münch), *H. simplex* Eisenack and *Plectograptus macilentus* (Törnquist).

In the upper part of its occurrence, it is associated with *Saetograptus chimaera* cf. *chimaera* (Barrande), *Pristiograptus dubius* (Suess), *P. dubius tumescens* (Wood), *Neodiversograptus beklemishevi* Urbanek, *Lobograptus scanicus parascanicus* (Kühne), *L. scanicus scanicus* (Tullberg), *L. imitator* n.sp., *Holoretiolites erraticus* Eisenack, *H. mancki* (Münch) and *Plectograptus macilentus* (Törnquist).

Cuc. pazdroi is also common in erratic boulders (comp. p. 519) being in the present author's collection, most frequent in boulders: S. 32, Gdańsk-Wrzeszcz and S. 181, Czarnogłowy. In all boulders it is associated with nearly the same graptolite assemblage which may include the following species: *Saetograptus chimaera* (Barrande) and *S. chimaera cervicornis* Urbanek (very frequent), *Lobograptus scanicus parascanicus* (Kühne) or, less frequently, *L. scanicus scanicus* (Tullberg), *Pristiograptus dubius* (Suess), *Plectograptus macilentus* (Törnquist) (only in S. 32), *Holoretiolites mancki* (Münch) and *Neodiversograptus beklemishevi* Urbanek.

This assemblage leaves no doubt that, also in the fauna from erratic boulders, the occurrence of *Cuc. pazdroi* is restricted to the *scanicus* zone as currently defined. This conclusion well coincides with data, supplied by Kühne (1955, p. 386). The earlier data of Urbanek (1954, 1958), indicating the occurrence of *Colonograptus colonus compactus* Wood, are misleading (in fact, these are senile rhabdosomes of *Saetograptus chimaera*) and the species in question surely does not occur in the *nilssoni* zone.

Cuc. pazdroi have been recorded in situ, from Thuringia (Jaeger, 1955, 1959) and from the Holy Cross Mountains (Góry Świętokrzyskie), Poland (Urbanek, 1958; Tomczyk, 1962), in all cases from the *scanicus* zone as currently defined.

Systematic position. — Although being nominally the type species of *Cucullograptus*, *Cuc. pazdroi* occupies a separate position among the entire assemblage of the Cucullograptinae. Owing to the complete lack of intermediate forms, its relation to other members of the subfamily remains, to a considerable extent, unknown.

The most reliable conclusion is that *Cuc. pazdroi* constitutes a separate lineage of cucullograptids, characterized by a different principle of construction of its apertural apparatus. The latter is expressed by the presence of a transversely expanded aperture and by strongly convex apertural lobes. The new interpretation of the fusellar structure in the right apertural lobe slightly diminishes its differences from apertural lobes in other cucullograptids (comp. p. 336). Its globular shape may be considered a new character (right lobes in other cucullograptids are flat). The fusellar structure of the right lobe is determined by the presence of the ventral node and by overhanging of the fuselli along the dorsal wall of metatheca. Such overhanging of fuselli is known in other cucullograptids but its combination with the globular (convex) shape of the lobe is entirely new. In the left apertural lobe, its globular shape may be considered a feature common with the *aversus* lineage. The fusellar structure of the left apertural lobe may be characterized by the presence of a ventral node and a dorsal attachment of fuselli along the dorsal margin of aperture instead of a fusion with a node.

Cuc. pazdroi may be theoretically derived from the "stem lobograptids" as its early offshoot, but its relationship to early representatives of the *hemiaversus-aversus* lineage also cannot be denied. In spite of the growing material available, no transient form, uniting the *pazdroi* lineage with the remaining cucullograptids, has been known so far and, therefore, its real relationship with other groups cannot be established. A comparison of *Cuc. pazdroi* from the lower with that from the higher horizon does not supply any evidence as to its descent.

Two theoretical possibilities have been indicated by Kühne (1955, p. 391) and Urbanek (1958, pp. 68, 72). Kühne, taking into account a possible stratigraphic order of appearance, was of the opinion that: "so liesse sich an eine Deszendenz des *M. aversus* von *M. eunebeni* (= *Cuc. pazdroi*) denken; von einer unbekannten Form mit symmetrischen Thekenlappen käme man zu *M. eunebeni* würde *M. aversus* folgen, bei dem der rechte Thekenlappen vollständig verschwunden ist".

Despite Kühne's opinion, Urbanek (1958) expressed the view that "...structure of the apertural lobes in *C. pazdroi* is specialized rather than primitive as compared with *C. aversus*" and that "...*Cucullograptus pazdroi* does not seem to be the true ancestral species in this evolutionary line" (p. 72). Urbanek derived *Cucullograptus* from ancestral forms with symmetrical apertural lobes, suggesting that the *Cuc. pazdroi* line originated by the lobograptid type structural modification of the right lobe (p. 68), or through the atrophy of this lobe and a secondary formation of a new lobe according to different structural pattern (pp. 68, 72). In the latter case, *Cuc. pazdroi* may be said to have passed through a one-lobed "*aversus* stage" in phylogeny (p. 72).

Both Kühne's (1955) and Urbanek's (1958) conclusions are now strongly denied by new data, indicating a rather separate descent of the *hemiaversus-aversus* lineage from the "stem lobograptids" (comp. p. 369) without any evidence of its relationship to the *Cuc. pazdroi* lineage. The descent of *Cuc. aversus* from *Cuc. pazdroi* is equally improbable (what is indicated by *Cuc. hemiaversus*, linking it with the "stem lobograptids") as passing of *Cuc. pazdroi* through a one-lobed "*aversus* stage" in phylogeny. The latter conclusion is indicated by an early appearance of *Cuc. pazdroi*, preceding the first signs of atrophy of the right lobe in the *Cuc. aversus* lineage, as shown by *Cuc. hemiaversus*. It seems, however, premature to speculate any more on the ancestry of *Cuc. pazdroi*. The conclusion that it represents a side branch which, for a long time, evolved simultaneously with the *aversus* lineage, seems to be very likely (comp. also considerations on pp. 369—370).

In spite of the separate position, occupied by *Cuc. pazdroi* among the Cucullograptinae, the structure of subapertural part of thecae and the shape of the "gracilized" cucullograptid sicula testify to its membership in this subfamily.

Nomenclatorial remark. This form, recently described from the Baltic erratic boulders (Urbanek, 1955, 1958; Kühne, 1955) is doubtlessly conspecific with one of the forms, figured in Holm's unpublished plates, housed at Riksmuseum in Stockholm. This form was briefly mentioned and figured by Bulman (1938, p. 31, Fig. 20, c), being subsequently considered by Urbanek (1954, p. 79, Engl. summ.) and Kühne (1955, p. 386) to be conspecific with *Cuc. pazdroi*. On the other hand, Bulman suggested (1953, p. 153) that "it seems not unlikely, however, that the *Monograptus* sp. from the Holm Collection figured in Bulman, 1938, Fig. 20 c, is referable to *M. crinitus*". Bulman stated, however, that "no really well-preserved examples of this species seem to be extant; even the figured specimens (Lapworth, Elles & Wood, 1913, Pl. 44, Fig. 3), preserved at

Birmingham University, are abraded and difficult to interpret". The same has been found by the present writer during his study on Birmingham Collection, in which he was unable to recognize the shape of thecae, especially the aperture. Studying the graptolites, identified by different authors as *Monograptus crinitus* Wood, the present author could ascertain that the latter species, in its current concept, produces a portmanteau for different "thin" forms of the Upper Silurian monograptids. The writer believes that the present knowledge of *M. crinitus* Wood provides unsufficient evidence for identifying it with *Cuc. pazdroi* and, moreover, he is inclined to think that the former represents a "nomen dubium" (a similar opinion was expressed by Dr. W. G. Kühne; 1958, personal communication).

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Warszawa, April 1966

REFERENCES

BARRANDE, J. 1850. Graptolites de Bohême, 1-74, Prague.

BEKLEMISZEW, W. N. 1957. Podstawy anatomii porównawczej bezkręgowców. I. Promorfologia. 1-491, Warszawa.

BULMAN, O. M. B. 1938. Graptolithina. *In*: O. H. Schindewolf (ed.), Handbuch der Paläozoologie, 2D, 2, 1-92, Berlin.

— 1950. Graptolites from the Dictyonema Shales of Quebec. — *Quart. J. Geol. Soc. London*, **106**, 1, 63-99, London.

— 1953. On the thecae of Monograptus scanicus Tullberg. — *Geol. Mag.*, **90**, 2, 131-136, Hertford.

— 1955. Graptolithina. *In*: R. C. Moore (ed.), Treatise on invertebrate paleontology, 1-101, Kansas.

— 1958. Patterns of colonial development in graptolites. — *J. Linn. Soc.*, Zoology, **44**, 295, 24-32, London.

— 1963. The evolution and classification of the Graptoloidea. — *Quart. J. Geol. Soc. London*, **119**, 401-418, London.

BOUČEK, B. 1933. Monographie der Obersilurischen Graptolithen aus der Familie Cyrtograptidae. — *Trav. Inst. Géol, Paléont. Univ. Charles*, **1**, 1-84, Praha.

BOUČEK, B. & PŘIBYL, A. 1952. Nové poznatky o cyrtograptidech z českého siluru a jejich stratigrafickém vyznamu. — *Rozpr. II Tř. Česk. Akad. Ved*, **62**, 9, 1-24, Praha.

BOWMAN, R. I. 1961. Morphological differentiation and adaptation in the Galapagos finches. — *Univ. Calif. Publ. Zool.*, **58**, 1-302, Berkeley.

DOGEL, V. A. 1954. Oligomeryzacja gomologičnych organov. 1-351, Leningrad.

EISENACK, A. 1935. Neue Graptolithen aus Geschieben baltischen Silurs. — *Paläont. Ztschr.*, **17**, 73-90, Stuttgart.

— 1942. Über einige Funde von Graptolithen aus Ostpreussischen Silurgeschieben. — *Ztschr. Geschiebef. Flachlandsgeol.*, **18**, 1, 29-42, Leipzig.

EISENACK, A. 1951. Retioliten aus dem Graptolithengestein. — *Palaeontographica*, C, Abt. A, 5, 129—163, Stuttgart.

ELLES, G. L. 1922. The graptolite faunas of the British Isles. — *Proc. Geol. Assoc.*, **33**, 168—200, London.

— 1925. The characteristic assemblages of the graptolite zones of the British Isles. — *Geol. Mag.*, **62**, 337—347, Hertford.

ELLES, G. L. & WOOD, E. M. R. 1901—1918. A monograph of British graptolites, Pts. I—IX. — *Palaeontogr. Soc.*, **21**, 171—539, London.

HADORN, E. 1955. Letalfaktoren, in ihrer Bedeutung für Erbpathologie und Genphysiologie der Entwicklung. 1—327, Stuttgart.

HORNÝ, R. J. 1962. Das mittelböhmische Silur. — *Geologie*, **11**, 8, 873—916, Berlin.

HUCKE, K. 1917. Die Sedimentärgeschiebe des norddeutschen Flachlandes. 1—178, Leipzig.

IVANOV, A. V. 1960. Pogonofory. *In:* Fauna SSSR, N. S., **75**, 1—271, Moskva-Leningrad.

JAANUSSON, V. 1960. Graptoloids from the Ontikan and Viruan limestones of Estonia and Sweden. — *Bull. Geol. Inst. Univ. Uppsala*, **29**, 289—336, Uppsala.

JAEGER, H. 1959. Graptolithen und Stratigraphie des jüngsten Thüringer Silurs.— *Abh. deutsch. Akad. Wiss.*, **2**, 1—197, Berlin.

— 1962. Das Silur (Gotlandium) in Thüringen und am Ostrand des Rheinischen Schiefergebirges. Symposium-Band 2 Int. Arbeitstag. Bonn-Bruxelles (1960), 108—135, Stuttgart.

— 1964. Beiträge zur regionalen Geologie Thüringens und angrenzender Gebiete sowie zu anderen Problemen. — *Abh. deutsch. Akad. Wiss.*, **2**, 27—51, Berlin.

JAEKEL, O. 1889. Über das Alter des sogenannten Graptolithen-gesteins. — *Ztschr. deutsch. Geol. Ges.*, **41**, 635—716, Berlin.

KOZŁOWSKI, R. 1949. Les Graptolithes et quelques nouveaux groupes d'animaux du Tremadoc de la Pologne (Graptolity i parę nowych grup zwierząt z tremadoku Polski). — *Palaeont. Pol.*, 3 ,1—235, Warszawa.

— 1953. Etude d'une nouvelle espèce du genre Corynoides (Badania nad nowym gatunkiem z rodzaju Corynoides). — *Acta Geol. Pol.*, **3**, 2, Consp. 68—81, Warszawa.

— 1956. Nouvelles observations sur Corynoididae, Graptolithina (Nowe obserwacje nad Corynoididae, Graptolithina). —*Acta Palaeont. Pol.*, **1**, 4, 259—269, Warszawa.

KRAFT, P. 1926. Ontogenetische Entwicklung und Biologie von Diplograptus und Monograptus. — *Paläont. Ztschr.*, **7**, 207—249, Stuttgart.

KÜHNE, W. G. 1953. The prosicula of Retiolites geinitzianus Barr. — *Geol. Mag.*, **90**, 6, 444—5, Hertford.

— 1955. Unterludlow-Graptolithen aus Berliner Geschieben. — *N. Jb. Geol. Pal. Abh.*, **100**, 3, 350—401, Stuttgart.

LACK, D. 1947. Darvin's finches. 1—209, New York.

LAPWORTH, CH. 1876. On Scottish Monograptidae. — *Geol. Mag.*, **3**, 2, Hertford.

MARTINSSON, A. 1963 (1962). The concealed Silurian of the Baltic area. — *Bull. Geol. Inst. Univ. Uppsala*, **42**, Appendix 2 (Autoref. of lecture 1962), 539—541, Stockholm.

— 1963. Kloedenia and related ostracode genera in the Silurian and Devonian of the Baltic area and Britain. — *Ibidem*, **42**, 1—63.

NAUMOV, D. V. 1960. Gidroidy i gidromeduzy morskich, solonovatych i presnovodnych bassejnov SSSR. *In*: Opredel. po faune SSSR, **70**, 1—585, Moskva-Leningrad.

NEWELL, N. D. 1960. The origin of oysters. Rep. XXI Session Norden, Part XXII, Proc. Int. Pal. Union, 81—86, Copenhagen.

PERNER, J. 1899. Etudes sur les graptolites de Bohême. 3b, 1—24, Leipzig-Prague.

POŻARYSKI, W. 1963. Jednostki geologiczne Polski (Engl. summary: Geological units of Poland). — *Przegl. Geol.*, **11**, 1 (118), 4—10, Warszawa.

PŘIBYL, A. 1948. Bibliographic index of Bohemian Silurian graptolites. 1—96, Praha.

REGNÉLL, G. & HEDE, J. E. 1960. The lower Palaeozoic of Scania. The Silurian of Gotland. Int. Geol. Congr. XXI, Guide to excursion A22 and C17, 1—86.

REMANE, A. 1956. Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik. I, 1—364, Leipzig.

REMELÉ, A. 1883. Untersuchungen über die Versteinerungsführenden Diluvialgeschiebe des Norddeutsches Flachlandes, I, 9—152, Berlin.

ROEMER, F. 1884/85. Lethaea erratica. — *Palaeont. Abh.*, **2**, 5, 1—173, Berlin.

ROHDENDORF, B. B. 1957. Paleoentomologičeskie issledovania v SSSR. — *Tr. Paleont. Inst.*, 66, 1—102, Moskva.

RUZHENCEV, V. E. 1947. Evolucija semejstva Medlicottidae Karpinsky. — *Vestn. AN SSSR*, **8**, 37—50, Moskva.

SCHEPOTIEFF, A. 1907. Die Anatomie von Rhabdopleura. — *Zool. Jb.*, Abt. Anat. etc., **23**, Jena.

STOLLEY, E. 1895. Die cambrischen und silurischen Geschiebe Schleswig-Holsteins und ihre Brachiopodenfauna. I. Geol. Theil. 1—104, Kiel-Leipzig.

TIMOFEEFF-RESSOVSKY, N. W. 1931. Gerichtetes Variieren in der phänotypischen Manifestierung einiger Generationen von Drosophila funebris. — *Naturwiss.*, **19**, 23—25, 493—497, Berlin.

— 1934. Über den Einfluss des genotypischen Milieus und der Aussenbedingungen auf die Realisation des Genotyps. Genmutation vti (venae transversae incompletae) bei Drosophila funebris. — *Nachr. Ges. Wiss. Goettingen*, Math. — Phys. Kl., N. F., Biol., **1**, 6, 53—106, Berlin.

TOMCZYK, H. 1958. Osady środkowego ludlowu nawiercone na Podlasiu w Żebraku koło Siedlec. — *Kwart. Geol.*, **2**, 4, 711—720, Warszawa.

— 1962. Problem stratygrafii ordowiku i syluru w Polsce w świetle ostatnich badań (Engl. summary). — *Prace Inst. Geol.*, **15**, 1—134, Warszawa.

— 1964. Stratygrafia syluru w północno-wschodniej Polsce. — *Kwart. Geol.*, **8**, 3, 506—523, Warszawa.

TULLBERG, S. A. 1883. Skånes graptoliter, II. — *Sver. Geol. Unders.*, *C*, **55**, 1—43, Stockholm.

URBANEK, A. 1953. O dwóch gatunkach Monograptidae (Sur deux espèces de Monograptidae). — *Acta Geol. Pol.*, **3**, 2, 277—297, Consp. 100—107, Warszawa.

— 1954. Some observations on the morphology of Monograptidae (Obserwacje nad morfologią pewnych Monograptidae). — *Ibidem*, **4**, 2, 291—306, Consp. 78—88.

— 1958. Monograptidae from erratic boulders of Poland (Monograptidae z głazów narzutowych Polski). — *Palaeont. Pol.*, **9**, 1—105, Warszawa.

— 1960. An attempt at biological interpretation of evolutionary changes in graptolite colonies (Próba interpretacji biologicznej zmian ewolucyjnych w koloniach graptolitów). — *Acta Palaeont. Pol.*, **5**, 2, 127—234, Warszawa.

— 1963. On generation and regeneration of cladia in some Upper Silurian monograptids (O rozwoju i regeneracji gałązek w koloniach pewnych górno-sylurskich Monograptidae). — *Ibidem*, **8**, 2, 135—254.

WALKER, M. 1953. The sicula of Monograptus scanicus Tullberg. — *Geol. Mag.*, **90**, 3, 224—225, Hertford.

WHITTINGTON, H. B. 1954. A new Ordovician graptolite from Oklahoma. — *J. Paleont.*, **28**, 5, 613—621, Menasha.

WILLEFERT, S. 1963. Graptolites du Silurien et du Lochkovien de Touchent (Maroc Central). — *Notes Serv. Gèol. Maroc*, **23**, 172, 69—94, Rabat.

WORTHINGTON, E. B. 1940. Geographical differentiation in fresh waters with special reference to fish. *In*: J. Huxley (ed.), The new systematics, 287—302, Oxford.

ADAM URBANEK

MORFOLOGIA I EWOLUCJA CUCULLOGRAPTINAE (MONOGRAPTIDAE, GRAPTOLITHINA)

Streszczenie

W pracy przedstawiono rezultaty badań nad budową i rozwojem astogenetycznym przedstawicieli podrodziny Cucullograptinae Urbanek, 1958, wyjaśniono przebieg i mechanizm ich ewolucji, jak również ustalono znaczenie stratygraficzne poszczególnych gatunków.

Opisano 14 gatunków i podgatunków Cucullograptinae, z czego 4 gatunki i 2 podgatunki są nowe. Materiał opracowany pochodzi: 1) z próbek rdzenia wiertniczego otworu Mielnik n/Bugiem, I. G. 1, wykonanego przez Zakład Rud Żelaza Instytutu Geologicznego w Warszawie; próby te przekazane zostały autorowi niniejszej pracy w celu zbadania występującej w nich fauny graptolitowej; 2) z bałtyckich głazów narzutowych wieku górnosylurskiego, pochodzących z moren Polski Północnej, zwłaszcza Pomorza.

Przy preparowaniu graptolitów stosowano zarówno chemiczne, jak i standartowe metody badania, używane przy opracowywaniu graptolitów w tym stanie zachowania.

W części ogólnej omawia się dokładnie pochodzenie materiału, określając bliżej stosunki stratygraficzne utworów sylurskich w wierceniu Mielnik n/Bugiem oraz pochodzenie i stanowisko stratygraficzne zbadanych głazów narzutowych.

Na podstawie występowania Cucullograptinae w sylurze Mielnika n/Bugiem można zaproponować podział stratygraficzny górnej części tzw. warstw mielnickich, wydzielonych przez H. Tomczyka (1962) dla syluru platformowego Polski. W pracy przeprowadza się porównanie proponowanego podziału stratygraficznego z powszechnie dotychczas przyjętym podziałem brytyjskim dla równowiekowych serii dolnego ludlowu oraz z alternatywnym podziałem, opartym na występowaniu Saetograptinae.

Dokładne poznanie budowy i rozwoju kolonii różnych przedstawicieli Cucullograptinae pozwoliło przeprowadzić analizę anatomiczno-porównawczą ich morfologii oraz ustalić pewne prawidłowości ewolucji zbadanej grupy graptolitów.

Analiza zmian ewolucyjnych sikuli Cucullograptinae pozwoliła po raz pierwszy prześledzić proces mikroewolucji tej części kolonii w obrębie określonej grupy graptolitów. Ustalono, że u Cucullograptinae polegała ona na progresywnej gracylizacji, tj. na stopniowym skracaniu się i upraszczaniu budowy sikuli. Analiza zachodzących zmian pozwala na wysunięcie przypuszczenia, że sprowadzały się one do procesu fetalizacji osobnika znajdującego się w sikuli (sikulozooida). Porównanie obrazu ewolucji sikuli u Cucullograptinae ze zmianami jej w innych grupach Graptoloidea pozwala na wstępną klasyfikację zależności między ewolucją sikuli i pozostałych tek rabdozomu. Rozważa się także przypuszczalne znaczenie fetalizacji sikulozooida, jako czynnika morfogenetycznego w ewolucji pozostałych tek kolonii u Cucullograptinae.

W przeciwieństwie do sikuli, pozostałe teki rabdozomu Cucullograptinae cechowała wyraźna tendencja do progresywnego różnicowania budowy. Zmiany ewolucyjne wyrażały się głównie w powstaniu i rozwoju złożonego aparatu aperturalnego, przy czym zbadany materiał pozwala określić główne etapy tego procesu, który zachodził niezależnie w poszczególnych liniach ewolucyjnych Cucullograptinae. Prymitywne gatunki *Lobograptus* (*L. progenitor* n.sp., *L. simplex*, *L. exspectatus*) mają aparat aperturalny bilateralnie symetryczny i stanowią pod względem morfologicznym tzw. S-kukullograptidy. Pozostałe gatunki *Lobograptus* cechowała, wraz z rozwojem aparatu aperturalnego, tendencja do powstania jego asymetrii przez przerost prawego płata aperturalnego. Stanowią one grupę tzw. R-kukullograptidów (*L. scanicus* z trzema podgatunkami, *L. imitator* n.sp., *L. invertus* n.sp. i *L. cirrifer* n.sp.). Odrębną grupę morfologiczną reprezentują przedstawiciele rodzaju *Cucullograptus*, u których występuje tendencja do przerostu lewego płata aperturalnego. Stanowią one tzw. L-kukullograptidy, reprezentowane przez *Cuc. hemiaversus*, *Cuc. aversus* z dwoma podgatunkami i *Cuc. pazdroi*.

Ewolucja tek u Cucullograptinae cechowała się znamiennymi rysami, do których należą: 1) koncentracja zmian ewolucyjnych na części aperturalnej teki, przy względnie dużej stałości budowy pozostałych części teki; 2) tendencja do rozwoju rozbieżnych kierunków wtórnej asymetrii aparatu aperturalnego.

Pierwsza cecha charakteryzująca ewolucję tek u Cucullograptinae daje się dobrze porównać z obrazem zróżnicowania u współczesnych Pogonophora, u których Iwanow (1960) stwierdził, że zmiany ewolucyjne polegały głównie na modyfikacjach budowy aparatu czułkowego, przy względnie dużej stałości w budowie reszty ciała. Omawia się przypuszczalne znaczenie przystosowawcze tego zjawiska w ewolucji Cucullograptinae, podkreślając, że świadczy ono, iż podstawowe kierunki ewolucji określone były powstaniem odrębnych mechanizmów pobierania pokarmu.

Powstanie asymetrii aparatu aperturalnego zdaje się świadczyć o rozwoju wtórnej asymetrii części miękkich ciała, zwłaszcza aparatu czułkowego. Asymetria tego aparatu zdaje się stanowić cechę skorelowaną z określonym stopniem jego rozwoju morfologicznego. Podkreśla się równocześnie różnice, jakie zachodzą między stabilnym, nie podlegającym większym zmianom ewolucyjnym, charakterem asymetrii R-kukullograptidów oraz progresywnym charakterem asymetrii większości L-kukullograptidów. W pierwszym przypadku mamy przypuszczalnie do czynienia z pewnym przerostem aparatu czułkowego z prawej strony ciała, bez równoczesnej jego redukcji na stronie przeciwnej. Natomiast u tych L-kukullograptidów, u których asymetria ma charakter progresywny, hypertrofia aparatu czułkowego z lewej strony łączyła się przypuszczalnie z jego redukcją po przeciwnej stronie ciała. Proces ten uruchomił prawdopodobnie mechanizm kompensacji morfofizjologicznej, stanowiący zapewne jeden z czynników przerostu aparatu czułkowego z lewej strony ciała zooidów.

Zbadanie zmian astogenezy, jakie zachodziły w ewolucji Cucullograptinae, doprowadza do wniosku, że głównym sposobem pojawiania się nowych cech filogenetycznych była u nich tzw. introdukcja dystalna. W rezultacie tego procesu, nowe cechy pojawiały się wpierw tylko w tekach dystalnej części rabdozomu, aby następnie stopniowo, w poszczególnych ogniwach danej linii ewolucyjnej, obejmować bardziej proksymalne części kolonii. Omawia się także pewne przypadki odstępstwa od reguły introdukcji dystalnej nowych cech filogenetycznych. Odnoszą się one do nielicznych i mniej istotnych cech morfologicznych, które pojawiają się w tej grupie graptolitów drogą introdukcji proksymalnej. Ponieważ większość cech, w tym wszystkie cechy o większym znaczeniu morfologicznym, wykazują introdukcję dystalną, ewolucja Cucullograptinae dostarcza niezwykle przekonywujących dowodów na znaczenie tego sposobu powstawania nowych cech w filogenezie tek. Pewien wyjątek od reguły introdukcji dystalnej stanowi też asymetria R-kukullograptidów, która — zgodnie z wcześniej wysuniętymi przypuszczeniami (Urbanek, 1960) — pojawia się apolarnie, tj. przejawia się mniej więcej jednakowo u wszystkich osobników kolonii.

Analiza rozprzestrzeniania się nowych cech w rezultacie filogenetycznych modyfikacji astogenezy potwierdza wcześniej wypowiedziane poglądy (Urbanek, 1960), że sprowadza się ono do zmian ekspresywności i penetracji określonych czynników genetycznych.

W pracy dyskutuje się także zagadnienie organizacji kolonii graptolitów. Starano się wykazać, że kolonie Graptoloidea reprezentują takie stadium integracji, przy którym procesy osobnicze, określające charakter morfofizjologiczny poszczególnych zooidów kolonii, nie zostają jeszcze całkowicie zniwelowane. Uważając takie kolonie za szczególny przypadek integracji grupy osobników (populacji), uzasadnia się słuszność stosowania pojęć „penetracja" i „ekspresywność' dla opisu zjawisk, zachodzących przy filogenetycznych modyfikacjach astogenezy. Przy rozważaniach tych przytacza się poglądy krytyczne, przekazane autorowi niniejszej pracy w listach Dra. L. Van Valena (American Museum of Natural History, New York).

Przez zestawienie danych morfologicznych i stratygraficznych uzasadniono pewne wnioski, odnoszące się do filogenezy i taksonomii Cucullograptinae. Podkreśla się odmienne znaczenie morfologii tek dystalnych i proksymalnych dla ustalania stosunków rodowych. U zbadanej grupy graptolitów, pierwsze mają znaczenie przyszłościowe, „profetyczne", z uwagi na zasadę introdukcji dystalnej nowych cech filogenetycznych. Pozwalają one w pewnym stopniu określić dalszy kierunek ewolucji. Drugie, przeciwnie, są najmniej zmodyfikowane, zachowują najdłużej mało zmienione cechy ancestralne i pozwalają w ten sposób określić budowę cech właściwą przodkom. Takie znaczenie tek dystalnych i proksymalnych nie jest jednak absolutne, lecz zależne od sposobów filogenetycznych modyfikacji astogenezy, właściwych danej grupie graptolitów.

Uwzględniając powyższe kryteria, starano się ustalić stosunki filogenetyczne w obrębie Cucullograptinae. Najstarszym i najbardziej prymitywnym przedstawicielem tej grupy jest *Lobograptus progenitor* n.sp., który zapoczątkowuje zarazem rozwój pierwszej linii ewolucyjnej Cucullograptinae, stanowiącej ich pierwotny pień rozwojowy ("stem lobograptids"), zaś *L. simplex* zajmuje stanowisko centralne wśród wszystkich Cucullograptinae, reprezentuje bowiem stadium strukturalne, od którego dokonała się przypuszczalnie radiacja tej grupy, dająca w rezultacie 4 lub 5 oddzielnych linii rozwojowych. W rozwoju każdej z tych linii przeważały procesy ewolucji kierunkowej nad procesami dywergencji (Pl. VIII i IX). Odrębne stanowisko zajmuje jedynie *Cucullograptus pazdroi*, który nie łączy się wyraźnie z głównym pniem rozwojowym Cucullograptinae. Stanowi on albo linię boczną, która wyodrębniła się wcześnie i allopatrycznie, lub też ma inne pochodzenie, niż pozostali przedstawiciele tej grupy. Z tego względu Cucullograptinae są raczej koncepcją morfologiczno-taksonomiczną, niż filogenetyczną.

Pochodzenie Cucullograptinae nie może być obecnie wyjaśnione. Jednak podobieństwo proksymalnej części kolonii prymitywnych przedstawicieli *Lobograptus* (*L. progenitor* n.sp., *L. simplex*) do proksymalnej części rabdozomu wczesnych linograptidów (*Neodiversograptus nilssoni*) wydaje się świadczyć o pokrewieństwie tych dwóch szczepów. *N. nilssoni* jest jednak zbyt wyspecjalizowany, aby można go było uważać za przodka *L. progenitor* n.sp. — najstarszego ze znanych przedstawicieli Cucullograptinae. Dlatego wysunięto przypuszczenie, że przodkiem wspólnym dla Cucullograptinae i Linograptinae mógł być linograptid, reprezentujący preneodiwersograptidowe stadium ewolucji.

W części systematycznej podaje się opis następujących przedstawicieli Cucullograptinae:

Lobograptus Urbanek, 1958
L. progenitor n.sp.
L. simplex Urbanek, 1960
L. exspectatus exspectatus Urbanek, 1960
L. exspectatus bicornis n.subsp.
L. scanicus parascanicus (Kühne, 1955)
L. scanicus amphirostris n.subsp.
L. scanicus scanicus (Tullberg, 1883) sensu Bulman, 1953
L. imitator n.sp.
L. invertus n.sp.
L. cirrifer n.sp.

Cucullograptus Urbanek, 1954
Cuc. hemiaversus Urbanek, 1960
Cuc. aversus cf. *aversus* (Eisenack, 1942)
Cuc. aversus rostratus Urbanek, 1960
Cuc. pazdroi Urbanek, 1954.

АДАМ УРБАНЭК

МОРФОЛОГИЯ И ЭВОЛЮЦИЯ CUCULLOGRAPTINAE (MONOGRAPTIDAE, GRAPTOLITHINA)

Резюме

В работе приводятся результаты изучения строения и астогенетического развития представителей подсемейства Cucullograptinae Urbanek, 1958, выяснены ход и механизм их эволюции, а также установлено стратиграфическое значение исследованных видов.

Дано также описание 14 видов и подвидов Cucullograptinae, из которых 4 вида и 2 подвида являются новыми. Изученный материал происходит: 1) из керна скважины Мельник над Бугом, I. G. 1, пробуренной Лабораторией Железных Руд Геологического Института в Варшаве. Образцы из этой скважины переданы автору настоящей работы с целью изучения присутствующей в них фауны граптолитов; 2) из балтийских эрратических валунов верхнесилурийского возраста, происходящих из морен Северной Польши, главным образом Поморья.

При препарировке граптолитов были применены как химические, так и обычные методы исследования, которыми пользуются исследователи при изучении граптолитов такой сохранности.

В общей части подробно обсуждается происхождение материала, определяются точные стратиграфические взаимоотношения силурийских осадков в скважине Мельника над Бугом, а также происхождение и стратиграфическое положение изученных эрратических валунов.

На основании распространения Cucullograptinae в силурийских отложениях Мельника над Бугом предлагается стратиграфическое деление верхней части так называемых мельницких слоев, выделенных Г. Томчиком (H. Tomczyk, 1962) для платформенного силура Польши. В настоящей работе проводится сравнение предлагаемого стратиграфического деления с общепринятым английским делением для одновозрастных серий нижнего лудлова, а также с альтернативным делением, основанным на распространении Saetograptinae.

Точное познание строения и развития колоний разных представителей

Cucullograptinae позволило автору произвести анатомическо-сравнительный анализ их морфологии, а также определить некоторые закономерности эволюции изученной группы граптолитов.

Анализ эволюционных изменений сикулы Cucullograptinae позволил впервые проследить процесс микроэволюции этой части колонии в пределах определенной группы граптолитов. Установлено, что у Cucullograptinae она заключалась в прогрессивной „грацилизации”, то есть в постепенном укорачивании и упрощении строения сикулы. Анализ происходящих изменений позволяет предположить, что они сводились к процессу фетализации особи, находящейся в сикуле (сикулозооид). Сравнение эволюции сикулы у Cucullograptinae с изменениями ее в иных группах Graptoloidea дает возможность предложить предварительную классификацию зависимости между эволюцией сикулы и остальных тек рабдосомы. Рассматривается также предполагаемое значение фетализации сикулозооида как морфогенетического фактора в эволюции остальных тек колонии у Cucullograptinae.

В противоположность сикуле, остальные теки рабдосомы Cucullograptinae отмечались отчетливой тенденцией к прогрессивному дифференцированию строения. Эволюционные изменения выражались, главным образом, в образовании и развитии сложного апертурного аппарата, причем изученный материал позволяет определить главные этапы этого процесса, который происходил независимо в отдельных эволюционных ветвях Cucullograptinae. Примитивные виды *Lobograptus* (*L. progenitor* n. sp., *L. simplex, L. exspectatus*) имеют билатерально-симметричный апертурный аппарат и морфологически составляют так называемые S-кукуллограптиды. Остальные виды *Lobograptus* отмечались совместно с развитием апертурного аппарата тенденцией к возникновению его асимметрии через гипертрофию правой апертурной лопасти. Они составляют группу так называемых R-кукуллограптидов (*L.scanicus* с тремя подвидами, *L.imitator* n.sp., *L. invertus* n. sp. и *L. cirrifer* n. sp.). Особой морфологической группой являются представители рода *Cucullograptus*, у которых имеется тенденция к гипертрофии левой апертурной лопасти. Они составляют группу так называемых L-кукуллограптидов, представленных видами *C. hemiaversus, C. aversus* с двумя подвидами и *C. pazdroi.*

Эволюция тек у Cucullograptinae отмечалась характерными чертами, к которым принадлежали: 1) концентрация эволюционных изменений на апертурной части теки, при относительно большой устойчивости строения остальных частей теки; 2) тенденция к развитию расходящихся направлений (дивергенция) вторичной асимметрии апертурного аппарата.

Первую черту, характеризирующую эволюцию тек у Cucullograptinae можно хорошо сравнить со способом дифференцирования у современных Pogonophora, у которых Иванов (1960) констатировал эволюционные изменения, заключающиеся, главным образом, в дифференцировке строения щупальцевого аппарата при относительно большой устойчивости в строении остального тела. Обсуждается вероятное приспособительное значение этого явления в эволюции Cucullograptinae, подчеркивая, что свидетельствует оно о том, что основные направления эволюции были определены возникновением особых механизмов для собирания пищи.

Возникновение асимметрии апертурного аппарата может свидетельствовать о развитии вторичной асимметрии мягких частей тела, особенно щупальцевого аппарата. Асимметрия этого аппарата составляет черту, коррелятивно связанную с определенной степенью его морфологического развития. Одновременно подчеркиваются различия, которые имеют место между стабильным, не подвергающимся заметным эволюционным изменениям, типом асимметрии R-кукуллограптидов и прогрессивным характером асимметрии большинства L-кукуллограптидов. В первом случае вероятно имеем дело с некоторой гипертрофией щупальцевого аппарата с правой стороны тела, без одновременной его редукции на противоположной стороне. Зато у тех L-кукуллограптидов, у которых асимметрия имеет прогрессивный характер, гипертрофия щупальцевого аппарата с левой стороны, возможно, сочеталась с его редукцией на противоположной стороне тела. Этот процесс, вероятно, включал механизм морфофизиологической компенсации, являющейся, по всей вероятности, одним из факторов гипертрофии щупальцевого аппарата с левой стороны тела зооидов.

Изучение изменений астогенеза, происходящих в эволюции Cucullograptinae, приводит к выводу о том, что главным способом возникновения новых филогенетических признаков была у них так называемая дистальная интродукция. В результате этого процесса новые признаки появлялись сперва только в теках дистальной части рабдосомы, чтобы потом постепенно, в отдельных звеньях даной эволюционной линии, охватывать более проксимальные части колонии. Рассматриваются также некоторые отклонения от принципа дистальной интродукции новых филогенетических признаков. Они касаются только немногих и менее существенных морфологических признаков, которые появляются в этой группе граптолитов путем проксимальной интродукции. Большинство признаков, в том числе все признаки большого морфологического значения, возникают путем дистальной интродукции, а эволюция Cucullograptinae дает чрезвычайно убедительные доказательства значения этого способа возникновения новых признаков в филогенезисе тек. Некоторым исключением от принципа дистальной интродукции является тоже асимметрия R-кукуллограптидов, которые, согласно с ранее выдвинутыми предположениями (Урбанэк, 1960), возникают аполярно, то есть проявляются более или менее одинаково у всех особей колонии.

На основании анализа данных о появлении и развитии новых признаков, являющихся результатом филогенетических модификаций астогенезиса, подтверждаются ранее высказанные взгляды (Урбанэк, 1960) о том, что это развитие сводится к переменам экспрессивности и пенетрации определенных генетических факторов.

В настоящей работе рассматривается также вопрос организации граптолитовых колоний. Автор стремится доказать, что колонии Graptoloidea представляют такую стадию интеграции, при которой процессы индивидуальные, определяющие морфофизиологический характер отдельных зооидов колонии, еще не исчезают целиком. Принимая такие колонии как особенный случай интеграции группы особей (популяция), доказывается правильность применения понятий „пенетрация" и „экспрессивность" в описании явлений, происходящих при филогенетических модификациях астогенеза. В этих рассуждениях приводятся критические взгляды, переданные автору настоящей работы в письмах Д-ра Л. Ван Валена (Dr. L. Van Valen; Amer. Mus. Nat. History, New York).

В результате сопоставления морфологических и стратиграфических данных обоснованы некоторые выводы, касающиеся филогенеза и таксономии Cucullograptinae. Подчеркивается иное значение морфологии дистальных и проксимальных тек для установления родовых отношений. В изученной группе граптолитов первые имеют „профетическое" значение, учитывая принцип дистальной интродукции новых филогенетических признаков. Они позволяют в некоторой степени определить дальнейшее направление эволюции. Вторые, наоборот, являются наименее модифицированными, сохраняют наиболее долго мало измененные анцестральные признаки и позволяют таким способом определить строение, свойственное предкам. Такое значение дистальных и проксимальных тек, однако, не абсолютное, а зависимое от способов филогенетических модификаций астогенеза, характерных для данной группы граптолитов.

Принимая во внимание вышеизложенные критерии, автор стремился установить филогенетические соотношения в пределах Cucullograptinae. Самым древним и наиболее примитивным представителем этой группы является *Lobograptus progenitor* n. sp., который открывает одновременно развитие первой эволюционной линии Cucullograptinae, представляющей их первоначальную филогенетическую ветвь („stem lobograptids"), *Lobograptus simplex* же занимает центральную позицию среди всех Cucullograptinae и представляет либо структурную стадию, от которой, вероятно, произошла радиация этой группы, дающая в результате 4 или же 5 отдельных линий развития. В развитии каждой из этих линий доминировали процессы направленной эволюции над процессами дивергенции (Пл. VIII, IX). Особое положение занимает только *Cucullograptus pazdroi*, который не соединяется отчетливо с главной филогенетической ветвью Cucullograptinae. Он представляет или боковую линию, которая обособилась ранее и аллопатрически, или его происхождение иное, чем остальных представителей этой группы. В этом отношении Cucullograptinae основаны скорее всего на концепции морфологически-таксономической, чем филогенетической.

Происхождение Cucullograptinae не может быть в настоящее время выяснено. Однако сходство проксимальной части колонии примитивных представителей *Lobograptus* (*L.progenitor* n. sp., *L.simplex*) с проксимальной частью рабдосомы ранних линограптидов (*Neodiversograptus nilssoni*) могут свидетельствовать о родстве этих двух ветвей. *N.nilssoni* однако слишком специализирован, чтобы можно было считать его предком *L. progenitor* n. sp. — наиболее древнего из известных представителей Cucullograptinae. Поэтому автор настоящей работы предполагает, что общим предком Cucullograptinae и Linograptinae мог быть линограптид, представляющий пренеодиверсограптидную стадию эволюции.

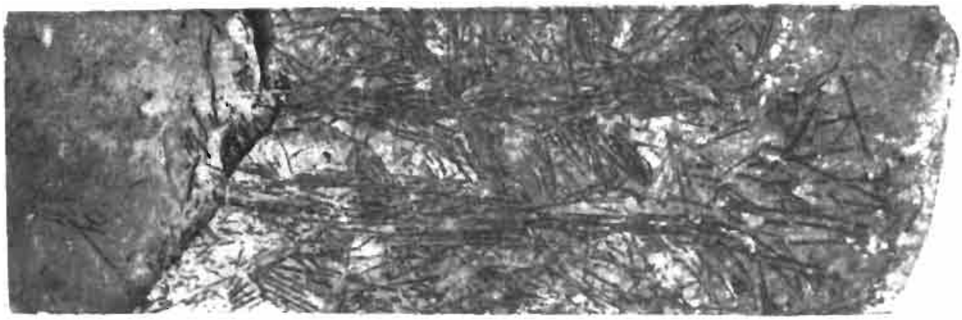
В систематической части дано описание следующих представицелей Cucullograptinae:

Lobograptus Urbanek, 1958
L. *progenitor* n.sp.
L. *simplex* Urbanek, 1960
L. *exspectatus exspectatus* Urbanek, 1960
L. *exspectatus bicornis* n.subsp.
L. *scanicus parascanicus* (Kühne, 1955)
L. *scanicus amphirostris* n.subsp.
L. *scanicus scanicus* (Tullberg, 1883) sensu Bulman, 1953
L. *imitator* n.sp.
L. *invertus* n.sp.
L. *cirrifer* n.sp.

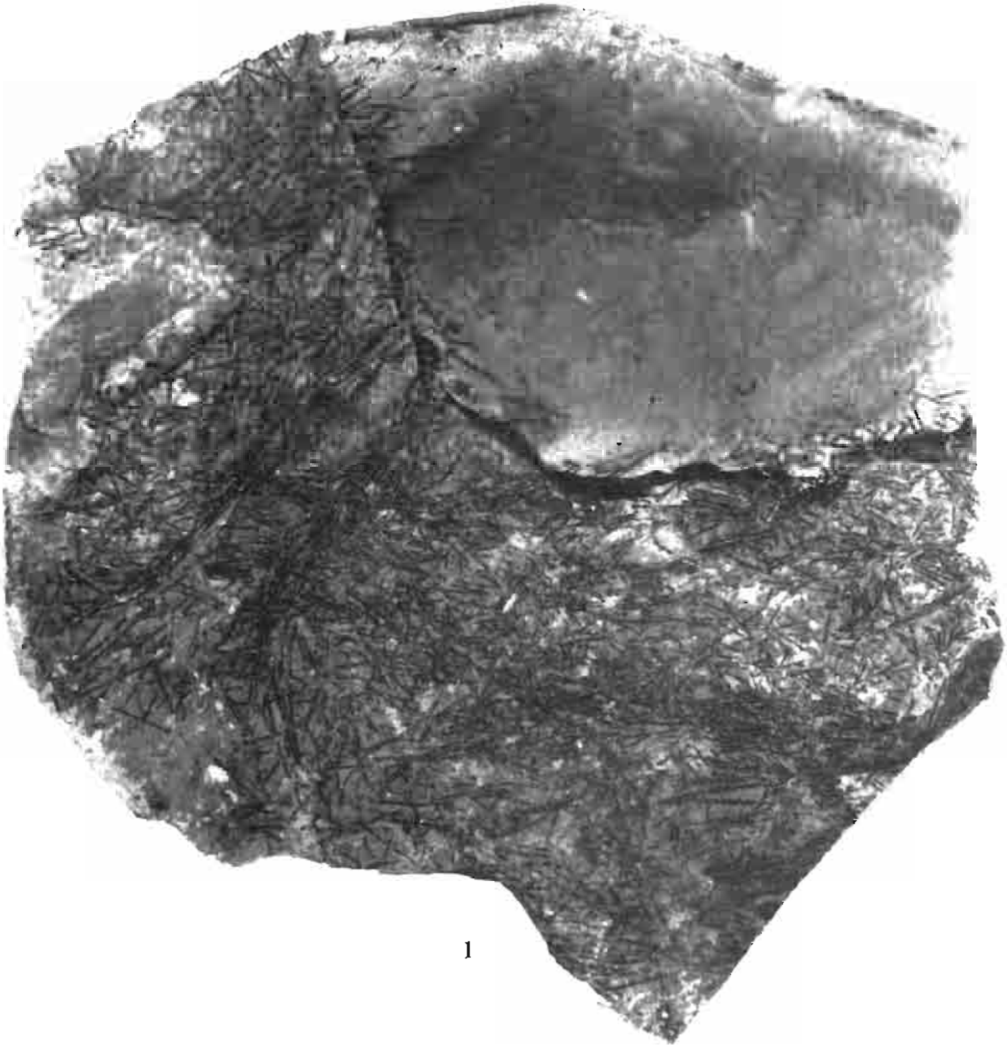
Cucullograptus Urbanek, 1954
Cuc. *hemiaversus* Urbanek, 1960
Cuc. *aversus* cf. *aversus* (Eisenack, 1942)
Cuc. *aversus rostratus* Urbanek, 1960
Cuc. *pazdroi* Urbanek, 1954.

Plate XLVI

Graptolite assemblage preserved on the surface of erratic boulder S. 181, Czarnogłowy (Western Pomerania). *1* Fragment of boulder with great accumulation of rhabdosome fragments, showing predominance of *Lobograptus scanicus parascanicus* (Kühne) and *Cucullograptus pazdroi* Urbanek; rhabdosomes are mostly randomly oriented, only in some parts showing parallel arrangement; slightly reduced (ca. 0.86). *2* Enlarged detail of the surface; ca. × 1.1.



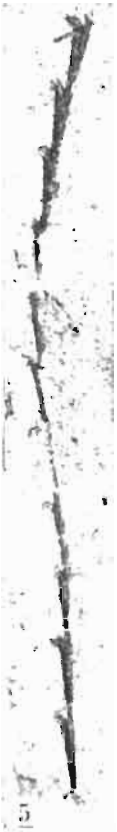
2



1


8


6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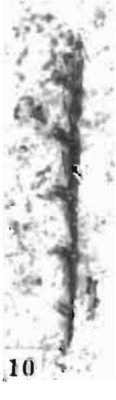
9


3


1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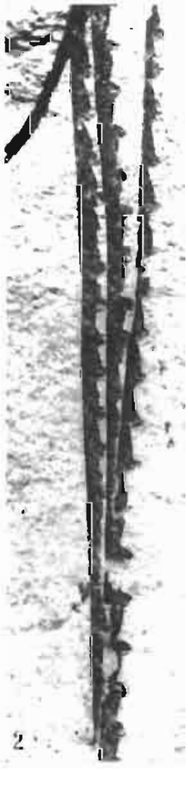
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4

Plate XLVII

Some examples of states of preservation of the Cucullograptinae on the rock surface. *1* — *Lobograptus scanicus parascanicus* (Kühne), a distal fragment of rhabdosome in reverse aspect; *2* — *L. scanicus scanicus* (Tullberg) sensu Bulman, three fragments of rhabdosome in both aspects; *3* — *L. cirrifer* n.sp., a distal fragment of rhabdosome in reverse aspect; *4* — *Cucullograptus hemiaversus* Urbanek, a distal fragment of rhabdosome in reverse aspect; *5*—*10* — *Cuc. aversus rostratus* Urbanek, different parts of rhabdosome in reverse (*7*,*9*) and obverse (*5*, *6*, *8*, *10*) aspects (Mielnik deep-boring, approximate depth: *1*—993.6, *2*—982.9, *3*—940.25, *4*—952.9, *5*, *8*, *9*, *10*—922.1, *6*, *7*—923.1 m); *1*—*2* ca. × 4; *3*—*6*, *8*—*9* ca. ×6; 7, *10* ca. × 7.