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MONOGRAPTIDAE FROM ERRATIC BOULDERS OF POLAND

(MONOGRAPTIDAE Z GŁAZÓW NARZUTOWYCH POLSKI)

BY

ADAM URBANEK

(WITH 68 TEXT-FIGURES, 7 TEXT-PLATES
AND 5 PLATES)

WARSZAWA 1958
PAŃSTWOWE WYDAWNICTWO NAUKOWE

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PREFACE

The material studied consists of a collection of graptolites which Professor **Roman Kozłowski**, Head of the Institute of Palaeontology at Warsaw University, turned over in 1952 to the present writer for investigation, also of graptolites recovered from erratic boulders at a later date by the writer and by his colleagues. Sincere thanks are here due to all of them.

The writer is under a special obligation to Professor R. **Kozłowski** for his untiring assistance throughout the four years work on the present paper. Professor **Kozłowski**'s kind suggestions and help proved most valuable, and warmest thanks are herewith conveyed to him.

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Palaeozoological Laboratory
of Warsaw University and
of the Polish Academy of Sciences
Warszawa, 1957

GENERAL PART

INTRODUCTION

The fossils, which form the subject of this paper, are graptolites of the family Monograptidae LAPW., collected from Silurian erratic boulders in Northern Poland.

Graptolites from erratic boulders in Northern Europe attracted the attention of palaeontologists in the past. F. HEIDENHAIN (1869) and K. HAUPT (1878) were the first to deal with them; today, however, their work is only of historic interest.

F. ROEMER (1885) and O. JAEKEL (1889) continued this work. R. KRAFT (1926) made valuable observations concerning ontogenetic and astogenetic development, from material recovered from Baltic erratic boulders. Both, KRAFT and previously C. WIMAN (1893) had used chemical methods of preparation by treating calcareous rocks with hydrochloric acid.

A. MÜNCH (1938) turned his attention to particular problems of monograptid morphology and was the first to describe specimens illustrating the mode of cladogenesis in the Cyrtograptidae.

A. EISENACK, one of the pioneer workers on microfossils from erratic boulders, devoted some of his papers to graptolites, including the monograptids (1942).

In recent years, papers on graptolite faunas from Silurian erratic boulders have been published by O. M. B. BULMAN (1953), W. G. KÜHNE (1953, 1955), A. URBANEK (1953, 1954) and M. WALKER (1953*a*, 1953*b*).

The use of chemical methods of preparation has enabled a more detailed study of graptolite morphology to be undertaken, notably in the works of R. KOZŁOWSKI and BULMAN. A more detailed description of the morphology of the Monograptidae is now possible on the basis of suggestions put forward by these two authors.

The Silurian boulders of Lower Ludlow age contain most graptolites. Wenlockian erratics yield markedly fewer, whilst none have been discovered from the Lower Silurian by the present writer. The predominance of the Lower Ludlow fauna in the erratic boulders makes the papers analysing the same graptolite association collected «in situ» of special interest to the present author. In particular these are: S. A. TULLBERG (1882/83) on Scanian graptolites, E. M. E. WOOD (1900) on the Lower Ludlow of Great Britain and B. BOUČEK (1936) on the Lower Ludlow of Bohemia. Papers based on material collected «in situ», from which graptolites have been prepared out of their matrix, are of considerable value for the elucidation of important problems of monograptid morphology. Those of C. WIMAN (1893, 1895) and I. COX (1933) ought to be mentioned here. Researches of G. L. ELLES (1922) and recent papers by BOUČEK and A. PŘIBYL (1942, 1951) are of marked importance in elucidating general phylogenetic relationships and evolutionary patterns of the monograptids.

Owing to the stratigraphic significance of the monograptids, this group has for a long time past been made the subject of extensive studies. They were, however, concerned mainly with faunal or more exactly bio-stratigraphical problems and thus only few of them dealt with problems of morphology and evolution. Most of the research work on monograptids was based on shale material, which is mostly unsuitable for anatomical studies, yet they were the «malum necessarium» for the majority of geologists and palaeontologists. On the other hand, graptolites preserved in limestones or marls, mostly undeformed, open up quite new palaeontological prospects [1].

Silurian erratic boulders represent a commonly known lithological type, named by the German authors «Graptolithengestein». They are limestones or marls with a characteristic colouration — from a bluish grey to a grey-green tint, massive, compact, usually strongly effervescent in hydrochloric acid, often strongly glauconitic. Both, the lithological and the faunal aspects of these erratic boulders have been comprehensively described by A. **Remelé** (1883) and F. **Roemer** (1885). Two types of them have been differentiated by **Remelé**. To one he refers more or less rounded boulders of argillaceous massive limestone, without signs of bedding, to the other flat boulders of marl, usually of a somewhat lighter colour. Both types were present in the material studied by the writer.

Tullberg's and **Remelé**'s supposition, that the majority of erratic boulders of the type of «Graptolithengestein» comes from concretions which originally must have been set within shale series, seems also very probable. These concretions being more resistant to transport and weathering processes constitute now the chief element among the Silurian erratic boulders.

It is noteworthy that in the Silurian graptolite series in the Holy Cross Mts. of Poland, as well as in the Bohemian Barrandian formations, calcareous, marly and sideritic concretions are mostly associated with the Lower Ludlovian, they are more rare in the Wenlockian and entirely absent from the Valentian. These conditions may explain the predominance of Ludlovian and Wenlockian rocks also among erratic boulders containing a graptolite fauna, inasmuch that in these series concretions occur, to which the present erratics owe their origin. It is thus probable that over the extensive areas of the Silurian sea sedimentation has taken place after an uniform manner and that these concretions in some degree indicate the definite stratigraphical horizon with corresponding graptolite fauna.

The derivation of erratic boulders has been roughly outlined in the above mentioned papers of **Remelé** (1883), F. **Roemer** (1885) and O. **Jaekel** (1889). The material has presumably been mostly derived from the area now occupied by the Baltic sea between the islands of Öland, Gotland and Scania. To some extent it may be derived from the area now exposed in Scania, where the occurrence is noted of outcrops of the so-called «Cardiolaskiffer», investigated by G. **Linnarson** (1875) and **Tullberg** (1880, 1882/3), and later by S. L. **Törnquist** (1889), G. **Holm** (1899), J. C. **Moberg** & **Törnquist** (1909), **Moberg** (1911) and E. **Hede** (1915). A general view of the stratigraphy of Gotland which also may be a source of erratic boulders, Ludlovian and Wenlockian, is contained in **Hede** (1942). The Silurian series in Scania, stratigraphically corresponding to the Lower Ludlow, attains there, according to **Tullberg** (1883), a thickness of over 1100 m. The lithological and faunal aspects of this series correspond well to the majority of Silurian erratic boulders.

The main part of the material to be described has been collected from the Baltic shore, mostly in Western Pomerania. Erratic boulders are not rare in the province of Mazury and in Central Poland, but monograptids are almost completely lacking, even though Ordovi-

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[1] W. G. KÜHNE (1955, p. 355) has done some interesting calculations. Out of 12 morphological characters differentiated by him, as many as 11 may be studied in isolated material, while only 7 in material recovered from shales.

cian limestones and the so-called Baltic limestones («Ostseekalk» of German authors) with *Orthograptus gracilis* (Roem.), and Beyrichia limestone, are common. Marly graptolite limestones are less resistant to destruction and distance of transport is, therefore, here the decisive selective agent.

To sum up, the present paper has been based on the fauna recovered from about 100 erratic boulders. The initial number of boulders subjected to chemical preparation was nearly double that figure. Many of the boulders, however, either yielded no graptolites at all, or they were destroyed in the course of preparation owing to their bad state of preservation.

The boulders here considered have been collected from the following 13 localities: Dziwnów, Gdańsk (Wrzeszcz), Jarosławiec, Lubin, Łebcz, Międzyzdroje, Niechorze, Orłowo, Poznań (Czerwonak), Rewal, Śrem, Ustka, Władysławowo, and Isle of Wolin. Particular boulders are marked with successive numbers and lettered S. (= Silurian), to distinguish them from Ordovician boulders which were deposited in the Palaeozoological Laboratory in Warsaw.

Not infrequently boulders found in certain localities show very particular lithological and faunal features. Most probably they constitute «packets» derived from one locality and one horizon. Thus, for example, boulders from Lubin were uncommonly argillaceous and resistant to chemical treatment, while those from Gdańsk with the same graptolite assemblage dissolved far more readily. The boulders from Jarosławiec, which are distinctly smaller than both previously mentioned, yielded a fauna in an exceptionally satisfactory state of preservation. On the whole it seems that the degree of carbonization and decomposition of graptolite specimens is not uniform in the different boulders. In some cases the periderm is wrinkled and partly decomposed. In others the chitin has been impregnated by pyrite or limonite.

Finally, it was possible to identify from the studied material the following 14 species:

Monograptus (Monograptus) priodon (Bronn)
M. (Monograptus) uncinatus Tullb.
Colonograptus colonus (Barr.)
Saetograptus chimaera (Barr.)
Cucullograptus pazdroi Urbanek
C. aversus (Eisenack)
Lobograptus scanicus (Tullb.)
L. parascanicus (Kühne)
Pristiograptus bohemicus (Barr.)
P. nilssoni (Lapw.)
P. dubius (Suess)
Pristiograptus sp.
Monoclimacis haupti (Kühne)
M. micropoma (Jaekel).

The majority of the species here described are known also from the Silurian deposits of Sweden. Only two forms are known exclusively from erratic boulders, i. e.: *Cucullograptus aversus* and *Lobograptus parascanicus*. *Cucullograptus pazdroi* was found «in situ» and occurs in the Lower Ludlow of Thüringia (Jaeger, 1955) and the Holy Cross Mountains, Poland (see p. 66). This species must be also present in the Silurian of Sweden, from where specimens in Holm's collection have come (see p. 66). Among the species here described, *Monoclimacis* *haupti* and *M. micropoma* are so far unknown from Sweden. Both these species are quite frequent in the fauna of erratic boulders and occur doubtless in Silurian series of Sweden. According to KÜHNE's opinion (1955, p. 367) *M. haupti* may indicate a horizon rather above the *scanicus*-zone. This view needs, however, further evidence because the stratigraphical range of the mentioned species is not established exactly.

The material thus obtained has enabled a study to be made of the morphology and in most cases also of the ontogeny and astogeny of these forms and has led the author to a revision of their systematic position.

The graptolite fauna in the Silurian erratics is accompanied by an assemblage of other fossils studied by ROEMER (1885, p. 363-379). The forms associated with the graptolites here considered are the Cardiolae (*C. interrupta* SOW.), the Orthoceratidae and an occasional abundance of crinoids. Chitinous microfossils such as Scolecodonta and Chitinozoa were frequently observed in the residue of the solution.

TAXONOMY OF THE FAMILY MONOGRAPTIDAE

The systematics within the family Monograptidae, established by C. LAPWORTH (1873) doubtless present a very complicated and difficult problem[2]. The main difficulty consists in that this group, seemingly displaying great uniformity of general morphology, is actually strongly differentiated in details. At the same time, it is difficult to ascertain causes of these similarities and differences and their taxonomic value. Thus, for example, the simple type of thecal structure encountered in representatives of *Pristiograptus*, as in *P. dubius* SUESS, may be regarded either as primary since it is noted among the oldest monograptids (*Monograptus? acinaces* TQT., *M.? gregarius* LAPW., *M.? concinnus* LAPW.), or as resulting from secondary simplification. This latter view was adopted by ELLES (1922, p. 185) with regard to some Ludlovian representatives of *Pristiograptus*.

The occurrence of actual relationship, therefore, as well as homeomorphy are here accepted as plausible explanations, the homeomorphy, in its broadest meaning, probably including cases of convergency, and of evolution both parallel and regressive.

The phylogenetic relationships within the monograptids are still uncertain. The principal task, for the present at least, is to elucidate the morphological relations within this group and to establish correct and uniformly defined taxonomic units. The elucidation of views regarding the real evolutionary lines will be possible after a full analysis of the stratigraphy of forms whose morphology is already well known. Earlier literature relating to the systematics of monograptids has been compiled and critically reviewed in ELLES & WOOD classical work «Monograph of British Graptolites» (1901-1918). There is, therefore, no need for reverting thereto. The present paper will only discuss and tentatively enumerate the most outstanding papers published on this subject within the last forty years or so. The monograptid systematics as given by ELLES & WOOD regarded this group as consisting of three genera, viz. *Monograptus* GEINITZ, *Rastrites* BARRANDE and *Cyrtograptus* CARRUTHERS. Genus *Monograptus*, at that time intentionally broadly understood, was split up into 7 groups, each of which was made to include forms morphologically similar.

This conception was rather one of temporary compromise between the great variety of species and the lack of criteria for their generic grouping. The systematics of mentioned

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[2] In this chapter some general problems are discussed, including conclusions drawn from the chapter on comparative anatomy (see p. 13).

authors were consequently artificial though some groups were sufficiently consistent. Neither did Elles & Wood take account of the previously described and established genera *Pristiograptus* (Jaekel, 1889), *Monoclimacis* (Frech, 1891) and *Spirograptus* (Gürich, 1908), though their groups I, III and VII by their range do correspond fairly well to these genera. The majority, however, of the later writers, with the exception of Bulman and others, used these generic names. Bulman had many a time stressed the probable polyphyletic descent of *Monograptus*. Yet he is of the opinion that an inadequate knowledge of the phylogeny of this group does not allow the splitting of Monograptinae into more genera than those of *Monograptus* and *Rastrites*. The remaining generic and subgeneric names are regarded by him as synonyms (1955, p. 92). This standpoint (comp. p. 7) does not seem sufficiently founded since in many cases the morphology of the monograptids has been investigated as well as that of other graptoloid groups. Some of these, e. g. the diplograptids have been divided on the structure of thecae and not on phylogeny, inasmuch as in taxonomy one needs to consider not only the question of origin, but also the extent of morphological similarities and differences.

Elles & Wood's conception contains, however, some statements not admissible from the present standpoint. For example, *M. priodon* (Bronn) has been referred to the group «with uniform thecae» though it is now known that in this form too, the proximal thecae differ considerably from the distal ones in the structure of processes and that it fully corresponds to the «biform» group. Also the whole group of species near *M. scanicus* has been placed side by side with *M. priodon* though their morphology differs decidedly.

The British authors have based their taxonomic classification on the evidence of distal rather than of proximal thecae. Since they are of the opinion that in the Dichograptidae, Dicranograptidae and Dimorphograptidae the distal thecae are more diagnostic specific characters than the proximal thecae, and «there can be little doubt, therefore, that in the matter of the classification of the species in Monograptids the characters of the mature portion of the polypary should similarly take systematic precedence of those of the earlier portion» (Elles & Wood, 1901-1918, p. 361).

On the other hand, Elles emphasized the particular significance of the proximal thecae and arrives at the conclusion that «it is necessary always to study particularly the thecae that are developed at the proximal end of the rhabdosome, for here it seems the vigour of the organism was greatest; hence in the progressive forms it is in that portion of the rhabdosome that new elaborations are first developed and in the retrogressive forms it is sometimes the only place where they retain signs of former elaboration» (1922, p. 179).

To the present writer both these standpoints are acceptable in spite of their contradictory character; the significance of particular parts of rhabdosome may vary in relation to different evolutionary processes. It is theoretically possible that in «progressive series» distal thecae reflect the original thecal type and this may be significant for establishment of the ancestry. Studies done by the present writer, however, seem to confirm the view that the proximal end of the rhabdosome is its particularly significant part, so that its analysis can throw much light as to the descent and systematic position of the forms under consideration. In *Saetograptus* and *Colonograptus* for instance (comp. p. 46) the distal thecae are not diagnostic in the establishment of their systematic position, while the structure of the proximal thecae, most particularly that of their apertural processes, better clears up their descent. Therefore, it seems very probable that, for purposes of taxonomy in groups of smaller rank (subfamilies, genera), the significance of the proximal thecae is greater than that of the distal thecae, but we cannot entirely neglect the structure of the distal ones.

Later studies have brought new conceptions which were, however, mostly incomplete and did not permit a full revision of the systematics of all the forms here noted. A general review of the literature, in which new taxonomic units have been established, is given below.

Bouček (1933) excluded from the family Monograptidae the genera *Cyrtograptus* Carr., *Diversograptus* Manck and *Linograptus* Frech, establishing for them a new family — the Cyrtograptidae.

T. H. Yin (1937) divided the Monograptidae into two subfamilies: Monograptinae and Cyrtograptinae, and established a new genus — *Streptograptus* — characterized by a spirally coiled apertural shield (genotype *M. nodifer* Tqt.). R. Hundt (1943) distinguished a number of graptolite families such as the Demirastritidae, Pernerograptidae, Diversograptidae and others. Recently, quite a number of smaller generic and subgeneric units has been established within the Monograptinae. These are namely *Pernerograptus* (Přibyl, 1941), *Pristiograptus (Colonograptus)* and *P. (Saetograptus)* (Přibyl, 1942), *Monograptus (Globosograptus)*, *Monograptus (Mediograptus)* (Bouček & Přibyl, 1948), *Tyrsograptus* (Obut, 1950), *Cucullograptus* (Urbanek, 1954). These new genera, together with previously described *Pristiograptus* (Jaekel, 1889), *Monoclimacis* (Frech, 1891), *Spirograptus* (Gürich, 1908), *Demirastrites* (Eisel, 1911) and *Streptograptus* (Yin, 1937) have made the systematics of the Monograptinae still more complicated.

A. M. Obut (1950) established a new genus *Campograptus* (genotype *M. communis* Lapw.) as one of the spirally coiled genera for which he proposed to establish a new subfamily, Spirograptinae. The peculiarity of *Campograptus* is rather doubtful. It was established on the basis of the hypothesis that the coiled shape of the rhabdosome was of taxonomic value. This conception is rather uncertain. As for the structure of the thecae *Campograptus* is referable to typical *Monograptus*.

Lately, A. T. Mu (1955) has concluded that different species within the genus *Spirograptus* are actually of different origin, their only common character being the spiral coiling of the rhabdosome. He suggests the transfer of forms having apertures provided with spines *(Monograptus turriculatus)* to genus *Monograptus* as the subgenus *Spirograptus* and of forms having triangular thecae provided with «scepellum» *(M. spiralis)* — to the genus *Demirastrites* as the subgenus *Obutograptus* Mu. The genus *Tyrsograptus* Obut would then be synonymous with *Spirograptus* Gürich. The latter name has the priority while *M. turriculatus* is the genotype for both.

Přibyl (1946) made the first attempt to compile all the available data concerning the systematics of the monograptids. The essential feature of his new taxonomy is that he retains the monograptids as a broadly conceived systematic unit including in it the subfamily Cyrtograptinae. It, thus, embraces all the uniserial Silurian graptolites, being subdivided into a number of subfamilies, i. e.

Monograptinae
Cyrtograptinae
Diversograptinae
Demirastritinae
Rastritinae
Pristiograptinae
Pernerograptinae

Přibyl's conception of classification seems to be purely pragmatic rather than a theoretically evidenced taxonomy, inasmuch as the author does not discuss any criteria and gives no reasons for his systematic division. Since, however, his paper is an attempt to give a general scheme of monograptid systematics, with the inclusion of the lately introduced taxonomic units, it may constitute a starting point for further discussion.

The present writer is of the opinion that the actual separation of the new genera and subgenera in the Monograptidae is reasonable. In the case of such a complex group, the possibility of a separation of a number of the new taxonomic units even «a priori» may be expected. Since the establishment of new units is not by itself a disquieting element, the negative attitude towards the possibility of the present separation of such new units does not seem convincing.

Nevertheless adequate morphological evidence should be postulated for the establishment of new taxonomic units. Evidently the species, that are known only as compressed specimens, are not of great value for diagnostic criteria, though doubtlessly a closer analysis even of such specimens could certainly produce better results. It is only a more thorough study of various representatives of the monograptids than can provide adequate evidence for working out their natural systematics. The writer's view does not quite concur with that of Bulman (1938, p. 82) when he writes that «subdivisions of the genus, to be of real value, must be deferred until far more is known of the main lines of evolution». The present writer namely believes that the correct knowledge of phylogenetic relations will be acquired through more detailed studies of the morphology and the time distribution of forms as well as through the determination of their correct systematic position and not «vice versa».

Even if the above uncertainties are taken into account, the writer is inclined to infer that Přibyl's (1946) conception of monograptid systematics may be a useful working scheme for further improving the taxonomy of this graptolite group.

The material here studied provides evidence for modifying some of that author's statements. According to Přibyl, the genus *Monoclimacis* Frech has also been referred to the subfamily Monograptinae. Unfortunately, no arguments are quoted by that author in favour of his hypothesis. The present writer may only suppose that the essential point here is probably that in *Monoclimacis* the processes in the apertural region are in the shape of semilunar lobes which may be derivative of the «hooked» type processes in Monograptinae, e. g. *M. priodon*, *M. uncinatus* etc. This was noted by Frech (1891) when he wrote that it is possible that both in *Monoclimacis spinulosa* (Tullberg) and in some representatives of the former genus *Pomatograptus* (e. g. *Monograptus micropoma* Jaekel), these processes are in fact a «Deckelorgan». The present writer agrees with the opinion expressed by Kühne (1955, p. 380-381) that both last mentioned forms are very closely related. For this reason he refers them both to the genus *Monoclimacis* Frech (comp. p. 95).

It should nevertheless be stressed that, as is evidenced by the present study, apertural lobes in *Monograptus* and in *Monoclimacis* constitute morphologically quite distinct structures. In *Monograptus* these lobes are derivatives of the distal wall of metatheca, while in *Monoclimacis* they are «sui generis» structures connected with the mesial edge of the next theca. Hence these structures cannot be homologized. In *Monoclimacis* the apertural lobe arises on the protheca of the theca ($n + 1$) and corresponds to the mesial edge of *Climacograptus* rather than to the apertural lobes of *Monograptus*. The fine structure of this lobe is also entirely different from the normal fusellar structure common in the lobes of *Monograptus* (comp. fig. 18, 21, 67, 68 and p. 48, 93). It is, therefore, asserted here that the apertural lobes in *Monoclimacis* are special processes not homologous with those of the other monograptids. Fig. 1 illustrates the morphological relations as they would have hypothetically existed on the inference that the mesial edge in *Monoclimacis* originated from the partial reduction of the «hooked» type lobe *(A, A')* and also the actual anatomical conditions ascertained in representatives of the genus *Monoclimacis (B, B')*.

These conditions are a strong argument against the recognition of a close relationship between *Monograptus* and *Monoclimacis*. These genera cannot, therefore, be placed in the same taxonomic group.

And yet it seems quite probable that the type of apertural processes observed in *Monoclimacis* developed independently in various stocks of Graptoloidea. The dorsal lip in the aperture of *Holmograptus callotheca* (Bulman) (Dichograptidae), described by Kozłowski (1954), corresponds to the apertural lobe of *Monoclimacis*, and similar conditions will be noted in a form recorded as *? incisus* Kozł. At present it is difficult to determine precisely the correct systematic position of the genus *Monoclimacis* Frech. It is characterized not only by a particular structure of the apertural lobes, but also by the presence of a ventral excavation such as is not encountered in other monograptids. In the present writer's opinion, this genus may, therefore, be connected with certain species of *Pristiograptus* s. s. (= *Pristiograptus* (*Pristiograptus*)). Even Frech (1891, p. 621-622) in his discussion on the origin of *Monoclimacis* did not deny the possibility of phylogenetic connections between this form and *Pristiograptus leptotheca*, *Pristiograptus* being in this case an ancestral form. Recently A. T. Mu (1948, p. 225-226) was inclined to accept this view on the standpoint that *Pristiograptus* was the ancestral form of 5 graptolite stocks, one of which would lead «from cylindrical *(Pristiograptus* form of thecae — *A. U.)* to sigmoid, with a well developed excavation *(Monoclimacis)*».

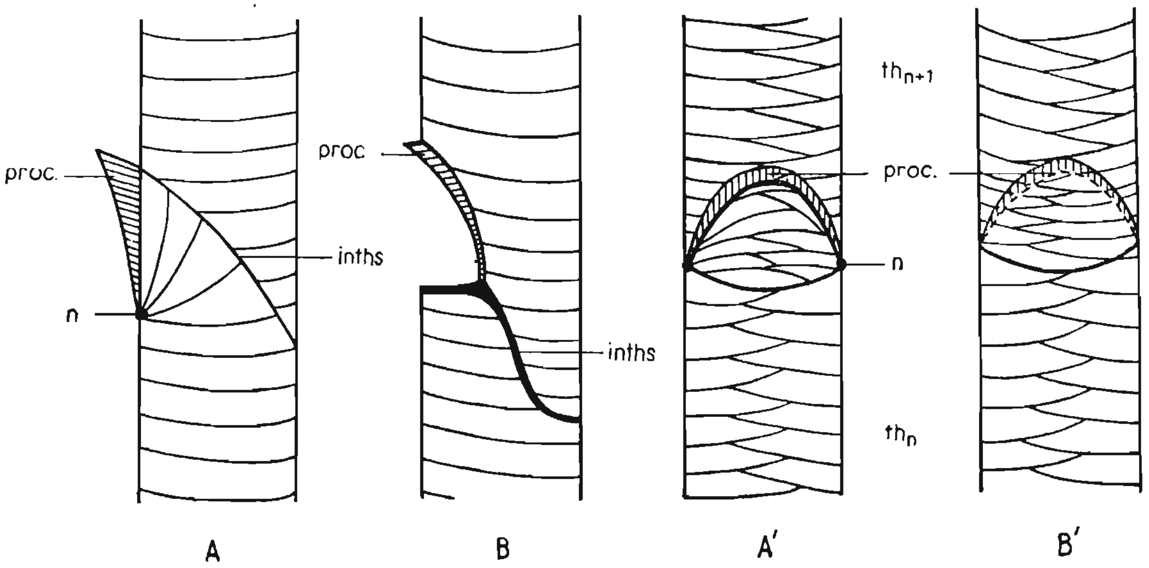

Fig. 1

Fusellar structure of thecae in *Monoclimacis*

A, *A'* theoretical pattern based on supposition that apertural structures of *Monoclimacis* and *Monograptus* are homologous; *B*, *B'* actually confirmed structure in examined representatives of *Monoclimacis*

inths interthecal septum, *proc* apertural process, *n* node, *th*$_n$ proximal theca, *th*$_{n+1}$ distal theca.

Further explanations — in text.

Discarding, however, for the time being the problem of the origin of *Monoclimacis* as insufficiently clarified, let us ascertain the very close resemblance between some representatives of *Monoclimacis* and those of *Pristiograptus*. It is interesting to note the intergradation with regard to the extent of excavation in both these forms. The species *haupti* (Kühne) is here regarded as a representative of *Monoclimacis* since the degree of excavation shown by it is not less than that in the typical representatives of *Monoclimacis* (comp. p. 89), while the edge round the excavation produces a thickened list corresponding to the apertural lobes of other species of *Monoclimacis.* In other representatives of *Pristiograptus* a faintly marked flattening of the ventral region is encountered which might be regarded as equivalent to the excavation. These are, naturally, purely morphological evidence and do not provide decisive proof of the real existence of phylogenetic connections between the two genera. In any case, *Pristiograptus* and *Monoclimacis* may tentatively at least be placed nearer to one another until more detailed studies will provide a closer determination of their mutual relations.

The origin of forms included in *Monoclimacis* FRECH is somewhat perplexing. The essential feature here is doubtlessly the thecal structure, which resembles BULMAN's figures of *Climacograptus typicalis* (BULMAN, 1932, pl. 4, fig. 33, 38 a-b). Photographs here published (comp. pl. V, fig. 3-4) of *Monoclimacis micropoma* (JAEKEL) sufficiently stress this likeness. Similarly, the fusellar structure of the thecae shows a striking resemblance (fig. 62, 63) outside of the differences existing between the uniserial and biserial forms.

The author of the genus *Monoclimacis* considered the direct relationship between *Climacograptus* and *Monoclimacis* «as greatly probable» (FRECH, 1897, p. 621). And yet he did not exclude the possibility of the derivation from *Monoclimacis* of secondary pristiograptic forms. HABERFELNER in 1932 (*fide* PŘIBYL, 1946, p. 21 — English text) advanced a similar view suggesting that *Pristiograptus dubius*, *P. vulgaris*, *Colonograptus colonus* and others may possibly have descended from *Monoclimacis.* To the present writer this suggestion does not seem strongly founded with regard to the origin of forms referred in the present paper to Saetograptinae *(Saetograptus, Colonograptus)*, but it is in fact difficult to deny that some forms of *Pristiograptus* could actually have evolved from *Monoclimacis* by the reduction of the excavation and of the mesial edge.

When discussing the origin of *Monoclimacis* and its relationship to *Climacograptus*, it is hardly admissible that the thecal resemblance is here one of convergence only, inasmuch as they agree in other features, the fusellar structure particularly so. Such concordance may be regarded as the expression of a homology rather than of analogy. Hence the probability of the supposition that the group ancestral to the monograptids was heterogenic and traceable back to various evolutionary lines of the diplograptids. The genus *Dimorphograptus* is not at present considered as the true intermediate link between the diplograptids and the monograptids, but rather as a side branch in which certain tendencies have been expressed common in the evolutionary line of the latter group (BULMAN, 1955, p. 74). Still it may be expected that thecae were differentiated already «ab origine», within the group of true ancestors of the monograptids as they were within *Dimorphograptus* (probably a collective genus). This was probably due to their descent from different phylogenetic stocks. It may be inferred that *Monoclimacis* has descended from graptolites which, though displaying the *Monograptus* type of structure, had thecae of the *Climacograptus* type, similarly as in *Dimorphograptus extenuatus* ELLES & WOOD (= *Metadimorphograptus* PŘIBYL).

The first representatives of *Monoclimacis* FRECH made their appearance in the Upper Llandovery. Until now this genus was believed to have become extinct towards the end of the Wenlockian, however, the upper boundary of its range ought to be moved up to the Middle Ludlow.

According to PŘIBYL (1946) *Pristiograptus* belongs to the subfamily of Pristiograptinae in which three subgenera are distinguished, i.e: *Pristiograptus (Pristiograptus)*, *P. (Saeto-*

graptus) and *P. (Colonograptus)*. These subgenera are markedly uniform morphologically, the two latter being more closely related and, in the present writer's opinion, they should be separated from this group. An attempt is made here (comp. p. 46) to show that these genera have descended from *Monograptus (Monograptus)*, since their essential diagnostic character, i. e. the structure of apertural processes, can be derived from the apertural lobes of certain monograptids. Numerous facts indicate that the «colonus» and «saeta» types of apertural processes are morphologically closely related, both being derived from the «hooked» type of apertural lobes, as in *M. (Monograptus) priodon* (BRONN). Probably, the *Colonograptus* processes represent a more primitive stage of the splitting of the single apertural lobe into two lateral ones. In *Saetograptus* these lobes became coiled along the paramedian edge and developed into a tubular process subsequently subject to additional modification (comp. p. 56).

This evidence justifies a revision of the formerly accepted systematic position of the subfamily Pristiograptinae. Only the forms referable to *P. (Pristiograptus)* and tentatively also to *Monoclimacis* ought to be referred in this subfamily. The other subgenera should be separated into independent genera and established into a new subfamily — the Saetograptinae n. subfam. — whose diagnosis is given on p. 11. This would be a unit of marked homogenity in respect of morphology and probably also of phylogeny, embracing representatives of various intermediate evolutionary stages of the tubular process from the apertural lobe of the Monograptinae.

The forms which show monofusellar structure of the lateral apertural lobes (comp. p. 62) and are characterized by a peculiar form of the thecae with long and slender prothecae and with metathecae displaying ventral curvature, should be placed close to the Monograptinae and the Saetograptinae. Some of these forms are characterized by a relatively simple structure of the apertural lobes, as for example in such species as *Monograptus scanicus* TULLBERG and *M. parascanicus* KÜHNE. These closely related forms also represent different evolutionary stages of the asymmetry of lobes. The new genus — *Lobograptus* n. gen. — is established to include these forms.

One of the stocks descended from the forms closely related to *Lobograptus parascanicus* (KÜHNE) has adopted a different trend of evolution leading to a strong development of asymmetry even to the obliteration of one of the lobes or to a greater complexity in the structure of the lobes themselves. This type of structure is represented by *Cucullograptus* URBANEK, to which (besides the genotype) *Monograptus aversus* (EISENACK) should be referred, as it displays a similar structure of lobe and type of asymmetry (comp. p. 72).

It seems beyond doubt that *Lobograptus* n. gen. and *Cucullograptus* form a group of species closely related, from the morphological and phylogenetical point of view, for which a new subfamily is established — the Cucullograptinae n. subfam. — whose diagnosis is given on p. 11.

We thus have three subfamilies of great morphological similarity. The Monograptinae might then be considered as the ancestral group which became differentiated by way of various evolutionary processes so as to give rise to two new subfamilies. In this light, the systematics of the monograptids would be as given below. It includes a revision of those groups only which are represented in erratic boulders, whilst a revision of the remaining subfamilies will not be possible until further material has been obtained to provide a better knowledge of their morphology.

This revision of the systematics of the monograptids is mainly based on thecal morphology whose patterns outlined by general structural features such as curvature, excavation, relations of protheca to metatheca, seem of important taxonomic significance. An analysis of the structure of the apertural region and its processes is, however, the most conspicuous feature. The admissibility of homologization of these structures would be the decisive question in separating or connecting certain groups. Compared with these important and diverse morphological features, the remaining characters in the monograptids, such as the shape of the rhabdosome are probably of far less taxonomic significance.

On the basis of the above, the following classification of the family Monograptidae is suggested:

Family **Monograptidae** LAPWORTH, 1873

A. Subfamilies represented in the writer's collection:

Subfamily **Monograptinae** LAPWORTH, 1873

Thecae straight or triangular, with round or elliptical aperture, provided with an unpaired process in the form of a lobe which is the prolongation of the dorsal wall and shows a zigzag suture (difusellar structure). The lobe hooked or lobate, or spirally coiled.

Monograptus (Monograptus) GEINITZ, 1852

Genotype: *M. (Monograptus) priodon* (BRONN).

Processes bent and not touching the rhabdosome.

Monograptus (Streptograptus) YIN, 1937

Genotype: *M. nodifer* TQT.

Processes strongly bent and touching the rhabdosome.

A. T. MU has recently (1955) referred to this genus, as a separate subgenus, forms characterized by a helical curvature of the rhabdosome: *M. (Spirograptus)*. Inadequate knowledge of the structure of the thecae prevents us from ascertaining the presence in these forms of a central lobe in addition to lateral apertural spines. In other words we do not feel sure whether they are to be placed closer to the Monograptinae or the Saetograptinae.

Subfamily **Saetograptinae** n. subfam.

Thecae straight, cylindrical, without ventral curvature, with round or elliptical aperture, provided with two lateral processes produced by the side walls of metatheca (monofusellar structure). The processes are ear-like *(Colonograptus)* or spine-like *(Saetograptus)* in shape.

Colonograptus (PŘIBYL), 1942

Genotype: *C. colonus* (BARR.).

Aperture provided with two ear-like lateral processes, with distal margin medially bent.

Saetograptus (PŘIBYL), 1942

Aperture provided with two lateral processes in form of spines formed by tubular folding of fuselli.

Subfamily **Cucullograptinae** n. subfam.

Thecae long, with fine, long straight protheca in the proximal part, showing ventral curvature distally. Aperture round or slit-like, provided with two apertural lobes, derived from side walls of metatheca, and having monofusellar structure. Occasionally, lobes asymmetrical or showing reduction of one lobe.

Lobograptus n. gen.

Genotype: *Monograptus scanicus* Tullb.

Aperture round, provided with asymmetrical or sub-symmetrical lobes formed by lateral wall of metatheca. Lobes flat, formed by the arched curvature of fusellus joined together by two nodes.

Cucullograptus Urbanek, 1951

Genotype: *C. pazdroi* Urb.

Aperture slit-like, provided with processes of complex structure, in the form of two curving lateral hood-like lobes. Right lobe larger, the left always smaller or atrophied.

Genera *Monograptus (Mediograptus)* and *Monograptus (Globosograptus)* Bouček & Přibyl 1948 are perhaps referable to this subfamily, but it is at present hardly possible to establish a boundary clearly separating these forms from subfamilies Monograptinae or Cucullograptinae.

Subfamily **Pristiograptinae** (Gürich), 1908

Thecae straight, cylindrical, with ventral wall straight or provided with more or less strong excavation. Aperture round, without apertural processes, or provided with characteristic apertural lobes.

Pristiograptus (Jaekel), 1889

Genotype: *P. frequens* Jaekel (=M. *dubius* Suess?).

Thecae straight, cylindrical, with ventral wall nearly or quite straight. Aperture without any supplementary structures.

Monoclimacis Frech, 1897

Genotype: *M. vomerina* Frech.

Thecae provided with more or less strong ventral excavation. On mesial edge of excavation a protruding list or lobe made up of numerous fine fuselli not producing an oblique suture. Aperture round.

B. Subfamilies not represented in the writer's collection:

Subfamily **Pernerograptinae** Přibyl, 1946

Rhabdosome with arcuate curvature, distally mostly straight. Thecae of «biform» type, the proximal provided with a dorsal lobe (*Monograptus* type), the distal straight (*Pristiograptus* type).

Representatives: genus *Pernerograptus* Přibyl, 1941.

Subfamily **Demirastritinae** Přibyl, 1946

Rhabdosome arcuate or spirally coiled. Thecae of «biform» type or homogeneous, the distal always triangular and provided with a peculiar shield, the so-called «scepellum».

Representatives: genus *Demirastrites* Eisel, 1912. A. T. Mu (1955) separates it into two subgenera: *D. (Demirastrites)* and *D. (Obutograptus)*. The latter has the subgenotype *Graptolithus spiralis* Geinitz. Some of the forms at one time referred to the genus *Spirograptus* (*s. l.* Přibyl, 1944) ought now to be placed here.

Subfamily **Rastritinae** Přibyl, 1946

Rhabdosome slender, thread-like, with arcuate or spiral coiling. Thecae tubular and completely isolated, placed on convex side of rhabdosome.

Representatives: genus *Rastrites* Barrande, 1850.

COMPARATIVE MORPHOLOGY OF THE FAMILY MONOGRAPTIDAE

A comparative study of the morphology and the fine structure of the peridermal tissue of graptolites leads to more general problems. The periderm here actually is a glandular zooidal secretion, to some extent analogous with such structures as the zooidal tubes of Polychaeta sedentaria, *Phoronis* or the chitinous exoskeleton of hydrozoans. In graptolites, however, the connection of the exoskeleton with soft parts must have been much closer than that in the above named groups. The same take place in the case of recent *Rhabdopleura*, which seems closely related to graptolites. In the latter group certain details in the morphology of the soft parts were quite distinctly reflected in the structure of exoskeleton in such a way as in *Rhabdopleura* but considerably more. It is only in Cephalodiscidea, among representatives of Pterobranchia, that conditions in this respect are somewhat different. Here the morphology of zooids differs but slightly, while their chitin structures (coenecia) are strongly differentiated.

When considering the mechanism of the development of periderm it is quite reasonable to suppose that in Cephalodiscidea the morphological differences of its chitinous derivatives are referable rather to differences of physiology and secretionary behaviour than to those of anatomy of the zooids. In graptolites, however, the mechanism of periderm secretion was exceptionally constant, whence comes the great stability of its fusellar structure in different parts of the rhabdosome. Outside of this, the periderm excellently reflects the budding and developmental processes of the individuals in the colony. All these are points enabling a study of the comparative anatomy of peridermal structures to be undertaken with a view to distinguishing the homologous from the analogous parts of the rhabdosome.

The fusellar structure is apparently the chief element in the analysis of the various peridermal structures. Its study leads to a very satisfactory determination of the relation of a given element to the axis of thecal symmetry. Derivatives of the ventral and dorsal walls should always be difusellar with a zigzag suture. Derivatives of lateral walls should be monofusellar. This is most essential in respect to apertural processes. The establishment of the primary topographic position, with consideration of details of fusellar structure, seems to provide a basis for an analysis of the peridermal structures in graptolites.

STRUCTURE OF SICULA AND ORIGIN OF FIRST THECA

The sicula may be regarded as the first theca in the graptolite colony, characterized, however, by certain particular features of structure. It is known to consist of two parts called the prosicula and metasicula (Kraft, 1926, p. 222, 226).

The shape of the prosicula is very much the same in all the graptoloids. It is in the form of a cone with walls of structureless chitin, closed apically and ending with a nema, while on the other side it opens into an aperture.

A characteristic helical line and longitudinal threads are visible on the wall of the prosicula. The helical line has also been described in the Dendroidea (Kozłowski, 1948, p. 19). It seems to be a constant character of all Graptolithina. It is less readily discernible in the monograptids than in the diplograptids. The number of longitudinal threads (Kraft's «Längsverstärkungsleisten») varies in monograptids, but there are three of them in most cases. They consist of thin bands of thickened periderm, stretching across its surface from the apex of the prosicula and often extending to the region of the apertural border. They are situated externally on the surface of the periderm, as shown by microtome sections of the prosicula (fig. 2).

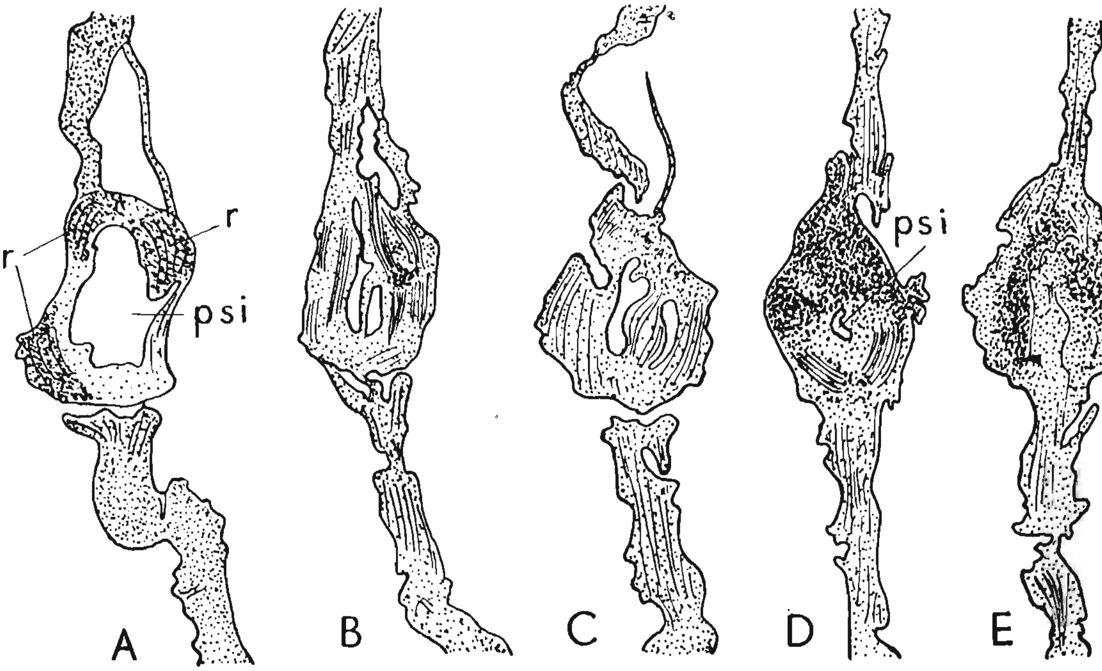

Fig. 2

Saetograptus chimaera (Barr.)

Transversal microtome sections cut through the top of prosicula; longitudinal threads (*r*) converging into nema (*n*), *psi* prosicula (S. 36, Jarosławiec); × 600. Somewhat diagrammatically.

The longitudinal threads (*r*) converge on the apex of the prosicula and fuse into the nema (fig. 2, *n*). In diplograptids the apical part of the prosicula has been shown to be separated from the rest by a chitinous membrane (diaphragma). The apical part here forms a tubule with the helical line on their surface and the thickened longitudinal threads extending over its wall. Further the longitudinal threads are fused together into the true nema (Kraft, 1926, pl. 6). No such apical diaphragm has thus far been recorded in monograptids where the beginning of nema also seems different. The longitudinal threads there become fused with the nema immediately on the top of prosicula, instead of persisting free for some time united by a chitinous membrane only, as in the diplograptids (fig. 17, 59). In any case, in the majority of monograptids which have so far been investigated, the tops of the prosiculae are damaged, while the nemae present are of the regenerating type (see p. 38). This is an obstacle in the study of the initial morphological structure of the apical portion of the sicula.

The structure of the nema is an open question too. Some authors consider it to be tubular and are of the opinion that the nema possesses a median canal (Bulman, 1938, p. 35; 1944, p. 25), while others regard it as a solid chitin fibril (Kozłowski, 1953, p. 75, French text). The present writer's observations also indicate that the nema is in monograptids a solid rod. The free spaces within the nema encountered in microtome sections are probably artefacts. As shown by microtome sections of the rhabdosome of *Saetograptus chimaera* (Barr.), *Pristiograptus dubius* (Suess) and *Cucullograptus pazdroi* Urbanek, the nema is mostly a continuous structure and in all fragments which are fairly well preserved it is a solid rod. An exceptionally well preserved specimen of *Cucullograptus pazdroi* has enabled the microscopic structure of the nema to be examined under high magnification (fig. 3). The nema is seen to be made up of numerous concentrically superimposed layers of chitinous substance. This would corroborate Kozłowski's opinion regarding the nema as a product of the soft tissues which surrounded it on the outside (1948, p. 91).

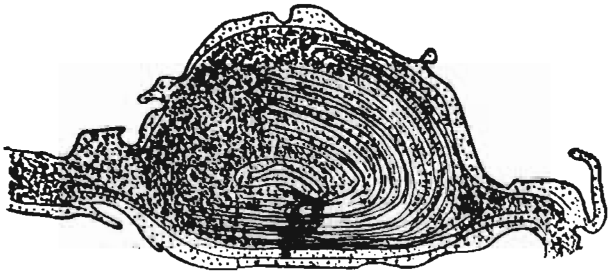

Fig. 3

Cucullograptus pazdroi Urb.

Transversal section of nema showing concentric layers of chitin substance (S. 32, Gdańsk-Wrzeszcz); × 1250 approx.

The nema is probably homologous with the basal disc of the dendroids since it occupies the same position and is of the same origin, having originated from extrathecal tissues. This explains the analogies in the microstructure of the nema and of the cortex layers in dendroids (laminar structure).

The nema often shows spiral coiling round its own axis. It is readily recognizable on nemae of young rhabdosomes. Kraft (1926, p. 242) connected this coiling with adaption to rotary movements around the long axis of the rhabdosome.

It is interesting that A. Frey-Wyssling (1948) ascertained spiral growth as usual for organic chitin threads. This is applicable for example to the growth of sporangiophors of some *Phycomyces* which move spirally, while increasing in length, as well as to certain animal organs such as the bristles of some arthropods. It is, therefore, possible that the biological adaptive function of such structures as the nema or the helical line may be due directly to the physico-chemical growth properties of the chitin skeleton mentioned by Frey-Wyssling.

Distally the prosicula is provided with an aperture whose margin is occasionally thickened to form an apertural ring. This is not, however, always the case.

Kozłowski supposes the prosicula to be the product of an oozooid from which, through probably intricate processes of histological metamorphosis, the metazooid responsible for building up the metasicula has evolved (1948, p. 98-101). With reference to this conception Urbanek (1953, p. 290) stresses that the check in growth during metamorphosis occurring here is indicated by the presence of the thickened apertural ring of the prosicula. This might reasonably constitute the ring marking the check of growth. According to Urbanek, the essential difference in the peridermal structure of the pro- and metasiculae may lie in the absence or presence of the preoral lobe supposedly responsible for the fusellar secretion type.

The formation of the zooid with a trimeric body structure resulting from metamorphosis, would apparently be simultaneous with that of the preoral lobe containing most of the chitin producing glands.

The metasicula is thus that portion of the sicula showing fusellar structure. In microtome section no cortical layer is recognizable as a definite structural element. It is possible that in monograptids the cortical layer does not exist in the same way as in dendroids, although the secondary thickening of the periderm does actually take place here. It is, however, difficult to acquire better knowledge of this problem because of the poor state of preservation of the periderm in monograptids.

The virgella begins to develop ventrally, at some distance from the aperture of the prosicula (fig. 4). The structure of virgella in monograptids fully agrees with that in other graptoloids. The basal part is made up of fuselli strongly thickened about the zigzag suture. Hence every fusellus produces a process-like element in the next part of virgella. The fuselli are attached to its borders and thus thicken the border (text-pl. VII, 1, 2 — see p. 85).

In the majority of the monograptid species studied to date the metasicula is provided with peridermal rings. They are visible as dark peridermal thickenings. Their number varies within a single species. Their position as well as genesis have been discussed. **Kraft** (1926, p. 234-235) was of the opinion that the peridermal rings are the «Stillstandsgürteln» and that they mark the levels where apertural growth had been checked longer. According to **Kozłowski** (1948, p. 53), these rings are placed obliquely to the fuselli, and we do not know of any cases where the aperture of the sicula would terminate at a thickening in the form of a ring. This refutes the idea of any connection between rings and apertural growth breaks. **Kozłowski** considers them to be secondary elements of cortical origin, external to the periderm.

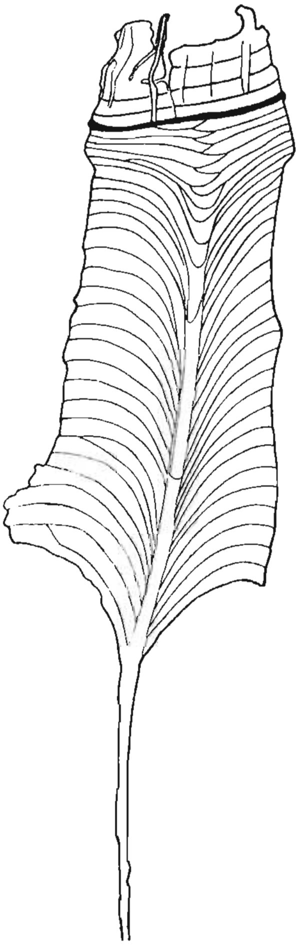

Fig. 4

Monograptus sp.

Fusellar structure of virgella (S. 36, Jarosławiec); × 100 approx.

Urbanek (1953, p. 288-290) has investigated the connection between peridermal rings and the aperture. The majority of rings do not, in fact, seem to have any connection with the aperture. The two first rings, however, are an exception. The first lies on the boundary line between the prosicula and the metasicula. It is actually the apertural ring of the prosicula, and prosiculae provided with just such a ring have been known prior to the development of the earliest fuselli in the metasicula. The other ring of the apertural type is the so-called budding ring. It is formed on the sicula ventrally where the first thecal bud is produced. During the sinus stage it constitutes a cylindrical thickening of the border of the metasicula, and is subsequently enclosed in the ring which surrounds the metasicula. This ring often unites with that on the protheca of the first theca, as is shown in fig. 48. The remaining peridermal rings are supposed to have no direct connection with the aperture.

Observations of M. **Walker** (1953, p. 364) have shed new light on this problem. This author has proved from microtome sections that the peridermal rings are internal, i. e. that they are situated on the inner surface of the metasicula wall. The first ring on the boundary line between the prosicula and the metasicula is often of some special shape, that of the letter *T* marked by suitable darkening, while the other rings are represented by convex thickening of secondary material with concentric layers superposed on fusellar material.

Microtome sections cut from the material here investigated fully confirm Walker's conclusions (fig. 5, 6).

The peridermal rings are actually internal structures. Only those rings whose apertural origin has been shown here (the apertural ring of the prosicula and the bud ring) illustrate different conditions. They are more or less symmetrically arranged on both sides of the periderm (comp. fig. 6; text-pl. III, 4-7, and VII, 6-7). The apertural ring of the prosicula is marked on both sides of the periderm, not always very distinctly (fig. 6 *A*, *B*). This will appear clearer if we take it for granted that the ring was actually of apertural origin. It is recorded even from siculae lacking the remaining peridermal rings (fig. 5 *C*).

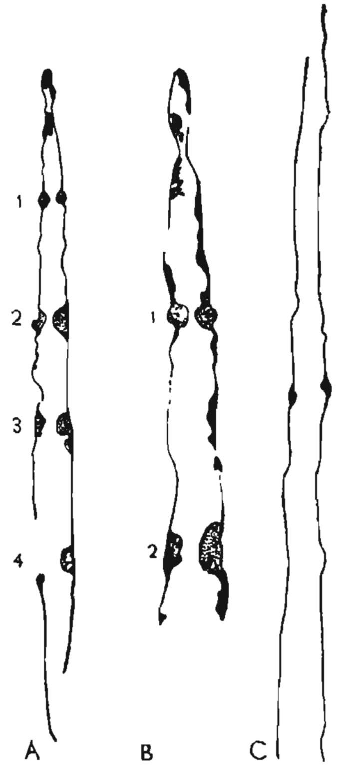

Fig. 5

Longitudinal section of sicula showing peridermal rings

A, *B* — *Monoclimacis haupti* (Kühne), *1-4* successive peridermal rings of sicula; *C* — *Pristiograptus dubius* (Suess), ringless form (S. 125, Niechorze); *A* × 100 approx., *B-C* × 200 approx.

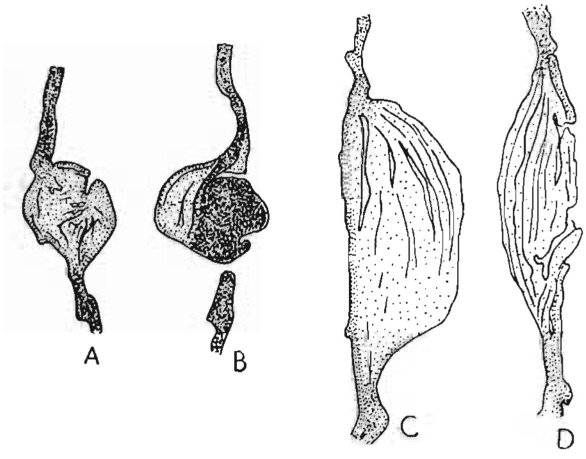

Fig. 6

Monoclimacis haupti (Kühne)

Peridermal rings of sicula — details of the same specimen as in fig. 5-*B*; *A*, *B* apertural ring of prosicula, *C*, *D* second ring of metasicula; × 900 approx.

The budding ring is always found on the outer as well as the inner peridermal side. This is shown in microtome cross sections of the rhabdosomes of *Saetograptus chimaera* and *Pristiograptus dubius* (text-pl. III, 4-5 and VII, 6-7). The other rings are always only internal. On the other hand, however, Walker's observations regarding the shape of the apertural ring of the prosicula have never been confirmed on the present author's material. It may be a matter of a strong individual variation displayed by this element.

The satisfactory state of preservation has led to a more profound investigation of the structure of peridermal rings of the metasicula. In conformity with information published by **Walker** they have a concentrically layered structure and have obviously grown by the gradual deposition of chitinous material (fig. 6 *A-D*). Nevertheless the significance of the peridermal rings continues to be an open question. **Kraft**'s view respecting the direct connection between the aperture and the rings cannot be held as reasonably justified in the case of most rings. It may be that the peridermal thickenings only indicate places where some portion of the body abounding in chitin-bearing glands mostly stopped, as for example during the contraction of the zooid and its retreat into the theca. Finally, rings may perhaps develop at the point separating the zooidal metasoma from its peduncle.

In monograptids the number of rings varies within the same species and they are differently spaced. Both ringed and ringless forms are encountered within one species, e. g. *Saetograptus chimaera*, *Pristiograptus dubius* (**Cox**, 1933; **Urbanek**, 1953; **Walker**, 1953). It is possible that the ringless forms were characterized by relatively rapid growth hindering sufficient deposition of chitin substance in places where the zooid was stationary. Similar specific dimorphism of siculae has also been ascertained in *Colonograptus colonus* (comp. p. 50).

For some time the mode of budding of the first theca in the monograptids remained an open question. **Kraft** (1926, p. 236) described it as an active pushing apart of the fuseli by the bud. But **Cox** (1933, p. 427), when analyzing the structure in the initial bud regioln, excluded the possibility of purely mechanical factors. **Kozłowski**, however (1948, p. 56), was the first to ascertain the actual mode of budding in monograptids and defined it as being apertural and opposed to that in diplograptids defined as perforating.

Eisenack (1942) distinguished two stages in this process. The first one called «sinus» consists in the formation of a sinus or apertural notch to the right of the virgella. This takes place by a special arrangement of the fuselli on the right side of the metasicula. They are namely arched and linked basally by a sort of node made of the thickened chitin (comp. fig. 23, 46, 60). After some time the sinus notch is closed up on the right side by a band of fuselli and this is the «lacuna» stage.

The same pattern occurs in all recorded monograptids. But some abnormal cases are described below (comp. p. 30).

Subsequent to the «lacuna» stage, the growth of the metasicula continues for some time. As a rule the development of the first theca or rather of its protheca goes simultaneously with the formation of the aperture of the definitive metasicula. This aperture is always provided with a virgella and a dorsal lip. The virgella is always a rod or spine protruding beyond the aperture, while the shape of the dorsal lip varies. Occasionally there is no process on the dorsal side of the metasicula. This is a characteristic feature of the Cucullograptinae (comp. fig. 41). If this process is present, it constitutes an ovate dilatation on the margin, more pointed in older individuals (Monograptinae, Saetograptinae, some of the Pristiograptinae), or even trapezoidal, e. g. in *Pristiograptus bohemicus* (**Barr.**) (comp. fig. 49 *C*).

The nature of the dorsal process in the aperture of the metasicula of *Pristiograptus nilssoni* (**Lapw.**) is distinctly characteristic, consisting of an asymmetrically placed and unpaired apertural spine (comp. fig. 52-55).

The morphology of the metasicula shows the complete structural pattern of a normal theca. The porus may be regarded as an equivalent of the prothecal aperture, the bud ring would correspond to the ridge-like thickening on the edge of the interthecal septum. The basal portion of the metasicula, comprising the porus, would constitute, broadly speaking, the equivalent of the protheca. The remaining part of metasicula would correspond to the metatheca. Naturally, the structure of the sicula, as compared with the other thecae, is quite distinct, but this does not alter the essential morphological conformity.

The length of the sicula in the Lower Ludlovian monograptids is in most cases less than 2 mm, most being from 1.6 to 1.7 mm. In this they differ from the primitive representatives of that family from the Lower Llandovery. Forms having relatively short siculae, i. e. from 1 to 2 mm in length, such as *Monograptus difformis, M.? atavus, M.? sandersoni,* occur frequently alongside forms with long siculae. In *M.? acinaces, M.? gregarius* (zone 18) the sicula was 5 mm long, in *M.? cyphus* — 4 mm. Forms with siculae as large as these are not encountered later in the monograptids.

Kozłowski (1948, p. 51), from information published by Elles & Wood, inferred that large siculae are associated with fairly large rhabdosomes and «vice versa». The only exception here would be that of *M.? gregarius,* cited by Kozłowski and belonging to the archaic forms mentioned above. Such a correlation does seem to exist in the case of forms whose colonies are of normal size (Wenlock), whereas it is not applicable to species showing secondary reduction of the number of individuals in a colony (comp. p. 30). *Monoclimacis ultimus* (Perner) seems to be a representative of such forms. It has a rather large sicula — up to 1.9 mm in length, while the average length of its rhabdosome does not attain 2 cm, in most cases being about 1.3 cm. The Wenlockian *M. (Monograptus) priodon* (Bronn) with a similar length of sicula (about 1.5 mm) was a form of gigantic size since its rhabdosome reached a length of 12 to 15 cm.[3]

Similarly in the Wenlockian *Pristiograptus dubius* (Suess), with length of sicula approx. 1.7 mm, the length of rhabdosome was up to 10 cm. On the other hand, Saetograptinae from the Lower Ludlow with a similar length of sicula — from 1.6 to 1.8 mm — were characterized by considerably shorter rhabdosomes. In *Colonograptus colonus* (Barr.) it attained a length of from 4 to 6 cm, in *Saetograptus chimaera* (Barr.) — from 2 to 4 cm. *Lobograptus scanicus* (Tullb.), with a length of sicula of 1.2 mm, had a rhabdosome 15 cm in length. The gradual reduction of the number of indivuduals in a colony suggests that in the case of such forms as *Monoclimacis ultimus* (Perner) the length of the sicula is a conservative character inherited from ancestors with longer rhabdosomes.

Siculae in various monograptid species and genera may resemble each other. It is hardly to be supposed that this is an expression of processes similar to those observable during ontogeny and referred to as the «ontogenetic convergence of phylogenetically related forms» (Haeckel, 1903). Neither does it seem probable that this should be an expression of K. Baer's law that specific characters appear during the last stages of ontogeny. It is hardly to be inferred that laws of ontogeny may be fully transfered to the astogenetic processes expressed by the development of the colony, particularly since metasiculae are occasionally provided with apertures showing strong characteristic differentiation on which they are specifically identifiable. The morphological homogeny of monograptid siculae together with the relatively strong differentiation in the morphology of other details are nevertheles striking facts. It is thus seen that the siculae have undergone only insignificant changes during the evolution of this group.

Urbanek (1953, p. 294-296) made an attempt to estimate the extent of the differences of several features of the siculae in order to determine their taxonomic significance. *Saetograptus chimaera* (Barr.) and *Pristiograptus dubius* (Suess) were selected for that purpose as being most abundant in the fauna from erratic boulders. The results of this analysis led in principle to the specific identification of siculae in a mixed population of both these spe-

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[3] R. Hundt (1933) mentions the length of some rhabdosome fragments of *M. (Monograptus) priodon* as being 19.5 cm, asserting that one of the German collectors had in his possession a specimen of *M. flemingi* from Wenlock measuring 75 cm. This was a species with the sicula about 1.6 cm long. More complete list of large-sized rhabdosomes in monograptids is quoted by G. Regnéll (1949).

cies. It should be stressed that these forms are not only specifically distinct but belong to different subfamilies. The specific identification of siculae among closely related congeneric forms does not seem to be likely.

STRUCTURE AND MORPHOLOGY OF THECAE

Monograptid thecae are more or less cylindrical. The proximal end of a typical theca consists of fuselli which above a certain length do not produce a zigzag suture. This is the basal part of the theca in monograptids, homologous to the stolotheca in the dendroids (Kozłowski, 1948, p. 58). The homology here is based on the identity of position occupied by this part of the theca in relation to its remaining part and on the fact that it presumably contained the stolon. The basal end of the theca, provided with its own aperture leading into the next theca, is additional evidence in support of the opinion that it is a separate thecal segment.

Bulman (1951, p. 318) suggested that this part of theca should be called «protheca», while Urbanek (1953, p. 290-291) proposed the term of «metatheca» for the remaining part of theca. Both these names replace certain terms previously introduced by Münch (1938, p. 46) whose use did not prove altogether convenient. The basal part of the protheca (at a time when its fuselli have not yet produced a zigzag suture) has by Münch been called the «semitubus»; the distal end of protheca, when the ventral zigzag suture is being produced, has been called the «metatubus», while the segment corresponding with present meaning of metatheca has been called the «thecatubus». These terms have been discussed by Walker (1953, p. 13-14).

For reasons of comparative anatomy the theca ought rather to be divided into two portions, one of which is homologous with the stolotheca of the dendroids (protheca), the other one being so with the autotheca (metatheca). The point where thecal fuselli cease being attached dorsally to the sicula or to the nema, may be accepted as the boundary between the protheca and the metatheca. Their oblique sutures start producing there the distal zigzag suture.

The first theca differs somewhat in its structure from the remaining thecae. It begins in the upper right corner of the porus with arcuate single fuselli which do not become double to form a zigzag suture until they are some distance from the beginning of the theca. In this theca the protheca creep along the wall of the sicula turning from the right side of the sicula into the plane of rhabdosome symmetry. On the ventral side the fuselli produce a zigzag suture over practically the entire length of the protheca and the part equivalent to the semitubus of other rhabdosome thecae is here missing.

The dorsal wall of the metatheca (interthecal septum, Querseptum) produced by the joining of metathecal fuselli is, morphologically speaking, a most interesting structure, since its further continuation produces the ventral wall of the next theca. Thus the basal part forms the dorsal wall of theca n, while the distal part forms the ventral wall of theca $n + 1$. The zigzag suture thus partly constitutes the dorsal and partly the ventral suture.

Walker (1953, p. 367-368) has laid special stress on irregular fusellar structure in this wall, a fact known before her time. Short or intercalary fuselli are here wedged in between the normal fuselli of the basal part. Walker believes these fuselli as built up by zooid $n + 1$ and not by zooid n. They gradually increase so as to occupy the whole median part of the septum, and finally the distal part of septum is built up wholly by zooid $n + 1$.

Actually, however, the writer has never been able to ascertain the intercalary fuselli to have grown so as to attain the size of normal ones, which they successively replace (comp. p. 60, fig. 31, 57). On the contrary, they often disappear. The scheme advanced by Walker has not been confirmed. Neither does the cooperation of both zooids seem reasonably probable if we remember that the distal wall of the metatheca *n* had developed almost completely when the building up of the first prothecal fuselli was only started by zooid $n + 1$. Moreover, in *Saetograptus chimaera* (Barr.) we note that the theca *n* is already provided with a complete aperture and apertural processes, while theca $n + 1$ has not yet developed a complete protheca. This shows that the developmental pattern of the two zooids deviated somewhat from that advanced by Walker.

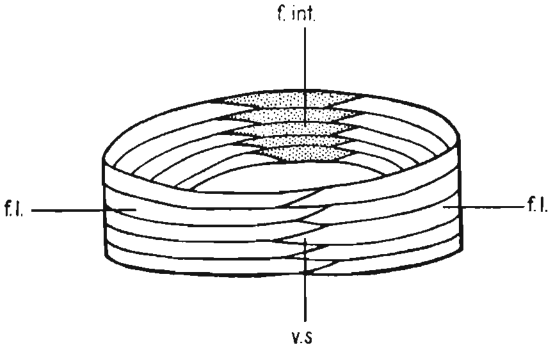

Fig. 7

Origin of intercalary fuselli on dorsal wall of metatheca (diagram)

f. l. lateral fuselli, *f. int.* intercalary fuselli on the dorsal wall, *v. s.* ventral zigzag suture.

Further explanations — in text.

Another hypothesis may, therefore, be proposed to interpret this most interesting phenomenon. One might for instance suppose that the zooid *n* built the fusellus first on the ventral side without producing them on the dorsal side, and that they were completed or joined by means of an intercalary supplementary fusellus. This was probably accompanied by additional bending of the zooid backwards. A diagrammatic drawing in fig. 7 illustrates this conception.

The closing up of the metathecal fuselli at a certain height gave rise to an aperture which the writer is inclined to call the aperture of the protheca. It is here that the bud of the next zooid emerged. The margins of the prothecal aperture, that of the dorsal wall particularly so, is secondarily thickened (see fig. 22, 51*A*, 64), constituting what Kühne (1954, p. 400) called the «annulus». The fuselli of the next protheca become attached to the lateral sides of the «annulus».

At the termination of its growth the metatheca develops an aperture. The apertural margin is usually provided with secondary thickening in the form of a roll. In monograptids the aperture may either be provided with such structures as apertural lobes, spines etc., or these may be missing.

Several types of these apertural processes may be distinguished. The apertural lobe, derived from the dorsal wall of the metatheca, is the most primitive and morphologically the simplest. It is a continuation of the fusellar system of the dorsal wall and has a corresponding zigzag suture running medially. On the lateral side the fuselli converge at about the midpoint of the aperture to a node. This is a peridermal thickening, joining together the fuselli. The Monograptinae (comp. p. 43, fig. 18, 21) are provided with this type of apertural lobes.

An analogous apertural type, however, being the derivative of ventral wall, is encountered in dendroid autothecae, as for instance in *Dendrograptus* (*D. cofeatus* Kozł.). Two principal varieties of this type of process occur in monograptids. One of them is called the «lobate» type and is found, for example, in *Monograptus lobiferus* (McCoy). Its characteristic feature is that the fuselli of the lobe do not unite into a node, but are attached, for a considerable distance to the lateral margins of the aperture. This gives rise to a sort of rooflet of apertural wall. The other variant is called the «hooked» type. The fuselli are united into one node and a covering is developed over the aperture (for example *M. (Monograptus) uncinatus* (Tullb.)). But the two types of lobes resemble each other very closely.

An instance of this type of apertural lobe, calling for special consideration, is observed in the apertural processes of *M. (Monograptus) priodon* (Bronn). At the sides of the dorsal lobe spine-like process are symmetrically arranged and are very similar to the processes in Saetograptinae. The last named species may in that respect be considered as leading towards the latter group.

Two other groups may be differentiated in addition to forms provided with a dorsal lobe. One of them has lateral ear-like or spine-like processes, the other one has true lateral lobes. Forms of the first group are those referred above (p. 11) to Saetograptinae *(Saetograptus, Colonograptus)*. Here we can observe two essentially distinct varieties of lateral process. One of them is the ear-like process of *Colonograptus*. Morphologically it may quite reasonably be derived from the dorsal lobate type.

In order to obtain this type of process, it only requires the fuselli within the lobe to no longer join in a middle zigzag suture. Further, the anterior edge of each process is formed by fuselli fused into a node, while the paraxial-posterior border consists of free fusellar edges.

Another variety is that of the spine-like apertural process. Here the process is folded into a tubule (Münch, 1938; Urbanek, 1953), while the free edge develops a protruding wing or petal. The edge of this lobe may develop additional processes or denticles (comp. p. 54). This type of process is encountered in *Saetograptus.*

In different specimens belonging to one species we may observe forms of processes intergrading between these two extreme types. Some of them, recorded in *Colonograptus*, are distinguished by a hooked process and faintly marked folding; others, recorded in *Saetograptus*, have, on the contrary, the folding less clearly marked than usually. Such forms are the extreme variants of these structures and shed some light on the evolutionary processes which may have occurred.

The type of process encountered in *Colonograptus* may, from the morphological point of view, be traced back to the hooked type of process, such as that of *M. (Monograptus) priodon* (Bronn). On the other hand, a tubular process like that in *Saetograptus* may be derived from the *Colonograptus* type by folding its anterior margin.

Naturally, this conception only involves the most general morphological connections that may be drawn from these structures, in particular from their fusellar structure. Hence it is a hypothesis grounded on solely morphological data, whereas the real course of phylogenetic processes must be left to future investigations. On the other hand, it seems most probable that morphological forms such as those mentioned above, have actually been the expressions of the various stages of this evolution.

This conception confirms the essential idea expressed by Elles (1922, p. 184) which derives the forms of the hooked type from those with a perfectly smooth aperture («progressive forms»). These are in turn believed to give rise to such forms as the Saetograptinae which, finally, led back again to forms with smooth apertures («retrogressive forms») (comp. p. 45). On the material here investigated, the writer thinks it reasonably correct to trace back forms such as *Colonograptus* and *Saetograptus* to those like *Monograptus priodon* (Bronn). Unfortunately, all stages of evolution represented by the «progressive forms» were inaccessible to the writer, neither did he find in his material any evidence to prove Elles' conception with regard to the final stage of the retrogressive line [4] (the passage of *Saetograptus* into forms o the *Pristiograptus* type). He does not, however, reject it as altogether improbable. Certain details of the problems connected with the evolution of apertural processes in Saetograptinae are discussed in the descriptive chapter of this work.

The aperture in Cucullograptinae represents the other principal type of aperture provided with lateral lobes. The simplest type of such lateral lobes is encountered in *Lobograptus* n. gen. (genotype: *M. scanicus* TULLB.). They are made of arch-like fuselli, convergent to an anterior and a posterior node (comp. fig. 35 *C*, 42). This type of process undergoes further complications, namely the lobes become asymmetric (one of them grows larger) and are pushed over the aperture. This type of modified lobe is observed in *Cucullograptus*. When considering the fusellar structure of such lobes it is possible to trace them back to the type represented by the lobe of *Lobograptus*. Some further details of the fusellar structure of lobes in Cucullograptinae are given on p. 67 and in fig. 32, 40, 42, 43, text-pl. IV. Apertural lobes of this type are fairly common. ELLES (1922, p. 185) also traced them back to the hooked type. This essentially is quite probable from the manner of formation of the posterior node simultaneously with a partial reduction of the dorsal wall of the simple lobe. The constitution of the posterior nodes and the splitting of the dorsal lobe seems to be a principal element in the evolution of this monograptid trend. The presence of two nodes imparts the arcuate shape to the fuselli. It might here be mentioned that the basal part of the process in *Colonograptus* and *Saetograptus* differs but little from the early evolutionary stages of the lobe in *Lobograptus*. Hence, at least in the present state of knowledge, this type of process may be derived from the apertural lobe of the hooked type.

The apertural lobes of some representatives of *Monoclimacis* FRECH constitute a distinct morphological type. These are very peculiar. Initially, the young theca lacks apertural lobes which are subsequently added as secondary structures on the boundary of the protheca and the next metatheca, in the form of a shield, with a crescent shape and special fusellar structure (comp. p. 94, fig. 68 *A-C*). This shield occupies, on the theca, a position equivalent to the so-called mesial list (BULMAN, 1938, p. 32-33) in thecae of *Climacograptus*. In this meaning it is also the equivalent of similar processes in diplograptids. It is distinguished by a peculiar structure since it consists of excessively numerous and very fine complete fuselli which do not produce a central zigzag suture, but extend from one end of the edge to the other end.

It is quite obvious that this structure is not homologous with the apertural lobes of Monograptinae, but that it constitutes a perfectly distinct type.

A frequent type of monograptid aperture is one lacking all accessories. Its border consists only of the free margin of the metatheca. This type is realized in *Pristiograptus*. The problem of primary simple or secondary simplified forms is connected with this type of apertural structure. In ELLES' opinion (1922), both types of the simple aperture are to be found in monograptids. In this sense *Pristiograptus* would group forms of similar morphology but different origin. At least, two groups of forms may be here differentiated: one uniting the primary simple forms and the other the secondary simplified, derived from forms initially provided with apertural processes (Saetograptinae, *Monoclimacis ?*). In support of this point of view are important differences in the thecal structure in some representatives of *Pristiograptus*. Thecae may be here cylindrical *(P. dubius)*, triangular *(P. bohemicus, P. nilssoni)*,

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[4] The terms «progressive» and «retrogressive» are here used for the sake of convenience only, to confront the views held by ELLES and those of the author. It may be that their choice is not too fortunate even if used in their formally morphological sense.

or long, tubular (*M. ? cyphus*, *M. ? acinaces*, our *Pristiograptus* sp.). Since, however, this is a hypothesis with insufficient evidence, the author here retains the genus *Pristiograptus* as a morphologically well defined group.

An analysis of the stratigraphical distribution of the various morphological types of aperture yields supplementary arguments supporting the conception advanced here of morphological connections between the apertural processes in monograptids. The type represented by the dorsal lobe is a very ancient one. *Monograptus lobiferus* McCoy is recorded from zone 19 (zone *M.? gregarius*, Lower Llandovery). These forms continue as far as zone 34 (zone *M. scanicus*) where they are represented by *M. (Monograptus) uncinatus* Tullb. This is, therefore, not only a most archaic but also a biologically very stable evolutionary line among the monograptids. *M. (Monograptus) priodon* (Bronn), a form probably ancestral to Saetograptinae, is recorded from zone 22 to 29 (zone *Monograptus turriculatus* — zone *Cyrtograptus linnarsoni*). The genera *Saetograptus* and *Colonograptus* appear in zone 33 (zone *Pristiograptus nilssoni*) and do not persist beyond zone 35 (zone *P. tumescens*)[5]. It seems probable that this was a relatively short-lived line. Between the extinction of *M. (Monograptus) priodon* and the appearance of the first Saetograptinae there is a stratigraphical gap in their occurrence which actually seems to correspond with the period of occurrence of unknown transitional forms.

The Cucullograptinae also seem to be recorded from the Ludlow and the Upper Wenlock only, though much caution must be here exercised in respect of evidence from flattened specimens, in order not to misinterpret a feature so characteristic as the structure of their apertural processes (comp. p. 75).

The process of the transformations of apertural lobes into spine-like structures may have occurred more than once in the history of monograptids, within some stocks it may have taken place more rapidly and at an earlier time than in others. The structure of *Monograptus? sedgwicki* (Portlock) is perplexing since its proximal end seems to be provided with processes of the dorsal lobe type, resembling this lobe in *M. priodon* (comp. Elles & Wood, 1913, p. 441-443; fig. 304 a-e), while in the distal end it has long processes, eminently similar to the apertural spine of Saetograptinae. This graptolite, recorded from zones 20-21, would thus seem to represent the intergradient type of structure, somewhat as is the case in *M. (Monograptus) priodon*. The apertural spines, however, here occupy only the distal end of the rhabdosome. If they were to be considered as a newly acquired character, then the mode of their appearance would differ from that which had occurred during the evolution of Saetograptinae on the boundary between the Wenlockian and the Ludlovian. Should, on the other hand, the spines be considered as a palingenetic character, then this form could, according to Elles' opinion, be held as a representative of the progressive evolutionary stage of the monograptids.

Monoclimacis is another very ancient stock among those in which we are interested. Its first representatives appear as early as zone 20 (zone *M. ? convulutus*), while the uppermost range of this stock ought to be placed as high as the Middle Ludlovian.

Pristiograptus, according to what has been stated previously, is probably not monophyletic. Within it are united very ancient forms recorded as early as zone 18 (Lower Llandovery), such as *M. ? concinnus*, *M. ? cyphus*, and probably later forms that realized a *Pristiograptus*-like appearance through the reduction and disappearance of apertural processes.

Thus, generally speaking, the stratigraphical distribution of the forms here considered

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[5] It seems very probable that *M.? testis* (Barr.) is also referable to *Saetograptus*, although reckoned to belong to *Monograptus* by others (Přibyl, 1948). However, the presence of long apertural spines and the probable loss of dorsal lobes are arguments against this latter point of view. The Saetograptinae would thus begin in the uppermost Wenlockian.

makes the correctness of previously advanced morphological inferences very probable. A schematic diagram plotted in fig. 8 illustrates some of the connections here advanced.

In view of strong morphological differences, the significance of several apertural accessories must have been also varied. Changes of function must have followed differences of morphology. The function of protecting the zooid seems to have been most general and one assignable to all of the apertural processes. Such specialized processes as *Cucullograptus* lobes may have additionally played the part of a «hydrodynamic tunnel» where the movements of the zooidal tentacles were instrumental in the formation of currents favourable to food-gathering.

Spine-like processes, besides their protective function, may have also been useful as balancers, particularly so in the sicula and in the proximal end of the rhabdosome (Kraft, 1956, p. 229).

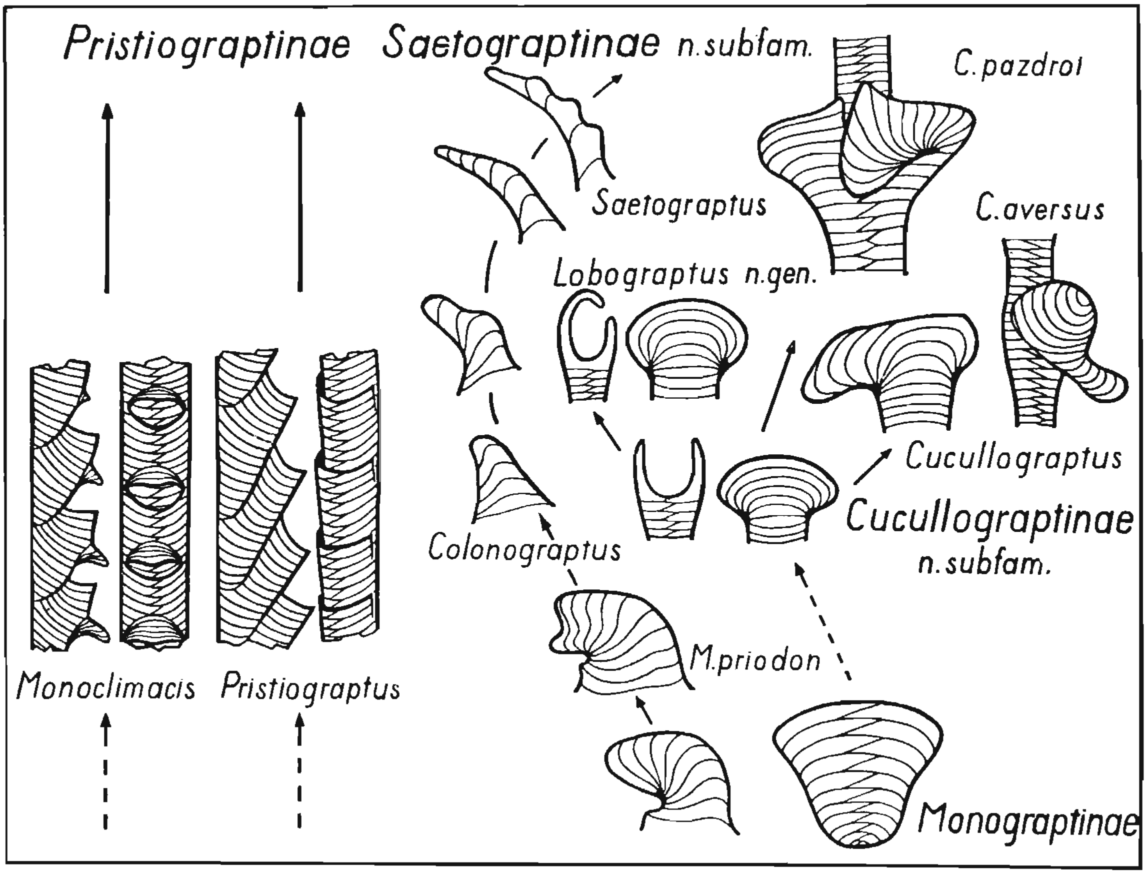

Fig. 8
Diagram showing the morphological relationship of different apertural structures in some Monograptidae.

According to M. Hemman (1943) the apertural spines of monograptids may be separated into two types. One of them is the fixed process, such as is encountered in *Colonograptus* and *Saetograptus*. The other one, on the contrary, is long, elastic and mobile, as are the processes in *Spirograptus* (= *M. turriculatus*) and *Obutograptus*. Hemman considered this to have been an apparatus, producing «vivifying currents» and vertical motion «bei der Einbettung in den weichen Schlamm».

As far as *Spirograptus* is concerned, it is regretted that its apertural accessories are not better known, but with respect to *Obutograptus*, whose apertures have been described by Bulman (1932, p. 13-15), Hemman's conception does not appear probable (comp. p. 6).

Quite a peculiar function is ascribed by Obut (1949, p. 24-25) to certain apertural accessories. In the case of *Spirograptus* this author supposes that the fine elongated apertural processes of this form served as ducts of sexual products. Although some processes do have a tubular form, it seems entirely improbable that they may have had this function. It was hardly to be associated with a zooid analogous to that of Pterobranchia where the pore of the gonoducts is situated on a prominence in the distal part of metasoma. Besides, it also seems that what Obut describes as the true gonades (1947, p. 880, fig. 1 A-F) in all probability constitutes but a chitin thickening on the free border of interthecal septum. Similar structures, in the same state of preservation, have been described by J. Perner (1899, I) from thin sections as «renforcement piriforme» of the internal aperture (= aperture of protheca). Perner's figures fully agree with Obut's (1947) figure 1-E. Probably we are dealing here with the same structure but differently interpreted. The structures described by Obut cannot in reality have any connection with the reproductive organs in graptolites, though Perner's description of the microstructure of the «pear-like» thickening in the internal aperture approaches that given by Obut (1947, fig. 1-E). The inside of this element is occupied by a dark substance, by Perner called the black layer («couche noire»), while on the outside there is an external layer («couche épidermique») containing wedges or inclusions occupied by the cuniform layer («couche en coins») or the columnar layer («couche à colonettes»). These two latter layers have probably resulted from secondary mineralization, taking place during the process of fossilization. This gives a picture similar to that which Obut has interpreted as a system of straight canals leading to the cavity of spermatophor (sperma sac) represented by the thickening of the interthecal septum. Obut's observations are based on species of *Monoclimacis* which actually do, occasionally, display a strongly marked thickening on the edge of the aperture of the protheca (see fig. 64 on p. 92). On the evidence of microtome sections it may be ascertained that the Perner's black layer and Obut's «mass of carbonized spermatozoa» truly correspond to the fusellar layer, while the external layer of lighter colour (Perner's «couche épidermique» and Obut's «straight canals») constitutes only a thickening of the secondary chitin layer.

After a more comprehensive analysis of apertural processes in graptolites known in flattened state of preservation only, it will be possible to determine their systematic position more exactly. *Saetograptus leintwardinensis* (Hopk.) e. g. has perhaps such a structure of apertural processes as *Monoclimacis* and ought to be referred to the latter genus. Side views of these processes seem to be similar to processes in representatives of *Saetograptus* (*S. salweyi* Hopk., *S. chimaera* (Barr.)), but their position is quite different. In fact, the apertural processes in *S. leintwardinensis* are mesial. This was known previously but was interpreted as a result of the bad state of preservation (Elles & Wood, 1901-1918, p. 402). In extremely well preserved specimens it is, however, possible to confirm that these processes are quite independent of apertural borders and are situated on a slightly protruding mesial edge. Their paired nature is rather doubtful. In any case these processes cannot be considered as homologous with such a structure in *Saetograptus* and correspond to mesial processes in *Monoclimacis*. Similar conclusions are suggested by the opinion, expressed by Tomczyk: «...apertural processes situated on outer surface of thecal walls in points equally or nearly so distant from apertures of adjacent thecae. Shape, especially of some thecae, is rather peculiar resembling those of *Monoclimacis* type» (1957, Polish text p. 58, fig. 17; pl. 8, fig. 4-6).

The metathecal aperture in monograptids may be variously shaped. In the majority of cases it is circular or elliptical (most Monograptinae, Saetograptinae, Pristiograptinae), but it may also be slit-like (part of the Cucullograptinae).

The apertural region may be separated from the basal part of theca by a sort of neck. An extreme expression of this type of aperture has been ascertained in Rastritinae, while a less extreme form is encountered elsewhere, for instance in *Cucullograptus*. In extreme cases isolation leads to lack of the truly interthecal septum. In such cases the thecae rise independently from the protheca which forms some sort of tube joining both thecae. A characteristic appearance is imparted to the thecae by less extensive isolation. Elles (1922) distinguished this type of thecae as the «triangulate type» represented in *Monograptus triangulatus.*

Two more essential types of thecae may be distinguished in monograptids: 1) the *Pristiograptus* type with straight cylindrical thecae, occasionally with distended apertural part. This is a type analogous to the *Dichograptus* type of the Ordovician Graptoloidea; 2) the other is the *Monoclimacis* type, with theca provided with a ventral prothecal excavation. This is very similar to the climacoidal type of theca noted in some diplograptids.

The mutual relation of thecae may also differ. In the first place this is expressed by the extent of thecal overlap. This overlap may range from nothing in isolated thecae or a very slight overlap in proximal thecae only, as in *Lobograptus scanicus* (Tullb.), to very strong overlap as in *Saetograptus chimaera* (Barr.).

During astogeny the thecal morphology undergoes different changes. In some monograptids these changes consist not only in changes of size or extent of isolation, but in structure too. In certain monograptids thecae of the proximal region have a different appearance than those of the distal part. On the whole they intergrade gradually from the proximal to the distal end of the rhabdosome, being subjected to a certain morphological sequence. Nevertheless, the contrast between the proximal and the distal part may be considerable. *M. (Monograptus) priodon* (Bronn), *Saetograptus chimaera* (Barr.), *Colonograptus colonus* (Barr.) may serve as better known examples of such forms. These are features long familiar to graptolite workers; forms of this kind have been called «biform».

Elles (1922) has advanced arguments to support the view that the proximal region is of particular significance in evolutionary processes, because it is in this region that any new characters are said to appear (comp. p. 5). T. S. Westoll (1950) has explained the «biformism» of certain monograptids by application of the «potential hypermorph» concept[6]. According to his view a «biform» monograptid may be regarded as a form potentially hooked throughout the rhabdosome if we suppose that such a shape of aperture is determined by corresponding size of thecae. Owing to restricted capacity for growth distal thecae, however, cannot always attain the particular apertural shape, linked with a definite size of theca. «Retrogressive series» in light of Westoll's views «may be regarded as neotenic modification of enlarged thecal form» (p. 505).

Bulman (1951), however, on the basis of detailed analysis of some «biform» monograptids belonging to «progressive series», critically estimated Westoll's concept. According to Bulman, this concept may be, eventually, a possible interpretation of the «retrogressive line», but in the majority of cases not only do changes in the distribution of existing thecal types

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[6] Hypermorphism is defined as «the prolongation of the development by addition of stages at its end» (Carter, 1954, p. 322). This is, therefore, a phenomenon analogous to Severtsov's anabolia. Potential hypermorphism would thus define a process whereby the addition of new stages is potentially possible, but never takes place owing to the abbreviated development of a part of individuals in the colony.

occur, but quite new thecal patterns must be involved. This latter phenomenon cannot be sufficiently explained by WESTOLL'S hypothesis.

According to BULMAN a colony of graptolites is subject to common genetic control. Evolutionary changes may take place here either by means of changes affecting all the individuals in the colony or only a defined group of them. In BULMAN'S opinion, the astogenetic process in graptolites is quite peculiar, but it comes nearest to the ontogeny of polymeric animals, such as the Arthropoda, for instance. Here we can also note a decline of the morphogenetic gradient, while metamere displaying the highest specialization are proximal.

In his conclusion BULMAN accepted ELLES' (1922) hypothesis that new thecal forms commonly originate in the proximal part of the rhabdosome «with the corollary that the factor concerned loses its potency as the colony ages» (p. 328).

The present writer, however, cannot accept WESTOLL'S interpretation of the so-called «retrogressive series» in monograptids because his own observations show that both, ancestors (*Monograptus priodon*) and descendants (Saetograptinae), are «biform» throughout all the evolutionary process under consideration (comp. p. 44, 46, 50). No changes in the degree of «biformism» can be noted among *M. priodon* and *Colonograptus* or *Saetográptus*. Differentiation in the thecal pattern between proximal and distal parts is well marked in both cases and the only difference that really existed is the presence or absence of apertural lobe. The evolution in this line displays some qualitative changes in structure which can be described neither in terms of a hypermorph concept nor in terms of neotenic changes in the structure of the colony.

Whichever of the previously mentioned hypotheses we accept for explanation of «progressive line», both the modifying and suppressing factors remain very obscure. An application of «growth gradient» hypothesis in the form proposed by J. HUXLEY (1950) seems to be very hopeful. On the other hand, however, THORNSTEINSSON'S investigations (1955) on cladial generation in *Cyrtográptus* indicate that the contemporary thecae both on main branch and on cladia display the same thecal pattern. If so, the thecal type depends on the age of the colony, not on the place occupied by thecae in the rhabdosome (or, in other words, on the distance from the beginning of colony). This rather confirms BULMAN'S view that the colony age is responsible for simplification of distal thecae.

Going back to ELLES' main conception as regards the mode of appearance of new characters in the phylogeny of graptolites, we are inclined to note there the number of analogies with SCHINDEWOLF'S theory of proterogenesis. Naturally, the theory of proterogenesis is concerned with the ontogeny of individuals and not with those occurring in colonies. Still there is some remote resemblance between the two phenomena. Nevertheless, the appearance in the early ontogenetic or astogenetic stages of new characters does not, apparently, constitute the only mode of evolution. Some exceptions to that rule have already been quoted by BULMAN, in the case of *Monograptus decipiens* and *M. communis*. Among graptolites, however, the most striking forms are those expressing a transition from the biserial to uniserial type of rhabdosome. Proximal thecae beginning with the first (Dimorphograptidae) were reduced in some forms and these are more numerous. In others, however, though the proximal thecae were also to be reduced, yet the theca *th* 1^2 was present and did not suffer reduction (*Peiragraptus* STRACHAN; I. STRACHAN, 1954).

One of the expressions of astogenetic thecal variability is also that adjacent edges, dorsal and ventral, draw closer distally, viz. that thecal apertures are more densely assembled. In some species (*Saetograptus chimaera*, *Colonograptus colonus*) this is shown quite distinctly and with relative regularity (see URBANEK, 1953, p. 293), in others no marked changes are discernible with regard to the distance of thecae as astogeny advances (*Monoclimacis häupti* (Kühne)) and it may be said rather to oscillate nearer a certain average than to be subject to definite changes. Occasionally, the distance even increases instead of decreasing *(Pristiograptus bohemicus, Monoclimacis micropoma)*. A form described by Elles & Wood as *Monograptus remotus* (1901-1918, p. 461-462, text-fig. 319, pl. 46, 9 a-b) provides the most extreme example since here the distance between thecae markedly increases distalward. At one time it was the only known form displaying such a feature. Today this does not seem so rare, hence the diminuation of distance between thecae in the course of astogeny is not an absolute rule.

The presence on proximal thecae of peridermal rings, fully equivalent to such rings on the metasicula, is a noteworthy feature among graptolites. Their presence has been ascertained by Urbanek (1954, p. 303-305, Consp. p. 84-85) in *Lobograptus scanicus* (Tullb.) and quite recently also in *Pristiograptus bohemicus* (Barr.) (see p. 78, fig. 50). In both these cases there are individuals either possessing or lacking these rings, exactly as it is with regard to the rings of the metasicula. Thecal rings seem to be exactly analogous with rings of the metasicula. In microtome sections they are seen to be also secondary peridermal thickenings of the inner surface of the wall being, however, less marked (fig. 51 *A*).

The ring of the first theca, situated near the porus, is a most particular form of thecal ring. As a rule it is not completely closed and occurs in practically all of the investigated species. Its presence, therefore, seems to be a rule.

Urbanek (1954, p. 305) links the presence or the lack of rings in conspecific forms to intraspecific variation which may have been of geographical or of historical nature.

RHABDOSOME AS A WHOLE

The definite morphological succession manifested by individuals of monograptid colonies allows us to regard the rhabdosome as a whole. It is characterized by certain definite features of which the shape of the rhabdosome comes foremost. Monograptid rhabdosomes may be straight or nearly so *(M. (Monograptus) priodon, M. (Monograptus) uncinatus)*; or with a ventral curvature (i. e. with a concave ventral side), as in *Saetograptus chimaera*, *Pristiograptus dubius* and particularly so in *P. bohemicus*; or again with a dorsal curvature (i. e. with a concave dorsal side) in forms like *M.? revolutus* and *M.? difformis*. Occasionally, within the proximal area, the curvature is dorsal changing into ventral distally (e. g. *P. nilssoni*, with its «dorsi-ventral curvature»). The morphological significance of the rhabdosome curvature in monograptids has not yet been clarified. Elles & Wood (1901-1918, p. 360-362) have assigned to it some taxonomic significance by separating certain groups of Monograpti into corresponding sub-sections characterized by a definite type of curvature. Nevertheless in forms usually characterized by ventral curvature *(Saetograptus chimaera)* all degrees of expression of this character are observed, some few forms even showing dorsal curvature. No great importance should, therefore, be attached thereto. Likewise there is no connection between the type of rhabdosome curvature and thecal structure. Some Monograpti showing fundamental differences of thecal morphology may realize the same type of curvature. This may be illustrated by Monograpti with a dorso-ventral curvature of rhabdosome: some of them have straight thecae with a *Pristiograptus* aperture *(P. nilssoni)*, others have dorsal apertural lobes with triangular thecae *(Monograptus lobiferus, Streptograptus becki)*. Forms with spine-like apertural processes (*Tyrsograptus* Obut (= *Obutograptus* Mu)), as well as those with dorsal lobes approaching the hooked type (= *Spirograptus* s. s.) both display characteristic spiral curvature of the rhabdosome. A similar pattern is followed in other types of rhabdosome curvature. From this one may infer that similar shapes of rhabdosome developed independently in many monograptid groups, being perhaps of some adaptive significance. The writer agrees with A. T. Mu's opinion that «the coiled rhabdosome is not a generic character, for a great number of species belonging to different genera may have the same character. It is thus unsafe to group some forms in one genus based on their coiled rhabdosome alone» (1955, p. 8). These remarks are in the same way applicable to other types of rhabdosome curvature.

It is difficult to establish the numerical maximum of individuals in monograptid colonies on material from erratic boulders. In the majority of cases we have young rhabdosomes which probably had not yet completed their growth or fragments of older rhabdosomes. Bulman (1955, p. 44) quotes «50-100 for typical *Monograptus*, and no more than 10 to 20 in the late Ludlow monograptids». The gradual reduction of the number of individuals in a colony is observed, according to Bulman, in the course of evolution within this graptolite line too.

ABNORMALITIES OF DEVELOPMENT AND STRUCTURE

When analyzing the structure of many monograptids we may, with relative frequency, note examples of variations which exceed the limits of normal variation and should rather be considered an expression of abnormality or monstrosity.

Some of these cases have apparently been caused by disturbances taking place during the normal course of budding and development processes of the colony. Disturbances of this kind involve a certain number of individuals of the rhabdosome; the succeeding ones resume their normal type.

In other cases abnormalities are observed in individual thecae only. These are probably the result of disturbances in the growth or ontogenetic development of a simple individual in the colony. Such abnormalities are most often associated with the changes of the shape of the aperture, its processes etc.

To the first group we may refer an interesting abnormality of the budding process of the second zooid, observed in *Saetograptus chimaera cervicornis* Urbanek (pl. III, fig. 3 *a-c*). A fragment of the rhabdosome consists of five proximal thecae with a protheca of the sixth theca. An abnormal development of the first theca is markedly noticeable. It is a nearly straight tube, almost completely isolated from the other thecae, adjoining the second theca along a small distance in the basal region only. The apertural end of the theca is provided with two triangular processes, resembling the «colonus» type of apertural processes, hence markedly different from those characteristic of this species. The next thecae, on the other hand, have normal apertural processes permitting the specific identification of the specimen. In the antero-posterior plane the theca has a constant diameter (about 0.5 mm) over its entire length, while in the lateral plane the basal part of the theca is somewhat narrower than the apertural end due to depressions formed by the side walls (pl. III, fig. 3 *a*). The theca is slightly inclined to the left and its basal end communicates with the inside of the metasicula by means of a pore. On the distal wall, placed somewhat below mid-height, is a sub-circular foramen about 0.19 mm in diameter. The edges of the foramen are slightly thickened and provided with a secondary chitin list. After decolouration of the specimen the fuselli are seen to end abruptly without producing an oblique suture (fig. 9 *op*). At its basal end the theca is completely closed up, there is no prothecal aperture in the proper place and the theca does not communicate with the second theca. The second theca has an essentially normal structure. It shows a slight sigmoid curvature of the basal end, adjoining the base of the first theca, not, however, communicating with it. At the base of the left wall of this theca, a subtrigonal foramen is discernible (fig. 9 *os*) on its base, about 0.19 mm long, being slightly longer than its two sides each 0.14 mm in length. One of these sides touches the fusellar part of the second protheca, while the other side and the base of the foramen are rimmed by an area of structureless chitinous membrane. The surface of the membrane is strongly wrinkled and folded thus

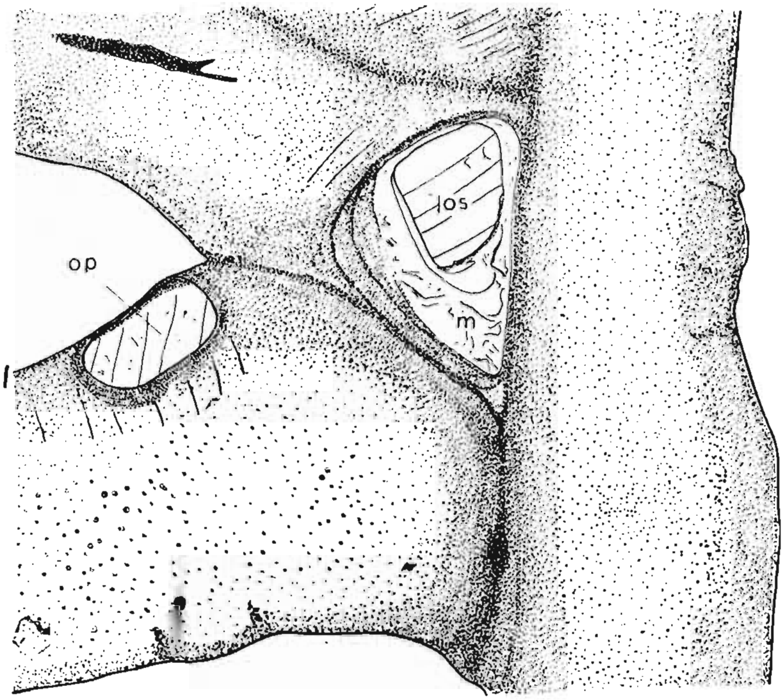


Fig. 9

Saetograptus chimaera (BARR.)

Portion of rhabdosome showing bases of 1st and 2nd theca — abnormal mode of budding of 2nd theca visible (S. 36, Jarosławiec); × 100 approx.

m chitinous membrane, *os* opening of stolon, *op* perforation opening.

resembling the regenerative periderm (fig. 9 *m*). The chitinous membrane and the foramen occupy jointly a larger trigonal area, which constitutes a magnified reproduction of the foramen contour. The base of this larger triangle is 0.34 mm long, the sides 0.25 mm each.

The shape and size of the first theca seem to suggest abnormalities in the ontogeny of the first zooid, due to factors unknown. They caused a relative retardation of the budding process in the second zooid, which did not appear before the metatheca of the first zooid had already reached an advanced stage of development. This resulted in the second zooid being as it were enclosed in the interior of the first theca. Probably, when making its way to the outside, the zooid succeeded in perforating the distal wall of the theca, thus giving rise to a kind of perforation pore, as is suggested by the structure of this foramen. Subsequently, owing either to the participation of a resorption process, or to secondary healing processes, the edges of the foramen were secondarily smoothed, as in the budding of the first theca in diplograptids. From the diameter of the foramen we can at the same time learn the dimensions of the young zooid which had to squeeze in through this foramen. We might imagine that the autozooid first began to form a fusellus spanning by an arch the base of the first theca with the edge of the metasicula. The first fusellus was set at a certain distance from the junction of the first theca with the edge of the sicula. A free space was thus formed which, upon the penetration of the zooid into the interior of the second theca, was partly sealed up by the chitinous membrane. The remaining contracted foramen probably enabled the stolon to enter. The budding of the third zooid had a normal course; the second theca normally communicates with the third by means of the prothecal aperture. Similar conditions prevail in all the remaining thecae.

It will be reasonable to infer that the stolon, joining the first and the second zooids, persisted constantly within one of its parts, as an «extrathecal stolon». It was situated outside of the thecae between the openings which were used by it to «leave» and to «enter» the inside of thecae. It should be stressed that it left no traces of its course such as peridermal thickenings or other secondary structures. This indicates that in monograptids, like in other Graptoloidea, the stolon had definitely lost the ability to excrete chitin. Its existence is, however, beyond doubt, as will be confirmed by the presence of peridermal foramina which could not in this case be entirely closed up owing to the presence of the stolon.

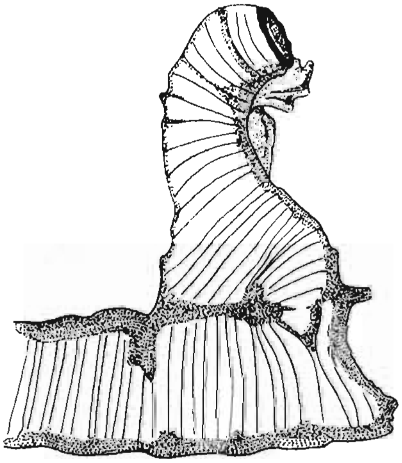


Fig. 10
Monograptidae (gen. et spec. indeterm.) Abnormal shape of 1st theca and reduction of rhabdosome (S. 37, Isle of Wolin); × 80 approx.

Another example also referable to the first group of abnormalities is the interesting colonial reduction observed in one single case. The specimen is represented by the sicula and the first, abnormally developed theca only (fig. 10). Hence it can only be identified as belonging to the Monograptidae, without generic and specific determination. The first theca has developed here as a tubule of nearly uniform width, showing a sigmoid curvature. As compared with the rest of the theca, the base is prominently wider. The aperture is in the form of a circular foramen, somewhat contracted in relation to the diameter of the terminal part of theca. It is provided with a thickened edge and the theca is slightly inclined to the left and completely isolated. The prothecal aperture is missing altogether as is also the perforation pore through which the bud of the second zooid might have been able to emerge. We may suppose that in this case the succeeding thecae were never produced and that the whole rhabdosome consisted of the sicula and of the first theca only. This would provide an example of extreme abnormal colonial reduction. The abnormality here would be analogous to conditions normally prevailing in genera *Corynoides* Nich. and *Corynites* Kozł.

It is difficult to establish the causes of this anomaly. The budding in the first zooid was quite normal, although the pore is uncommonly near to the apertural edge of the metasicula, being separated by two or three fuselli only. The change, which deviated the course of ontogeny into an abnormal direction had, therefore, taken place within later growth stages of the zooid. On the ventral wall of the metatheca there are supplementary abnormal processes on the periderm.

Another example suggesting a stronger disturbance of the normal rhythm of budding is that provided by rhabdosome curvature in *Saetograptus chimaera*. Here the first theca protrudes to the right in relation to the plane of symmetry, while the second theca is inclined to the left. In the remaining thecae this abnormality must have, probably, been done away with, but unfortunately the thecae are damaged in the specimen under consideration (fig. 11). The curvature of the first is accompanied by asymmetry of the apertural processes, the right of them being normally developed, while the left one has been reduced to a triangular ear.

Anomalies in the structure of the sicula and of other organs connected with it, noted by the writer, are also of interest. They are the frequent occurrences of «manifold nema» probably connected with the formation of a regenerative nema (see p. 38). Since in many species this is a common process and may be considered as the physiologically normal mode of formation of this organ, it is difficult to delimit the normal and abnormal expression of nemae.

Anomalies in the regeneration processes, however, occasionally lead to the formation of a certain number of regenerative threads, which do not become fused into the solid filament of the nema (fig. 12 *A*, *B*). This gives rise to several regenerative nemae, every one of them being the prolongation of one of the threads. Fig. 12 *A* illustrates the occurrence of a double nema in *Saetograptus chimaera cervicornis*. The writer has also observed the occurrence of threefold nema in *Monoclimacis haupti* (in a specimen which has been destroyed during attempts at decolouration). We do not know the entire length of these manifold nemae. Similar examples described by Eisenack (1941) in the case of *Climacograptus*, also consist of relatively short chitin threads. These manifold nemae fused perhaps into a solid filament at a certain distance from the apex of the prosicula. This pattern of development has been described by Bulman (1944, I, p. 29) in *Cryptograptus tricornis* Carruthers. Double threads of the nema were joined there at a considerable distance from the apex of the prosicula producing the so-called «bifurcating nema». This process has probably also some connection with that of regeneration, though Bulman writes that in some cases the apex of the prosicula is apparently undamaged. The peculiar shape of nema in the case of this latter species may be also referable to modification of sicula and linked with the partial reduction of its periderm.

It is rather difficult to establish reasonable causes responsible for the formation of manifold nemae. In the case of the initial nema-the longitudinal ribs of the prosicula seem to coalesce automatically owing to the conical shape of prosicula. If, however, the apex of the prosicula is destroyed, the regenerative threads become separated and may not necessarily touch one another.

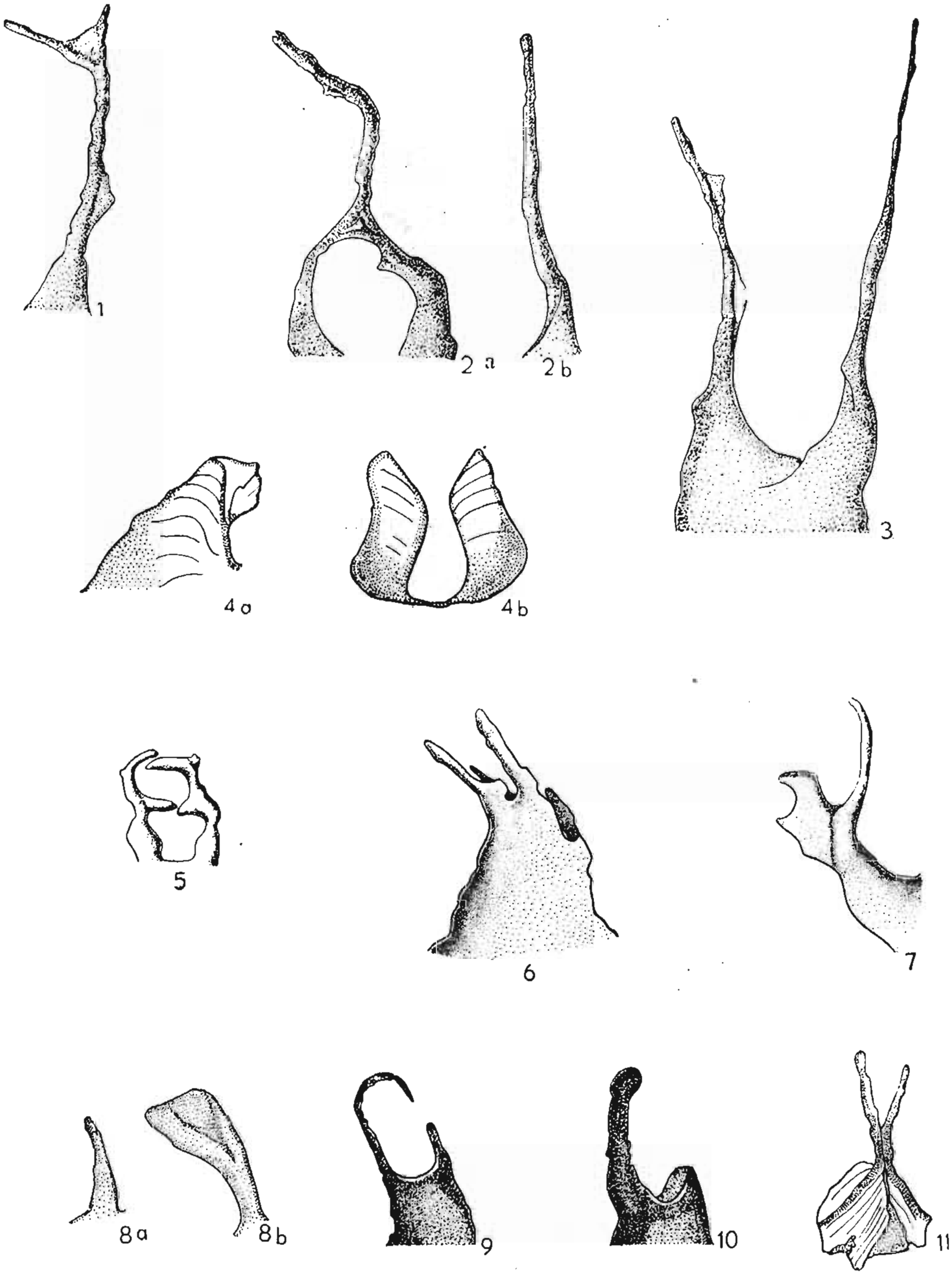
Fig. 11

Saetograptus chimaera (Barr.)

Curvature of the rhabdosome axis (S. 32, Gdańsk-Wrzeszcz); × 37 approx.

Anomalies observed near the pore present noteworthy examples of abnormalities of the sicula. The writer is inclined to call such structures «twin pores», since two pores are then formed. One of them occupies a normal position on the right side, while the supplementary pore is to the left side. Fig. 13 illustrates the first example of this type. It shows the distal end of metasicula with two discernible pores. The left is in the «lacuna» stage, the right —

TEXT-PLATE I



Abnormalities of virgella and apertural processes

Fig. 1. *Pristiograptus dubius* (SUESS), abnormality of virgella (S. 32, Gdańsk-Wrzeszcz); × 100 approx.

Fig. 2. *Saetograptus chimaera salweyi* (HOPK.), *a* coalescence of apertural processes in 1st theca, *b* normal shape of apertural process in 2nd theca of the same rhabdosome (S. 108, Rewal); × 100 approx.

(explanations continued on the next page)

the «sinus» stage, and its development seems retarded as against that of the first one. It is an interesting fact that, their position excepted, both pores display normal structure, since the niche formed by them owes its existence to the characteristic curvature of the fuselli.

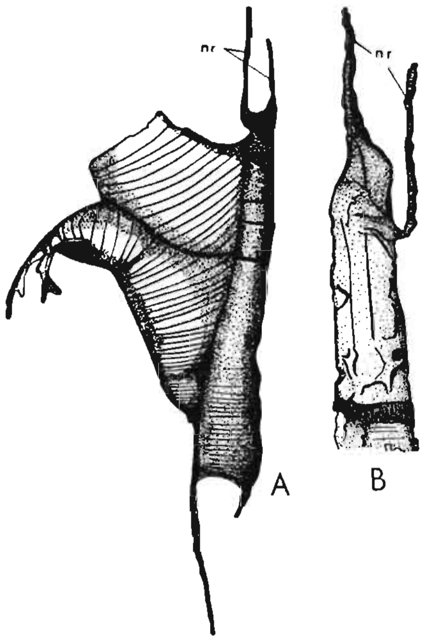


Fig. 12

A — *Saetograptus chimaera cervicornis* URB. Stage with 2nd theca and double nema, *nr* regenerative nema (S. 36, Jarosławiec); × 33 approx.

B — Monograptidae (gen. et spec. indeterm.) Sicula with double nema, *nr* regenerative nema (S. 36, Jarosławiec); × 100 approx.

The other example differs somewhat from the first one (fig. 14 *A*, *B*), since the structure and dimensions of the two pores do not agree. The right pore is of normal structure, and in an advanced stage, part of its protheca being already developed. The left pore is considerably larger and it is far from being normal. Its niche consists of fuselli which break off as a free edge before reaching the virgella. The upper edge is provided with a kind of brim consisting of fuselli, in the form of a gently upturned periderm thickened distally. Perhaps this part may actually be regarded as the protheca in the process of development, though this is not confirmed by its structure.

All «twin pores» of this type in all probability develop as a result of the acceleration of the budding processes. This may have resulted in the almost contemporaneous formation from the metazooid of two succeeding zooids. A pattern is thus produced resembling somewhat that of the budding process in diplograptids.

Finally, abnormalities of the virgella may also be observed on the sicula. These should rather be referred to the other group of anomalies since they are associated with ontogenetic disturbances of one theca only. In one case, that of *Pristiograptus dubius*, the virgella was terminally bifurcated (text-pl. I, fig. 1). One of the bifurcations, i. e. the right, is slightly longer and set at an angle of about 70° to the other one, which forms the prolongation of the basal end of virgella. A peridermal membrane spans the two branches. There is moreover a sub-triangular process to the left of the median area of the virgella. This abnormality resembles the structure of the dorsal processes, described by BULMAN (1932,

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(continued)

Fig. 3. *S. chimaera cervicornis* URB., asymmetrical shape of apertural processes in Ist theca (S. 104, Dziwnów); × 100 approx.

Fig. 4. *Colonograptus colonus* (BARR.), excrescence on apertural processes of Ist theca: *a* lateral view, *b* distal view (S. 19, Poznań); × 33 approx.

Fig. 5. *Saetograptus chimaera cervicornis* URB., abnormal shape of apertural processes in Ist theca, distal view (S. 36, Jarosławiec); × 40 approx.

Fig. 6. *S. chimaera cervicornis* URB., double apertural processes of the 3rd theca (S. 36, Jarosławiec); × 80 approx.

Fig. 7. *S. chimaera cervicornis* URB., abnormal shape of apertural processes of Ist theca (S. 36, Jarosławiec); × 70 approx.

Fig. 8. *S. chimaera* (BARR.), *a* normal shape of apertural process in 4th theca, *b* shovel-like shape of apertural process in 5th theca of the same rhabdosome (S. 108, Rewal); × 50 approx.

Fig. 9. *S. chimaera* (BARR.), curvature of virgella (S. 32, Gdańsk-Wrzeszcz); × 100 approx.

Fig. 10. *Pristiograptus dubius* (SUESS), excrescence on virgella (S. 32, Gdańsk-Wrzeszcz); × 100 approx.

Fig. 11. *Monoclimacis haupti* (KÜHNE), splitting of virgella (S. 148, Jarosławiec); × 80 approx.

p. 30, pl. 8, fig. 5·6) in the case of a sicula in *Lasiograptus hystrix* Holm. There the processes also bifurcate, a peridermal membrane being enclosed between them.

In another case the virgella is prominently thickened, and terminates in an additional swelling (text-pl. I, fig. 10). Sometimes the usually straight virgella is curved arcuately over the aperture with the apex retreating to the rear (text-pl. I, fig. 9). An interesting example of a bifurcated virgella in *Monoclimacis häupti* (Kühne) is shown in text-pl. I, fig. 11. The virgella is here split medially and the two ramifications diverge at an angle.

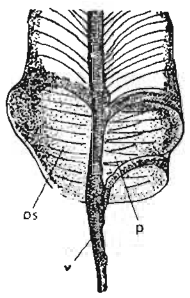

Fig. 13
Saetograptus? sp. Metasicula with double pore, *p* pore in the «lacuna» stage, *ps* pore in the «sinus» stage, *v* virgella (S.36, Jarosławiec); × 67 approx.

In numerous cases the presence may be noted, on some thecae, of peridermal excrescences shaped as crests, spines, etc. Examples of these «ulcerations» in *Monoclimacis haupti* (Kühne) are of special interest. The periderm is covered over considerable areas by numerous protuberances and nipple-like roughnesses of chitinous substance (pl. V, fig. 5). On the whole it has not been ascertained that these «ulcerations» are connected with processes of regeneration of that part of the periderm. They may, perhaps, be the results of a morbid affection of the extrathecal membrane covering the periderm, caused by the presence of some parasites or by their encystment.

Occasionally such excrescences have a fusellar structure as for instance in the case of a rhabdosome of *Colonograptus colonus* (text-pl. I, fig. 4*a*, *b*). The excrescence, discernible on the apertural process, is obviously a secondary product, as is indicated by the sharp boundary between it and the remaining part of the process.

The apertural region and more particularly the apertural processes are parts of the theca showing most extensive variation. Some examples of the development of processes obviously, do not fit into normal variations. Ample evidence in this respect has been provided by *Saetograptus chimaera* (Barr.). The fusion of processes belongs to this type of abnormality. Occasionally (text-pl. I, fig. 2*a*, *b*) an «arcade-like fusion» of both processes takes place with a single process starting there from. This is so, however, in only one theca, the others being provided with normal processes (text-pl. I, fig. 2*b*). Sometimes the process is spade-like in shape. This is caused by the broadening out of its terminal part, while, as stated above, processes of adjacent thecae or even the second process in the same theca retain their normal pattern (text-pl. I, fig. 8*a*, *b*). Text-pl. I, fig. 3 illustrates a markedly striking example of this. The right process resembles the type common in *Saetograptus chimaera salweyi*, while the left one comes closer to that common in *Saetograptus chimaera cervicornis*.

The pattern figured in text-pl. I, fig. 6 is of particular interest. We have there a duplication of processes, there being two processes symmetrically placed on each side of the theca. The adjacent thecae have, however, but one pair of processes. This duplication of processes may perhaps be associated with secondary zooidal budding. If so, the presence of two zooids within one theca would perhaps explain the two pairs of processes. Some other cases of peculiar shape of processes are figured (text-pl. I, fig. 5, 7).

One of the *Saetograptus chimaera* specimens illustrates an example of the occlusion of the first theca. The specimen is a fragmentary rhabdosome with 7 thecae (pl. II, fig. 2). The first theca has a normal structure, that of the aperture excepted, since the left process is missing, while the right shows a rather unusual development. Its aperture is completely sealed by a film of chitin, consisting of the peridermal membrane, apparently rather thick and non-transparent. The membrane is strongly wrinkled and slightly domed.

This type of occlusion is probably an unusual occurrence in Graptoloidea, while similar examples have often been described in other groups of graptolites. Of the dendroids, *Dictyonema wimani* has been described in this respect by Bulman (1933, p. 24) and *Dictyonema wysoczkianum* by Kozłowski (1948, p. 43-44). In Camaroidea (Kozłowski, *l. c.*, p. 173) occlusion is expressed so frequently that the majority of thecae are occluded. The frequency of this occurrence in Dendroidea and Camaroidea prevents the possibility of a complete analogy with the occlusion in monograptids as given above, where it is a rare phenomenon.

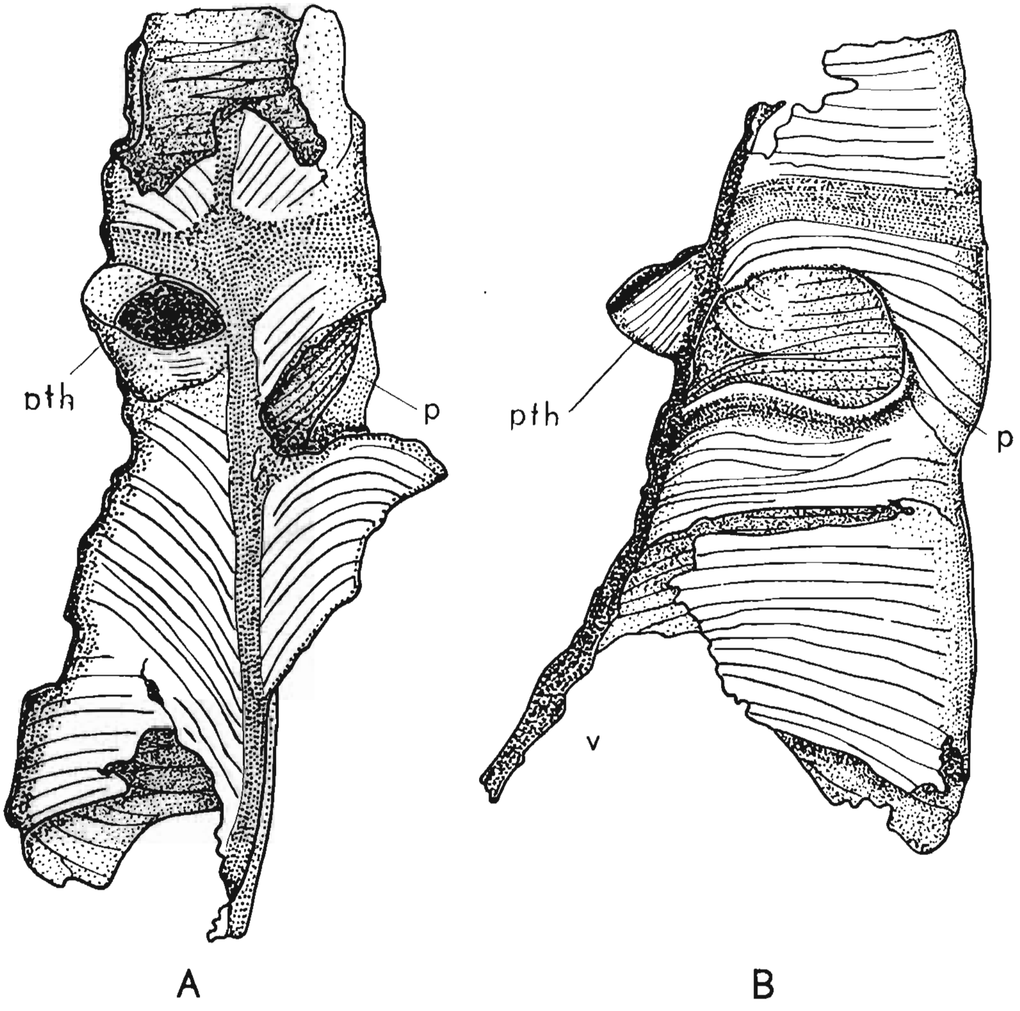

Fig. 14

Saetograptus? sp.

Sicula with double pores: *A* ventral view, *B* right lateral view, *p* pore, *pth* protheca, *v* virgella (S. 32, Gdańsk-Wrzeszcz); × 133 approx.

After Kozłowski (1948, p. 173) autothecal occlusion in Camaroidea is associated with zooidal encystment. The causes of occlusion in dendroids are not so clear owing to the presence of secondary chitinous products in the interior of the autothecae. In our case the lack of one of the processes and an anomalous shape of the second one suggests here some damage or wound inflicted on the zooid, probably leading to its necrosis which was preceded by the sealing up of the theca by the occluding membrane.

REGENERATION

Regeneration and reconstruction of damaged periderm are quite frequent among graptolites. Their occurrence has been described previously (Kraft, 1926; Bulman, 1932; Eisenack, 1940; Kozłowski, 1948).

Peridermal regeneration in graptolites may be separated into two groups. In one of them the regenerated parts have fusellar structure and usually supplement or replace the damaged or destroyed areas on the edge of the aperture. In the second group the destroyed area is situated far from the aperture. The regenerated area then consists in most cases of a thin structureless membrane. Kozłowski (1948) has described both these types in older graptolites.

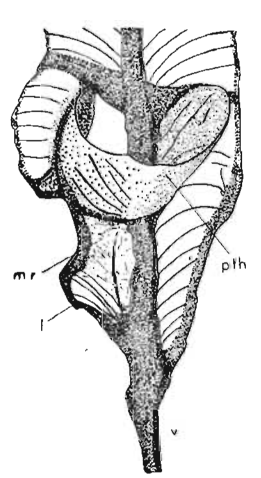

Fig. 15
Monograptidae (gen. et spec. indeterm.)
Regeneration of a portion of metasicula: *mr* regenerative membrane, *l* thickening margin, *pth* protheca, *v* virgella (S. 116, Rewal); × 100 approx.

A description of the first type of peridermal regeneration in Graptoloidea has been given by Kraft (1926, pl. 12, fig. 1-3) illustrated in *Orthograptus gracilis*.

The second type of regeneration has not so far been described from the Graptoloidea. A monograptid sicula showing this (gen. et sp. indet.) is therefore worthy of note. The regenerative membrane is placed to the right of the virgella in the pore region (fig. 15). The free edge is provided with a thickened list. The damage inflicted, probably extensive, has been filled up by a structureless chitin membrane with a strongly wrinkled surface *(mr)*. In this case, though the damage was inflicted to the edge of the theca so that it could have been filled up by fusellar periderm, no such structure is discernible. Hence it may probably be referred to stronger disturbances responsible for damage to the zooid.

An example in *Pristiograptus* sp. (fig. 58 *C*) seems to be of similar nature. Here the regenerated area constitutes part of the metathecal wall imparting to it its abnormal shape. The regeneration periderm is also a structureless chitin membrane.

Besides examples of the regeneration and reconstruction of periderm, the regeneration of the nema is also frequently displayed by graptolites. It has been more closely investigated by Eisenack (1941). He has ascertained in *Climacograptus* frequent damage to the apex of the prosicula which also involves the destruction of the nema. Nevertheless, secondary fibres develop on the edges which by their fusion give rise to a secondary nema — the «Ersatznema» of Eisenack. In a particular case described by Eisenack, the regeneration nema was formed directly on the fuselli of the metasicula after the complete destruction of the prosicula. The development of the nema must have been associated with fairly extensive processes of regeneration.

An analogous occurrence has been described by Urbanek (1953) in the monograptid *Saetograptus chimaera* (Barr.). Here again the destruction of the initial nema was connected with the breaking off of the apical part of prosicula. The formation of the regeneration nema was preceded by the development of bands broader than the initial threads which were subsequently fused into a secondary nema. The foramen resulting from the destruction of the apex of the prosicula became later rimmed by a secondary thickening list (fig. 16). Urbanek stresses also the frequency of this process. He has noted it in 40 out of 43 specimens examined of *Saetograptus chimaera cervicornis*, and in 22 out of the 33 studied specimens of *Pristiograptus dubius*. In several specimens belonging to the latter species secondary sealing up of the prosicula foramen has been detected.

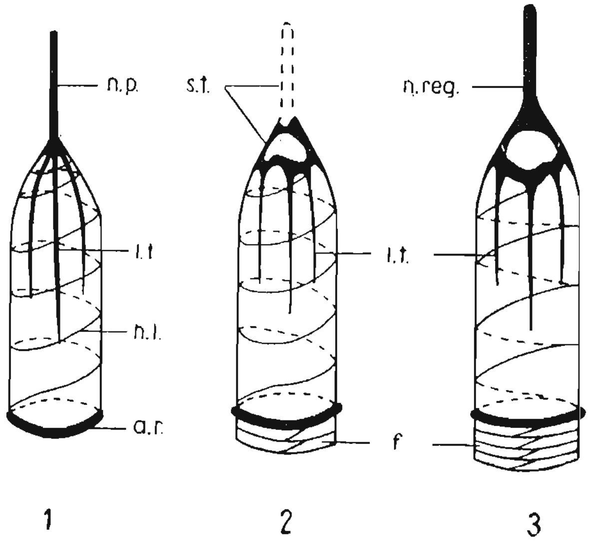

Fig. 16

Diagram showing mode of origin of regenerative nema in Monograptidae, *1-3* successive stages

n. p. primary nema, *l. t.* longitudinal threads, *h. l.* helicoidal line, *a. r.* apertural ring, *n. reg.* regenerative nema, *s. t.* secondary thickening, *f* fuselli.

The writer has recently noted a similar pattern of regeneration in *Monoclimacis haupti* (Kühne) (see fig. 59 *A-C*). Occasionally, an apical opening is already discernible in young prosiculae, subsequently rimmed by the thickening list. The list is later stretched out into a single fibre of the nema (fig. 61 *A-C*) without the fusion into one of the several initial fibres.

Present data indicate that both in diplograptids and monograptids the reconstruction of the nema is very frequent, so much so that most of the rhabdosomes have their own regeneration nemae. Even in old rhabdosomes of *Saetograptus chimaera* we may see that the apex of the prosicula is broken off with secondary fibres fusing above it into a regenerative nema. Hence, this type of construction of an organ of such vital significance for the entire colony must be recognized as normal and as the result of the normal course of some physiological process.

Causes responsible for the destruction of the apical portion of prosicula are rather puzzling. In addition to purely mechanical agents, such as water movements, Eisenack (1941) has suggested injuries by animals of prey or by the necrosis of tissues. But the frequency of this process suggests a more constant factor. Necrosis of tissues would be acceptable upon recognition of the partially necrotic character of oozooidal metamorphosis in the metazooid. As a result the tissues of the prosicula would after some time die out, the prosicula becoming a hollow chitinous tubule readily destructible. Nevertheless a conception of this kind does not fully clarify these phenomenons if it be remembered, that the sicula must have then been covered by an extrathecal membrane, made up of soft tissues. A search should, therefore, be made for causes directly responsible for the breaking off of the nema together with the extrathecal surrounding membrane. A study of the biological function of the nema may perhaps clear up these facts. A graptolite colony was probably suspended by the nema, attached as an epiplanktonic organism to floating algae. Since, therefore, the fate of the whole colony depended on a hairbreadth, i. e. on the strength of the nema, the graptolites tended to produce a nema that was neither too weak nor irreplaceable. The great regenerative ability of that organ is thus referable to its biological function. It seems that the majority of cases of the breaking off of the apex of prosicula and of the initial nema had occurred during the transition period of life of the graptolite colony, when it was changing its mode of life from a planktonic larva to an epiplanktonic graptolite colony. Being attached by the still weakly developed nema the young colony was greatly exposed to every kind of injury, much more so than in later stages when the nema thickened and became attached to the periderm not at one point only, viz. the apex of the prosicula, but along a large distance of the rhabdosome as well. It is most probable that the replacement of the initial nema by the secondary nema evolved gradually. At first it may have been an accessory structure but its great adaptive importance probably rendered it a normal developmental process in most epiplanktonic graptolites.

Our unsatisfactory knowledge of the biology of Recent Pterobranchia, nearest to graptolites, does not allow us to draw analogies between the regeneration processes in these two groups of animals. And yet Schepotieff (1906, 1907) mentions having observed many examples of the regeneration of the soft parts in *Rhabdopleura*, most particularly so of the pre-oral lobe and tentacles. Kozłowski (1948, p. 75) described the regeneration of the skeletal parts in recent *Rhabdopleura normani*. It is an illustration of the breaking off and regeneration of the zooidal tube, markedly resembling the fusellar regenerated structures in graptolites.

INTRASPECIFIC VARIATIONS

Monograptid species, so far closely investigated, display strong variations of many characters. Besides purely quantitative characters, such as the dimensions of rhabdosomes and thecae, extensive qualitative variation is also displayed. Those to be enumerated below are the shape of the apertural processes, which are excessively variable, as in *Saetograptus chimaera* and *Colonograptus colonus*, also the presence or absence and the number of peridermal rings on the metasicula and on the proximal thecae.

Specific identification is therefore difficult within the several genera. It appears that in many cases the variation range in different species fits in excellently with respect to many characters. Even in forms so widely different, as those of *Saetograptus chimaera* and *Pristiograptus dubius* it has been seen that the majority of quantitative indices of the sicula show markedly similar range of variation (Urbanek, 1953, p. 104, French text). The pattern is much the same in respect of the index of thecae within 10 mm in the proximal part of the rhabdosome. In *Saetograptus chimaera*, which is distinguished by a rather weak ventral curvature of the proximal part of the rhabdosome, rhabdosomes showing dorsal curvature may nevertheless be observed.

Some species display exceptionally strong variations. Among them is *Saetograptus chimaera* (Barr.) (see p. 56) which has, undoubtedly, been most closely studied from this point of view. Still we do not know whether the variation, occasionally sufficiently strong to denote several subspecific forms, is referable solely to extreme internal differentiation of population (sympatric variation) caused by the assembling of mutations within them, or to allopatric viz. geographical differentiation. Some geographically vicarious forms of so cosmopolitan a species as *Glossograptus quadrimucronatus* (= *Orthograptus quadrimucronatus* Hall) (see R. Ruedemann, 1919, p. 63; 1947, p. 452) might supply evidence for the conception that sympatric variation in graptolites could become allopatric variation. This species has evolved within the wide area of its distribution four vicarious forms. Two of these are recorded from

America, one from Scotland, and one from Australia. All these forms represent completely analogous though different morphological types. In each of them we note an extensive elongation of the apertural processes of a certain group of thecae, that group being, however, different in each of the geographical stocks. In some there are thecae 6-7 or 5-7, in others theca 10. If RUEDEMANN's observations were made correctly, this would be one of the most interesting examples of geographical variation, as ascertained from fossil material. Still it is beyond doubt that numerous local endemisms recorded in various graptolite faunas are referable to geographic variation. Some other, but similar examples of geographical variations in graptolites were discussed by BULMAN (1933 *b*, 1950).

But the marked intraspecific variation of graptolites ascertained on fossil material from erratic boulders cannot be interpreted as the expression of geographic variation (see p. 56). The fossil material is obtained from sediments of a relatively small area in the same sea basin. With the probable planktonic mode of life of these graptolites we cannot infer any isolation between the various populations of these organisms. Neither can we expect results of spatial isolation, expressed by the presence of so-called «clines», in view of the small area from which the material has been collected. The strong variation may have been here caused by certain other agents among which those relating to genetics and population mechanism did play some part. It seems probable that Silurian graptolites lived in markedly large populations, where the genetic effective size of population (N) was considerable. Genetic variation within one population increases accordingly to its size, hence we can note extensive variation within the several fossil populations.

Nevertheless, the «variation spectrum» in the several populations is by no means relatively homogeneous; on the contrary, we note a certain segregation of variations. Variants of one type predominate in certain boulders, those of another type — in others, occasionally their numbers may be uniform (see p. 57). If geographic variation is not taken into consideration for the reasons previously given, the causes will have to be looked for among historical changes of population structure. Subspecific forms such as varieties of *Saetograptus chimaera* are probably the expression of the «zonal evolution» of this species (see A.W. ROWE, 1899). Various morphological forms predominate in certain stages of specific evolution, constituting index forms among representatives of a given species at some definite moment of its history. It should therefore probably be possible to separate here, as in the case of many other fossil organisms, certain «sub-zones» within which the biometric characterization of one species would differ from that of its population within lower or higher horizons. Such forms are by F. A. SCHILDER (1952, p. 20) justly called «chronotypes» (Chronotypus) of the given species. They represent the position occupied by a species in time in the same way as vicarious subspecies do so with relation to space.

A verification of the conception here advanced is somewhat difficult. Information available concerning the occurrence of intraspecific monograptid forms is still very inadequate. If, however, it is accepted that erratic boulders may and probably actually are derived from different horizons of the same sedimentary series, it seems altogether reasonable to suppose that forms yielded by them are referable to various evolutionary stages of these species.

The most convincing evidence of the actual occurrence of such a process in graptolites is supplied by their widely distributed and relatively long-lived species. An example of marked interest is that provided by *Dictyonema flabelliforme* (EICHW.). A number of varieties have been separated within this species, such as var. *typica*, var. *sociale*, var. *norvegica*, var. *anglica* (KJERULF, BRÖGGER, BULMAN). These varieties are characteristic of clearly defined zones within a zone proper to that index fossil. For example, L. Størmer (1940, p. 162) has ascertained that at least the following four «sub-zones» may be differentiated within the Oslo region:

2e δ *Dictyonema flabelliforme anglica* Bulman
2e γ *D. flabelliforme norvegica* (Kjerulf)
2e β *D. flabelliforme* f. *typica* Brögger
2e α *D. flabelliforme sociale* (Salter)

We should thus have a «zonal evolution» of that very species. The several «chronotypes» differ slightly but quite distinctly in the number of dissepiments, their shape, the position of bithecae etc. Transitional forms between these varieties are observed.

A new and complete revision of the mentioned graptolite fauna (Bulman, 1954) permits a more detailed analysis of varieties in *Dictyonema flabelliforme* s. l. According to Bulman's authoritative opinion, the varietal forms are not restricted to a particular horizon, but may occur through the succession accompanied by particular «index» forms. These varieties show greater or lesser overlap, appear in underlying and persist to overlying zones, below and above their own horizons. Predominance of particular forms indicates and justifies, however, the establishment of the mentioned subzones. This character of time-distribution of intraspecific varieties in *Dictyonema flabelliforme* fully agrees with the here described distribution pattern for varieties of *Saetograptus chimaera* in erratic boulders.

This collective conception of the species *D. flabelliforme* has recently met with criticism on the part of Obut (1953, p. 39). In his opinion they may be held to constitute a group of species, independent though closely related and occupying a distinct stratigraphic position. He believes that regarding them as intraspecific varieties makes the investigation of their actual phylogenetic connections more difficult.

That author's standpoint does not, however, seem well grounded in view of the fact that a stratigraphic zone cannot be regarded as decisive for the specific rank of fossils. Zonal supremacy leading to the false theory of «horizonal influence» was subjected to criticism by F. A. Bather (1910, Quart. J. Geol. Soc., No. 66). In practice even stratigraphers, Elles, for example (1923, p. 89), are in favour of establishing a «species group» even in the case of index species[7]. Obut's objections are thus hardly acceptable even from a purely pragmatic point of view.

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[7] «Species group or gens may be considered to be the aggregate of all the species which possess in common large number of essential properties and are continuously related in space or time».

SYSTEMATIC PART

Family **MONOGRAPTIDAE** LAPWORTH, 1873

Subfamily MONOGRAPTINAE (LAPWORTH, 1873), YIN 1937

Genus **MONOGRAPTUS (MONOGRAPTUS)** GEINITZ, 1852

Monograptus (Monograptus) priodon (BRONN), 1834

(text-fig. 17-20; pl. I, fig. 1-2)

1834. *Lomatoceras priodon* BRONN; H. G. BRONN, Lethaea geognostica..., I, p. 56, pl. 1.
1932. *Monograptus priodon* (BRONN); O. M. B. BULMAN, On the Graptolites..., p. 10-11, pl. 1, fig. 1-11.
Further references:
1901-1918. G. L. ELLES & E. M. E. WOOD, British Graptolites, p. 418.
1948. A. PŘIBYL, Bibliographic Index..., p. 32.

Material. — This species has been prepared from one boulder only (S. 161, Jarosławiec). The specimens are most satisfactorily preserved, but few in number. They are: a prosicula, a young metasicula, two fragments of proximal part of rhabdosome, a distal part, detached thecae and apertural lobes.

Description. — Rhabdosome proximally straight, or somewhat curved dorsally.

Sicula (fig. 17 *A*, *B*) straight, with apex reaching second theca.

Prosicula (fig. 17 *A*) from 0.44 to 0.50 mm long, with a relatively blunt apex, diameter of aperture approx. 0.1 mm. Apertural ring of prosicula strongly expressed. Longitudinal threads well marked. No helical line visible in the examined specimens owing to poor state of preservation. The specimen of young metasicula (fig. 17 *B*) has the apex perforated and the opening rimmed by thickened lines later uniting into the nema. This is probably a regenerative nema.

The metasicula attains a length of 1.10 mm. The initial part of virgella with characteristic arrangement of fuselli (fig. 17 *B*) is well visible. No rings are discernible, probably owing to lack of older specimens. Aperture of metasicula nearly simple, dorsal lip very slightly expressed; diameter of aperture 0.29 mm, length of virgella 0.96 mm.

Thecae straight, without ventral curvature. Dorsal wall of metatheca stretched out into a strongly hooked lobe (fig. 18; pl. I, fig. 1-2). On the side of these lobes lateral processes are discernible which in this species were ascertained for the first time by BULMAN (1932, p. 11). The fusellar structure of the apertural lobe is analogous to this structure in the dorsal wall of metatheca. It consists of two series of fuselli (difusellar lobe). But the true zigzag suture is missing, as the fuselli are very long and wide, reaching almost to the margins of the lobe (fig. 18 *A*, *B*). Apertural lateral processes are symmetrically placed on both sides of the lobe.

The processes of proximal thecae of the rhabdosome are distinctly longer (approx. 0.22 mm in the first 6 thecae) than those on the distal thecae, where the process is approx. 0.07 or 0.08 mm long. Processes of proximal thecae produce a kind of apertural spine and display, as ascertained by the writer, a tubular structure. Hence, the spines here very closely approach those described in *Saetograptus* (fig. 19). Distally, however, the apertural processes are relatively short and ear-like, in which the broader base rests on the antero-lateral margin of theca (pl. I, fig. 1). The fusellar structure of processes in distal thecae is shown in fig. 20. The periderm there is as a rule very much thickened, hence the fuselli are not readily recognizable. Such a process has a monofusellar structure but it develops similarly e. g. as the virgella or the dorsal lip of metasicula, viz. by way of a local increase in the width of fuselli. Generally speaking, these processes come quite near to those in *Colonograptus*, differing only in the smaller degree of isolation of lateral lappets.

Taking into consideration these marked structural differences in proximal and lateral thecae, *M. (Monograptus) priodon* (Bronn) may be regarded as a species of the biform type.

In the proximal part of the rhabdosome the number of thecae in 10 mm is approx. 11-12, while Bulman states that in his specimens it is 12-13; 7.5 to 8 thecae fit in the first 5 mm of the proximal part.

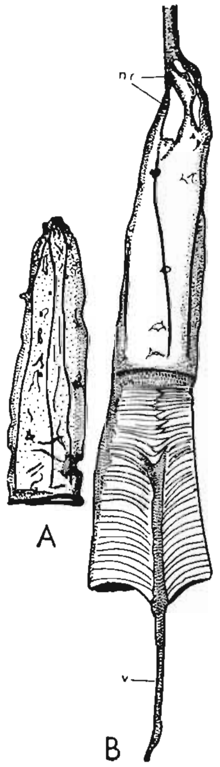


Fig. 17
Monograptus (Monograptus) priodon (Bronn)
A prosicula with longitudinal threads and appertural ring, *B* young sicula with regenerative bands visible (*nr*) and apertural ring. Details of the fusellar structure of virgella (*v*) (S. 161, Jarosławiec); × 80 approx.

Measurements (in mm):

a) Distance of ventral margins of lobes

Thecae	*Distance*	*Thecae*	*Distance*
1-2	0.49	5-6	0.65
2-3	0.49	6-7	0.72
3-4	0.57	7-8	0.76
4-5	0.60	8-9	0.80

b) Width, length and height of lobes

No. of theca	*Maximum width of lobe*	*Length of process*	*Height of rhabdosome with lobe*
1	0.44	0.22	0.73
3	0.66	0.22	0.95
6	0.80	0.22	1.10

The growing distance between thecae is probably connected with the decreasing overlapping of lobes.

The maximal width of apertural lobe, as measured on distal fragments of the rhabdosome, was ascertained to be 1.20 mm.

Faunal assemblage and stratigraphical distribution. — In the author's material, *M. (Monograptus) priodon* (Bronn) is encountered quite isolated, without accompanying fauna. More exact determination of the stratigraphic age of the boulder, from which it was recovered, is hardly possible. However, it probably fits into the distribution range recognized for this species, namely from Gala-Tarannon to the Lower Wenlock.

Systematic position. — Undoubtedly, this is one of the most abundant and most characteristic of all monograptids and its position as genotype for genus *Monograptus* is not incidental.

According to Elles & Wood (1901-1918, p. 420), this species makes its appearance during Gala-Tarannon within the *M. crispus* horizon, being initially less numerous than the related forms *M. marri* and *M. pandus*. Gradually, however, its number increased and it attained its maximal numerical development at the base of the Wenlockian where it is the most abundant of all graptolites. It persists, though in diminishing numbers, up to the *M. riccartonensis* horizon when it is replaced by *M. flemingi*, a species probably descended from it. It was thus a relatively long-lived form and examplifying a cosmopolitan species recorded from all the six continents (Bulman, 1955, p. 17). It must have, therefore, been a prosperous species which had reached its adaptive peak within its group, being an example of a relatively constant species. Elles (1922, p. 184) stresses most particularly its significance in the evolution of monograptids. In her opinion, this form descends from graptolites with a perfectly smooth aperture (*Pristiograptus* type), like *M. cyphus*, passing to the «priodon» type (comp. p. 22) through forms with gradually increasing apertural curvature, in the following succession: *M. cyphus*, *M. revolutus*, *M. difformis*, *M. argenteus*, *M. clingani*, *M. sedgwicki*, *M. marri*, *M. priodon*.

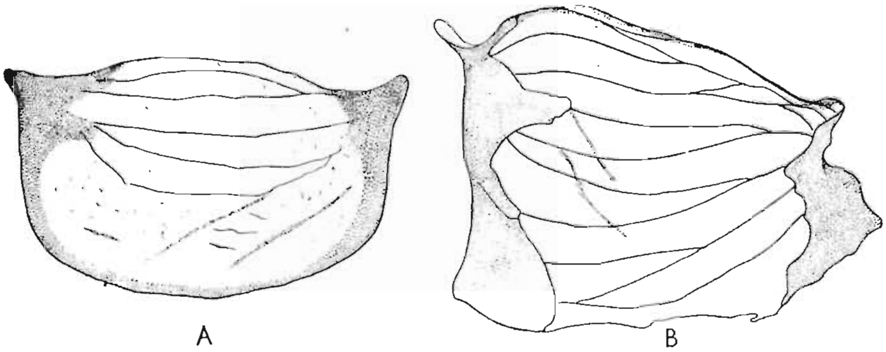


Fig. 18

Monograptus (Monograptus) priodon (BRONN)

Fusellar structure of apertural lobes: *A* outer, ventral view, *B* inside, dorsal view (S. 161, Jarosławiec); × 30 approx.

This group is believed to have attained the peak of its evolution («acme») at the «priodon» type. According to Elles (1922, p. 185) *M. (Monograptus) priodon* may be considered as an ancestor of the «retrogressive line», leading to simplified structure of processes and secondarily returning to the «hooked» form and even to a *Pristiograptus* type of aperture, namely: *M. priodon*, *M. flemingi* var. *compactus*, *M. colonus*, *M. tumescens*.

G. Elles' inferences are mostly based on forms known in a flattened condition only, hence they need supplementary studies to confirm this hypothesis. Material available to the present writer is insufficient to take up a discussion on the first, «progressive» stage of the evolutionary line leading up to *M. priodon*, though on the whole he believes the conceptions advanced by the eminent British author to be very sound. On the other hand, knowledge of the structure of *M. (Monograptus) priodon* and of Saetograptinae sheds light on the second evolutionary stage of this stock, called by Elles «retrogressive».

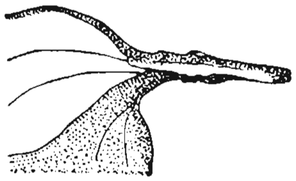


Fig. 19
Monograptus (Monograptus) priodon (Bronn)
Lateral process of proximal theca showing tubular structure, anterior view (S. 161, Jarosławiec); × 60 approx.

Arguments supporting the evolution from the apertural lobes of *M. priodon* to «hooked» typė processes, such as «colonus» or «chimaera», are quite sound. A confirmation of their further reduction, however, down to the pristiograptid form, need additional evidence. These arguments have been summed up in the chapter on comparative morphology (see p. 22).

These facts explain the morphology of *M. (Monograptus) priodon* Bronn. This might be the ancestral form of the subfamily Saetograptinae. The proximal processes in *M. priodon* are of the same type as those in *Saetograptus*. From this form, in the course of the reduction of lobes and partial reduction of distal lobe to a small ear-like processes, the typical «biform» *Saetograptus* may readily have descended. Thecal «biformism» in Saetograptinae would not thus be secondary, but on the contrary, primary, inherited from such early monograptid forms as «priodon».

Hence the proximal end of the rhabdosome in *Saetograptus* does not seem to constitute a progressively differentiated part in relation to *Colonograptus*, but rather to be a primary structure.

What relationship exists between *Colonograptus* and *Saetograptus?* May *M. (Monograptus) priodon* be regarded as their common ancestor?

In the writer's belief this is not a problem for actual solution. Arguments have been advanced (see p. 22) making *Colonograptus* and *Saetograptus* closely related. *M. (Monograptus) priodon*, however, has proximal processes of a more complicated nature than those of *Colonograptus*. Theoretically speaking two conceptions are reasonably admissible:

1) that two evolutionary lines have proceeded from *M. priodon*, both characterized by a reduction of the middle dorsal lobes, but one of them, the *Colonograptus*, being additionally associated with a secondary structural simplification of processes in the proximal thecae (diagram I);

2) the existence may be supposed of an initial form which had not been «biform» and had a «colonus» type of process and apertural lobes in all its thecae. Two lines may have descended from this form: one could have produced the initial tubular folding of processes in the proximal thecae *(M. (Monograptus) priodon)*, and simultaneously also a reduction of the dorsal lobes, the other line only a reduction of dorsal lobes *(Colonograptus)* (diagram II). Further observations are, however, required for a solution of this problem.

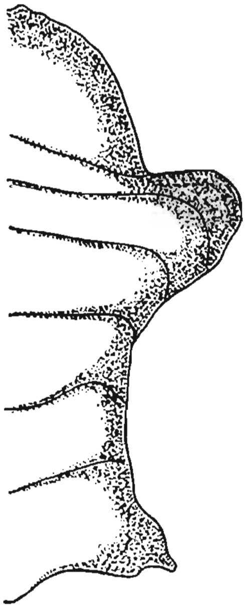
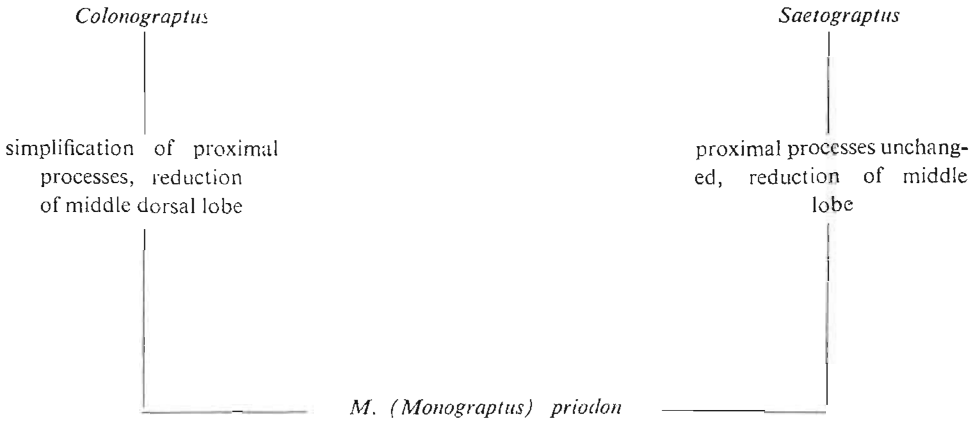


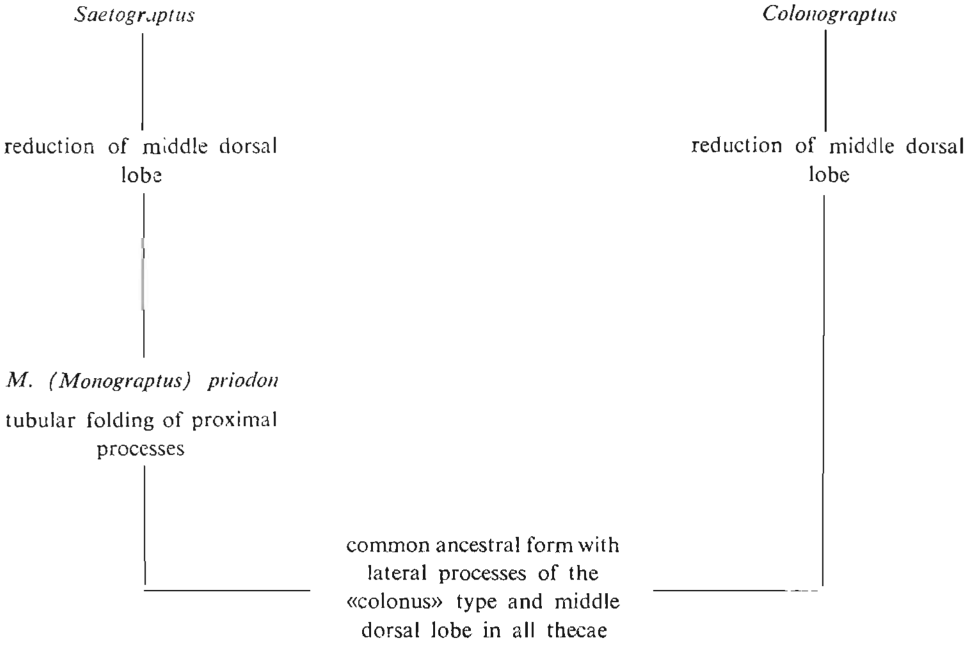
Fig. 20
Monograptus (Monograptus) priodon (Bronn)
Lateral process of distal theca, lateral view (S. 161, Jarosławiec); × 60 approx.

HYPOTHETICAL PHYLOGENETIC RELATIONS BETWEEN MONOGRAPTINAE AND SAETOGRAPTINAE

I.



II.



Monograptus (Monograptus) uncinatus TULLBERG, 1883

(text-fig. 21, 22; pl. I, fig. 3)

1883. *Monograptus uncinatus* TULLBERG; S. A. TULLBERG, Skånes Graptoliter, II, p. 30-31, pl. 1, fig. 24-25.
1911. *Monograptus uncinatus* cf. *orbatus* WOOD; G. L. ELLES & E. M. E. WOOD, British Graptolites, p. 427-428, fig. 290 a-b; pl. 43, fig. 1 a-d.

Material. — This species has been recovered from three erratic boulders: S. 38 (Jarosławiec) has yielded several proximal parts of rhabdosome, partly damaged; S. 19, 20 (Poznań) have each yielded several proximal parts (rhabdosomes with 4-5 thecae). The state of preservation is fairly satisfactory, although the specimens bear signs of slight mechanical damage they can be readily prepared.

Description. — Rhabdosome proximally straight. Sicula straight, 1.85-2.41 mm in length (two specimens), terminating below the protheca of the third theca.

Prosicula not closely investigated owing to lack of adequate material. Length of prosicula approx. 0.45 mm, aperture provided with distinct apertural ring.

Metasicula with rings, in most cases there are two and a bud ring. The latter frequently not completely closed and ramified. In one case, the bud ring only is present. Aperture with a blunt lip. Diameter of aperture in plane of symmetry from 0.22 to 0.26 mm, virgella strong, with an average length of 0.60 mm.

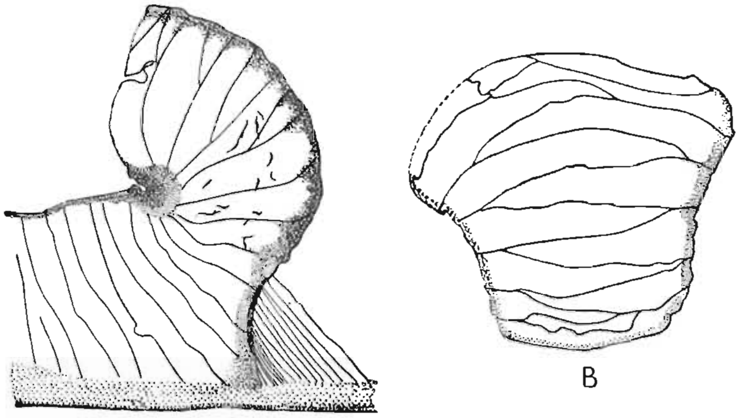


Fig. 21

Monograptus (Monograptus) uncinatus TULLB.
Fusellar structure of theca and apertural lobes: *A* lateral view, *B* top view (S. 38, Jarosławiec); × 100 approx.

Thecae straight, cylindrical, relatively short and high. In their basal part inclined at an angle of 45° to the long axis of the rhabdosome. First theca begins near aperture of metasicula. Dorsal wall of metatheca extends into a lobe ventrally curved as a kind of helmet resembling the apertural lobes in *M. (Monograptus) priodon* BRONN (hooked type of apertural lobe). These lobes, however, are without lateral processes, only their free lateral margins protrude somewhat. The free margin of lobes is in the form of a rather small, irregular brim (pl. I, fig. 3). These lobes are in nearly close contact with the ventral wall of thecae (markedly more so than in *M. (Monograptus) priodon*). There are no differences in the degree of curvature or they are unimportant between the proximal and the distal thecae. The fusellar structure of apertural lobes is completely analogous to that in *M. (Monograptus) priodon*. The fuselli are markedly high, they do not produce a zigzag suture but overlap nearly to the very margins of lobes (fig. 21). Antero-ventral fuselli converge into a kind of node. The periderm here is thickened and dark coloured (fig. 21 *A*, *B*).

It was possible to study the internal structure in microtome sections (fig. 22). The paramedial section shows the contour of apertural lobes and secondary thickenings on margins of apertures in prothecae, metathecae and metasiculae. They are in the shape of prominent lists. The bud ring of metasicula has the outline of a moderate list; it is developed on both sides of the wall of metasicula, on the inside as well as on the outside (see p. 16, 17).

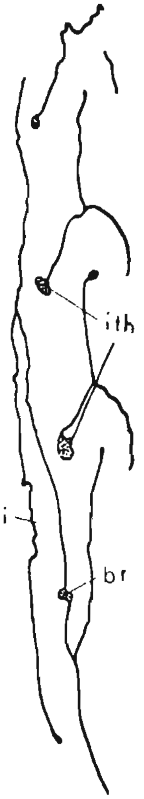


Fig. 22

Monograptus (Monograptus) uncinatus Tullb. Longitudinal microtome section of proximal part of rhabdosome, showing secondary roll-like thickenings corresponding to bud ring, free margin of interthecal septum and apertural margins (S. 38, Jarosławiec); × 30 approx.

ith thickening of interthecal septum, *si* sicula, *br* bud ring.

Measurements (in mm):

Thecae	*Width of apertural lobes*	*Height of rhabdosome with lobes*
1	0.57	0.76
3	0.80	0.91

Faunal assemblage and stratigraphical distribution. — In all boulders this species is found in association with a fauna typical for the Lower Ludlow, namely: *Pristiograptus dubius* (Suess), *P. bohemicus* (Barr.), *P. nilssoni* (Lapw.) and *Colonograptus colonus* (Barr.).

Tullberg also writes that this species occurs together with *M. nilssoni* and *M. dubius* within the lowest horizons of the «*Cardiola* skiffern» in Scania.

Systematic position. — *Monograptus uncinatus* Tullb. is probably a representative of the conservative, «bradytelic» line within the *Monograptus (Monograptus)* group. Together with the closely related and contemporary species *M. (Monograptus) unguiferus* Perner, it belongs to the last representatives of this subgenus which becomes extinct simultaneously during Lower Ludlow times. The evolutionary line represented by *M. (Monograptus) priodon* was a progressive («tachytelic») line, probably ancestral to the Saetograptinae. It became extinct rapidly being survived by the bradytelic *M. (Monograptus) uncinatus* line. This constitutes one more fact confirming the frequent occurrence of relative longevity of the bradytelic lines as compared with the tachytelic lines (comp. G. G. Simpson, 1944, p. 125-148). It is so probably because the tachytelic line, when already on its way to transformations, is either subject to rapid evolution or loses its adaptive equilibrium and becomes extinct.

Morphologically this species may be regarded as more primitive than *M. priodon*, as is also indicated by its apertural process, a simple lobe without lateral processes. *M. (Monograptus) unguiferus* Perner, a form very close to it, differs in the shape of the thecae with the apertures more closely spaced and with higher lobes. *M. (Monograptus) uncinatus* has been described by Tullberg from Scania. Elles & Wood (1901-1918) have described its variety from Wales under the name of *M. uncinatus* var. *orbatus*, and referring here as a second variety, *M. micropoma* (p. 425) described by Jaekel.

Bouček (1936, p. 20), however, has united into one species the type form *M. uncinatus* with its variety *micropoma* Wood, since both these forms, in his opinion, do not differ sufficiently to warrant their separation. The present writer, however, believes that the structure of thecae in *M. micropoma* Jaekel makes reasonable not only its specific separation but also its recognition as the representative of a distinct genus, viz. *Monoclimacis* Frech (see p. 95).

Subfamily SAETOGRAPTINAE n. subfam..

Genus COLONOGRAPTUS (Přibyl), 1942

Colonograptus colonus (Barr.), 1850

(text-fig. 23-25; pl. I, fig. 4, 5)

1850. *Graptolithus colonus* Barrande; J. Barrande, Graptolites de Bohême, p. 42, p. II, fig. 2-3 (non fig. 1, 4, 5).
1955. *Monograptus colonus* (Barrande); W. G. Kühne, Unterludlow-Graptolithen..., p. 370-372, fig. 5 A-B.
Further references:
1942. A. Přibyl, Revision der Pristiograpten..., p. 4-5, text-fig. 2, No. 1-34.

Material. — 1. Boulder S. 19 (Poznań): with few specimens mostly of proximal parts, in bad state of preservation, but with rich associated fauna. 2. Boulder S. 38 (Jarosławiec): with numerous specimens in satisfactory state of preservation, with occasional flattened examples. Several rhabdosomes with 5-8 thecae, a few with 10 thecae. A dozen or more proximal parts (with 2-4 thecae). Siculae numerous, but not sufficient to establish a complete astogeny. 3. Boulder S. 16 (Łebcz): with fragmentary proximal parts of the rhabdosome.

Description. — Rhabdosome proximally straight. Approx. 15 thecae in 10 mm at proximal part of the rhabdosome, of which 8-9 fit in the first 5 mm.

Sicula nearly straight or slightly curved ventrally (fig. 23 *A-C*, 24). Apex of prosicula terminating below third protheca. Length of sicula 1.40 to 1.52 mm.

Prosicula, measured in one specimen only, with length of 0.44 mm. Apex broken off and encircled by two secondary bands.

Metasicula, with aperture 0.19-0.34 mm in diameter, provided with a small rather pointed dorsal lip. Virgella moderately long, from 0.38 to 0.57 mm. Ringed and ringless forms (Urbanek, 1954, p. 303) occur within this species, both may be present in the same erratic, as for example in boulder S. 16 (Łebcz) (comp. fig. 17 on p. 304, Urbanek 1954).

The ringed form has usually 4 or 5 peridermal rings, the bud ring included. Frequently a branch of the bud ring extends into the interior of first theca as an incomplete thecal ring.

The ringless form is distinguished by complete lack of peridermal rings, the apertural ring of prosicula and the bud ring being also absent. In the studied material ringless forms are on the average slightly larger than the ringed forms. This observation, however, may hardly be generalized. Apertural diameter of metasicula in ringed forms is from 0.19 to 0.24 mm, that in ringless forms being 0.22 to 0.34 mm.

Colonograptus colonus belongs to the «biform» type, displaying considerable differences in structure of proximal and distal thecae. In this species, the first 4 thecae of the rhabdosome are to be regarded as proximal. These cylindrical thecae, without ventral curvature, have 2 lateral processes in the form of triangular lappets with monofusellar structure. The distal lappet wall is medially folded (fig. 25 *A*, *B*). Fuselli discernible on lateral walls are arcuate and widened, producing elevation. These fuselli become considerably thinner on the antero-ventral edge and converge into a sort of node, while on the postero-dorsal side they end at the free edge (fig. 25 *A*, *B*). In certain cases the proximal processes resemble those of *Saetograptus* (fig. 25 *C*, *D*). They are then curved downward and produce a kind of «knee», the postero-dorsal edge being occasionally slightly infolded, which further increases their resemblance to *Saetograptus*. These structures may be interpreted either as mutations analogous with the morphological type of *Saetograptus* (GOLDSCHMIDT's «systemic mutations»), or as anomalies. Secondary excrescences are sometimes to be noted on processes (text-pl. I, fig. 4 *a*, *b*).

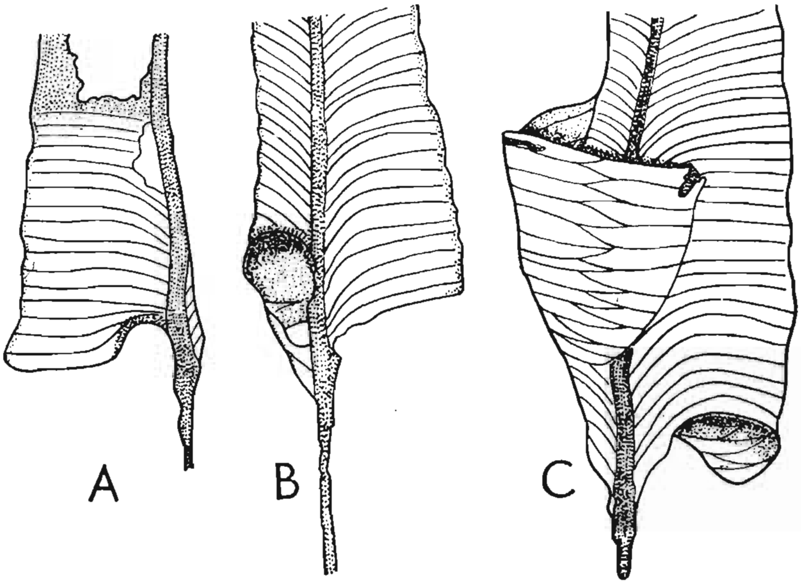


Fig. 23
Colonograptus colonus (BARR.)
Budding of 1st theca: *A* «sinus» stage, *B* «lacuna» stage, *C* prothecal segment of 1st theca (S. 38, Jarosławiec); × 70 approx.

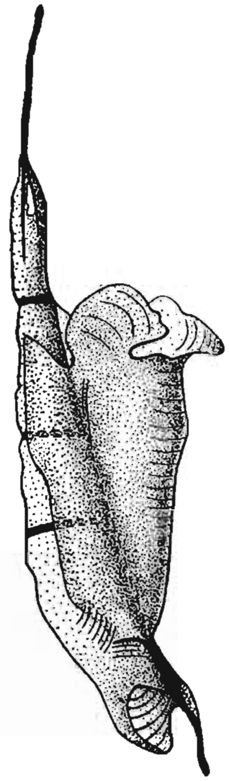


Fig. 24
Colonograptus colonus (BARR.)
Rhabdosome in 1st theca stage (S. 19, Poznań); × 37 approx.

Distal thecae have much shorter processes though essentially of the same type as in the proximal thecae. These processes are laterally directed and their side edge is not curved. They grow successively smaller, gradually becoming nearly obliterated, so that thecae 14-15, and the following, differ no more from those of the *Pristiograptus* type.

Within the proximal part the processes are also gradually reduced, however the difference between the first 4 thecae and the remaining ones is readily recognized.

Faunal assemblage and stratigraphical distribution. — Within the investigated boulders this form occurs in association with the following fauna: *Monograptus (Monograptus) uncinatus* TULLB., *Saetograptus chimaera* (BARR.), *Pristiograptus dubius* (SUESS). The first two species constitute an association typical of the Lower Ludlow.

According to Příbyl (1948, p. 80), *Colonograptus colonus* occurs in Bohemia within the *Pristiograptus nilssoni — Lobograptus scanicus* zones. It has been described from Europe and North America.

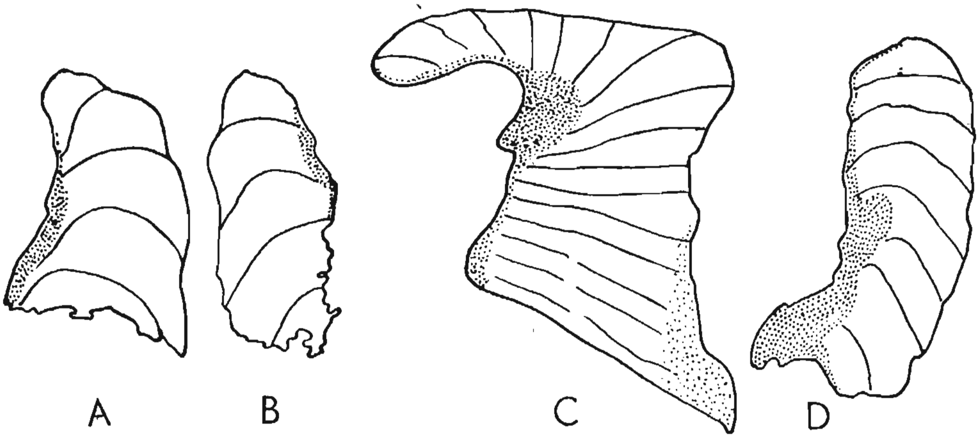


Fig. 25
Colonograptus colonus (Barr.)
Normal (*A, B*) and abnormal (*C, D*) fusellar structure of apertural lobes in proximal thecae;
A, C lateral view, *B, D* distal view (S. 19, Poznań); × 90 approx.

Measurements (in mm):

Thecae	*Distance between ventral margins of thecae*	*Thecae*	*Distance between ventral margins of thecae*
1-2	0.46	8-9	0.65
2-3	0.46	9-10	0.65
3-4	0.57	10-11	0.76
4-5	0.57	11-12	0.68
5-6	0.57	12-13	0.68
6-7	0.57	13-14	0.76
7-8	0.65	14-15	0.84

Thecae	*Width of rhabdosome (thecal aperture)*	*Thecae*	*Height of rhabdosome*
1	0.30	1	0.49
3	0.46	3	0.72
6	0.72	6	1.06
		12	1.37

Systematic position. — Wood (1900, p. 466) has described a British variety of this species, var. *compactus* Wood, characterized by a greater number of thecae (14-16) in 10 mm. The form here described is probably referable to this variety.

Together with the other closely related species this form occurs in the lowermost parts of the Ludlow, within the *Pristiograptus nilssoni — Lobograptus scanicus* zones, and belongs rather to the short-lived forms.

Colonograptus colonus (Barr.), together with other species of this genus, such as *C. roemeri*, *C. lochkovensis* and others, belongs to forms which, on their morphology, may reasonably be derived from certain *Monograptus (Monograptus)* species (comp. p. 10, 22, 46). The only open question is whether the apertural processes in *Colonograptus* have been formed by way of gradual accentuation of lateral processes in a mode analogous to that seen in *M. (Monograptus) priodon* (Bronn), or simply by separation of two rows of fuselli through disappearance of the oblique distal sutures within the apertural lobe of metatheca. If the latter supposition be accepted, processes of this type may be derived from such forms even as those of *M. (Monograptus) uncinatus* Tullb. The variety of processes manifested in large *Colonograptus* populations from the Lower Ludlow probably does not appear to have influenced the further evolution of this genus. It merely seems to be the expression of a phenomenon, asserted in other groups also (Simpson, 1944, p. 214-215), that variation often increases just before extinction: «The unfavorable environmental changes produce population attenuation and subdivision with small local groups adaptively unstable and prone to fixation of inadaptive mutations» (*l. c.*, p. 215). Moreover, this line after a relatively rapid period of prosperity very soon died out.

Genus **SAETOGRAPTUS** (Přibyl), 1942

Saetograptus chimaera (Barrande), 1850

(text-fig. 26-31; pl. II, fig. 1-4; pl. III, fig. 1-3; text-pl. II, III)

1850. *Graptolithus chimaera* Barrande; J. Barrande, Graptolites de Bohême, p. 52, pl. 4, fig. 34-35.
1953. *Pristiograptus (Saetograptus) chimaera cervicornis* Urb.; A. Urbanek, Sur deux espèces de Monograptidae, p. 278-284, fig. 1-7.
1953. *Monograptus chimaera* (Barr.); M. Walker, Development of *Monograptus dubius* and *M. chimaera*, p. 370-373, fig. 4-6.
1955. *Monograptus chimaera* (Barr.); W. G. Kühne, Unterludlow-Graptolithen, p. 372-379, fig. 6.
1956. *Pristiograptus (Saetograptus) chimaera chimaera* (Barr.); H. Tomczyk, Wenlock and Ludlow..., p. 55-56, pl. 8, 2, text-fig. 16 b.
Further references:
1942. A. Přibyl, Revision der Pristiograpten..., p. 12, text-fig. 3, No. 1-2.

Material. — Several dozen older rhabdosomes in excellent state of preservation, partly complete (with 10 to 25 thecae), numerous young rhabdosomes (1-2 thecae) and several tens of siculae in earliest stages of ontogeny. Periderm of specimens yielded by some boulders (Gdańsk-Wrzeszcz) is strongly carbonized and does not clear readily, while in specimens from other boulders (Jarosławiec, Łebcz) the fusellar structure is easily discernible even without clearing. This species was extracted from numerous boulders: Dziwnów (S. 54, 100, 104), Gdańsk-Wrzeszcz (S. 32), Jarosławiec (S. 36, 145, 146, 149), Lubin (S. 118), Łebcz (S. 16), Międzyzdroje (S. 141, 143), Pobierów (S. 115), Poznań (S. 19, 21), Rewal (S. 108, 110) and Władysławowo (S. 106, 111).

Description. — *S. chimaera* is doubtlessly one of the best known graptolites since it has been more than once thoroughly investigated on etched specimens in a satisfactory state of preservation (particularly so by Urbanek, 1953; Walker, 1953; Kühne, 1955). The description below is confined to a general statement of its morphology with particular stress laid on the problem unsettled in the papers here mentioned.

Rhabdosome straight, often, however, slightly curved ventrally. Sicula somewhat bent in adults with a mean length of 1.76 mm (from 1.28 to 2.04 mm), terminating below the third protheca. Prosicula with a mean length of 0.46 mm. In larger specimens the helical line poorly discernible. In majority of prosiculae the apex is damaged and the periderm is missing over a certain area. Regenerative nema is usually formed by fusion of 3 secondary strips.

Metasicula with virgella arising at a mean distance of 25 mm from aperture of prosicula. Aperture of metasicula with the greatest diameter 0.24 mm in length and with a relatively short and rather blunt dorsal lip. Number of peridermal rings on metasicula varies from 3 to 5. The occurrence is sometimes noted of forms either ringless or with two rings only, namely the apertural ring in the prosicula and the bud ring.

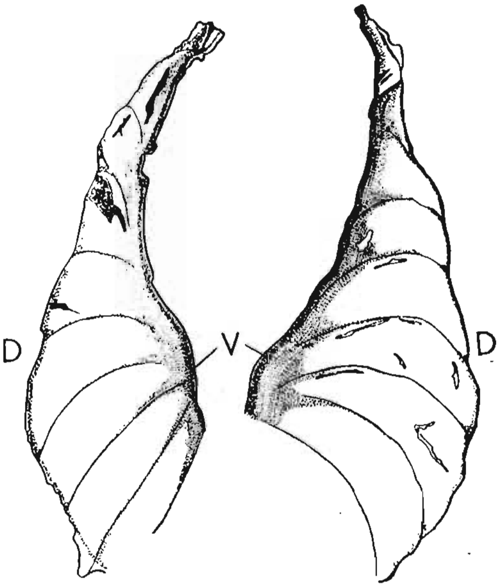


Fig. 26
Saetograptus chimaera (Barr.)
Fusellar structure of apertural process in proximal theca: *V* ventral border, *D* distal border (S. 54, Dziwnów); × 133 approx.

Thecae cylindrical, with sub-elliptical aperture. Th 1 with mean transverse diameter length of 0.24 mm, that of the longitudinal diameter being 0.28 mm, viz. ratio 0.86. During the astogeny a fairly constant aperture develops, proper to all distal thecae, with transverse axis growing longer (in 10th theca transverse axis 0.9 mm, longitudinal axis 0.65, 1.4 ratio) (for more detailed data see Urbanek, 1953, p. 293).

Aperture provided with paired lateral apertural processes displaying monofusellar structure (see fig. 26). In its basal region the process resembles those of *Colonograptus* and its ontogeny is analogous too (fig. 27), while the terminal portion elongates into a spine with the antero-ventral and the postero-dorsal edges folded together into a tube. During astogeny the shape of the processes changes. The processes of the first 3 thecae are mostly arched and frequently provided with supplementary elements (such as small lobes on the free edge); the next are shorter and more straight, finally thecae 8-10 have rather small blunt processes, directed postero-laterally (pl. III, fig. 1).

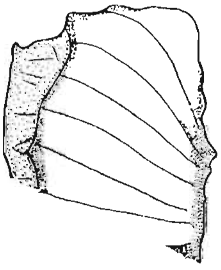


Fig. 27
Saetograptus chimaera (Barr.)
Early stage of formation of apertural process (S. 54, Dziwnów); × 100 approx.

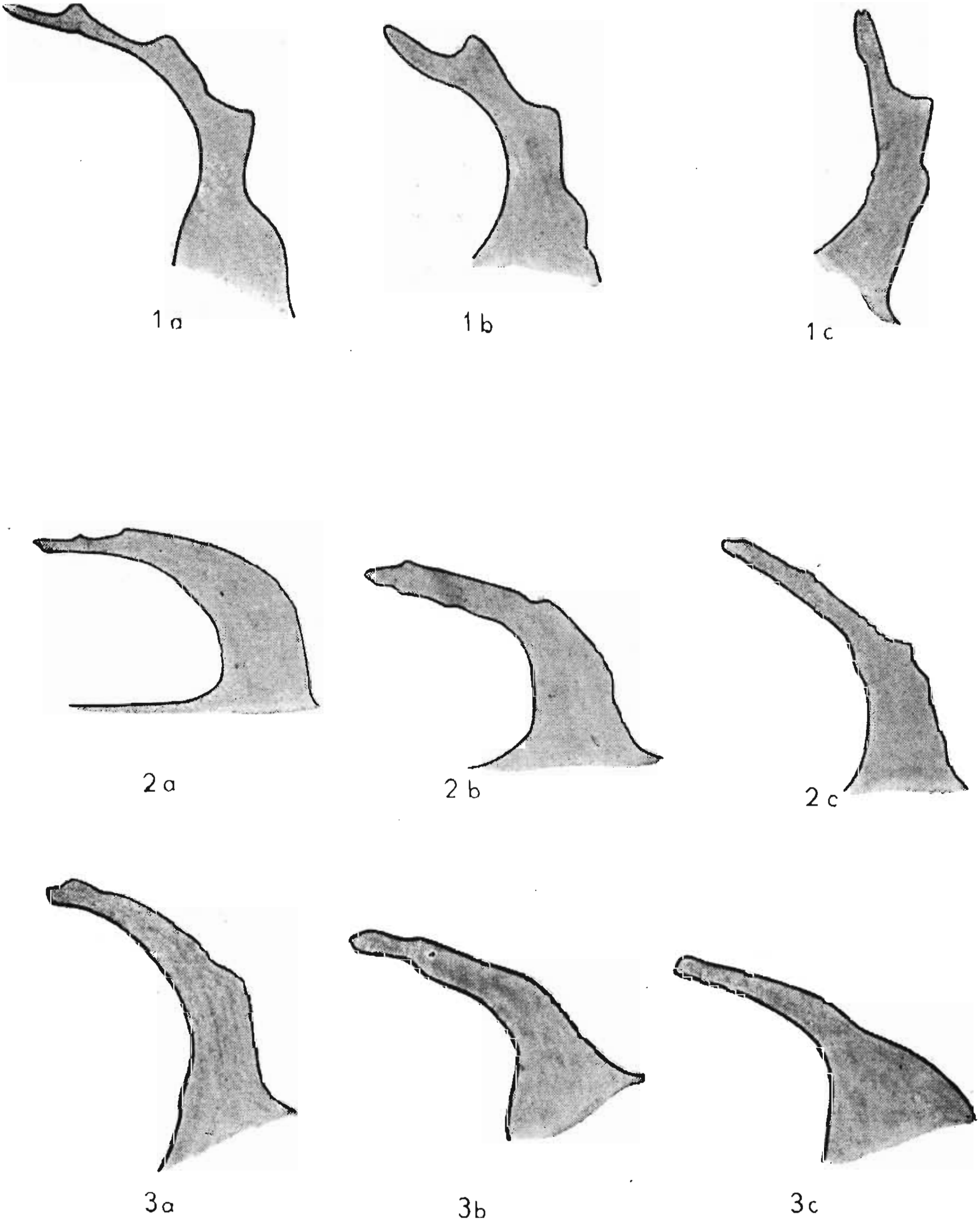
This type of apertural process was first described by Münch as «Röhrenstachel», in the case of a form incorrectly assigned by him to *M. colonus* (Münch, 1938, p. 48).

In 1953 the writer ascertained that a similar though still more intricate structure is shown by a form of *Saetograptus chimaera* which he separated under the name of *S. chimaera cervicornis* Urb.

Variation of apertural processes. — After a detailed study of the structural variations of apertural processes within *Saetograptus chimaera* (Barr.) the writer has now come to the conclusion that there may be differentiated several morphological types of apertural processes within this species. They may probably be regarded as expressions of strong intraspecific variation. These types are as follows:

1) with relatively short process whose postero-dorsal edge is not lobed. Tentatively

TEXT-PLATE II



Variation of apertural processes of first three thecae

Fig. 1. *Saetograptus chimaera cervicornis* (S. 36, Jarosławiec); × 105 approx.
Fig. 2. *S. chimaera chimaera* (S. 143, Międzyzdroje); × 105 approx.
Fig. 3. *S. chimaera chimaera* (S. 32, Gdańsk-Wrzeszcz); × 105 approx.

the writer regards this process as suitable for the typical form of *Saetograptus chimaera chimaera*[8] (text-pl. II, fig. 2 *a-c*, 3 *a-c*);

2) with process showing the same mean length but the postero-dorsal edge usually separated into 3 small lobes or denticles (the lobate-tubular type; URBANEK 1953, p. 281, fig. 4; text-pl. II, fig. 1 *a-c* in present paper). This type is characteristic of *Saetograptus chimaera cervicornis* URB. Denticles on the paramedian edge of apertural processes in *S. chimaera cervicornis* may be the result of a rather small genetic change, analogically to mutation of wings in *Drosophila*, described by R. GOLDSCHMIDT (1937) as «scalloped» abnormality. In both cases modification of shape seems to be connected with reduction of chitinous substance on the edges of these organs (*fide* G. S. CARTER, 1954, p. 84);

3) with markedly longer «hair-like» process whose postero-dorsal edge is not lobed. This type is characteristic of a variety probably identical with *Saetograptus chimaera salweyi* (HOPKINSON) (fig. 26 *A-B*; text-pl. I, 2 *b*).

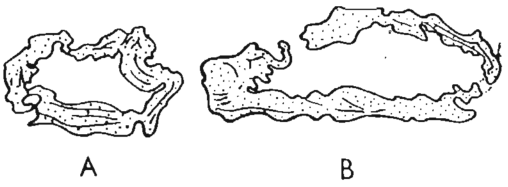


Fig. 28

Saetograptus chimaera (BARR.)

Transverse sections of terminal portion of apertural processes of 3rd theca (S. 36, Jarosławiec); × 625 approx.

A common feature of all these processes is that they are folded into a tubule. This may be established not only by observation of specimens in reflected light, but also on their microtome cross sections (comp. fig. 28).

The three types of processes here differentiated grade into each other showing an abundance of passage forms, this being on the whole a characteristic feature of intraspecific variations. Nevertheless, the extreme variants differ so much that neglect to separate them would mean inadequate knowledge as regards the extensive variability of this interesting species.

Intraspecific variations. — A certain number of varieties has been distinguished in this species. They are: *Saetograptus chimaera chimaera* (BARR.), *S. chimaera cervicornis* URB., *S. chimaera salweyi* (HOPK.), *S. chimaera semispinosus* (ELLES & WOOD).

This seems to suggest considerable intraspecific differentiation, supposedly analogous to «zonal evolution» in Upper Cretaceous *Micraster*, ascertained by ROWE (1899), or in the Liassic *Gryphaea* (TRUEMAN, 1922). Naturally, full confirmation of this hypothesis needs to be searched for in careful analysis of the material collected from all stratigraphical horizons. Since this procedure was impossible with isolated boulders, the writer wishes to advance some arguments which indirectly support the above interpretation.

It has been ascertained that the fossil populations, thanatocoenoses, yielded by particular erratic boulders, display a varying number of particular patterns — the differences being mainly in the processes — with the frequent predominance of one type.

The processes show strong variation and a number of their variable structural characters is listed below:

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[8] The definition of this form as *S. chimaera chimaera* may be contested on formal grounds, since we do not actually know what was the structure of processes in specimens which led BARRANDE to this specific diagnosis. Owing to the state of preservation of BARRANDE's specimens this question may be considered as permanently open, therefore the writer thinks it reasonable to accept the above stated solution.

1) nearly straight
2) curved
3) nearly touching the ventral wall of rhabdosome
4) curved laterally
5) laterally straight
6) not lobed
7) tri-lobed
8) with less than three lobes
9) strongly folded into a tube
10) weakly folded into a tube
11) bases of processes well separated
12) ,, ,, ,, closely set
13) ,, ,, ,, fused together

This is the qualitative aspect only of the features, but to a certain extent sufficiently characterizing the strong variability of processes. It presents a mosaic pattern, i. e. the particular features are not strictly correlated, though characters nos. 7, 2, 4, and 11 mostly occur associated. The other features show no such correlation, this also being a frequent feature of intraspecific variation.

The following are short morphological characteristics of some of these populations from particular boulders:

1) S. 36 (Jarosławiec) — with practically all rhabdosomes showing moderate or strong anterior and lateral curvature of processes. All forms with at least three lobes, bases of processes well separated — in all about 40 rhabdosomes;

2) S. 32 (Gdańsk-Wrzeszcz) — as in boulder S. 36, there are forms of the *cervicornis* type, with non-lobed processes or with poorly developed lobes *(chimaera chimaera)* — in all about 30 rhabdosomes;

3) S. 145 (Jarosławiec) — besides forms recognized as *chimaera cervicornis* and *chimaera chimaera*, forms with long hair-like processes probably the variety *salweyi*;

4) S. 34 (Dziwnów) — a predominance of forms with rather long and straight processes, approaching the «salweyi» type. Forms of the «cervicornis» type are present as an unimportant element (3-4) (in a score or so of rhabdosomes).

The remaining populations more or less approach one of the 4 types mentioned.

This striking polymorphic variability of *S. chimaera* (Barr.) may, in the writer's opinion, be referred to «zonal evolution».

It is true that variations in the morphological composition of populations may be regarded as the expression of geographical variations. Such a supposition, however, does not seem likely. The considered erratic boulders all come from localities within a relatively small area, where there can be no question of geographical differentiation of planktonic organisms. «Zonal evolution» seems to be the most reasonable explanation. It is nevertheless difficult — in spite of apparently precise stratigraphical evidence[9] — to determine the sequence of the particular varieties of *S. chimaera* (Barr.). Material yielded by erratic boulders may supply evidence for discussing such problems, but not, however, for their solution.

Varieties of Saetograptus chimaera and the problem of senile forms. — Urbanek (1953) separated *S. chimaera cervicornis* as a distinct sub-species differing from the type forms first of all in:

1) the greater distance of the beginning of the first theca from the aperture of the metasicula;

2) the different number of thecae in 10 mm, and in the maximum dimensions. The structure of processes was stated as barely comparable, due to the lack of corresponding

---

[9] Should we be in a position to advance a conception such as that of Jaeger (1955, p. 424, fig. 4), giving a full account with regard to the occurrence in Thüringia of Upper Silurian graptolites, we might then come nearer to a solution of this problem. That author, however, treats the species of *S. chimaera* collectively.

data (shaly material). Kühne (1955, p. 373-379) investigated a number of morphological details in *S. chimaera* and made the following remarks: «...mache ich folgende Beobachtung: während des Theka 1-und 2-Stadiums sind alle vorhandenen Dornen cervicorn. Beim Theka 3-Stadium sind die meisten Dornen cervicorn. Je älter das Rhabdosom ist, um so weniger cervicorne Dornen finden sich, obwohl auch noch ein Theka 10-Stadium mit drei cervicornen Dornenpaaren vorliegt ...cervicorne Dornen... mit zunehmenden Alter des Rhabdosoms seltener werden und die Tendenz haben zu verschwinden. Mit anderen Worten: cervicorne Dornen der drei proximalen Theken sind ein Jugendmerkmal von *M. chimaera*» (p. 376).

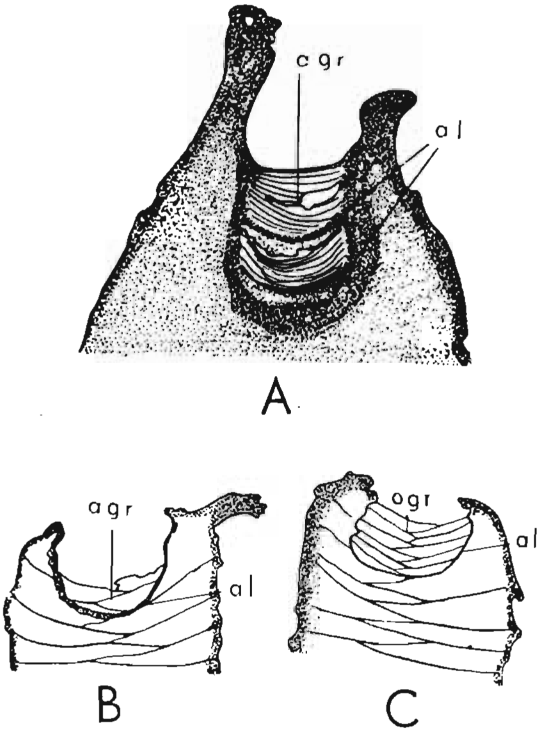


Fig. 29

Saetograptus chimaera (Barr.)

A — Dorsal wall of metatheca showing secondary growth of periderm (S. 31, Gdańsk-Wrzeszcz); × 100 approx.

B, C — Dorsal walls of metatheca in marginal region showing secondary growth, rhabdosome in 1st theca stage (S. 16, Łebcz); × 70 approx.

al older apertural levels, *agr* additional growth.

The disappearance of lobes in processes of *S. chimaera* is associated by Kühne with the secondary growth of peridermal material between the processes so as to produce a shield or dome (Haube) of the fused apertural processes. As indirect support of his opinion Kühne called attention to the fact that the majority of long old rhabdosomes are provided with fused processes in their proximal parts.

The writer's observations confirm Kühne's view in this. Pl. II, fig. 1 and pl. III, fig. 2 show old rhabdosomes or proximal parts of rhabdosomes provided with characteristic senile processes.

Kühne's arguments, however, lacked direct evidence confirming that the secondary «shield» proceeded from the fusion of lateral processes, not being so «ab origine». The present writer has been able to assemble fairly abundant material in this respect (fig. 29 *A-C*), which provides evidence that in the distal wall of metatheca secondary growth produces fusion of both processes. Fig. 29 *A* shows the distal wall of the first theca in an old rhabdosome, made transparent by strong clearing. It can be seen that the aperture of the younger zooid, marked by darker peridermal thickening, had been situated lower down, having been later elevated. Between the processes a wall has developed consisting of numerous narrow fuselli.

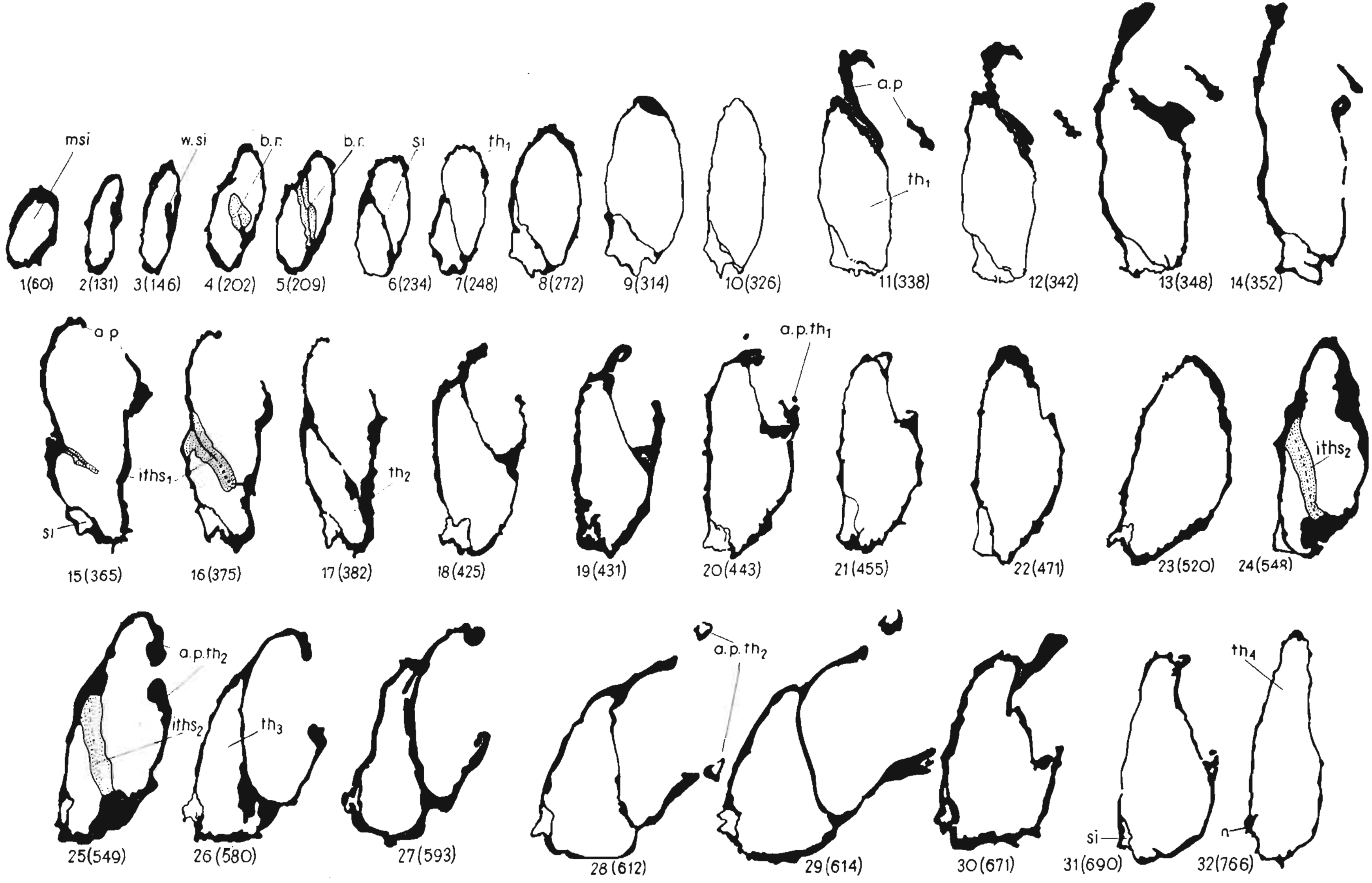
Saetograptus chimaera cervicornis Urb.

Serial transverse microtome sections of proximal part of rhabdosome; numbers in parenthesis correspond to actual numbers of sections cut at 3μ (S. 36, Jarosławiec); × 70 approx.

msi metasicula, *w. si* wall of sicula in region of 1st bud, *b. r.* bud ring, *si* sicula, th_1-th_3 numbers of thecae, *a. p*, apertural processes, $iths_1$-$iths_2$ successive numbers of interthecal septum, *a. p.* th_2 apertural processes of 2nd theca, *n* nema.

TEXT-PLATE III

(explanations on the left page)



A darkened line is discernible medially on the secondary wall, probably indicating the level at which the aperture had been temporarily situated.

Furthermore, the writer has succeeded in collecting material proving that the secondary formation of dorsal wall was not necessarily limited to later astogenetic stages. On the contrary, they may start very early. Fig. 29 *B*, *C*, for example, illustrate the presence of secondary distal wall as early as during the first or second thecal stage, which means that the portion rimmed by remnants of the original aperture is filled by an independent fusellar system. This may suggest that some thecae acquire shield-like process at an earlier stage than others. Perhaps this feature is to be associated with thecae which have closely set processes.

While agreeing with Kühne's conception regarding the occurrence of secondary growth in metatheca, the writer cannot accept some of his inferences. Kühne believes that the presence of lobed processes («cervicornis» type) is a juvenile character in the proximal thecae which is common to all representatives of this species. In connection with what has been said above regarding the variability of processes, the opinion of Kühne cannot be accepted. During development various processes realize common senile characters yet they are different at their beginning and this fact must form the basis for interpreting intraspecific differentiation in *S. chimaera* (Barr.).

Hence, though agreeing, naturally, with Kühne's statement that «Urbanek's und mein Material artlich identisch sind und zu *M. chimaera* gehören» [10] (p. 378), the writer wishes to lay stress on the eminently polytypical nature of this species by separating several morphological types. He believes that the particular intraspecific varieties are quite distinctly expressed.

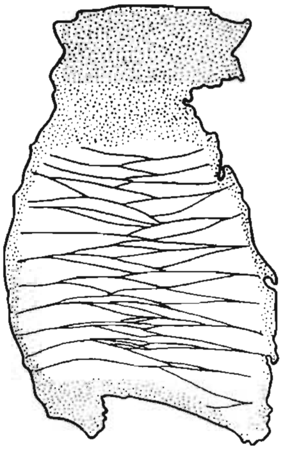


Fig. 30
Saetograptus chimaera (Barr.)
Fusellar structure of interthecal septum of proximal theca (S. 36, Jaroslawiec); × 40 approx.

Structure of dorsal wall of metatheca. — This interesting problem was analyzed by Walker (1953, p. 372-373, fig. 6 *A-C*). She noted that in *Pristiograptus dubius* (Suess) this wall, when passing into the metatheca of the next theca, displayed short interdigitate fuselli between the normal fuselli with the ventral zigzag suture. According to her view, these had been formed by the adjacent zooid. The interthecal septum would in this case be the product of both neighbouring zooids. However, in *Saetograptus chimaera*, Walker noted: «...in *chimaera* the change over along the septum occurs at a definite place, with no interdigitation as there is in *dubius*» (1953, p. 373).

The material investigated (fig. 30; fig. 31, *A-D*) represents the «interthecal septum» of the first 4 thecae of the rhabdosome in *Saetograptus chimaera* (Barr.). Here also we are dealing with fusellar «interdigitation»; in this respect this species does not differ from *Pristiograptus dubius*. Walker's observations would then only indicate the strong variability of this structure. A discussion of her interpretation of fusellar interdigitation is given on p. 20, 21.

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[10] Kühne stresses Urbanek's statement (1953, p. 100 of French text) that *S. chimaera cervicornis* has the pore rather distant from the aperture of the metasicula (0,78 mm). From measurement on Urbanek's figures 1-3, Kühne's result was only from 0.1 to 0.2 mm. Measurement methods may be partly responsible for the differences here, since the present writer's measurements were executed on transparent specimens, beginning from lower margin of the pore, while Kühne measured from the outside, and partly because our figure was the mean from 39 measurements. Naturally, these relations may vary in various forms.

Internal structure. — The internal structure of the rhabdosome in this species has been studied on microtome transverse sections. Text-pl. III, 1-2 shows a section of the metasicula passing between the pore and the aperture; sections 3-5 show the pore region with a distinct bud ring marked by peridermal thickening on both sides of the periderm. The next sections (6-10) are cut at several different levels of the first theca and of the sicula, the diameter of the latter decreasing continuously. Sections 11 and 12 cross the apertural region; the basal end of the left process and the thickened ventral margin of the aperture are discernible. Section 14 passes above the ventral margin of the theca, showing a transverse section of the right process and its tubular nature. Sections 15-17 provide a picture of the processes and of the interthecal septum; section 18 is that of the apertural region of the second theca, while the next sections cut the theca and its processes at different levels of the second theca. Section 24 shows the second metatheca and the third protheca with the thickened margin of the interthecal septum. The diameter of the sicula becomes markedly small, since in *Saetograptus chimaera* it terminated at the level of the third theca. Sections 28-30 are cut through the apertural region of the third theca. Cross sections of the basal and terminal margins of the processes are very distinctly seen. The latter show their tubular structure. Section 31 passes above the aperture of the third theca. Section 32 represents already the fourth theca. A thickening of the periderm corresponds to the nema on the dorsal wall.

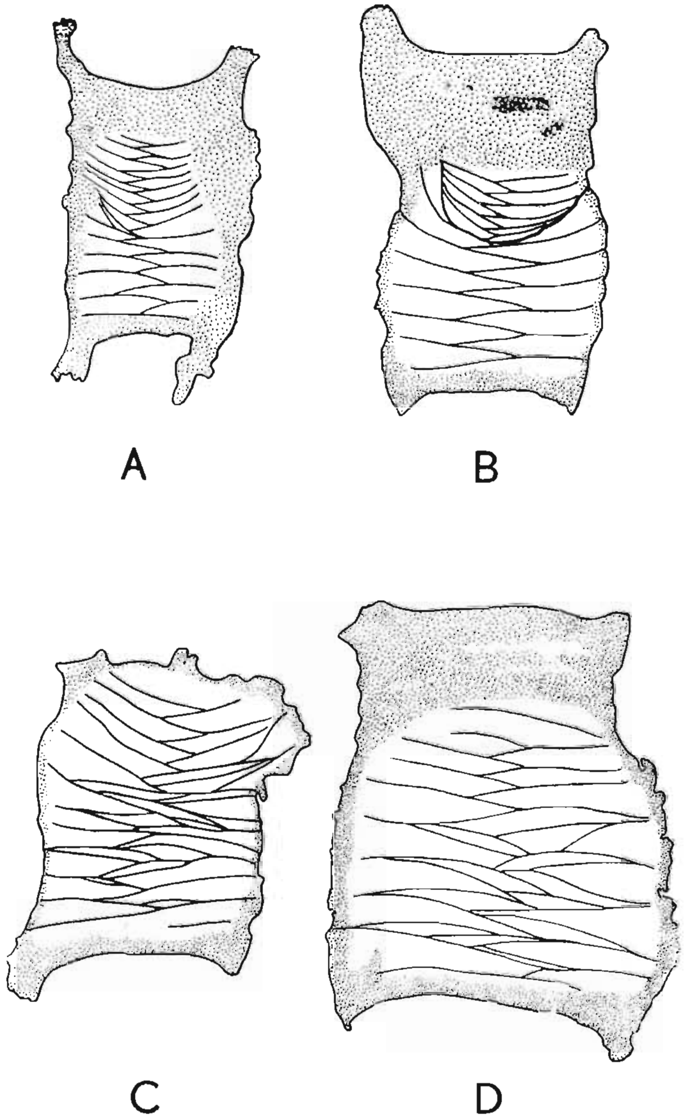


Fig. 31

Saetograptus chimaera (Barr.)

Fusellar structure of interthecal septum in four first thecae *A-D* (S. 36, Jarosławiec); × 50 approx.

Faunal assemblage and stratigraphical distribution. — This is the most common graptolite in faunas from erratic boulders. It occurs most frequently in association with: *Colonograptus colonus* (Barr.), *Cucullograptus pazdroi* Urb., *Lobograptus scanicus* (Tullb.), *Pristiograptus bohemicus* (Barr.), *Pristiograptus nilssoni* (Lapw.), *Pristiograptus dubius* (Suess), *Spinograptus spinosus* (WOOD), *Holoretiolites mancki* MÜNCH. Hence, it may be regarded as a form very characteristic of the Lower Ludlow.

Systematic position. — This typical species of *Saetograptus* has retained in the structure of its processes some traces of its descent from the Monograptinae. These processes are traceable back to the structure of the apertural lobes in *Monograptus (Monograptus)* (comp. p. 46). A fact of some interest is that the strong variability of apertural processes occasionally produces results analogous to processes in *Colonograptus*. Perhaps these are expressions of «analogous mutations» within related forms, and it may be that by way of such mutations *Saetograptus* was derived from *Colonograptus*.

It should be recalled that the tubular type of apertural process is a peculiar feature common to all forms of *Saetograptus*. Their specific differentiation, on the other hand, is expressed by differences of shape, number of the proximal type of thecae, presence of small side petals on the processes etc. Owing to considerable differences in the thecal structure of the proximal and distal parts, this genus must be regarded as «biform».

Subfamily CUCULLOGRAPTINAE n. subfam.

Genus **CUCULLOGRAPTUS** URBANEK, 1954

Cucullograptus pazdroi URB., 1954

(text-fig. 32-35; pl. IV, fig. 4; text-pl. IV-VI)

1889. *Pomatograptus becki* (BARRANDE); O. JAEKEL, Über das Alter..., p. 683-684, pl. 29, fig. 7-9.
1938. *Monograptus* sp.; O. M. B. BULMAN, Graptolithina, p. 31, fig. 20-c.
1954. *Cucullograptus pazdroi* URBANEK; A. URBANEK, Some observations..., p. 292-297, fig. 1-8.
1955. *Monograptus eunebeni* KÜHNE; W. G. KÜHNE, Unterludlow-Graptolithen..., p. 386-389, fig. 11-12.

Material. — From boulder S. 32 (Gdańsk-Wrzeszcz). Medial parts of rhabdosome most abundant, some specimens of distal margin, one specimen of sicula with first theca. State of preservation satisfactory, deformations unimportant. There is no specimen containing both the proximal and distal parts of rhabdosome.

Description. — Rhabdosome straight, after KÜHNE, up to and over 60 mm in length. About 8 thecae in 10 cm (KÜHNE, 1955, p. 388).

Sicula 1.05 mm long, straight, extending to approx. 2/3 of first theca.

Prosicula without distinct apertural ring.

Metasicula slightly curved ventrally in the pore region. Aperture with the longer diameter 0.12 mm and a short, hardly discernible lip. No peridermal rings.

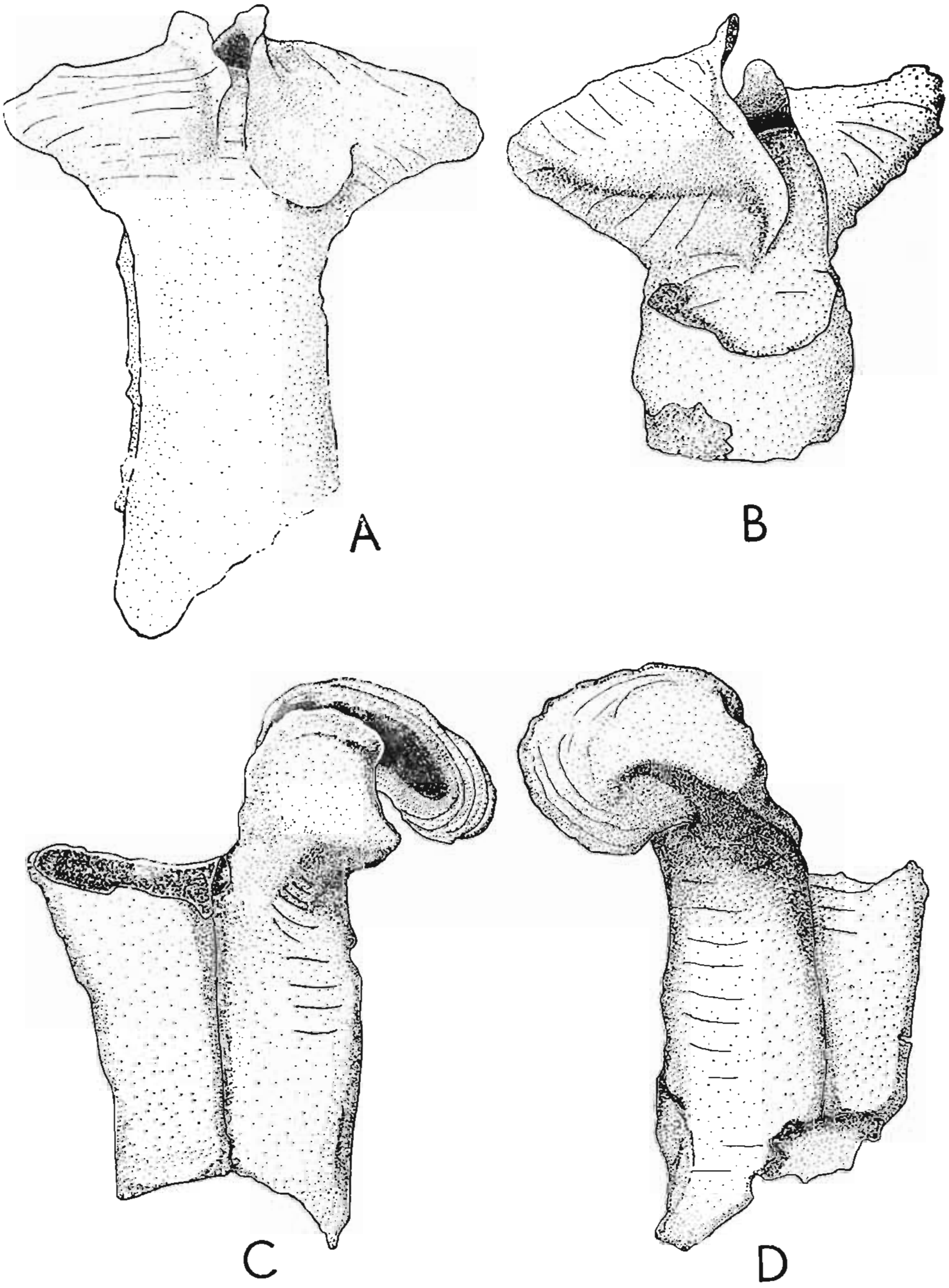
Proximal thecae are straight and long tubes. The distal ones much shorter and with ventral curvature. The slit-like aperture with peculiar apertural processes forming 2 asymmetric lateral hood-like lobes (fig. 32 *A-C*, 33 *A-C*, 34 *A-B*; text-pl. IV).

Left lobe much larger and extending perpendicularly to the longer rhabdosome axis. Free edge of the lobe with margin distinctly bent upwards like a brim (fig. 33, 34; text-pl. IV).

Right lobe markedly smaller, with a more symmetrical structure.

A study of the minute structure of the lobes on cleared specimens and on microtome sections has led to a complete reconstruction of their fusellar structure. The left lobe consists

TEXT-PLATE IV



Cucullograptus pazdroi URB.

Metatheca of a distal theca with apertural lobes: *A* ventral view, *B* dorsal view, *C* right side view, *D* left side view (S. 32, Gdańsk-Wrzeszcz); × 125 approx.

of a prolongation of the left series of the metathecal fuselli, disposed arcuately and transversely to the longer apertural axis. Ventrally the fuselli are attached to the apertural node and in passing to the dorsal part they fuse with the dorsal wall of the metatheca at some distance from its margin. Medially they form a protuberance (fig. 32 *A-C*). The spade-like ventral widening is only a fusellar outgrowth of this process.

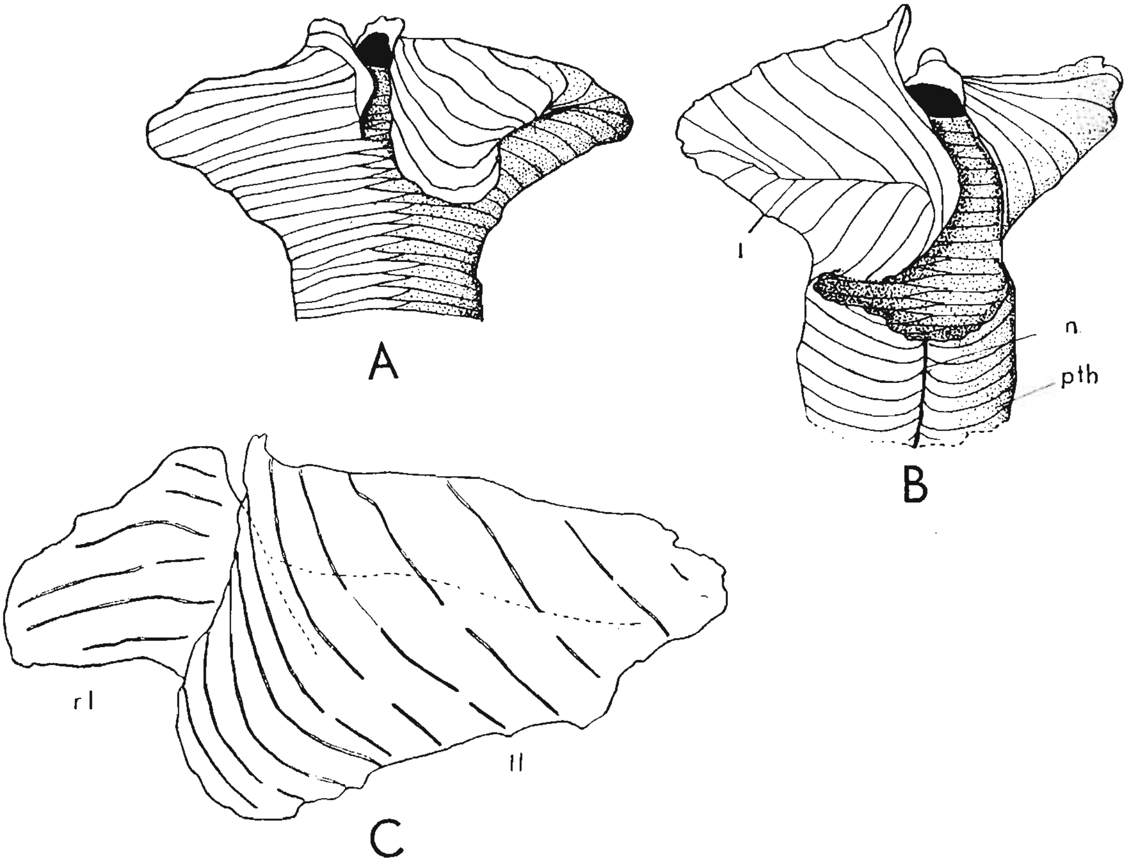


Fig. 32

Diagram of fusellar structure of apertural lobes in *Cucullograptus pazdroi* URB.: *A* ventral view, *B* dorsal view, *C* fusellar structure of the upper surface of apertural lobes (S. 32, Gdańsk-Wrzeszcz); *C* × 110 approx. *n* nema, *pth* protheca, *l* line joining fuselli, *ll* left lobe, *rl* right lobe.

The right lobe is constructed somewhat differently (fig. 32 *A-C*). Seen ventrally it is only an extension of the right series of fuselli, whose arrangement does not vary considerably. Starting from the upper surface of the lobe, the fuselli become gradually set at a different angle and they regain the ventral side by passing through the dorsal wall. Such a fusellus is thus seen to run out of the ventral side parallel to the metathecal fuselli, to go over the top of the hood-like structure (fig. 35 *A*) reaching its margin on the dorsal or upper surface. A small rim is produced by the addition of 2-3 fuselli.

In microtome sections transversal to the long axis of the theca (text-pl. V) a section of the protheca and metatheca (1-8) is first seen with a distinctly marked thickening of the nema (*n*), and then the apertural part with its neck. At first the lower elongated elements of both lobes (9-11) are to be seen, the axial section of lobes appearing next. Here the node (*nd*) is seen as a strong peridermal thickening, also the point where the left lobe is attached to the dorsal wall. Spaces between the peridermal walls are filled up with a spongy chitinous substance. The sections 9-16 show that the right lobe of the ventral wall is really an extension of the metathecal wall, having no true ventral wall. Also its dorsal part hangs down unattached at some distance from the dorsal wall. The following drawings (text-pl. V, 16-22) represent the successive sections including the uppermost parts of the left lobe (22).

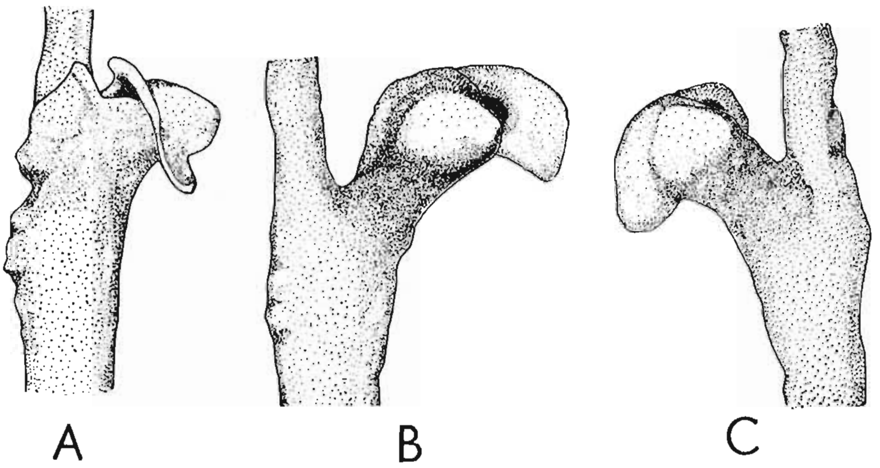


Fig. 33
Cucullograptus pazdroi URB.
Metatheca and apertural lobes of proximal theca: *A* ventral view, *B* right side view, *C* left side view (S. 32, Gdańsk-Wrzeszcz); × 80 approx.

Longitudinal sections (text-pl. VI, from left to right) first show the peridermal thickenings near the node (*nd*) and the place of attachment of the lobe to dorsal wall (1-4). In section 5 the relation of the left lobe to the dorsal wall of metatheca is clearly visible. Both apertural margins show list-like thickenings (5-7). Numbers 6-10 represent sections of the free portion of the left lobe. Beginning with fig. 8 the right lobe becomes visible. Its ventral wall is seen to be simply the prolongation of the ventral metathecal wall, while the dorsal part encircles the dorsal wall of the metatheca touching it at one point. The margin of the dorsal wall is strongly thickened. The last sections pass through the lateral lobe extension. Dorsally it is seen to form a slight downward bending of the wall (sections 16-18).

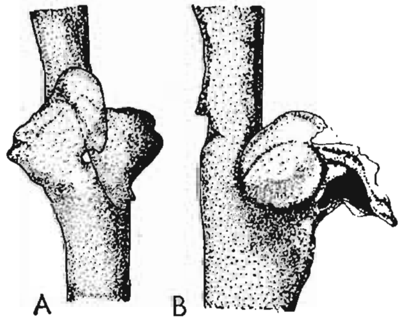


Fig. 34
Cucullograptus pazdroi URB.
Metatheca and apertural lobes of 1st theca: *A* ventral view, *B* right side view (S. 32, Gdańsk-Wrzeszcz); × 125 approx.

The interthecal distance is reduced in the course of astogeny. Length of first theca is 1.6 mm, maximum width of lobes 0.16 mm, height of lobes 0.12 mm. In the distal thecae these dimensions, as taken from detached fragments, increase to 0.76 mm in length of lobes and to 0.68 mm in their height. The overlapping grows stronger too, during astogeny. There is no overlapping at all in the first theca, while in the distal thecae it involves from 40 to 50%

of the thecal length. In the specimen examined here the aperture of the first theca is not isolated, while according to Kühne (1955, fig. 11-a) isolation may even reach 40% of the aperture. This would indicate strong variation in this respect within this species.

Faunal assemblage and stratigraphical distribution. — In the writer's material this graptolite occurs in association with: *Saetograptus chimaera* (Barr.), *Colonograptus colonus* (Barr.), *Lobograptus scanicus* (Tullb.), *Pristiograptus dubius* (Suess).

Kühne (1955, p. 386) also mentions *Lobograptus parascanicus* (Kühne). The Lower Ludlow may thus be regarded as the stratum typicum for this species. Jaeger (1955, p. 424) records *Monograptus pazdroi* from the Ludlow of Thüringia. When investigating graptolitic shales in Mójcza near Kielce (Holy Cross Mountains) the writer has noted the presence of a form within the *M. scanicus* zone, probably identical with *Cucullograptus pazdroi.*

Systematic position. — Descriptions by Urbanek (1954) and Kühne (1955) indicate the fairly frequent occurrence of this species within Lower Ludlow erratic boulders. It may be reasonably presumed that it has been found and even described under incorrect specific names.

In all probability a form described by Bulman (1938, p. 31, fig. 20-c) from the Holm Collection is specifically identical with *Cucullograptus pazdroi* (Urbanek, 1954; Kühne, 1955).

Likewise a graptolite described and figured by Jaekel (1889, p. 683-684, fig. 7-9) under the name of *Pomatograptus becki*, is identical with *Cucullograptus pazdroi* Urb. (Kühne, 1955).

It is also probable that a graptolite referred by Frech (1897, p. 644) to *Monograptus cygneus* Törnq. is in fact identical with this species.

Bulman (1953, p. 134) wrote 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*». The general characteristics of that species given by Wood (1900), the dimensions and stratigraphical distribution do not preclude the possibility of the identity of the form described by Wood with that of the present writer. It is, however, difficult to confirm this supposition since both, the holotype worked out by Bulman (1953) and the specimens described by Czech authors, are in a most unsatisfactory state of preservation. For the time being nothing very precise can be said in this respect. When looking through the descriptive types of the Bohemian graptolites in the National Museum in Prague, the writer had an opportunity of ascertaining that forms likely to belong to different species had all been referred to *Monograptus crinitus.* This is suggested by fig. 4 in a paper by Bouček (1936, p. 21, fig. 4 j-m), where forms have been figured by that author as *M. crinitus* Wood. If the specimen fig. 4-j (Narodni Museum, No. 25739) approaches fig. 298-c by Elles & Wood (1901-1918), then specimen No. 25742 shown in fig. 4-m by Bouček does not correspond to the

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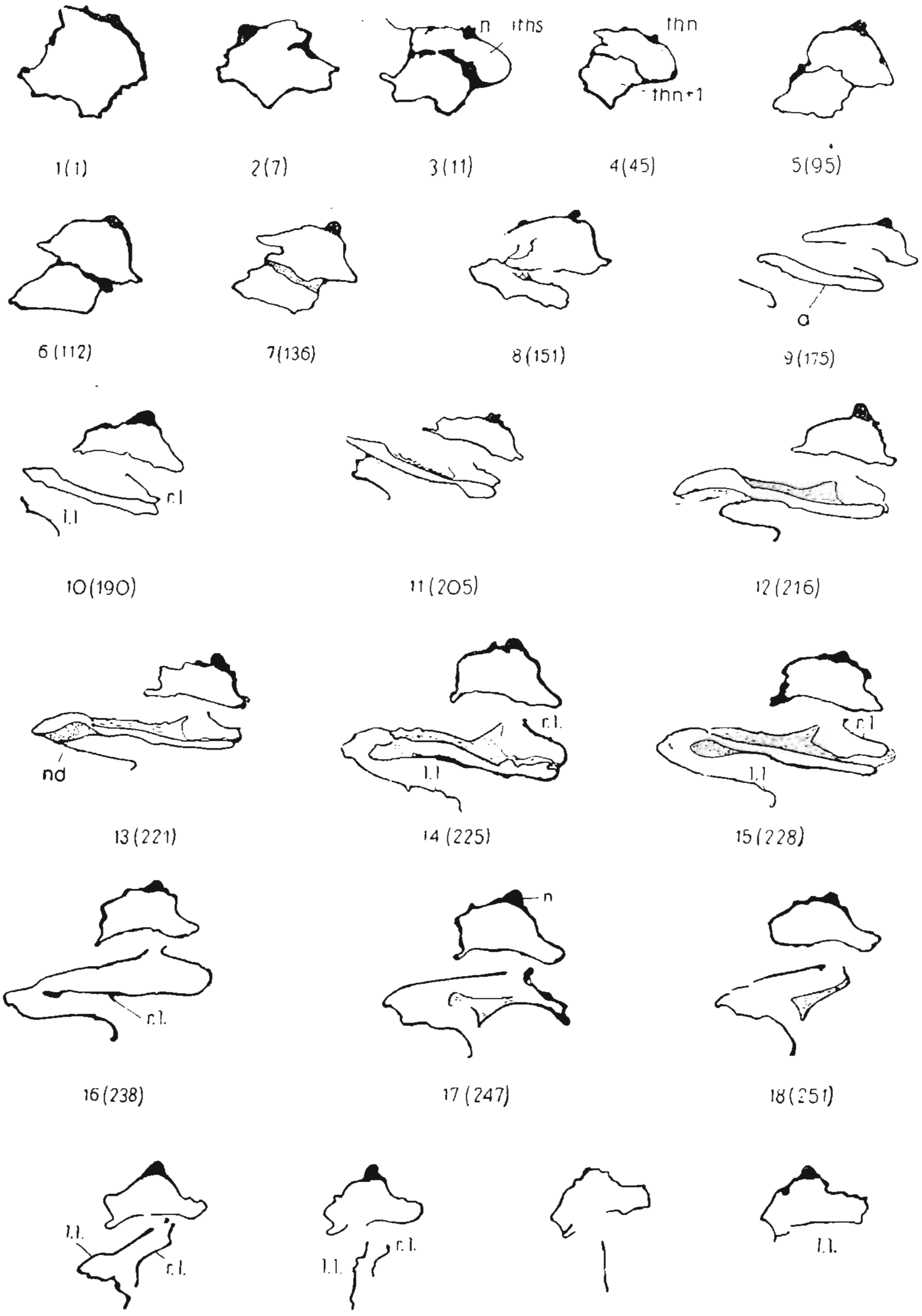
Cucullograptus pazdroi Urb.

Serial transverse microtome sections of theca; numbers in parenthesis correspond to actual numbers of sections cut at 5μ (S. 32, Gdańsk-Wrzeszcz); × 70 approx.

n nema, *iths* interthecal septum, th_n, th_{n+1} successive thecae, *a* aperture, *l. l.* left lobe, *r. l.* right lobe, *nd* node.

TEXT-PLATE V



1(1) 2(7) 3(11) 4(45) 5(95)

6(112) 7(136) 8(151) 9(175)

10(190) 11(205) 12(216)

13(221) 14(225) 15(228)

16(238) 17(247) 18(251)

19(255) 20(270) 21(279) 22(290)

(explanations on the left page)

former in thecal structure. They approach rather the proximal thecae of *Pristiograptus nilssoni* (Lapw.). This confirms the difficulty of identifying *M. crinitus* Wood. The writer is of the opinion that the present knowledge of this species provides insufficient evidence for identifying it with *Cucullograptus pazdroi*, which is now a well established species.

The structure of the apertural lobes in *Cucullograptus* is most peculiar; the forms nearest to it are *C. aversus* and *L. scanicus* (fig. 35, 40). These forms are linked with *Cucullograptus* by the general appearance of their lobes, which are a prolongation of the lateral metathecal walls made up of arched fuselli, also by their asymmetry *(Lobograptus scanicus, L. aversus)* and finally be the slit-like aperture *(L. aversus)*.

The left lobe may be regarded as homologous with the type described in *L. scanicus* (Bulman, 1953). It shows an additional fusellar structure which is absent in *L. scanicus*, furthermore it is situated above the aperture and has a hood-like shape. It is harder to connect the right lobe with the type of apertural lobes in *L. scanicus* and *parascanicus*. In a sense this lobe displays a fusellar structure exactly opposite to that of the «scanicus» type.

Lobe asymmetry in *Cucullograptus pazdroi* is the opposite of that in *Lobograptus scanicus*. In the former, the left lobe is larger, in the latter it is smaller. This calls for a search for the common ancestor of these forms among those provided with symmetrical lobes, such as *L. parascanicus*, from which both types of symmetry may have developed independently.

The slit-like aperture is correlated with the hood-like apertural lobes since it is encountered both in *Cucullograptus pazdroi* and in *C. aversus*. Both these forms display a common type of asymmetry, namely hypertrophy of the left side.

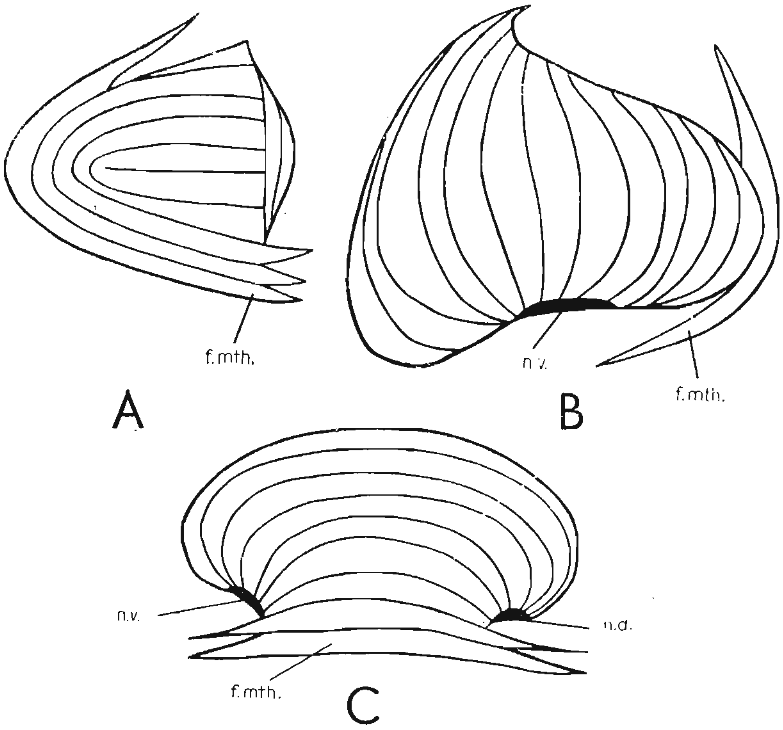
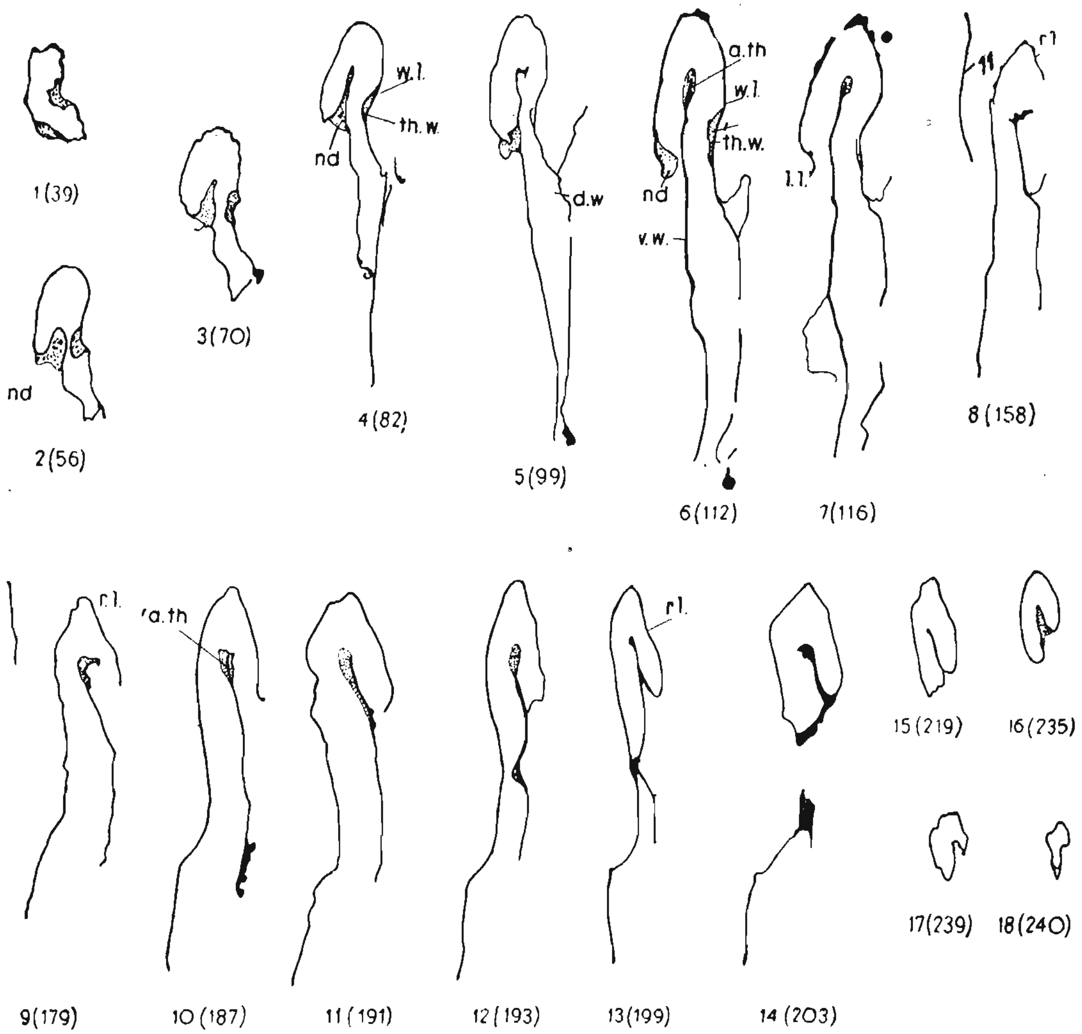


Fig. 35

Diagram of fusellar structure of apertural lobes in Cucullograptinae
A, B top view of right and left apertural lobes in *Cucullograptus pazdroi*, *C* apertural lobe in *Lobograptus scanicus*, lateral view
f. mth. fuselli of metatheca, *n. v.* ventral node, *n. d.* dorsal node.

A schematic diagram in fig. 35 shows the essential characters of the fusellar structure of lobes in *Cucullograptus pazdroi* and *Lobograptus scanicus*. Both lobes are shown diagrammatically from a lateral view (projected into a plan). The structural pattern of the «scanicus» lobe strikingly resembles that of the left apertural lobe in *Cucullograptus pazdroi*, while marked differences are displayed by the right lobe.

TEXT-PLATE VI



Cucullograptus pazdroi Urb.

Serial longitudinal microtome sections of theca; numbers in parenthesis correspond to actual numbers of sections cut at 3μ (S. 32, Gdańsk-Wrzeszcz); × 70 approx.
a. th thickening on apertural margin, *th. w.* thecal wall, *d. w.* dorsal wall, *v. w.* ventral wall, *w. l.* wall of lobe, *n* nema, *iths* interthecal septum, *l. l.* left lobe, *r. l.* right lobe, *nd* node.

In summing up morphological data concerning these related forms, the same conclusions may be drawn as those inferred from the diagram. The ancestral form admitted here is that of a graptolite with symmetrical apertural lobes. *L. parascanicus* fits to a certain extent into that model (comp. p. 23). Two evolutionary lines are supposed to have descended from a form of this type. The one giving rise to *Cucullograptus* (fig. 45) would be characterized by hypertrophy of the left lobe and the strongly modified structure of the right. Whether this would be effected by structural modifications of the «scanicus» type of lobe, or by the atrophy and secondary reconstruction of that lobe into a new shape (as suggested by *C. aversus*) is a problem difficult to solve.

Cucullograptus aversus (EISENACK), 1942

(text-fig. 36-40)

1942. *Monograptus aversus* EISENACK; A. EISENACK, Über einige neue Funde..., p. 34-38, pl. 2.
1954. *Monograptus aversus* EISENACK; A. URBANEK, Some observations..., p. 82-83 (Engl. text), fig. 9-12.
1955. *Monograptus* cf. *aversus* EISENACK; W. G. KÜHNE, Unterludlow-Graptolithen..., p. 389-391, fig. 13.

Material. — Very scarce, based on fragments of thecae from boulder S. 121 (Jarosławiec). No sicula available. The majority of metrical data is therefore taken from papers by EISENACK (1942) and KÜHNE (1955).

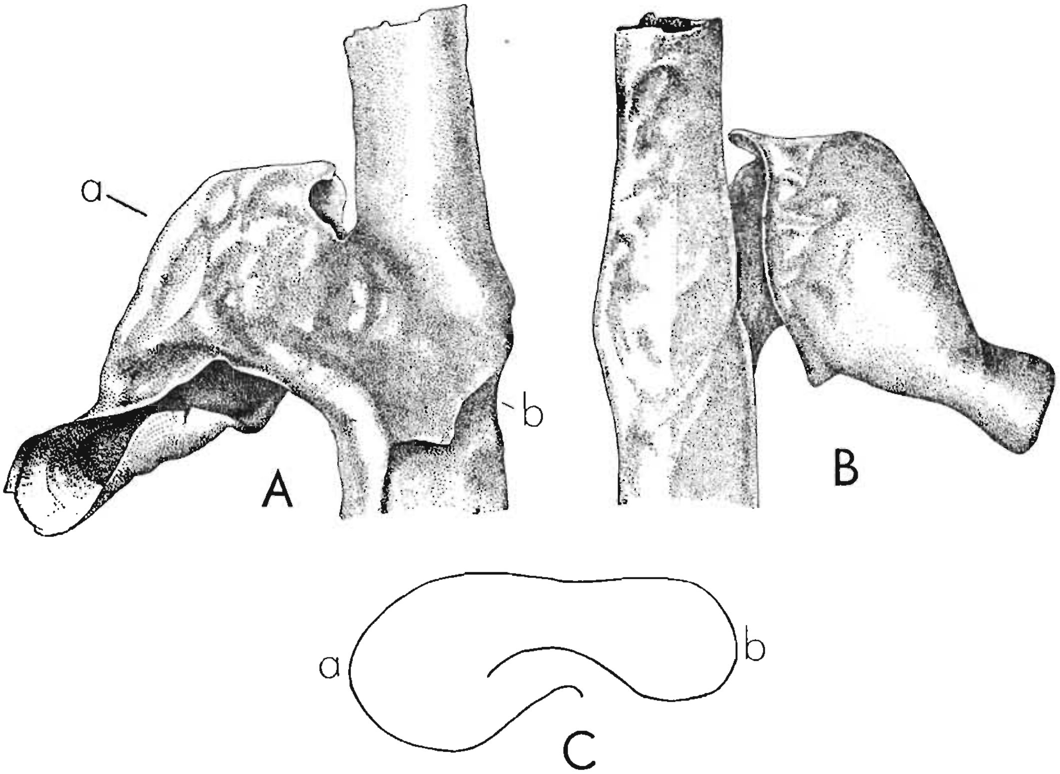


Fig. 36
Cucullograptus aversus (EISENACK)
Apertural region of theca: *A* left side view, *B* right side view, *C* diagrammatical section of the apertural lobe along the *a-b* line on fig. *A* (S. 121, Jarosławiec); × 140 (after URBANEK, 1954).

Description. — Rhabdosome straight. Proximal thecae straight, tubular and long; distal thecae shorter with a ventral curvature.

Sicula, 0.75 mm in length, somewhat bent ventrally (Kühne). Aperture with an extremely small, blunt dorsal lip.

Thecae, on the whole, of a type characteristic of Cucullograptinae (comp. p. 68). A slit-like, asymmetric aperture with one left apertural lobe only. It is a monofusellar lobe, derived from the left metathecal wall. Medially this lobe develops a strongly convex dome made up of arched and slightly thickened fuselli. These fuselli terminate freely at the dorsal margin, while on the ventral margin they are joined into a node (fig. 36, 39). The dorsal edge of the dome is free and medially it is slightly incurved so as to produce a brim (fig. 37, 38). The ventral margin of the process forms an expanded spade with its margin bent out fig. 39). This spade, folded into a tube, is made up of short, arcuate fuselli which, similarly to the incurving brim, constitute an outgrowth of the true process (fig. 40). Only a narrow slit separates the margin of the lobe from the ventral margin of the aperture (fig. 36 *C*).

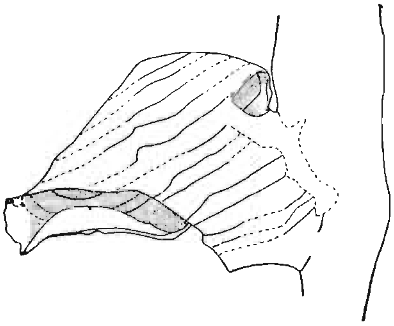


Fig. 37

Cucullograptus aversus (Eisenack) Fusellar structure of the apertural lobe, left side view (S. 121, Jarosławiec); × 100 approx. (after Urbanek, 1954).

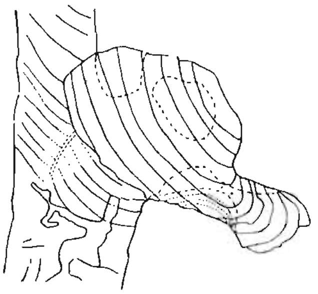


Fig. 38

Cucullograptus aversus (Eisenack) Fusellar structure of the apertural lobe, right side view. Discontinuous line marks the borders of lobe and aperture visible in transmitted light (S. 121, Jarosławiec); × 100 approx. (after Urbanek, 1954).

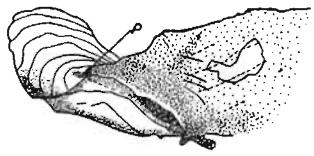


Fig. 39

Cucullograptus aversus (Eisenack) Ventral end of the apertural lobe, left side view. Flange of one of the margins visible, *p* point where fuselli come together. Discontinuous line marks fuselli of the counter part of the lobe (S. 121, Jarosławiec); × 100 approx. (after Urbanek, 1954).

Eisenack (1942) asserted that the apertural lobe in *C. aversus* was derived from the dorsal wall of the metatheca. His conception was that of a dislocation of the thecal plane of symmetry as a result of which the dorsal process had become lateral.

On his own material Urbanek (1954, p. 82-83) was of the opinion that this process is not actually a derivative of the dorsal wall since it consists of one fusellar series without a zigzag suture. It is thus a lateral structure, while the asymmetry is due to atrophy of the right lobe. This is a more advanced stage of the *Lobograptus scanicus* type of asymmetry, but affecting another antimere (left, not right).

Faunal assemblage and stratigraphical distribution. — Eisenack (1942) when describing this species did not discover any associated fauna determining its age. On the lithology of the boulder he believed it to be a Wenlockian form.

From the correspondence between the lithological character of his boulder with the «Colonus shales» of Sweden and on the presence of *Cardiola interrupta* Sow., Urbanek (1955) was rather inclined to refer this form to the Lower Ludlow. His view was confirmed by Kühne's observations (1955), who recorded this form in association with *Lobograptus scanicus* (Tullb.) and *Pristiograptus dubius* (Suess), which indicate Lower Ludlovian age.

Systematic position. — Urbanek (1954) expressed the opinion that this form probably belongs to the same group as *Lobograptus scanicus*, though the two species are not likely to be directly related.

Kühne (1955) held the view that this form descended from *Cucullograptus pazdroi* by an increase of asymmetry finally resulting in the complete atrophy of the right lobe.

Closer studies of the morphology of these two forms lead to a more precise determination of their phylogenetic relationships. *Cucullograptus pazdroi* does not seem to be the true ancestral species in this evolutionary line. The right lobe in this species cannot be fully homologized with the structure of the «scanicus» lobe type. Perhaps, the initial structure of the right lobe was of the «scanicus» type and was completely reduced, while the final right lobe, as actually observed in *C. pazdroi*, represents a new structure developed in the process of evolution. In any case both these species may be considered as descendants from a common ancestral form, while *C. pazdroi* may be said to have passed through an «aversus» stage (comp. p. 68 and fig. 45). According to this view the structure of the apertural lobes in *C. pazdroi* is specialized rather than primitive as compared with *C. aversus*.

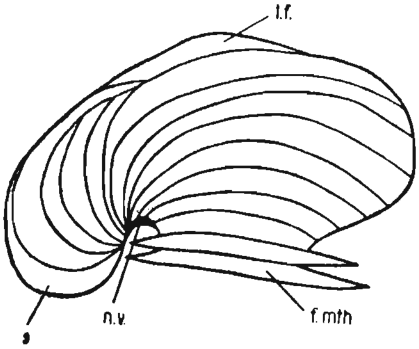


Fig. 40

Diagram of the fusellar structure of apertural lobe in *Cucullograptus aversus*. Lobe spread in a plain, lateral view

l. f. incurved portion, *s* shovel-like outgrowth, *n. v.* ventral node, *f. mth.* metathecal fuselli.

Genus LOBOGRAPTUS n. gen.

(for diagnosis see p. 12)

Lobograptus scanicus (Tullberg), 1883

(text-fig. 41-42; pl. II, fig. 5, 6)

1883. *Monograptus scanicus* TULLBERG; S. A. TULLBERG, Skånes Graptoliter, II, p. 26, pl. 2, fig. 38.
1885. *Monograptus scanicus* TULLBERG; F. ROEMER, Lethaea erratica, p. 117 (364), pl. 9, fig. 13 a-b.
1900. *Monograptus scanicus* TULLBERG; E. M. E. WOOD, On the Lower Ludlow..., p. 479, pl. 25, fig. 25 A-B, text-fig. 22 a-b.
1913. *Monograptus scanicus* TULLBERG; G. L. ELLES & E. M. E. WOOD, British Graptolites, p. 433-434, pl. 44, fig. 2 a-d, text-fig. 297 a-d.
1936. *Monograptus scanicus* TULLBERG; B. BOUČEK, La faune graptolithique du Ludlovien..., p. 21-22, fig. 4 e-i, pl. 2, fig. 9.
1953. *Monograptus scanicus* TULLBERG; O. M. B. BULMAN, On the thecae..., p. 131-136, fig. 1-3.
1953. *Monograptus scanicus* TULLBERG; M. WALKER, The sicula of *M. scanicus*..., p. 224.
1954. *Monograptus scanicus* TULLBERG; A. URBANEK, Some observations..., p. 84-85 (Engl. text), fig. 18-20.
1955. *Monograptus scanicus* TULLBERG; W. G. KÜHNE, Unterludlow-Graptolithen..., p. 291-292, fig. 14.

Material. — About 100 specimens, mainly distal parts, only a dozen fragments of proximal parts and 12 specimens of sicula with first theca. Boulders: S. 16 (Łebcz), S. 36 (Jarosławiec), S. 32 (Gdańsk-Wrzeszcz), S. 128, 130, 131 (Władysławowo) and S. 137 (Ustka). The last boulder contained a nearly monospecific fauna (several tens of specimens, with but a few *Saetograptus chimaera*), excellently preserved.

Description. — Rhabdosome gently curved. Proximal thecae straight, distal thecae ventrally curved.

Sicula straight, approx. 1.2 mm in length (fig. 41).

Prosicula from about 0.43 to 0.45 mm long, with conspicuous apertural ring, and discernible longitudinal threads.

Fig. 41
Lobograptus scanicus (Tullb.)
Sicula and 1st theca with peridermal rings (S. 137, Ustka); × 60 approx.
sir peridermal rings, *thr* thecal rings.

Metasicula about 0.75 mm long, provided with 1-3 peridermal rings. Bud ring indistinctly marked. Aperture nearly smooth, with margin slightly protruding at dorsal lip. Greater diameter of aperture 0.12 mm. Virgella about 0.3 mm long.

Thecae of form typical of Cucullograptinae, proximally long and narrow, without overlap; distally short with ventral curvature (fig. 42; pl. II, fig. 6).

Aperture narrow, with longitudinal axis, parallel to axis of rhabdosome. Provided with paired lateral apertural processes, showing monofusellar structure.

Each process made up of arcuately curved fuselli, converging both ventrally and dorsally into nodes (fig. 42). The right process larger than the left and protruding beyond it (pl. II, fig. 6). Free edge of process gently curved, medially producing a brim.

Structure of thecae recently described by Bulman (1953). In the course of astogeny the processes remain with no visible change, being similar in both proximal and distal parts of rhabdosome. Maximum diameter of process 0.17 mm in first theca and about 0.27 mm in distal thecae.

Length of first theca from 1.37 to 1.22 mm, nine tenths of length being involved in the protheca. The whole theca, therefore, is an extremely fine tube about from 0.06 to 0.12 mm in diameter, consisting almost exclusively of the protheca. The following thecae become longer (up to 1.7-2.00 mm); their length to width ratio, however, decreases when they are 1.2-1.37 mm long, and about 0.25 to 0.30 mm broad. Isolation of apertures diminishes and the protheca occupies only about six tenths of thecal length. Distally 8 thecae in 10 mm.

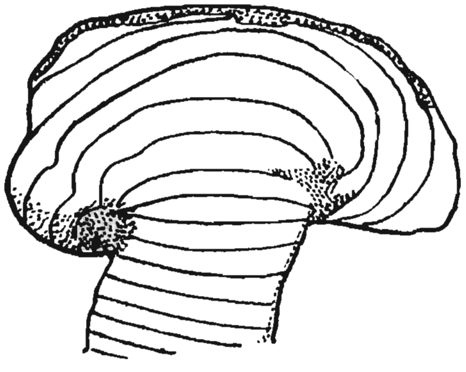


Fig. 42
Lobograptus scanicus (Tullb.)
Fusellar structure of apertural lobe (S. 137, Ustka) × 160 approx.

Urbanek (1954, p. 84-85) has shown that *Lobograptus scanicus* (Tullb.) occurs in two forms. One of them (figured by Walker, 1953) has no peridermal rings in the first theca, while the other (figured by Urbanek 1953, fig. 18-20), has a certain number of rings, termed thecal. These are peridermal thickenings completely analogous to the rings on the metasicula. They have recently also been noted by the writer in *Pristiograptus bohemicus* (Barr.). Available data suggest that rings of this type may have formed not on the first theca only, but also on the second, and even perhaps on further proximal thecae of the rhabdosome (Urbanek, 1954, fig. 19-20).

The presence of these two forms, analogous to the ringed and ringless forms of sicula in *Pristiograptus dubius*, *Saetograptus chimaera*, *Colonograptus colonus*, indicate strong intraspecific variations of some monograptids.

Faunal assemblage and stratigraphical distribution. — This well known form is the index species for zone 34. In erratic boulders it was accompanied by the following: *Saetograptus chimaera* (Barr.), *Pristiograptus nilssoni* (Lapw.), *P. dubius* (Suess), *P. bohemicus* (Barr.) *Monoclimacis micropoma* (Jaekel).

Systematic position. — This species was regarded as being related to typical representatives of *Monograptus (Monograptus)*, on the ground that its processes were of the same type as those in *M. (Monograptus) priodon* (Bronn).

Tullberg himself, the author of that species, writes that «Tekorna likna dem hos *Monogr. priodon*» (1883, p. 27). This probably made Elles & Wood (1913) assign *M. scanicus* to the same group as *M. priodon* (comp. p. 5).

Other writers (Bouček, 1936; Přibyl, 1948), on similar grounds, placed this species near to *M. (Monograptus)*.

Bulman (1953, p. 131) when describing the structure of apertural processes, was correct in stating that «this hooked appearance is deceptive». It cannot be doubted that *Lobograptus scanicus* (Tullb.) ought to be referred to the group which is characterized by lateral lobes and by similar thecal shape. But the asymmetry of lobes indicates that *Lobograptus scanicus* (Tullb.) belonged to a different evolutionary line from *Cucullograptus aversus* and *C. pazdroi.*

Lobograptus parascanicus (Kühne), 1955

(text-fig. 43, 44)

1955. *Monograptus parascanicus* KÜHNE; W. G. KÜHNE, Unterludlow-Graptolithen..., p. 392-393, fig. 15 A-D, 16 A-I.

Material. — Very meagre, some fragments of the distal parts, two proximal parts, one specimen of a single theca with incomplete sicula. Boulder S. 140 (Władysławowo). Due to poor state of preservation, fusellar structure not very distinct.

Description. — Rhabdosome straight, or nearly so. Sicula straight, with complete length of 0.75 mm according to Kühne (1955, p. 393). In our specimens sicula preserved as far as the pore region only (0.6 mm long), the apertural part being broken off. No dorsal lip.

Thecae similar to those in *L. scanicus.* The proximal are long, thin tubes consisting mainly of the protheca (fig. 44). The distal have a distinct ventral curvature. Width of second protheca approx. 0.1 mm, while in distal thecae it increases to 0.44 mm. Distal thecae spaced 0.60-0.95 mm (as measured on fragmentary specimens). According to Kühne, there are 7 thecae in 10 mm. Maximum length of distal lobes 0.27 mm.

Aperture with two lateral lobes of monofusellar structure, essentially similar to that in *L. scanicus*, but lobes differently shaped (fig. 43 *A-D*).

Free edge of lobes markedly more medially placed, so much so that the edges meet and even mutually overlap (fig. 43 *C*). A sort of shield is thus produced made up of two lobes, covering the aperture. The ventral margin of processes is either sub-circular (fig. 43 *A*) or stretched into a characteristic beak (fig. 43 *B*). This constitutes a kind of fusellar outgrowth analogous to those in *Cucullograptus* (fig. 43 *D*). Due to the overthrust of lobes they are — when seen from the side — lower than in *scanicus* and often provided with a beak, as mentioned above. These two types of lobes (fig. 43) are thus very different.

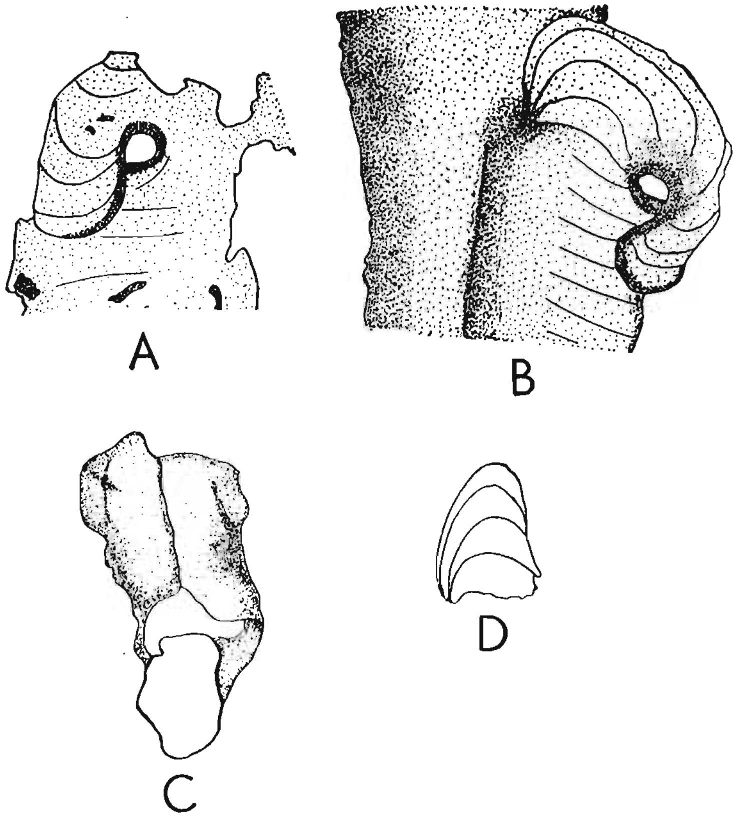


Fig. 43

Lobograptus parascanicus (KÜHNE)

Apertural lobes: *A* normal, *B* strongly elongated — lateral view, *C* apertural lobe — distal view, *D* fusellar outgrowth on the proximal end of lobe (S. 140, Władysławowo); × 80 approx.

There is no distinct asymmetry of lobes in *L. parascanicus*. Although, the lobes are not of equal size, it cannot be said that one of them is constantly larger than the other. It is thus a form with its asymmetry not yet definitely established.

Faunal assemblage and stratigraphical distribution. — In our material this form is accompanied only by *Monoclimacis micropoma* (Jaekel). Kühne has recorded it from an assemblage with *Lobograptus scanicus* (Tullb.). It is therefore a Lower Ludlovian form.

Systematic position. — This form has only been recorded from erratic boulders (Kühne, 1955). It is, however, very near to *Monograptus irfonensis* Elles (Elles & Wood, 1913, p. 429, fig. 292; pl. 43, fig. 3). The type of thecae and apertural parts seem to agree perfectly in both species. Elles has recorded *M. irfonensis* from the uppermost Wenlock (zone 31 with *Cyrtograptus lundgreni*). Since, according to these authors, «*M. irfonensis* presents a certain amount of resemblance to *M. scanicus*» — its occurrence in the Lower Ludlow is highly probable,

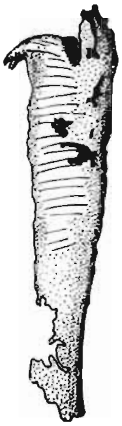


Fig. 44
Lobograptus parascanicus (KÜHNE)
Proximal theca (S. 140, Władysławowo); × 33 approx.

but seems to be identified there with *L. scanicus*. In a flattened condition the two species are almost indistinguishable. Since, however, the present writer has not been able to settle the question of their identity, he retains KÜHNE's species until the matter has been cleared up.

Nevertheless, the resemblance of *M. irfonensis* ELLES to *Lobograptus parascanicus* (KÜHNE) sheds some light into the problem of the evolution of this group. It seems very likely that the asymmetric Cucullograptinae may have developed during the Upper Wenlockian from forms such as *L. parascanicus* (KÜHNE) or from some other species closely related to it.

These forms are linked by their common thecal structures and by the general appearance of their apertural lobes. The fact that *L. parascanicus* is a form with relatively symmetrical thecal structures or with the asymmetry not yet stabilized, leads us to regard it as ancestral to both lines of Cucullograptinae which are characterized by hypertrophy of one of the antimeres (comp. fig. 45). The fact that it is a form contemporary with the highly modified forms of the Cucullograptinae cannot exclude this possibility, especially as the existence of this species in the Wenlockian is not inadmissible.

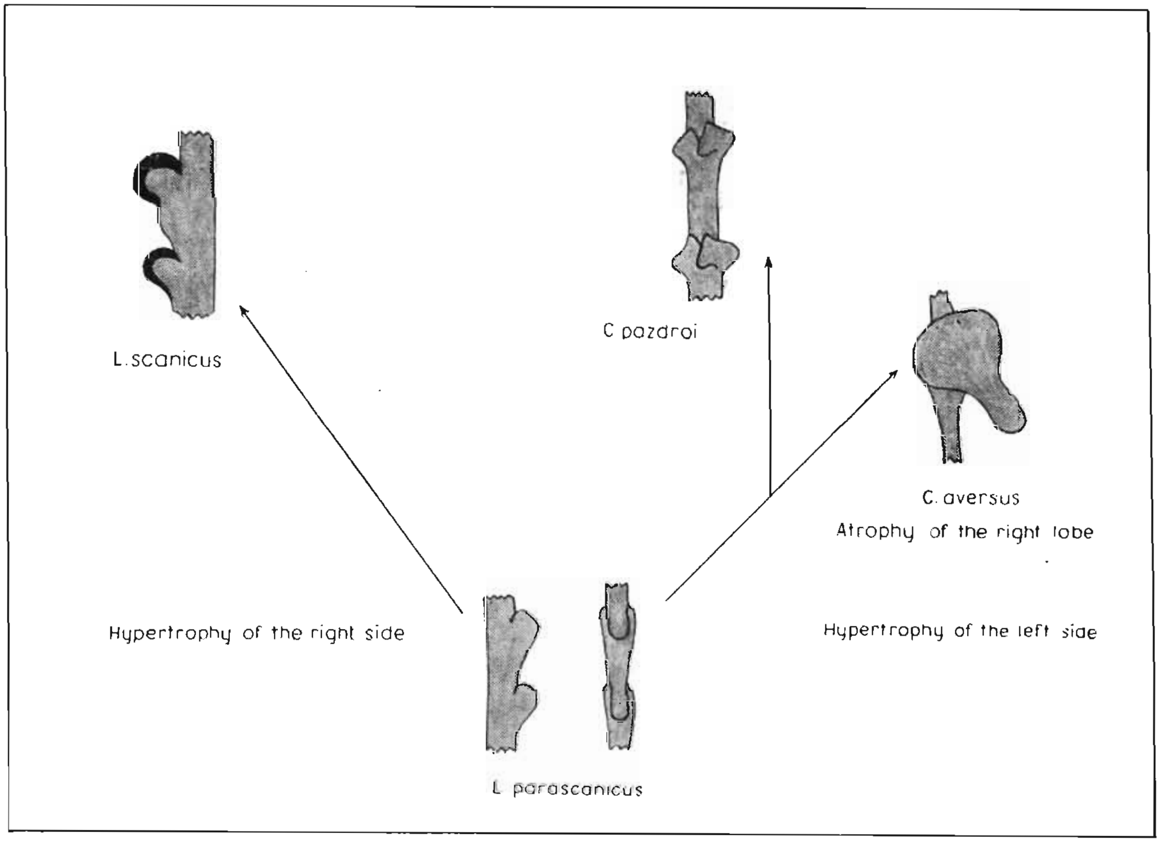


Fig. 45
Suppositive phylogenetical relationship among Cucullograptinae.

Subfamily PRISTIOGRAPTINAE (GÜRICH), 1908

Genus **PRISTIOGRAPTUS** (JAEKEL), 1889

Pristiograptus bohemicus (BARRANDE), 1850

(text-fig. 46-51; pl. IV, fig. 1-3)

1850. *Graptolithus bohemicus* BARRANDE; J. BARRANDE, Graptolites de Bohême, p. 40, pl. 1, fig. 15-18.
1855. *Monograptus bohemicus* (BARRANDE); W. G. KÜHNE, Unterludlow-Graptolithen..., p. 382-384, fig. 9 A-J.
Further references:
1936. B. BOUČEK, La faune graptolithique du Ludlovien..., p. 3, pl. 1, fig. 1-3.
1948. A. PŘIBYL, Bibliographic Index..., p. 68.

Material. — This species is very abundant in erratic boulders, being present in nearly every Upper Ludlovian boulder. The following boulders have yielded fairly copious material: S. 16 (Łebcz), S. 32 (Gdańsk-Wrzeszcz), S. 112 and 114 (Rewal, in great abundance), S. 122 (Dziwnów), S. 124 (Władysławowo), S. 136 (Niechorze), S. 154 (Jarosławiec). In all, the writer

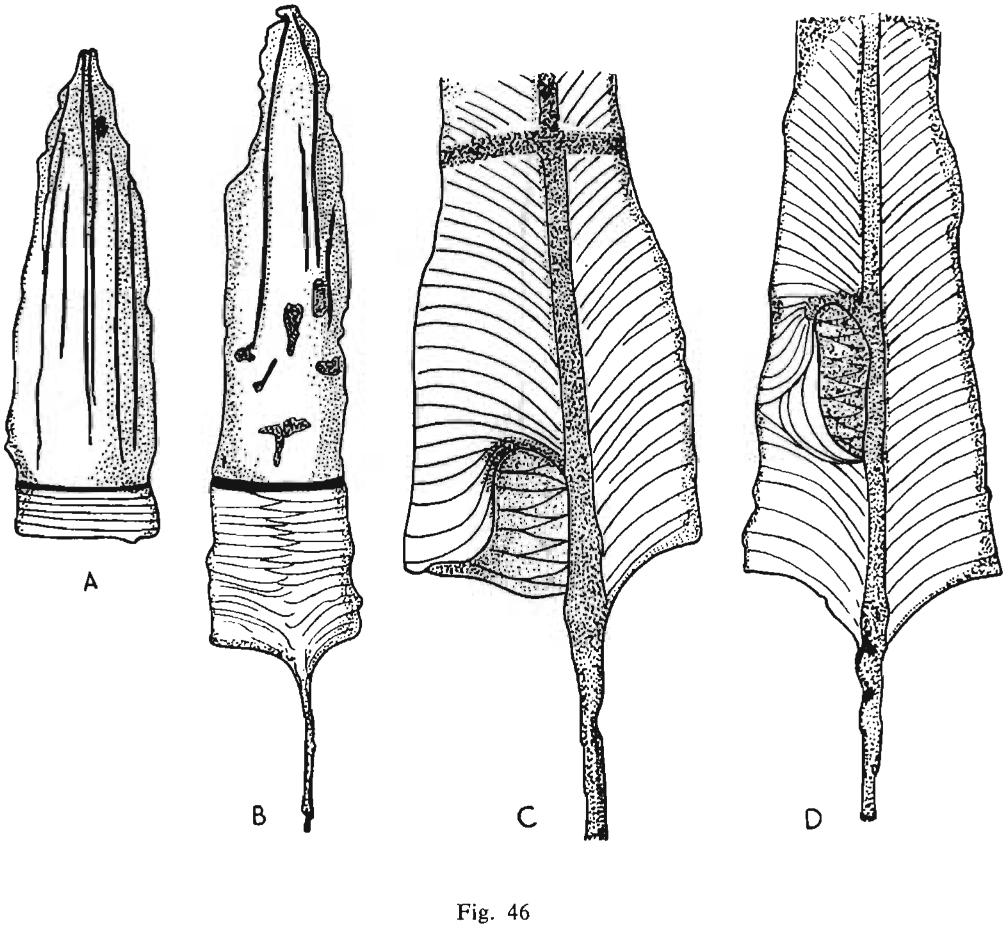


Fig. 46

Pristiograptus bohemicus (BARR.)

Development of sicula and 1st theca: *A* young metasicula, *B* young metasicula with virgella, *C* «sinus» stage, *D* «lacuna» stage (S. 112, Rewal); × 133 approx.

had at his disposal about 100 specimens, including well over 10 mature siculae. The other specimens were various fragments of the proximal and distal parts of rhabdosomes.

Description. — Rhabdosome with strong ventral curvature; this feature, however, varied considerably, there being almost straight and strongly curved rhabdosomes (comp. pl. IV, fig. 1-3).

Sicula with an average length ranging from 1.74 to 1.89 mm, ventrally distinctly curved. Apex under second protheca (fig. 46, 47).

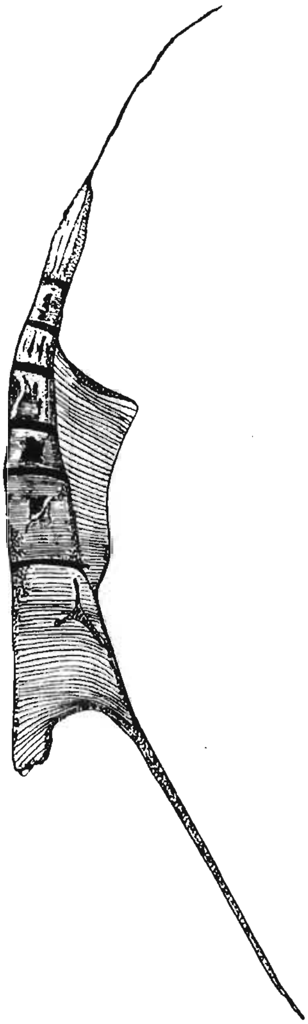


Fig. 47

Pristiograptus bohemicus (BARR.) Sicula and prothecal segment of 1st theca (S. 112, Rewal); × 38 approx.

Prosicula (fig. 46 *A*), with an average length from 0.37 to 0.48 mm, with numerous and well developed longitudinal threads. Apertural ring of prosicula usually strongly expressed as a list-like peridermal thickening.

Metasicula (fig. 46 *A-E*) with 4-7 peridermal rings, usually 5 (together with the bud ring). Towards the aperture the metasicula widens out strongly, so much so that the long axis of the fully developed aperture attains 0.37 to 0.40 mm. The aperture is commonly provided with a conspicuously long virgella (0.4 to 1.14 mm) and a well marked dorsal lip, which is subtrapezoidal with a broader base. The blunt free edge has a thickened list (fig. 49 *C*).

The development of the sicula agrees with the general pattern characteristic of Monograptidae (fig. 46, 47).

The formation of the pore passes through the «sinus» and «lacuna» stages (fig. 46 *C*, *D*). The first fuselli of the first theca are laid down in the right corner of the sub-triangular pore (fig. 46 *E*).

In *P. bohemicus* the thecae have a most characteristic shape because of their triangular outline (fig. 48, 49 *A*, *B*). The thecal aperture is smooth, without processes and shows marginal thickening. Their fusellar structure can be well investigated in cleared specimens (fig. 49 *A-B*). Protheca ($n + 1$) is formed by the superposition of fuselli which initially extend on one side to the metatheca (n) and to the nema on the other (fig. 49 *A*). A zigzag ventral suture is then produced (fig. 49 *B*). In proximal thecae the protheca occupies more than two thirds of the total thecal length; no important changes are noted in distal thecae.

The presence of thecal rings on the proximal thecae of the rhabdosome is an interesting feature, similar to *L. scanicus*. Ringed forms occur on proximal thecae of rhabdosome along with ringless forms (fig. 50 *A*, *B*). The specimen figured in fig. 51 *B* indicates that these rings may sometimes appear on later thecae also.

A microtome section (fig. 51 *A*) of a form with metasicular and thecal rings shows their internal position in relation to the wall. They are fully analogous structures. Frequently one branch of the bud ring passes into the interior of the first theca. Such morphological differentiation is probably an expression of intraspecific variation.

The distance between the ventral apertural margins and the width of the rhabdosome increases in the course of astogenetic evolution.

The distance between the ventral apertural margins is as follows: in th 1-2 — 0.72 to 0.87 mm, in th 2-3 — 0.72 to 0.95 mm, in th 3-4 — 0.76 to 1.06 mm, with a tendency to wide rather than to close spacing.

Height of rhabdosome is as follows: under th 1 — 0.49 to 0.57 mm, under th 3 — 0.65 to 0.80 mm, under th 6 — about 1 mm.

Owing to lateral flattening of the majority of rhabdosomes, probably resulting from their state of preservation, data relative to the width of the rhabdosomes cannot be regarded as very exact. They are as follows: in th 1 —0.15 mm, in th 2—0.19 mm, in th 3—0.19 mm. In distal fragments these figures increase up to 0.7 mm. There are 9-10 thecae in 10 mm.

Fig. 48

Pristiograptus bohemicus (Barr.)

Proximal part of rhabdosome (S. 147, Jarosławiec); × 23 approx.

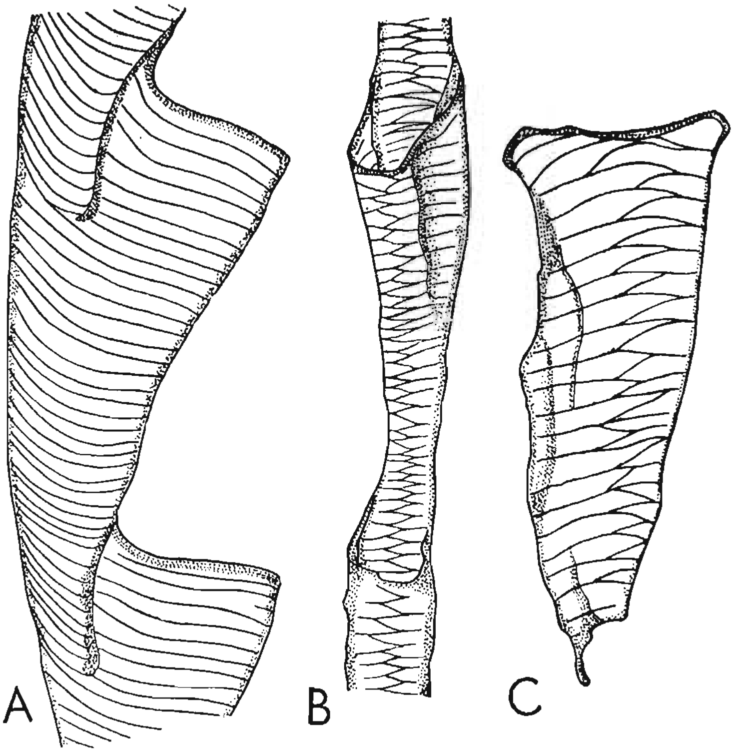


Fig. 49

Pristiograptus bohemicus (Barr.)

Fusellar structure of theca; *A* lateral view, *B* ventral view (S. 147, Jarosławiec); × 50 approx.; *C* fusellar structure of the dorsal lip of metasicula (S. 112, Rewal); × 120 approx.

Faunal assemblage and stratigraphical distribution. — This form occurs most frequently in association with the following species: *Pristiograptus dubius* (Suess), *P. nilssoni* (Lapw.), *Lobograptus scanicus* (Tullb.), *Cucullograptus pazdroi* Urb.

It is a cosmopolitan species recorded from Ludlovian deposits in Europe, Asia, North America and Australia. It is considered to be stratigraphically linked with the *P. nilssoni* (Lapw.) zone.

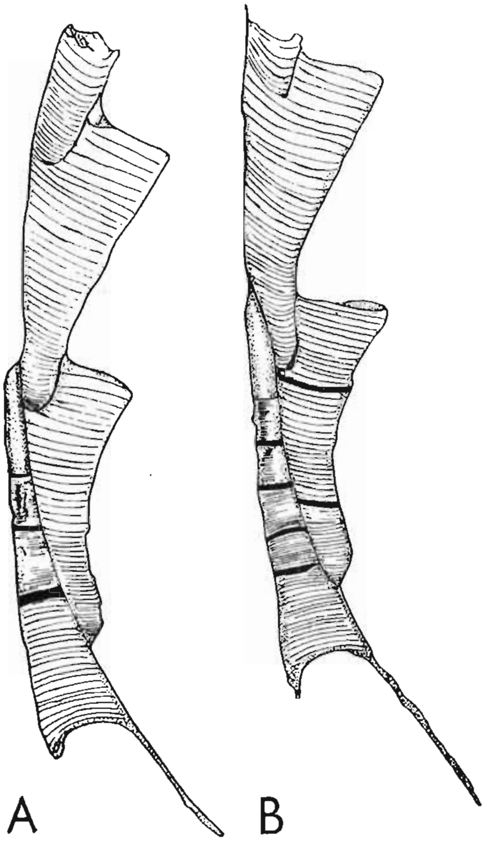


Fig. 50

Pristiograptus bohemicus (BARR.)

Young rhabdosomes in the same stage of development; *A* without thecal rings, *B* with thecal rings (S. 147, Jarosławiec); × 33 approx.

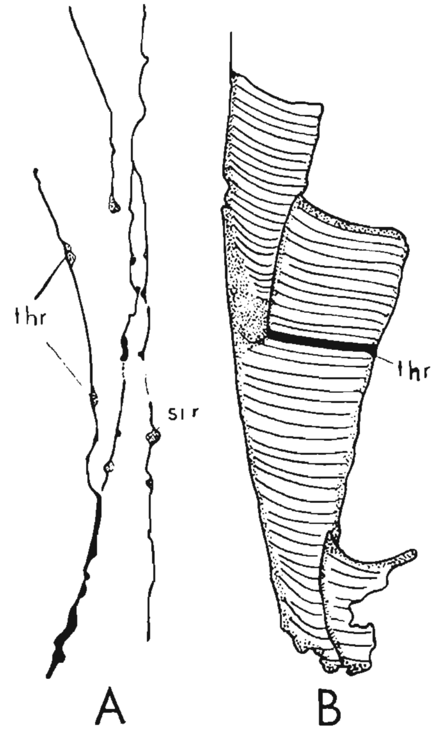


Fig. 51

Pristiograptus bohemicus (BARR.)

A longitudinal microtome section of rhabdosome with thecal rings, *B* distal theca with thecal rings (S. 147, Jarosławiec); × 33 approx.

thr thecal rings, *sir* peridermal rings of the sicula.

Systematic position. — This very typical representative of the genus *Pristiograptus* is characterized by strong ventral curvature of the rhabdosome. In outline, distal thecae closely resemble those in *P. dubius* (SUESS), while the proximal thecae approach those in *P. nilssoni* (LAPW.).

Pristiograptus nilssoni (LAPWORTH), 1876

(text-fig. 52-56)

1876. *Monograptus nilssoni* BARRANDE; C. LAPWORTH, Scottish Monograptidae, p. 315, pl. 10, fig. 7 a-e.
1954. *Pristiograptus (Pristiograptus) nilssoni* (BARR.); A. URBANEK, Some observations..., p. 83-84, fig. 13-16.
1955. *Monograptus nilssoni* (BARRANDE); W. G. KÜHNE, Unterludlow-Graptolithen..., p. 384-386, fig. 10.
1956. *Pristiograptus (Pristiograptus) nilssoni* (LAPW.); H. TOMCZYK, Wenlock and Ludlow..., p. 51-52, pl. 5, fig. 2, text-fig. 13 a-b.
Further references:
1936. B. BOUČEK, La faune graptolitique du Ludlovien..., p. 5, pl. 1, fig. 19-20.

Material. — Rare specimens of this species are to be found in nearly all erratic boulders, accompanied by *P. bohemicus* (BARR.) and its assemblage. The unsatisfactory state of preservation, however, of the available specimens, consisting mainly of minute rhabdosome fragments, prevents a detailed study of its morphology. It is interesting to note that Kühne (1955) has observed a similar condition. Somewhat more complete remains have been etched by the writer from erratic boulders S. 36, 38 (Jarosławiec) and S. 20 (Poznań). In addition to numerous rhabdosome fragments — proximal and distal — there are also several siculae.

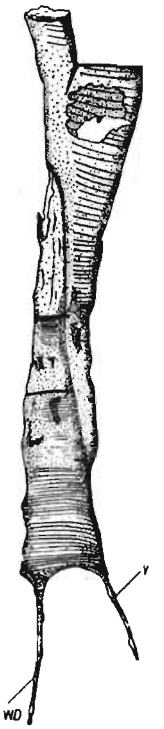


Fig. 52
Pristiograptus nilssoni (Lapw.)
Sicula and 1st theca; *v* virgella, *wd* dorsal process (S. 38, Jarosławiec); × 33 approx. (after Urbanek, 1954).

Description. — Sicula approx. 1.6 mm long, terminating at the boundary between the protheca and the metatheca of the first theca (fig. 52).

Prosicula up to 0.58 mm in length and 2.8 times shorter than the total length of sicula, with an apertural ring.

Metasicula approx. 1 mm long, with very few peridermal rings, in most cases only one besides the bud ring. Long axis of metasicula aperture approx. 0.3 mm. The dorsal margin strongly differentiated: in the plane of symmetry, instead of the usual lip, there is a small notch, bordered on both sides by wing-like lobes (fig. 53, 54). The right lobe stretches out into a long and thin, asymmetrical apertural spine. This spine is thus unpaired, being a derivative of the right fusellar series (monofusellar structure) and is at the right side of the zigzag suture (fig. 55). Though resembling the virgella, it differs from it in its fusellar structure: its basal part (fig. 55) consists of two slightly widened out fuselli, on which the terminal narrow end of the spine rests. The edges of the latter have list-like thickenings. The left lobe corresponds only to the basal part of the right spine.

The rhabdosome in *P. nilssoni* (Lapw.) has a strong dorsal curvature in the proximal part (comp. Elles & Wood, 1913, pl. 37, fig. 1 a-c) and a ventral curvature in the distal part. Although the material here studied does not contain rhabdosome fragments including both ends, still it has been possible to ascertain the proximal (fig. 56, *C*) and the distal parts (fig. 56, *A-B*).

Proximal thecae resemble those in *P. bohemicus*, the curvature excepted, whereas distal thecae show a gentle ventral curvature due to the abrupt increase in thecal width at the boundary between the protheca and the metatheca. Besides this, the ventral edge of the aperture of the metatheca is marked by a slight median notch making its edge analogous to the dorsal aperture of the metasicula.

Faunal assemblage and stratigraphical distribution. — The following forms are its most common associates: *Monograptus (Monograptus) uncinatus* Tullb., *Saetograptus chimaera* (Barr.), *Colonograptus colonus* (Barr.), *Pristiograptus dubius* (Suess).

This is an index species for zone 33, and a cosmopolitan form recorded from Europe, Asia, North America and Australia.

Systematic position. — Graptolites described by Barrande (1850) under this specific name, have by Perner been shown to be actually fragments referable to different species, two belonging to Cyrtograptidae, and one only (figured by Barrande in fig. 16) being *M. nilssoni*. It has, however, been shown by Bouček (1936, p. 5) that the latter is actually a fragment

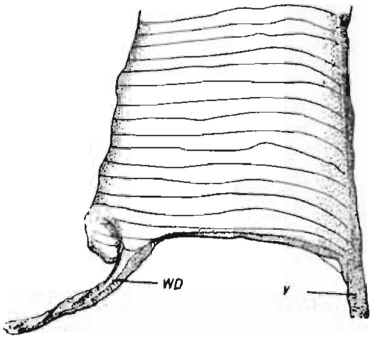


Fig. 53

Pristiograptus nilssoni (LAPW.)

Aperture of metasicula, right side view: *v* virgella, *wd* dorsal process (S. 20, Poznań); × 100 approx. (after URBANEK, 1954).

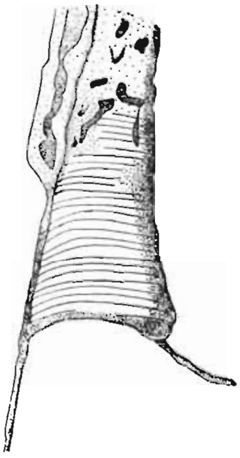


Fig. 54

Pristiograptus nilssoni (LAPW.)

Aperture of metasicula, left side view (S. 20, Poznań); × 58 approx. (after URBANEK, 1954).

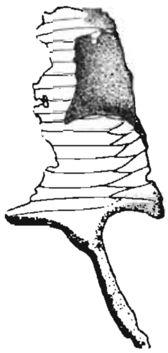


Fig. 55

Pristiograptus nilssoni (LAPW.)

Fragment of periderm near zigzag suture at base of dorsal spine of sicula (S. 20, Poznań); × 86 approx. (after URBANEK, 1954).

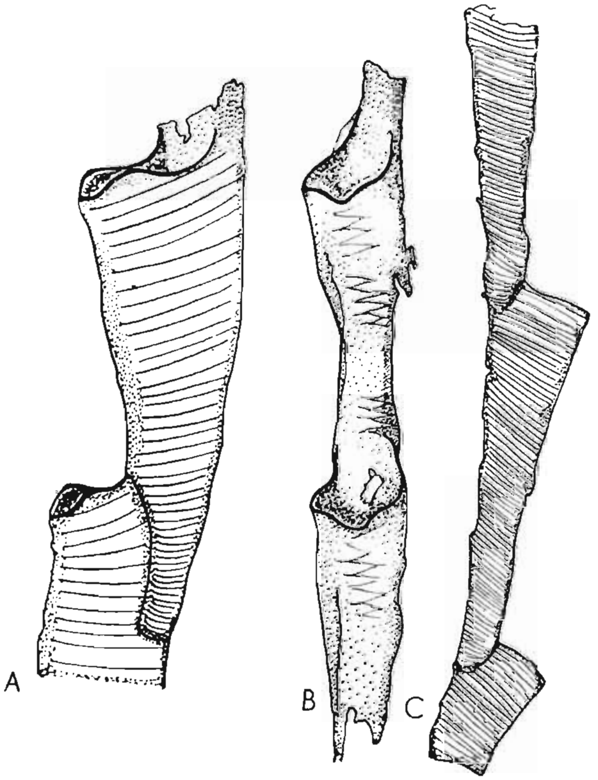


Fig. 56

Pristiograptus nilssoni (LAPW.)

Two fragments of rhabdosome with distal thecae: *A* lateral view, *B* ventral view (S. 36, Jarosławiec); *C* proximal thecae (S. 38, Jarosławiec), × 30 approx.

of *Cyrtograptus hamatus* Baily. Hence, according to that author, the priority of *P. nilssoni* belongs to Lapworth[11].

Morphologically *P. nilssoni* is most interesting since it displays a number of peculiar features. Those most characteristic are the rather exceptional curvature of the rhabdosome and the presence of an unpaired apertural spine of the metasicula, closely approaching the apertural spines of diplograptid metasiculae. The closest structural resemblance is here observed with the apertural spines of *Orthograptus gracilis* (Roem.) (comp. Kraft, 1926, pl. 7, fig. 5). Further growth, however, produces in *Orthograptus gracilis* two symmetrical apertural spines separated by a shallow notch, while in *P. nilssoni* (Lapw.) the right spine only is formed. Such apertural spines are very frequent in diplograptids. They have been described, for example, by Kraft in *Orthograptus gracilis* (Roem.) (lappenförmige Stacheln); by Bulman in various representatives of the genus *Climacograptus*, *Orthograptus* and *Lasiograptus*; by Cox in *Climacograptus inuiti* Cox; and by Walker in *Diplograptus* cf. *(Amplexograptus) maxwelli* Decker.

In monograptids, on the other hand, they are quite an exception. It is naturally difficult to establish whether these are cases of convergence or not.

It is interesting to note that up to now no concern has been shown regarding the presence of an asymmetric apertural spine in the metasicula of *P. nilssoni* (Lapw.). But this spine is clearly figured in text-fig. 241-a of Elles & Wood (1913, p. 370) though those authors do not mention it. Neither does Kühne (1955) mention this structural peculiarity though material of this species from erratic boulders is rather abundant.

Pristiograptus dubius (Suess), 1851

(text-fig. 57; pl. V, fig. 1-2; text-pl. VII)

1851. *Graptolithus dubius* Suess; E. Suess, Über böhmische Graptolithen..., p. 115, pl. 9, fig. 5 a-b.
1933. *Monograptus dubius* (Suess); I. Cox, On the structure..., p. 421-425, fig. 1-16, pl. 11.
1953. *Pristiograptus (Pristiograptus) dubius* cf. *dubius* (Suess); A. Urbanek, Sur deux espèces de Monograptidae, p. 101-102 (French text), fig. 8.
1953. *Monograptus dubius* (Suess); M. Walker, The development of *M. dubius*, p. 365-370, fig. 2-3.
1955. *Monograptus dubius* (Suess); W. G. Kühne, Unterludlow-Graptolithen..., p. 360-365, fig. 2.
Further references:
1943. A. Přibyl, Revision der Vertreter der Gattung Pristiograptus..., p. 4, pl. 1, fig. 4-6.

Material. — This species is very common in fauna from erratic boulders, being encountered in nearly every graptolite-bearing boulder. Most of the material here comes from erratic boulders: S. 16 (Łebcz), S. 19, 20 (Poznań), S. 36 (Jarosławiec), S. 110 (Rewal), S. 118, 123 (Lubin), S. 127, 130, 131 (Władysławowo) and S. 134 (Gdynia-Orłowo). There are about 50 proximal rhabdosome parts in a satisfactory state of preservation. Distal parts are less numerous. The great number of siculae has enabled a complete reconstruction of ontogeny.

Description. — Rhabdosome with slight ventral curvature in the proximal part.

Sicula with length ranging from 1.56 to 2.06 mm, an average of 1.73 mm.

Prosicula with a mean length of 0.39 mm. Older prosiculae in proximal fragments of rhabdosome often show some damage of apex (as many as 22 out of 33 specimens).

There are usually two elongated secondary strips rimming the opening thus formed.

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[11] This note of Bouček was not taken into account by the present writer in his paper of 1954.

Metasicula shows extensive variation of length ranging from 1.16 to 1.6 mm. Besides the virgella, the aperture of metasicula is provided with a blunt dorsal lip. In our specimens there are peridermal rings in the metasicula. The apertural ring of prosicula and the bud ring are nearly always developed and between them are from 3 to 5 intervening rings; in one case their number reached seven. On the other hand, completely ringless forms were also observed.

The latest researches, particularly those of Cox (1934), URBANEK (1953) and WALKER (1953) have clarified the ontogeny of siculae and of the first theca. It agrees with the general developmental pattern established for the monograptids. The virgella starts at a distance of 0.24 to 0.36 mm from the aperture of the prosicula. Apertural budding commences with the formation of a notch (EISENACK's «sinus»), by a curvature of the fuselli in the virgella area. The pore usually begins to develop at 0.65 to 0.9 mm from the aperture of the prosicula and at 0.7 mm from the aperture of the metasicula. This notch is subsequently closed up by the new fuselli. The first fuselli of the first theca form in the right corner of the pore.

The thecae are cylindrical with a smooth aperture and without any processes. The apertural margins are thickened. The majority of thecae increase in size and the width of the rhabdosome increases accordingly. At the mid-point of the first theca its width is 0.38 mm, while at the mid-point of the 13th theca it is from 1 to 1.24 mm. However, the growth rate of thecae here is slower than in for example *S. chimaera* (BARR.) (comp. pl. II, fig. 3, 4).

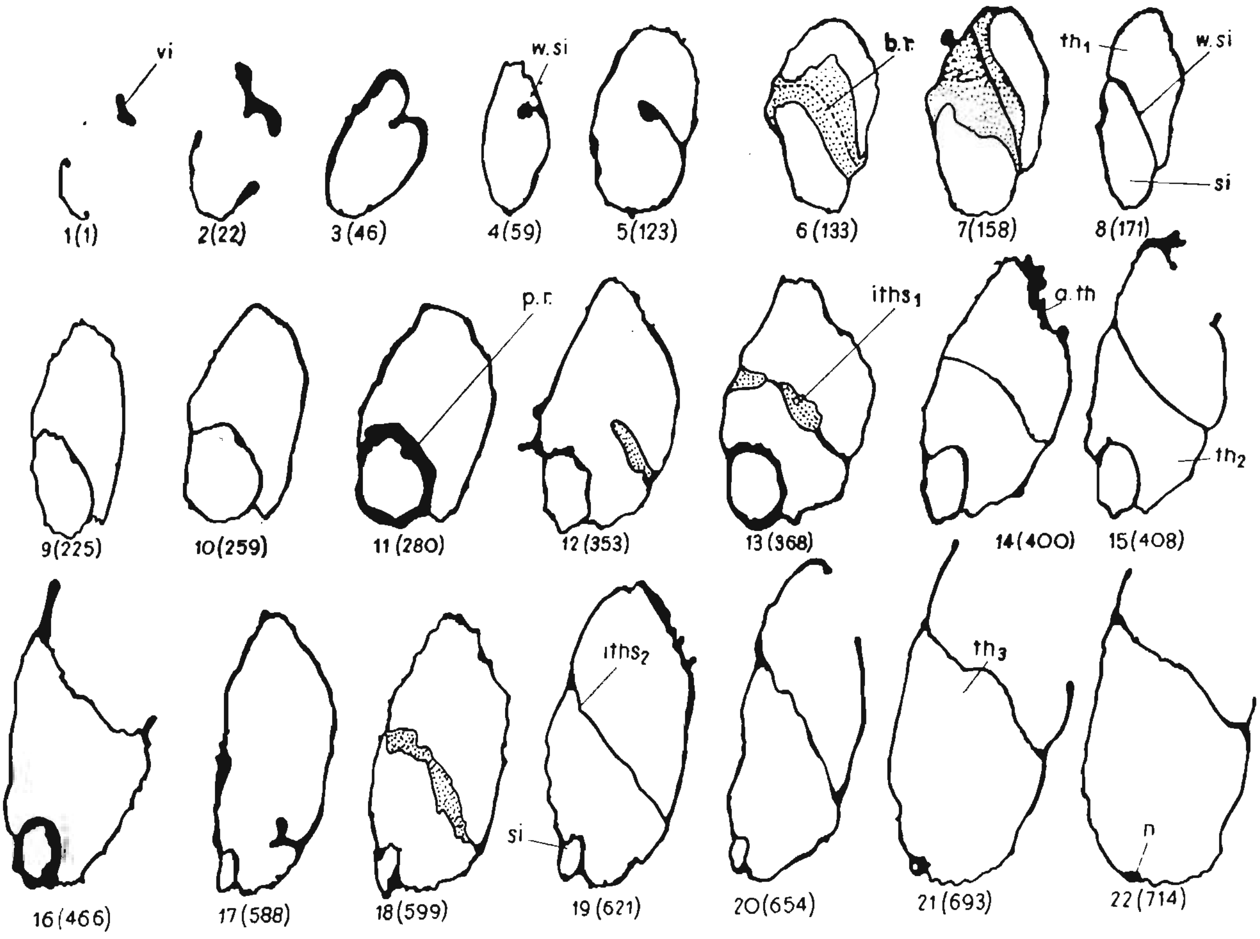
Text-pl. VII shows a series of microtome cross sections of the proximal part of the rhabdosome in *P. dubius*. Sections 1-2 are those of the virgella, 6-7 of the bud ring, other rings are shown in section no. 11. The development of the interthecal septum is well seen in sections nos. 12, 13, 17 and 18, the thickening of the thecal aperture — in sections nos.14, 19 and 22.

Structure of interthecal septum. — The irregularity of the fusellar structure of this part of the thecae in *P. dubius* has already been stressed by Cox (1934, p. 432-434). His interpretation of that phenomenon was similar to that advanced by BULMAN (1932, p. 27, fig. 15) regarding the fusellar structure in *Orthograptus gracilis*. Cox believed that in both these cases the irregularity of fusellar structure is due to its formation from «undifferentiated tissue from which the «zooids» were severally derived» (p. 434).

WALKER (1953, p. 367-368) has dealt with the same problem. According to her view, the basal end of the septum is formed by fuselli normally placed and producing the dorsal suture, while short, incomplete fuselli, formed by the next individual of the colony, are intercalated between these normal fuselli. There is thus, over some distance, an interdigitation of the fusellar systems of two zooids. In the upper part the fuselli of the younger zooid take up more and more space and finally they push out those of the preceding zooid (WALKER, 1953, fig. 3 *A-B*). WALKER is of the opinion that «the method described above is probably the main way in which the interthecal septum is formed».

The conception put forward by WALKER is an interesting one but difficult to prove. First of all, the rhythm of thecal formation shows that when the first fuselli of theca ($n + 1$) just appear, the theca n has almost definitely formed its aperture and has actually completed its growth. It is, therefore, difficult to understand how zooid $n + 1$ was able to build up the interthecal septum at a fair distance from its aperture, since its own protheca is still markedly small. Neither is it clear where the small fuselli intercalated on the septum belong to. WALKER refers them to individual $n + 1$, but with inadequate evidence. According to WALKER, the intercalated fuselli become bigger and change into normal fuselli of theca $n + 1$.

TEXT-PLATE VII



Pristiograptus dubius (Suess)

Serial transverse microtome sections of proximal part of rhabdosome; numbers in parenthesis correspond to actual numbers of sections cut at 3μ (S. 36, Jarosławiec); × 70 approx.

vi virgella, *w. si* wall of sicula, $iths_1$, $iths_2$ interthecal septum, *b. r.* bud ring, th_1-th_3 successive thecae, *si* sicula, *n* nema, *p. r.* peridermal ring, *a. th.* thickening of apertural margin.

Specimens, studied by the present writer, of *P. dubius* (fig. 57) and of *S. chimaera* do not provide any ground for such an interpretation. This structure varies markedly in the different specimens. Some of them might suggest an interpretation agreeing with that of Walker (e. g. septum of th 2 in fig. 57 *B*), in others, however, the arrangement is quite different e. g. th 1, th 3, th 4). There is no distinct increase in size of the intercalated fuselli corresponding to thecal growth and the disappearance of lateral ones. There is only a well marked border line between the part of septum with intercalated fuselli (zooid *n*) and that without them (zooid *n* + 1).

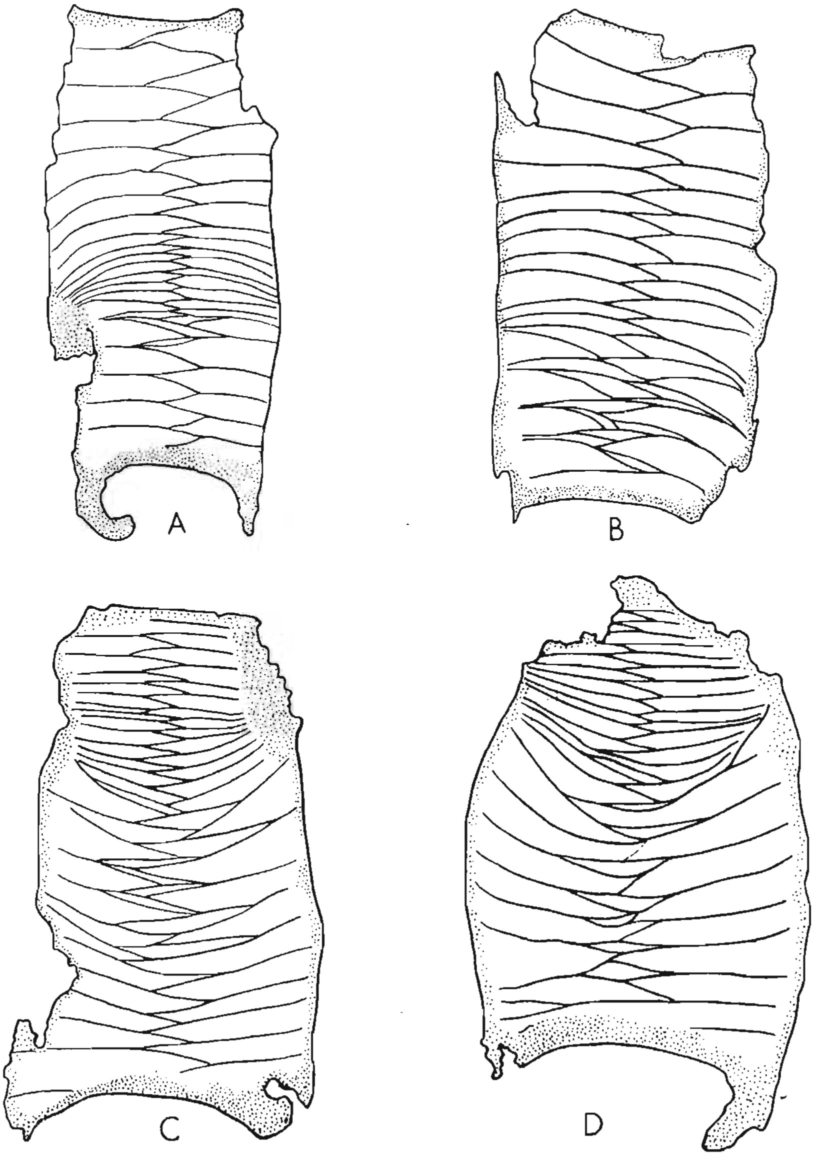


Fig. 57

Pristiograptus dubius (Suess)

Fusellar structure of interthecal septum in four first thecae *A-D* (S. 36, Jarosławiec); × 66 approx.

It is noteworthy that in *P. dubius* intercalated fuselli have also been ascertained by KÜHNE (1955, p. 363-364) on the dorsal side of the protheca, near the nema. No such occurrence has been observed in our material.

Faunal assemblage and stratigraphical distribution. — *P. dubius* is mostly found in association with: *Saetograptus chimaera* (BARR.), *Monograptus (Monograptus) uncinatus* TULLB., *Pristiograptus bohemicus* (BARR.), *Lobograptus scanicus* (TULLB.), *Gothograptus nassa* HOLM.

This is a relatively long-lived form, recorded throughout the Wenlock up to zone 34 (with *L. scanicus*) in the Lower Ludlow. It has been described from Europe, Asia, North America and Australia.

Systematic position. — In addition to the type form, two sub-species (*P. dubius latus* BOUČEK and *P. dubius ludloviensis* BOUČEK) have been distinguished on flattened specimens. It is rather difficult to determine to which of them the form studied here belongs. However, it comes closer to the type form.

In the form described by Cox (1934) and referred by him to *Pristiograptus dubius*, the peridermal rings were altogether missing on the metasicula.

URBANEK (1953) and WALKER (1953*a*) have described specimens of *P. dubius* having peridermal rings on the sicula. Together with these, a number of ringless forms was also recorded. Considering that this feature is subject to strong variation in *P. dubius* (SUESS) and in other monograptids as well, it may be regarded as being only the expression of intraspecific variation. The varying number of ringed and ringless forms within the different populations may thus probably express their genetic differentiation.

Pristiograptus sp.

(text-fig. 58)

Material. — Exceedingly poor, etched from erratic boulders S. 32 (Gdańsk-Wrzeszcz) and S. 58 (Jarosławiec). A few rhabdosome fragments, probably distal parts. No sicula. Specimens difficult to clear.

Description. — Thecae straight, very long and thin, with smooth aperture. In the apertural region theca widens slightly thus becoming funnel-like. Rhabdosome with a slight dorsal curvature (fig. 58 *A*, *B*).

Distance between ventral edges of apertures in adjacent thecae markedly great, being from 1.2 to 1.5 mm. Basal width of theca about 0.13 mm, height of rhabdosome in the apertural region about 0.25 mm. The thecal length distinctly exceeding their width. This gives the rhabdosome a thread-like appearance (fig. 58 *A*, *B*).

In one case (fig. 58 *C*) it has been possible to observe a damaged theca with the construction of a secondary wall in the apertural region. No fusellar structure has been detected on the regenerated part in spite of strong clearing.

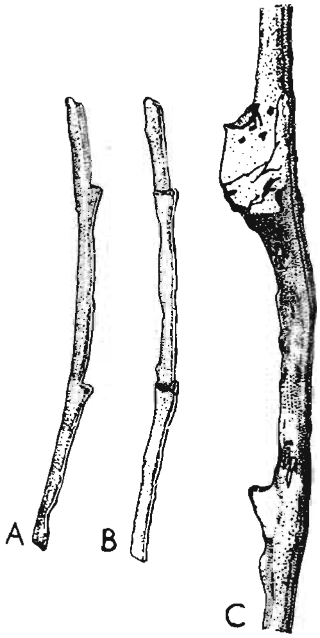


Fig. 58

Pristiograptus sp.

Fragment of rhabdosome: *A* lateral view, *B* ventral view; × 16 approx.; *C* abnormal shape of theca, probably caused by regeneration; × 33 approx. (S. 58, Jarosławiec).

Faunal assemblage and stratigraphical distribution. — This form was found in association with: *Monoclimacis haupti* (Kühne), *Saetograptus chimaera* (Barr.), *Lobograptus scanicus* (Tullb.).

Its occurrence is therefore referable to the Lower Ludlow.

Systematic position. — The fragmentary condition of our material does not permit a closer determination of the systematic position of this form. It seems to be identical with a form described by Kühne as *Monograptus* sp. (1955, p. 395-397, fig. 17). The only detectable difference is that the specimen of that author (fig. 17 *A*, *B*) has a slight ventral curvature of the theca, not noted in our material.

It is very likely that a form assigned by Bouček to *Monograptus crinitus* Wood (1936, p. 21, text-fig. 4-k) belongs to the species here considered. That form differs widely from other specimens also referred to *M. crinitus* Wood (fig. 4-j, l, m), while it closely approaches the thecal form in the species here studied.

In shape of the thecae *Pristiograptus* sp. differs strongly from other representatives of this genus, particularly from the Ludlovian forms. In the Llandovery, however, we encounter forms more similar in appearance to the ours, e. g. *M. (Pristiograptus?) sandersoni* Lapw. It is nevertheless hardly possible to determine the nature of this resemblance.

Genus **MONOCLIMACIS** Frech, 1891

Monoclimacis haupti (Kühne), 1955

(text-fig. 59-64; pl. IV, fig. 5)

1955. *Monograptus haupti* Kühne; W. G. Kühne, Unterludlow-Graptolithen . . ., p. 365-368, fig. 3 A-F.

Material. — About 60 fragments of proximal parts of rhabdosome, about 25 fragments of the distal parts and extremely numerous siculae belonging to all ontogenetic stages. Most of the material has been recovered from erratic boulders: S. 116, 155, 156 (Rewal), S. 125 (Władysławowo), S. 135 (Niechorze), S. 139 (Ustka), S. 148 (Jarosławiec). The majority of specimens are in a satisfactory state of preservation.

Description. — Rhabdosome with a slight ventral curvature in the proximal part. Thecae with ventral excavation.

Sicula attains a mean length from 1.76 to 1.4 mm; it is very slightly ventrally curved. It ends under the protheca of third theca (fig. 59 *A-C*, 60 *A-C*, 61 *A-C*).

Prosicula with length ranging from 0.56 to 0.48 mm (fig. 59 *A*, *C*). In the early stages fairly numerous, moderately thin, longitudinal threads are visible on the surface. They converge apically into the nema, which, however, is usually damaged. The margins of the apical opening thus formed become thickened and secondary bands are produced, while the threads disappear under the thickened periderm (fig. 61 *A*,*B*). These bands, usually two in number, fuse into the secondary regenerative nema. The youngest prosiculae display the helical line which it is hard to detect on older specimens. The aperture of the prosicula has a thickened apertural ring.

Metasicula with markedly conspicuous peridermal rings. In most cases three rings are present besides the bud ring. This is frequently not completely closed up. The aperture of the metasicula has the greater diameter from 0.15 to 0.20 mm, with the virgella protruding from 0.38 to 0.49 mm beyond the apertural margin.

The great number of available young siculae enable a complete analysis of the ontogeny (fig. 60 *A-C*). The formation of the pore is effected by the development of a notch («sinus» stage) subsequently closed up by a fusellar strip («lacuna» stage). The first thecal fuselli are formed, as usual, in the right corner. Fig. 61 *C* shows the final sicula with a fragment of the first protheca.

The thecae have a characteristic outline owing to a fairly strong ventral excavation which makes them similar to thecae in *Climacograptus*. The thecal aperture is smooth, without processes but provided with a thickened margin, almost perpendicular to the axis of the rhabdosome. The excavation is rimmed by a slightly thickened and somewhat protruding subcircular margin, constituting a flat area with a median zigzag suture. This flat area is formed as a result of the arched course followed by the fuselli as far as the margin, beyond which they bend down and continue flat (fig. 63 *A*, *B*). This margin may be the equivalent of the mesial margin in other species of *Monoclimacis* FRECH, more strongly protruding or

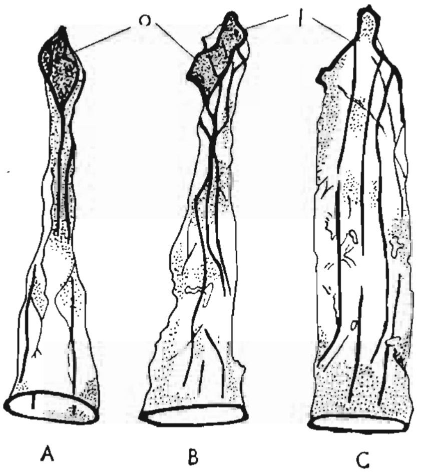


Fig. 59

Monoclimacis haupti (KÜHNE)

Prosicula, three sides, with apical opening rimmed by secondary list; *o* opening, *l* list (S. 58, Jarosławiec); × 120 approx.

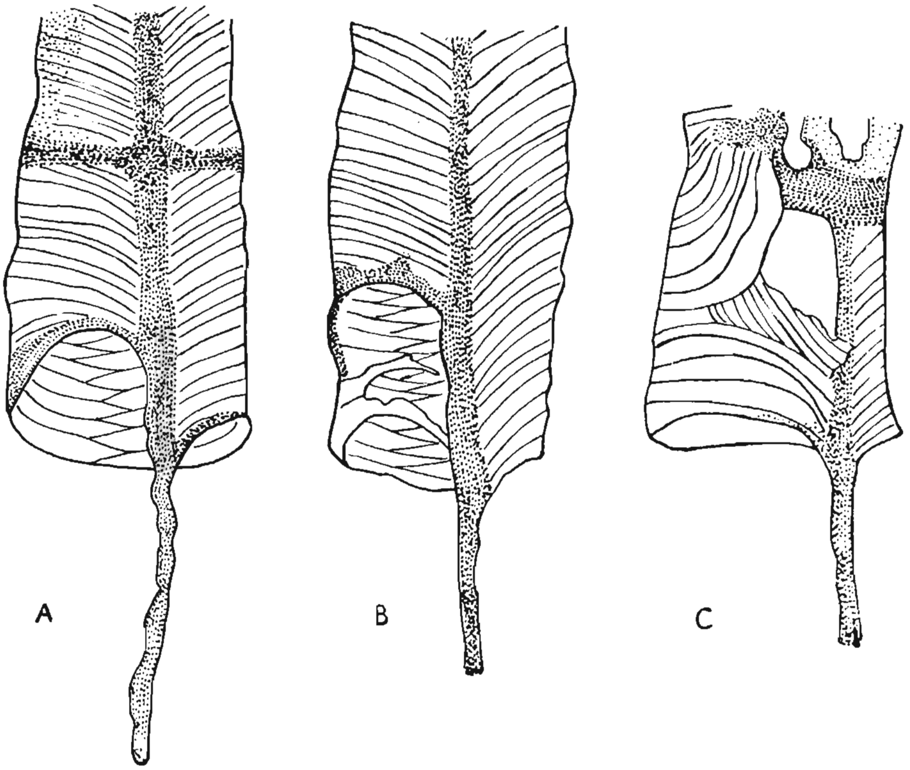


Fig. 60

Monoclimacis haupti (KÜHNE)

Budding of 1st theca: *A* «sinus» stage, *B* «lacuna» stage, *C* early fuselli of protheca (S. 135, Niechorze); × 133 approx.

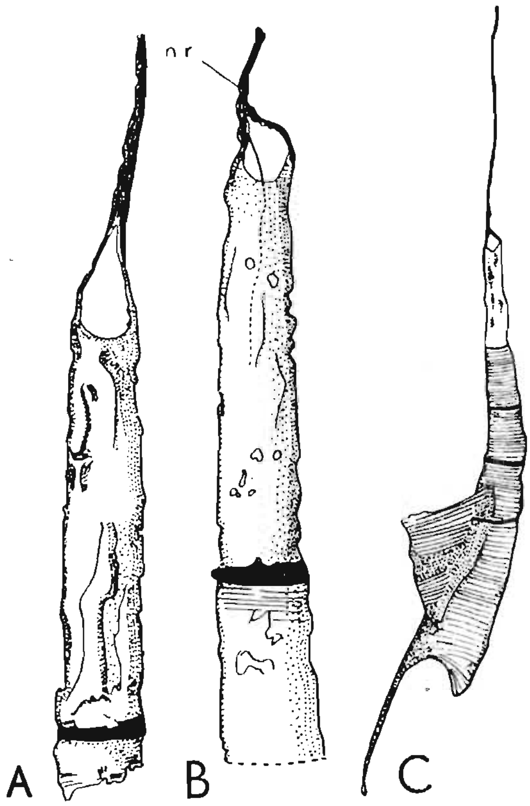


Fig. 61
Monoclimacis haupti (KÜHNE)
A, *B* prosiculae with apexes broken off and rimmed by secondary bands, *nr* regenerative nema (S. 135, Niechorze), × 120 approx.; *C* sicula with prothecal segments of 1st theca showing regenerative nema (S. 136, Niechorze); × 35 approx.

even provided with a list. The general structure here very much resembles the fusellar structure in *Climacograptus* as compared with a specimen from an Ordovician erratic boulder (fig. 62, 63 *A-B*). In that specimen the excavation is rimmed by a strongly thickened mesial list. A zigzag suture traverses the excavation medially. The pattern of fusellar structure is identical in both cases. In the proximal thecae the excavation is conspicuous, being somewhat less so but still quite distinct in the distal thecae. The aperture of the prothecae is always provided with a strongly developed apertural ring.

There is an average of 12 thecae in 10 mm, but about 7 thecae fit into the first five millimeters of rhabdosome length.

The distance between the ventral edges of apertures is in the respective thecae as follows (in mm):

Thecae	*Distance*	*Thecae*	*Distance*
1-2	0.58-0.73	7-8	0.73-0.80
2-3	0.58-0.80	8-9	0.73-0.88
3-4	0.66-0.80	9-10	0.73-0.88
4-5	0.66-0.80	10-11	0.80
5-6	0.66-0.77	11-12	0.88
6-7	0.69-0.80	12-13	0.80

They are thus seen to oscillate round a certain mean figure without directional changes.

The rhabdosome width is: in th 1 — 0.36 mm, in th 3 — 0.55 mm, in th 6 — 0.80 mm, in th 12 — 0.88 mm.

Their respective heights are: in th 1 — 0.58 to 0.66 mm, in th 3 — 0.88 to 1.10 mm, in th 6 — 1.20 mm, in th 11 — 1.50 mm.

Faunal assemblage and stratigraphical distribution. — In erratic boulders this species is accompanied by a poor assemblage of *Lobograptus scanicus* (Tullb.) and *Pristiograptus nilssoni* (Lapw.). The great resemblance of this species to *M. ultimus* (Perner) permits to suppose that form described from Thüringia as *Pristiograptus praeultimus* Münch (1942, p. 247-248, pl. 1, fig. 8-11; pl. 7, fig. 3), recorded from zone of *L. scanicus,* is actually conspecific with *M. haupti*. This needs, however, further investigations.

Systematic position. — *M. haupti* should be placed close to *M. ultimus* (Perner). Both these species are characterized by presence of ventral excavation of thecae and by similar

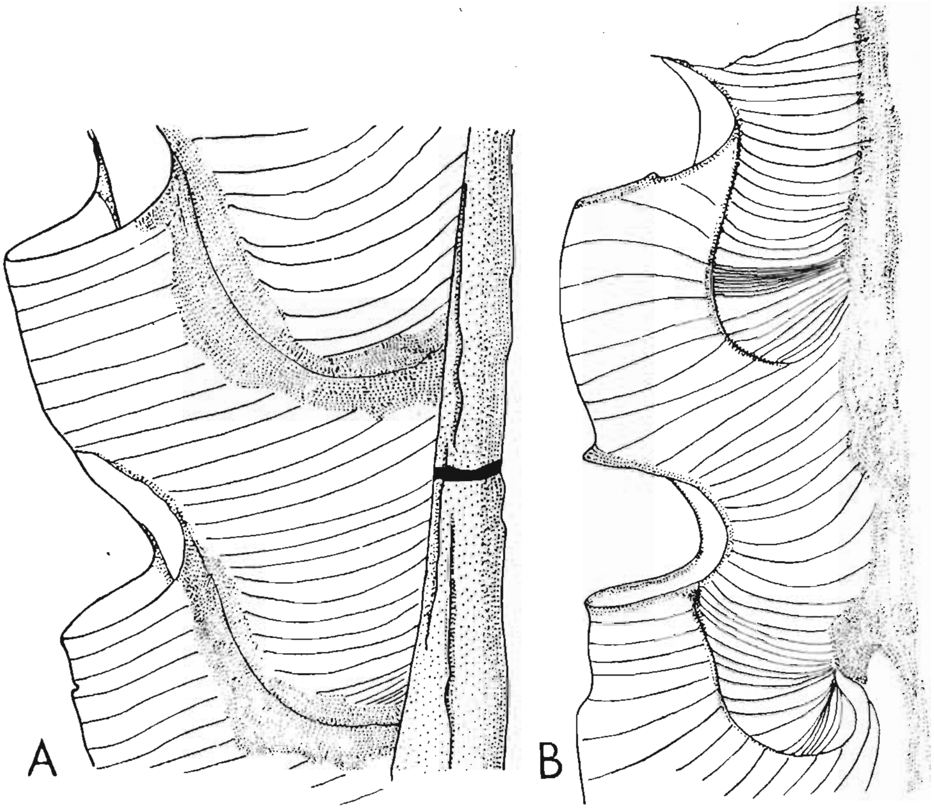


Fig. 62
Comparison of fusellar structure of thecae in (*A*) *Monoclimacis haupti* (KÜHNE) and (*B*) in *Climacograptus* sp., lateral view (*A* — S. 125, Władysławowo, *B* — Ordovician erratic boulder); × 80 approx.

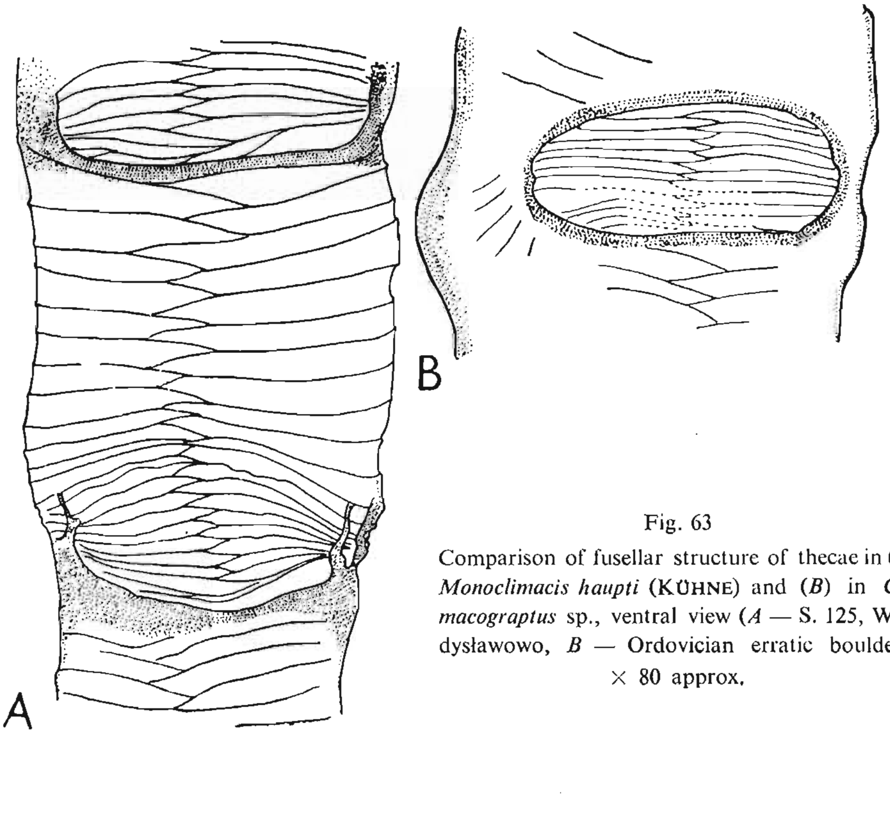


Fig. 63
Comparison of fusellar structure of thecae in (*A*) *Monoclimacis haupti* (KÜHNE) and (*B*) in *Climacograptus* sp., ventral view (*A* — S. 125, Władysławowo, *B* — Ordovician erratic boulder); × 80 approx.

curvature of sicula. Taking into account its probably early appearance, *M. haupti* may be considered as fore-runner of *M. ultimus*, or as offshoot of this trend, from which it is distinguished by different shape of first theca and oblique apertural border. The degree of excavation seems to be lesser in *M. ultimus*, as it can be seen in Bohemian descriptive types (fig. 65) (specimens figured by Přibyl, 1941, pl. 1, fig. 10, from Kosov, Narodni Museum, No. 26950, and by Perner, 1899, pl. 16, fig. 5). On the other hand, however, *M. gerhardi* Kühne has a great degree of resemblance to *M. ultimus* especially in the form of apertural border and presence of thecal excavation. The relationship between these forms and *M. ultimus* needs, however, further investigations.

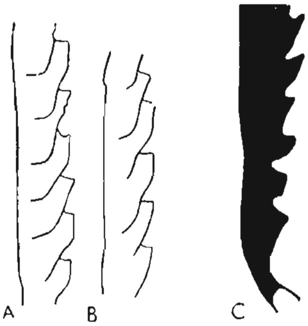


Fig. 65

Monoclimacis ultimus (Perner)
Natural sections (*A*, *B*) and outline of proximal part of rhabdosome (*C*); *A*, *B* — specimens from Kosov (Perner, 1899, pl. 16, fig. 5), *C* — specimen from Kosov (Přibyl, 1941, pl. 1, fig. 10); × 6 approx.

Kühne, who first described *M. haupti*, figured the holotype in a sketch picture only (1955, fig. 3 A-F), thus causing serious difficulties to the present writer in the identification of this species. The conclusion that our and Kühne's form are conspecific and that neither is identical with *M. ultimus*, was not reached until the author's 1958 visit to Berlin when the was able to examine the holotype and homoeotypes, thanks to the kind permission of Dr. H. Jaeger and Dr. W. G. Kühne.

The species here described should be referred to the genus *Monoclimacis* Frech. In a paramedial microtome section (fig. 64) it is easy to ascertain a markedly strong excavation, certainly no less than that in typical representatives of the genus *Monoclimacis*. The similarity is particularly striking in the natural sections of *Monoclimacis crenulata* as figured by Törnquist (1892, pl. 1, fig. 16). The agreement involves cross section of thecae, their excavation etc. In the writer's opinion, the thecal structure does refer this species to the genus *Monoclimacis* Frech. *M. ultimus* Perner and *M. gerhardi* Kühne are also referable to this genus. The poorly marked edges round the excavation are no exception here, since this is observed likewise in other species of this genus.

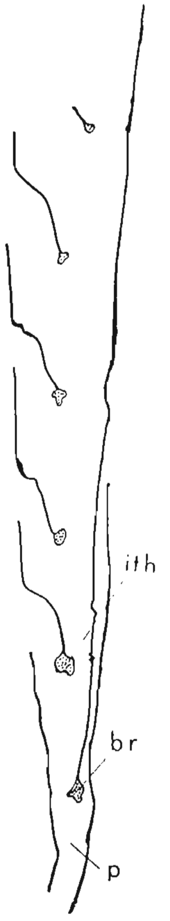


Fig. 64

Monoclimacis haupti (Kühne)
Longitudinal microtome section showing the thickening margin of interthecal septa and bud ring (S. 136, Niechorze); × 30 approx.
p pore, *br* bud ring, *ith* thickening on interthecal septum.

Monoclimacis micropoma (Jaekel), 1889

(text-fig. 66-68; pl. V, fig. 3-5)

1889. *Pomatograptus micropoma* Jaekel; O. Jaekel, Über das Alter..., p. 682-683, pl. 29, fig. 4-6.
1913. *Monograptus uncinatus* var. *micropoma* (Jaekel); G. L. Elles & E. M. E. Wood, British Graptolites, p. 428-429, fig. 291 a-b, pl. 43, fig. 2 a-c.
1955. *Monograptus micropoma* (Jaekel); W. G. Kühne, Unterludlow-Graptolithen..., p. 379-381, fig. 8 A-D.

Material. — The material available from boulders: S. 21 (Poznań), S. 54 (Dziwnów), S. 133 (Gdynia-Orłowo), S. 135 (Niechorze), S. 156 (Rewal), consisted of about 10 proximal fragments; 3 rhabdosomes of the senile type and several fragmentary siculae with 1-2 thecae, in an unsatisfactory state of preservation.

Description. — Two forms are represented in the above material; one with the mesial edge relatively short (pl. V, fig. 3) and the other with broad and hood-like edge (pl. V, fig. 4). This is probably due to ontogenetic thecal variation. The older thecae would probably take on a senile appearance characterized by a conspicuous mesial list. Individual differentiation is also noted here as some rhabdosomes grow senile-like earlier than others, as also occurs in *Saetograptus chimaera* (BARR.) (comp. p. 60).

Rhabdosome straight. Thecae with sigmoid curvature, and a process on the mesial edge.

Sicula from 1.85 to 1.90 mm. Aperture in metasicula with the longest axis about 0.15-0.16 mm, with a blunt dorsal lip. Apex of prosicula ends at level of metatheca 2.

Thecae (fig. 66, 67), th 1 excepted, sigmoidally curved. Ventral wall on the boundary between the protheca and the metatheca showing an excavation fully analogous to that in *Monoclimacis haupti* (KÜHNE). This excavation constitutes a flattened area rimmed by a subcircular edge reaching the edge of the aperture in the preceding theca. A medium zigzag suture traverses the area. As in *M. haupti* the excavation is formed by the flattening out of the prothecal fuselli. During ontogeny the thecae at first have no apertural lobes. The thecal aperture (*n*) ends straight and has a thickened margin while in the wall of the next protheca ($n + 1$) only an excavation is formed. At this stage of development the thecal arrangement agrees completely with that of *M. haupti* (KÜHNE).

Later, when the thecal aperture ($n + 1$) has already begun, a list (fig. 68 *A*) makes its appearance on the edge rimming the excavation, constituting the initial apertural lobe. In the course of ontogeny this list grows into a broad rim and finally takes on the shape of a shield (fig. 67 *A*, *B*). The structure of this lobe is most peculiar (fig. 68 *C*). It consists of extremely numerous and thin fuselli arched from one lateral end to the other without a median zigzag suture. This presents a marked contrast to the appearance of the thecal fuselli (fig. 68 *B*), while resembling the secondary growth of the apertural region in *Saetograptus chimaera* (BARR.) (comp. p. 58, fig. 29 *A-C*). Both these structures are formed when the theca is already completed and their peculiar fusellar structure has most likely some connection with it. Similar differences in fusellar structure have also been observed in *Idiotubus rectus* KOZŁ. The proximal thecal part of that form is made up of normal fuselli, while distally it consists of extremely fine fuselli (KOZŁOWSKI, 1948, p. 147-148, fig. 40). These features are, however, considered by KOZŁOWSKI as anomalous for this species and connected with an earlier check of thecal growth.

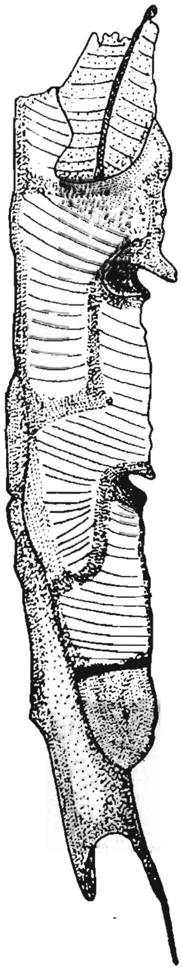


Fig. 66
Monoclimacis micropoma (JAEKEL)
Proximal part of rhabdosome, lateral view (S. 54, Dziwnów); × 36 approx.

The formation of apertural lobes of *Monoclimacis micropoma* so late in the ontogeny, if not in the senile, in any case in the mature stage, and distinguished by such a peculiar fusellar structure, is a special character of this species. Most particularly it is not homologous with the apertural lobes of other Monograptinae which, as we know (comp. p. 7), are derived from the dorsal wall of the metatheca and have a normal fusellar structure. The apertural lobes of *M. micropoma* are a kind of outgrowth built by the zooid (n) on the protheca ($n + 1$). Subsequent to the formation of the lobe, the apertural edge is raised when 1-2 fuselli are laid down joining the lobe. The aperture is thus conspicuously narrowed (fig. 66).

The distance between the ventral edges of the apertures is as follows (in mm):

Thecae	*Distance*	*Thecae*	*Distance*
1-2	0.58	5-6	0.66
2-3	0.58-0.73	6-7	0.73
3-4	0.58-0.80	7-8	0.73
4-5	0.73	8-9	0.73

Height of rhabdosome (without the process) is: under th 1 — 0.52 mm, under th 2 — 0.58 mm, under th 6 — 0.73 mm.

Width of rhabdosome is: under th 1 — 0.36 mm, under th 3 — 0.44 mm, under th 6 — 0.58 mm.

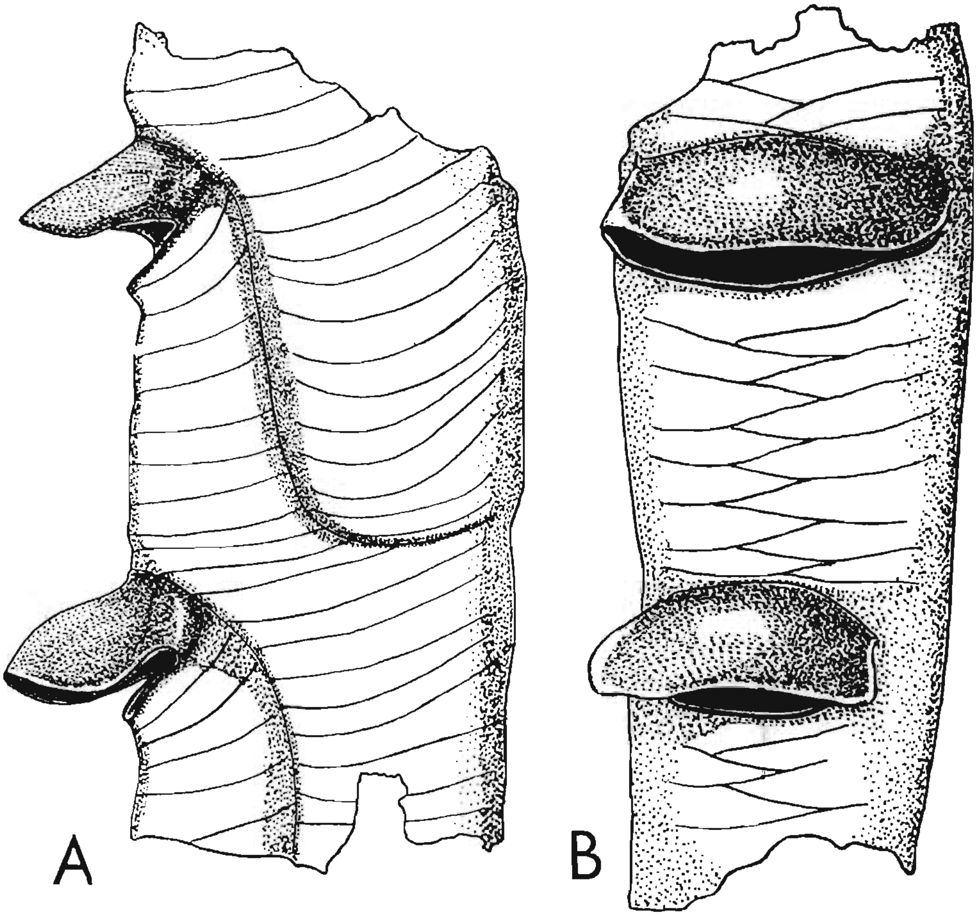


Fig. 67
Monoclimacis micropoma (JAEKEL)
Fusellar structure of thecae: *A* lateral view, *B* ventral view (S. 54, Dziwnów); × 53 approx.

There are 6 thecae on the first 5 mm and probably 9-10 thecae in 10 mm. Well developed lobes seen laterally protrude beyond the thecal edges; lobe of th 1 is about 0.07 mm long, that in other thecae from 0.22 to 0.26 mm.

Faunal assemblage and stratigraphical distribution. — This species occurs in association with: *Saetograptus chimaera* (Barr.), *Lobograptus scanicus* (Tullb.), *Pristiograptus nilssoni* (Lapw.), *P. bohemicus* (Barr.), *Monoclimacis haupti* (Kühne). It is therefore a typical Lower Ludlow form. Its occurrence has been recorded from erratic boulders and from Great Britain where it is regarded as typical of zones 33 and 34.

Systematic position. — Jaekel (1889) has referred this species to *Pomatograptus* (= *Monograptus* s. s.) on the presence of processes approaching the apertural lobes of *Monograptus priodon*.

Elles & Wood (1913) regarded it as a variety of *Monograptus uncinatus* Tullb., while Bouček (1936) made these two forms conspecific asserting that var. *micropoma* does not differ from *M. uncinatus* in a degree sufficient to warrant their separation.

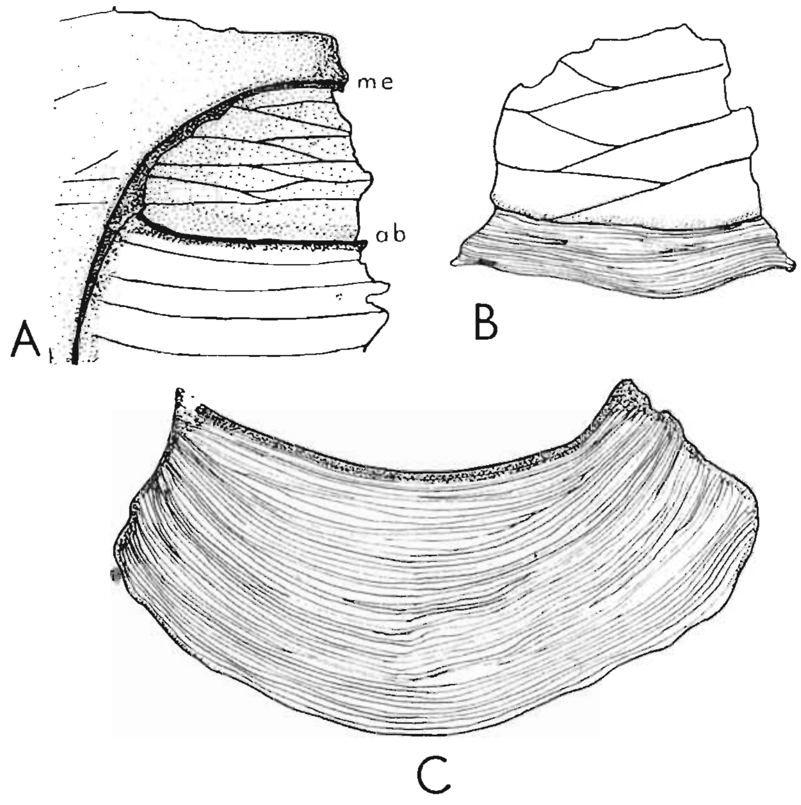


Fig. 68

Monoclimacis micropoma (Jaekel)

A mesial edge of a distal theca on first formation stage of the lobe, *me* mesial edge, *ab* apertural border; *B* apertural lobe, mesial edge with a fragment of lobe; *C* fusellar structure of apertural lobe (S. 54, Dziwnów); × 100 approx.

These opinions were not correct, inasmuch as the structure of the apertural lobes in *Monoclimacis micropoma* (Jaekel) is essentially different from those in *Monograptus priodon* and *Monograptus uncinatus*, these being non-homologous structures. The differences are so essential between these species that they not only warrant the specific separation of *Monoclimacis micropoma*, but also do not permit to place it near the above mentioned species (comp. p. 50).

Among the other species of the genus *Monoclimacis* the closest morphological relationship is shown by *Monoclimacis vomerina* (Nich.) and *M. spinulosa* (Tullb). According to Tullberg, however, the latter form occurs in the Lower Wenlockian (zone 25) so that there is a great stratigraphical gap between these species. On the other hand, it is possible that *Monoclimacis micropoma* has a direct phyletic connection with the group of *M. vomerina* (PŘIBYL, 1940 *b*), whose morphology is markedly similar. This latter group persists throughout the Wenlockian and it is replaced in the Ludlow by *M. micropoma*. It is not out of the question that *M. spinulosus*[12] is only a variation of the long-lived *M. vomerina,* which is subdivided into a number of varieties such as *basilicus*, *crenulatus* and *gracilis*.

On its thecal structure this species has even previously been placed close to forms referred to *Monoclimacis* FRECH (FRECH, 1897, p. 623-624; KÜHNE, 1955, p. 380-381), but at present only its real generic position is doubtless.

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[12] According to PŘIBYL (1940 *b*) *M. spinulosus* is only a synonym of *M. continens* TQT., 1881.

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PLATES

(All figures are retouched photographs)

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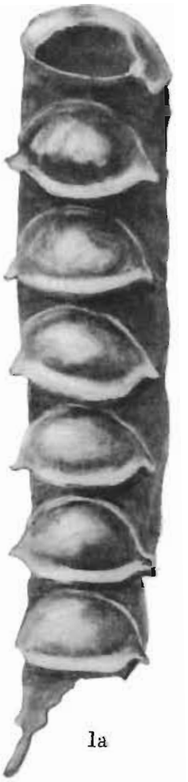
1a


1b


2a


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1


2


3a


3b


4a


4b


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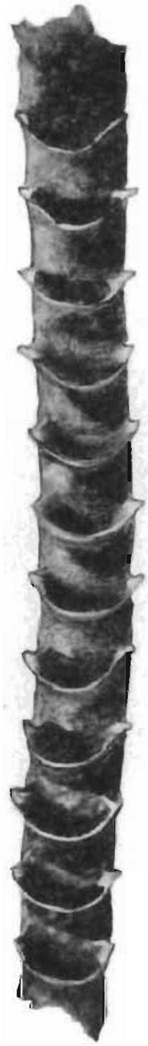
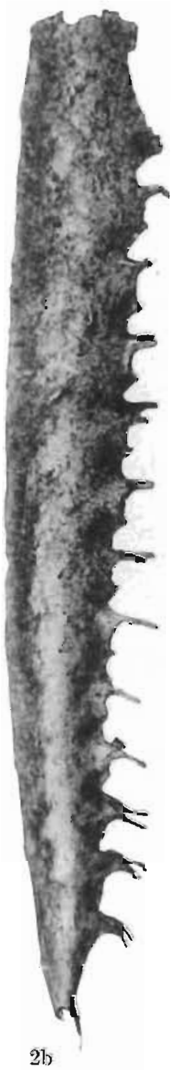

1a


1b


2a


2b


3a


3b


3c

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1

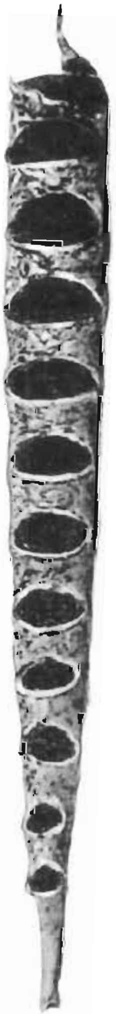

2


3


4a


4b


4c


5a


5b

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1a


1b


3a


4a


5


4b


3b


2a


2b

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