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LATE MONOGRAPTID FAUNAS AND THE PROBLEM
OF GRAPTOLITE EXTINCTION

KOREN T. N.: Late monograptid faunas and the problem of graptolite extinction. Acta Palaeontologica Polonica, 24, 1, 79—106, April 20, 1979.

Main trends and dynamics of evolution in the late graptoloids are traced on the basis of their morphology, geographical and stratigraphic distribution. Frequency distribution curve of Ludlovian-Pragian graptoloid species shows gradual but not uniform extinction. The periods of crises are followed by short intervals of increased diversification combined with a wider distribution of graptolite facies. Peaks of diversity show a regular downward trend by the end of the Pragian time. Lack of essential morphological novelties and decrease of taxonomic diversity are indicative of a biological regression of the group. Facies analysis of Late Silurian-Early Devonian deposits shows a substantial reduction of areas with typical graptolite shales and a simultaneous increase of carbonate and terrigenous sediments with mixed shelly-graptolite taphocoenoses. Decrease in carbonaceous organic matter may be evidence of an environmental change and reduction of microplankton biomass, the latter being the food resource for graptolites. Simplification of morphology to a single adaptive type, a great numerical abundance of Late Pragian populations may be indicative of the loss of ecological flexibility. Probable causes of extinction of graptoloids are discussed namely: internal organization of the colony, biocoenotic changes due to evolutionary improvements in other planktonic organisms, changes in biotops as a results of palaeogeographic reconstruction.

Key words: Extinction, graptolites.

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INTRODUCTION

In the history of graptoloid studies which are nearing their 150-th anniversary, late monograptids are the newest object of investigation. The first step towards recognizing the early Devonian monograptids was made by the stratigraphers in the sixties. Their correlations allowed to establish the Gedinian age of the *uniformis-hercynicus* Zone which had been considered Silurian. Then, the last decade featured a number of further important findings of graptoloids in the Devonian deposits, namely, in the Pragian Stage of the Barrandian and in its analogues in other regions.

At present, the late Silurian—early Devonian monograptids have been observed on all continents except South America and Antarctica.

In order to show the distribution of Pridolian, Lochkovian and Pragian monograptids, all known localities have been plotted on maps based on palaeomagnetic data (Smith *et al.* 1973; modified by Pickett 1975 and R.B. Rickards MS.). It was beyond the scope of my work to produce palaeogeographical or facies maps; therefore, what is shown here is the distribution of graptoloids, the generalized lithofacies type and rough outlines of the land masses according to the American and Soviet evidence. The Pridolian and Lochkovian graptolite-bearing deposits were found in the Cordilleran, Yukon, Arctic, Canadian or Appalachian regions of North America, in many localities of Northern Africa and Central Europe, in the Ural-Tien Shan region and also in Thailand, Malaya and Southern Australia. Pragian monograptids are recorded in fewer sections within the same territories. They are most widely distributed in North America (Nevada, Alaska, Yukon, the Canadian Arctic Archipelago), in the Ural-Tien Shan and Himalaya-Thailand folded areas. Their individual occurrences can be observed in the Barrandian and Bardo Mountains of Central Europe, Northern Africa and Southern Australia. As can be seen from the maps, the fossiliferous late-monograptid-bearing deposits are chiefly confined to the tropical belt, that is within the palaeolatitudes 40—45°N and 30°S.

Late Silurian and, probably, early Devonian geography knew no large land masses in the low palaeolatitudes, displaying a large southern continent and a multitude of smaller land masses in the northern hemisphere (Pickett 1975). This allowed for free migration of planktonic graptolites within one large equatorial basin. Late monograptids have a striking similarity of taxonomic composition in the assemblages of the same age in all regions under study.

The Upper Silurian—Lower Devonian graptolite-bearing deposits are chiefly the sediments of the miogeosynclinal zones of the basins. Monograptids occur in argillaceous shales, limestones, siltstones, sandstones and other rocks (fig. 1—3). They are most abundant in black carbonaceous-argillaceous shales and argillites. But in the Upper Silurian-Lower Devonian sections these deposits rarely build thick monotonous beds over large stratigraphic intervals. More often, thin bands or intercalations of graptolite shales alternate with limestones bearing benthic fauna. Some of the latest graptolites were found in the carbonate-shelly facies of Nevada, South Tien Shan and others.

Biostratigraphic investigations prove the stratigraphic importance of late monograptids. The Pridolian, Lochkovian and Pragian stages of the Barrandian are usually employed as standard units for subdivision of Upper Silurian—Lower Devonian deposits. The zonal subdivision is based on the succession of monograptid assemblages as traced in the sections of Barrandian, Thuringia, Poland, Canada, the USSR and other regions. A more accurate zonation was achieved due to global studies



Fig. 1. Distribution of graptoloids during the Pridolian. Reconstruction by Smith *et al.* 1973, modified by Pickett 1975 and Rickards R.B., MS. For all maps, lined shading indicates probable land areas; graptolite occurrences in different kinds of sediments: shaded circle — graptolite shales, quadrangle — mixed limestone and argillite successions, triangle — mainly carbonate deposits, cross — variable clastics and volcanics.

and correlation of boundary Silurian-Devonian deposits (Martinsson *ed.* 1977). The Pridolian of the Upper Silurian contains the *ultimus* (= *formosus*) and *transgrediens* Zone (Jaeger 1967). The latter can be subdivided into the *lochkovensis*, *bouceki*, *perneri* and *transgrediens* subzones. Zonation of this stage requires further study.

The Lochkovian stage is accepted as spanning the *uniformis* and *hercynicus* Zones, the two graptolite zones of world-wide distribution.

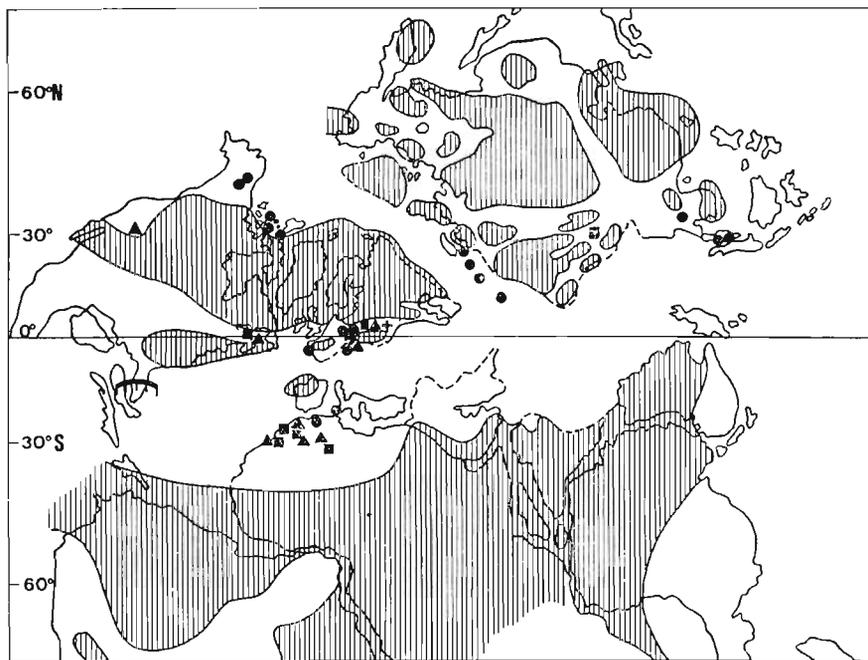


Fig. 2. Distribution of graptoloids during the Lochkovian. Reconstruction by Smith *et al.* 1973, modified by Rickards R.B., MS.

The zonal stratigraphy of Post-Lochkovian or Pragian deposits has been developed during the last decade on the basis of the Lower Devonian sections of Yukon, Alaska, Malaya, Thailand, Australia, Barrandian, Poland, the Ural-Tien Shan region and China. Establishment of a graptolite zonal sequence on the basis of the latest monograptid succession is not so easy due to the lack of continuous graptolite-bearing sections which would span the entire Pragian. For the present, the *falcarius*, *janicus* and *yukonensis* Zones can be traced in the Post-Lochkovian deposits of Europe and Asia. The *yukonensis* Zone is also widely distributed in North America and, possibly, present in Australia. The problem of monograptids of post-*yukonensis* age (the *pacificus* Zone, Churkin *et al.* 1970) is still open.

Thus, the stratigraphic distribution of late monograptids and their wide geographical extent permit broad time correlations together with tracing system and stage boundaries.

LATE SILURIAN — EARLY DEVONIAN MONOGRAPTIDS

This chapter deals with taxonomic composition, chief morphological characters, general trends and evolution of Pridolian, Lochkovian and Pragian monograptid fauna.

Taxonomy. — The late Silurian — early Devonian graptoloids belong to the family Monograptidae and the subfamily Linograptinae of the Cyrtograptidae. These taxonomic categories are discriminated owing to the presence or lack of sicular cladia. The Pridolian — Lochkovian monograptids are fairly diverse and abundant, forming the bulk of the assemblage. Multiramous linograptids disappear towards the beginning of the Pragian, giving way to the latest monograptid faunas.

Systematic stratigraphic investigations make use of monograptid species as the main taxonomic category. Being easily diagnosed due to their fairly distinct morphological and metric characteristics these

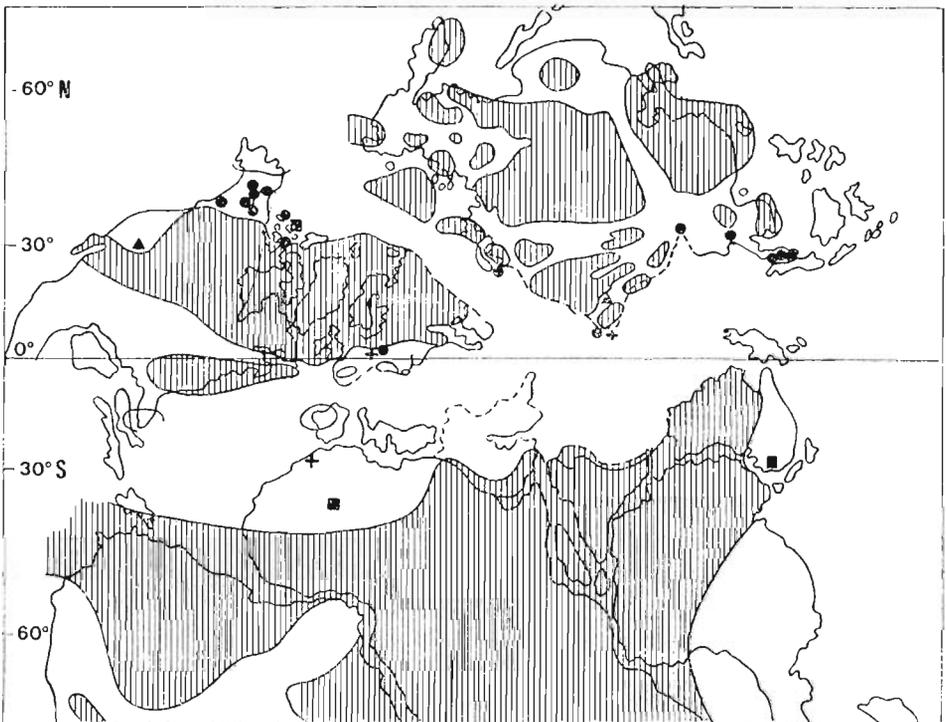


Fig. 3. Distribution of graptoloids during Pragian. Reconstruction by Smith *et al.* 1973, modified by Rickards R.B., MS.

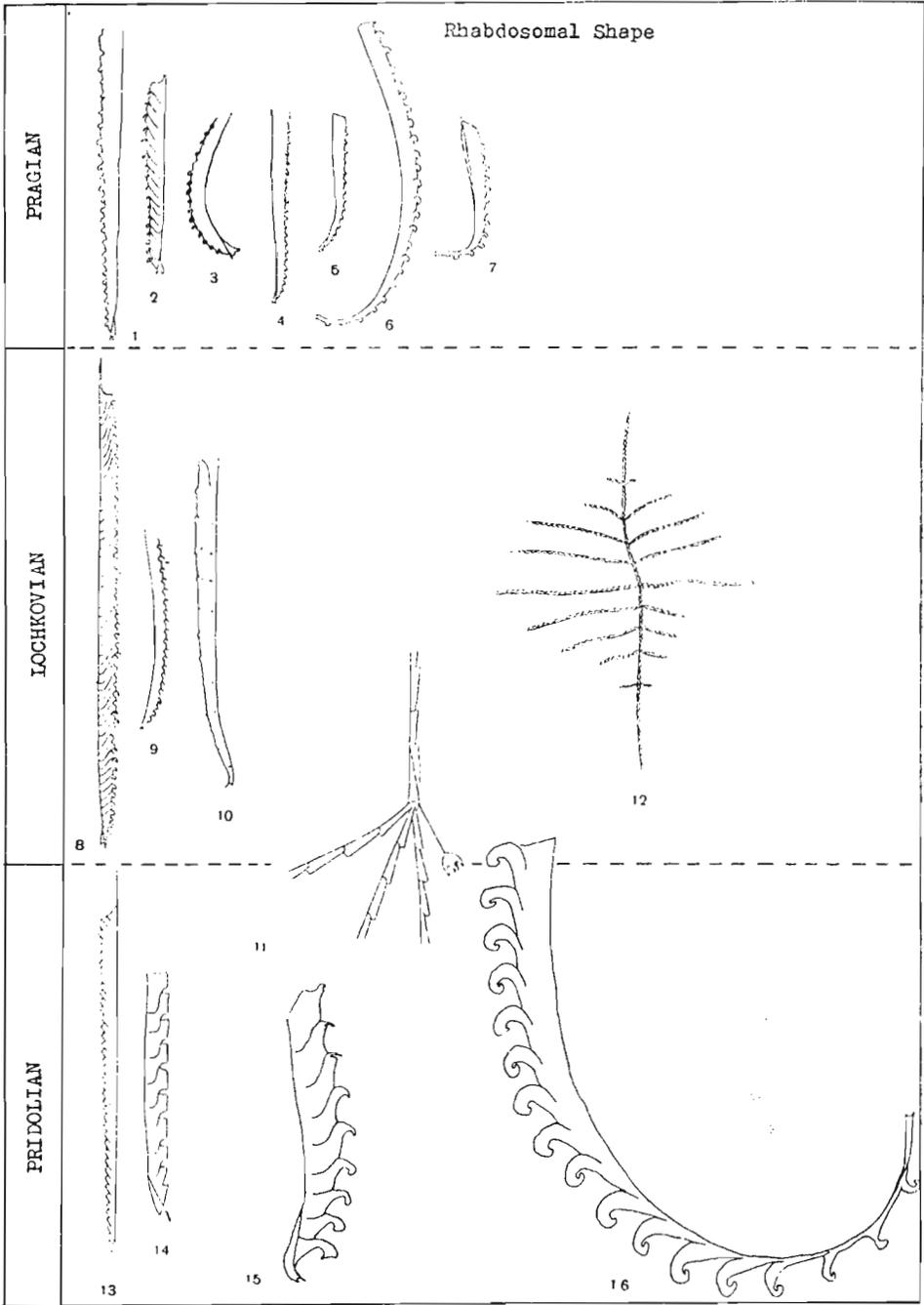
species are widely accepted. The generic categories, however, cannot be established so easily, as their scope and discriminatory criteria are highly debatable. Let us take some examples. The *ultimus* species can be found in literature under such generic definitions as *Monograptus*, *Monoclimacis*, *Pristiograptus*. The species of the *transgrediens* and *dubius* groups are referred by different authors either to *Pristiograptus* or *Monograptus*, while *lochkovensis* is classed with *Monograptus*, *Pristiograptus*, *Saetograptus* and others.

The genus *Monograptus* is usually regarded as a broad taxonomic category, a kind of a "portmanteau genus" (Bulman and Rickards 1970). According to Bulman's diagnosis (1970), it embraces almost every known species of late representatives of the family Monograptidae, varying in the structure and shape of aperture, and differing considerably from the apertural structure in *Monograptus priodon* — which is the type species. It is clear that *Monograptus s.l.* should be subdivided into smaller genera or subgenera, but the present knowledge of the details of their morphology and phylogeny is still insufficient for the purpose. It is possible that future studies of three-dimensional specimens isolated from the rock would yield some new revelations, similar to those made by Urbanek when investigating Ludlow monograptids (Urbanek 1958, 1960, 1966, 1970). The recent attempts at establishing new genera (Mu 1974; Tsegelnyuk 1976) do not seem convincing due to the lack of sufficiently distinct morphological criteria.

Morphology. — Our knowledge of morphology of Pridolian-Pragian monograptids depends upon the preservation of the material available for palaeontological study. It appears in the shape of flattened, semi-flattened or, more rarely, three-dimensional specimens in the rocks of variable composition. No three-dimensional rhabdosomes have been obtained yet by chemical treatment from deposits above the *formosus* Zone.

Late graptoloids display two types of colonies, single (*Monograptus*) and multiramous of which the latter either consists of several sicular cladia (*Linograptus*) or also have thecal cladia (*Abiesgraptus*). These

Fig. 4. Rhabdosomal shape of the Pridolian-Pragian graptoloids. 1 *Monograptus telleri* Jacks. et Lenz, South Tien Shan, Pragian, the author's collection; 2 *M. fanicus* Koren', South Tien Shan, the author's collection; 3 *M. falcarius* Koren', Pai-Khoi, the author's collection; 4. *M. craigensis* Jaeger, after Koren' 1975: pl. 10: 8, CGM 46/1075; 5 *M. yukonensis* Jacks. et Lenz, after Koren' 1975: pl. 9: 16, CGM 47/10875; 6 *M. n.sp. aff. yukonensis* Jacks. et Lenz, after Jaeger et al. 1969: fig. 1J; 7 *M. yukonensis fangaensis* Jaeg. et Stein, after Jaeger et al. 1969: fig. 1B; 8 *M. uniformis* Přibyl, after Jaeger 1966: fig. 1L; 9 *M. kayseri* Perner, after Jaeger 1977: fig. 1J; 10 *M. microdon silesicus* Jaeger, after Jaeger 1959: fig. 17e; 11 *Linograptus posthumus* Richter, after Urbanek 1963: text-pl. 17; 12 *Abiesgraptus tenuiramosus* Hundt, after Urbanek 1963: text-pl. 17; 13 *Monograptus transgrediens* Perner, after Teller 1964: tabl. 1; 14 *Pseudomonoclimacis minimus* Mikh., Kazakhstan, collection of Bandaletov S.M., Mikhajlova N.F. and the author; 15 *M. perneri kashakhstanensis* Mikhajlova, Kazakhstan, collection of Bandaletov S.M., Mikhajlova N.F. and the author; 16 *M. formosus* Bouček, Kazakhstan, collection of Bandaletov S.M., Mikhajlova N.F. and the author.



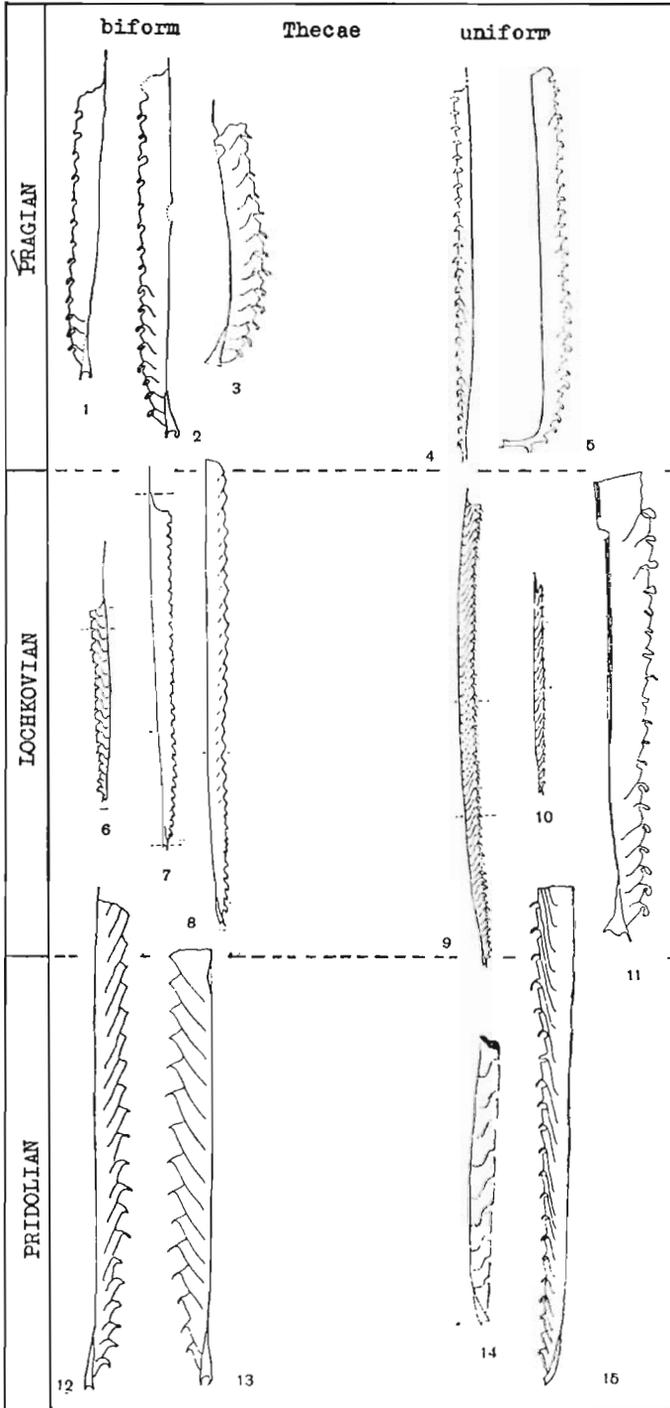
peculiarities of their astogeny serve as diagnostic characters of the subfamilies Monograptinae and Linograptinae. The shape of rhabdosome is fairly stable. Predominant are straight colonies with a length from 10 to 70—80 mm. The post-Ludlow time yields almost no monograptids of a ventral or spirally curved shape. Different lineages of Pridolian — Pragian graptoloids show a tendency to a dorsal curvature of the proximal part (*Monograptus perneri*, *M. falcarius*, *M. yukonensis*) or, more rarely, of the whole rhabdosome (*M. formosus*). Taken as a whole, however, late monograptids achieve a maximum simplification of the colony shape.

The structure and shape of the theca and, in particular, of its aperture account for the morphological diversity of late monograptid faunas. Alongside the colonies with a uniform *Pristiograptus* or *Monograptus*-type theca, there are abundant biform graptoloids. They have proximal introduction of new characters and vary as to the degree of its penetrance. The hoods or paired lateral lobes can be found in one to three most proximal thecae as is the case with *M. aequabilis* and *M. transgrediens*, or in fifteen to twenty five thecae — as in *M. lochkovensis*, *M. ramstalensis*. Reduction of apertural structure in the course of astogeny can be sudden — *M. aequabilis* or gradual, distinct in the distal part alone — *M. hercynicus*, *M. telleri*. Both the uniform and biform monograptids show a similar evolutionary stability of morphological structure, many of the species being long-living.

The morphological diversity of apertural structure in late Silurian monograptids is represented by the following major types:

1. dorsal or dorso-lateral hoods of fusellar structure which may be developed either in the proximal thecae or in most of the thecae, or in all the thecae of the colony (*M. similis*, *M. bouceki*);
2. apertural hooked processes being a continuation of dorso-lateral thecal walls; more or less coiled (*M. aff. balticus*);
3. simple paired lateral elevations in most proximal thecae (*M. transgrediens*) or in all thecae of the colony (*M. ultimus*);
4. unpaired dorsal shields bifurcating in the course of growth and terminated with long paired curved lobes (*M. lochkovensis*), having sometimes spinous processes (*M. willowensis*). The penetrance of this

Fig. 5. Pridolian-Pragian monograptids with uniform and biform thecae. 1 *Monograptus aequabilis notoaequabilis* Jaeg. et Stein. after Koren' 1975: pl. 8: 5, CGM 25/10505; 2 *M. fanicus* Koren', after Koren' 1975: pl. 8: 12, CGM 10/10505; 3 *M. falcarius* Koren', after Koren' 1978: fig. 40; 4 *M. thomasi* Jaeger 1966: fig. 1a; 5 *M. yukonensis* Jacks. et Lenz, after Lenz and Jackson 1971: fig. 5F; 6 *M. aequabilis aequabilis* Přibyl, after Jaeger 1977: fig. 1E; 7 *M. hemiodon* Jaeger, after Jaeger 1977: fig. 1G; 8 *M. ramstalensis* Jaeger, after Jaeger 1977: fig. 1F; 9 *M. uniformis angustidens* Přibyl, after Jaeger 1977: fig. 1B; 10 *M. microdon microdon* R. Richter, after Jaeger 1977: fig. 1B; 11 *M. hercynicus* Perner, after Koren' 1978: fig. 4a; 12 and 13 *M. willowensis* (Berry et Murphy): 12 Kazakhstan, collection of Mikhajlova N.F., 13 after Berry and Murphy, 1975: fig. 18d; 14 *Pseudomonoclimacis minimus* Mikh., Kazakhstan, collection of Bandaletov S.M., Mikhajlova N.F. and the author; 15 *Monograptus* sp.n. 2, Kazakhstan, collection of Mikhajlova N.F.



character varies throughout the colony: the first 2 to 15 thecae usually have apertural structures while the remaining thecae are of pristiograptid appearance;

5. an isolated triangulate theca, similar in shape to *M. spiralis* with paired lateral spines (the *M. formosis* group) (Rickards *et al.* 1977);

6. a straight pristiograptid theca without apertural apparatus throughout the colony (*Pristiograptus dubius*).

The apertural diversity sharply decreases by the beginning of the early Devonian (fig. 10). The Devonian monograptids preserve only the dorsal hoods of "uncinatus" type which can be observed either in the proximal thecae alone or in every theca of the colony. This is most probably a proof of a proximal introduction characteristic of all Pridolian — Pragian biform monograptids. The degree of bimorphism is used as a specific diagnostic character.

Besides the usual astogeny, different phylogenetic lines of late monograptids exhibit the following changes in the thecal structure and proportions:

1° progressive elongation of thecae associated with their considerable overlap (*M. transgrediens*, *M. lochkovenski*, *M. uniformis*);

2° appearance of a gentle or sharp genicular curvature of the free ventral wall (*Pseudomonoclimacis* div.sp., *M. ultimus*, *M. aequabilis*, *M. hemiodon*, *M. falcarius*, *M. telleri*).

The bulk of Pridolian — Pragian monograptids have a sicula of a common conical shape, straight or gently ventrally curved, showing some variation in size and shape (fig. 7). Some structural modifications of the sicula can be observed in a more or less developed dorsal process. The latest Pridolian monograptids have a long, wide and slightly curved dorsal process which is a most striking morphological characteristic (*M. telleri* — *M. yukonensis*, *M. aequabilis notoequabilis* — *M. fanicus*). Some Pridolian and, in particular, Lochkovian — Pragian monograptids display changes in the sicular shape of the terminal members of evolutionary lineages (*M. willowensis*, *M. hercynicus*, *M. falcarius*, *M. atopus*). Those changes consist of a sudden widening of the metasicular aperture, which acquires a trumpet-like shape and in the appearance of a sigmoidal curve in the lateral margin (a late zonal population of *M. hercynicus*, *M. falcarius*). The above changes, namely, the presence or absence of the dorsal process can be observed in all monograptids — in those with a straight or dorsally curved rhabdosome as well as in those varying in their apertural structure and the degree of thecal bimorphism. This evidences that there is no correlation between the changes in the above morphological characteristics.

Evolution. — The graptoloid evolution saw the last stage of morphophysiological progress in the appearance of uniserial scandent rhabdosomes with a monograptid type of development (the early Llandovery,

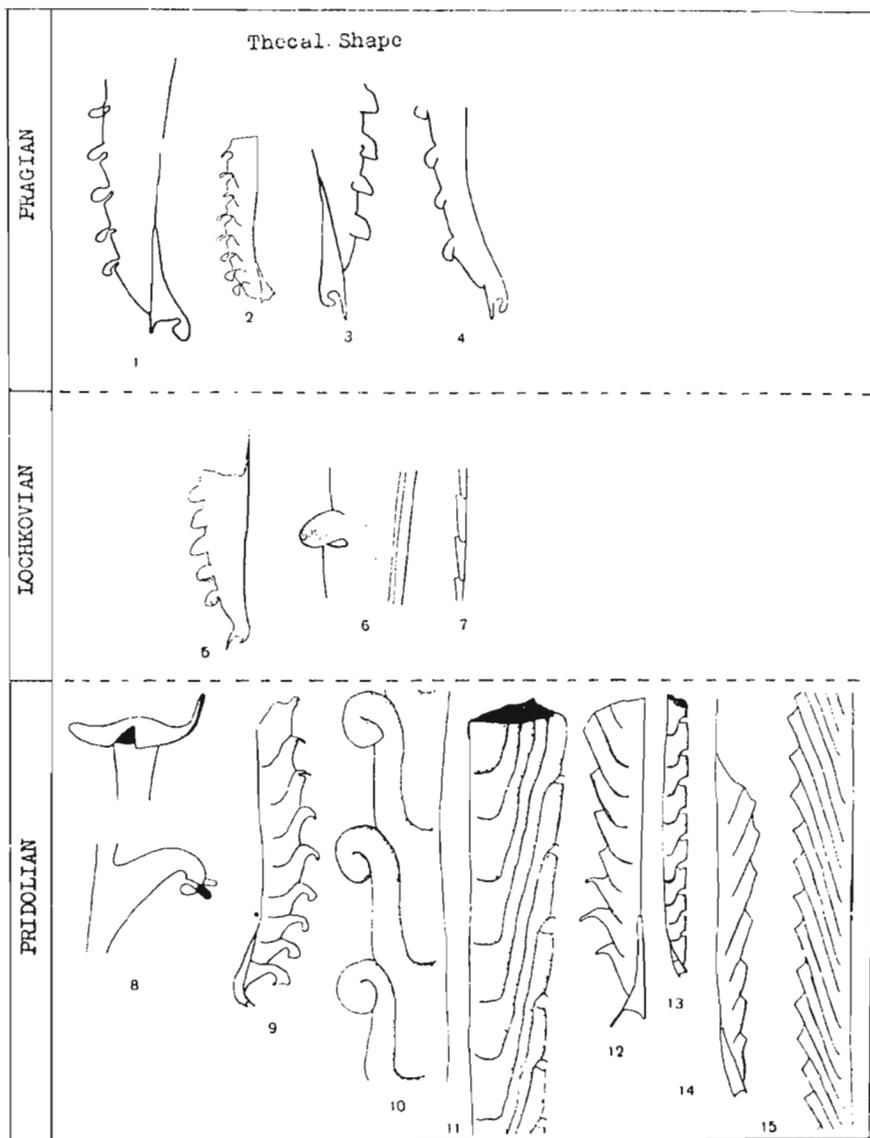


Fig. 6. Thecal shape of the Pridolian-Pragian monograptids. 1 *Monograptus fanicus* Koren' after Koren' 1974: fig. 3: 15 CGM 40/10875; 2 *M. falcarius* Koren', after Koren' 1978: fig. 4n; 3 *M. telleri* Lenz et Jacks., after Koren' 1974: fig. 3: 17; 4 *M. yukonensis* Jacks. et Lenz, after Koren' 1974: fig. 3: 23; 5 and 6 *M. uniformis* Přibyl: 5 after Jaeger 1959: fig. 16d; 6 after Rickards et al. 1977: fig. 44d; 7 *Linograptus* sp., after Urbanek 1963: text-pl. 17; 8 *Monograptus formosus* Bouček, after Rickards et al. 1977: fig. 37a; 9 *M. perneri kasakhstanensis* Mikh., Kazakhstan, collection of Bandaletov S.M.; 10 *Monograptus* sp.n. 3, Kazakhstan, collection of Bandaletov S.M.; 11 *Monograptus* sp.n. 2, Kazakhstan, collection of Bandaletov S.M.; 12 *M. wilowensis* (Berry et Murphy), Kazakhstan, collection of Bandaletov S.M., Mikhajlova N.F. and the author; 13 *Pseudomonoclimacis minimus* Mikh., Kazakhstan, collection of Bandaletov S.M., Mikhajlova N.F. and the author; 14 *Pristiograptus dubius* (Suess), Kazakhstan, collection of Bandaletov S.M., Mikhajlova N.F. and the author; 15 *Monograptus* sp.n. 1, Kazakhstan, collection of Bandaletov S.M.

the *persculptus* Zone; cf. Bulman's "monograptid grade", 1963). The entire subsequent Silurian and early Devonian history of the group is connected with evolution of monograptid fauna within the acquired grade of structure.

The appearance of the new structural type of the colony was followed by intense divergent idioadaptation (Severtsev 1967) through an extensive thecal differentiation. The peak of appearance and development of various structural types in monograptid theca was observed in the Llandovery. It is displayed by persistence of about twenty groups of related species and genera, while in the Wenlock their number is reduced to eight (Rickards *et al.* 1977: fig. 1). Thus, the monograptid fauna attains its evolutionary peak in the Llandovery to be followed by a long

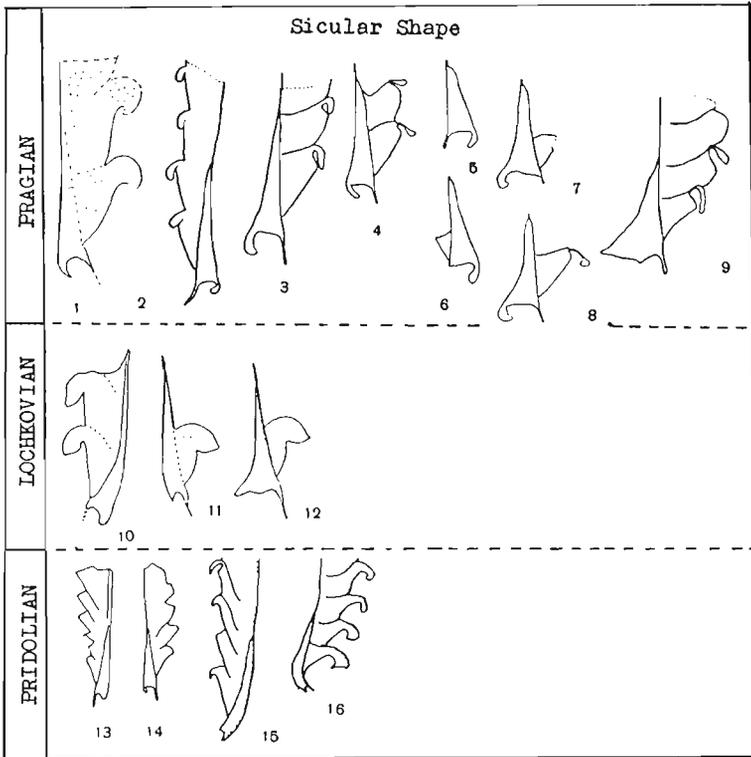


Fig. 7. Sicular shape of the Pridolian-Pragian monograptids. 1 *Monograptus thomasi* Jaeger, after Jaeger 1966: fig. 10; 2 *M. craigensis* Jaeger, after Koren' 1974: fig. 3: 21, CGM 40/10875; 3, 7 and 8 *M. fanaticus* Koren', South Tien Shan: 3 collection of the author; 7 and 8 after Koren' 1974: fig. 3: 9, 11, CGM 34/10875; 36/10875; 4-6 *M. aequabilis notoaequabilis* Jaeger et Stein, South Tien Shan: 4 collection of the author, 5 and 6 after Koren' 1974: fig. 3: 13, CGM 26/10875, 28/10875; 9 *M. falcarius* Koren', after Koren' 1974: fig. 3, CGM 31/10145; 10 *M. uniformis* Přibyl, after Rickards *et al.* 1977: fig. 44e; 11 *M. praehercynicus* Jaeger, after Jaeger 1966: fig. 1n; 12 *M. hercynicus* Perner, after Jaeger 1966: fig. 1m; 13 and 14 *M. transgrediens* Perner, after Koren' 1978: fig. 3c, d; 15 *Monograptus* sp.n. 2, Kazakhstan, collection of Mikhajlova N.F.; 16 *M. perneri kashakhstanensis* Mikhajlova, Kazakhstan, collection of Bandaletov S.M., Mikhajlova N.F. and the author.

period of biological regression of the group in spite of the appearance of new phylogenetic lines and periodic increase of specific diversity. On the Wenlock-Ludlow boundary all early Silurian phylogenetic lines disappear with the exception of individual representatives of long-living species of pristiograptid stem. It is these representatives that yield in the Ludlow a new burst of specific differentiation associated with the appearance of several new evolutionary lineages.

In order to demonstrate the dynamics of the late Silurian—early Devonian graptoloid evolution I have arranged a diagram of the total number of species reported from each zone (fig. 8). The diagram shows pulsations in the increase and decrease of specific differentiation expressed as steep, almost symmetrical slopes of the curve. Rapid extinction is common consequence of attaining the peak of diversity. The diagram displays two curves—of the total number of species and of the number of species transcending the zonal boundaries. Their outlines are in general symmetrical which is indicative of a certain proportion in the number of new and transient elements in the zonal assemblages. This regularity is gradually loosening during the early Devonian stage of monograptid evolution. As can be seen from the diagram the peaks of specific diversity in late Silurian—early Devonian graptoloids occur in the *nilssoni-scunicus* Zone of the Ludlow, the *lochkovensis* subzone of the Pridolian, the *uniformis* Zone in the Lochkovian and the beginning

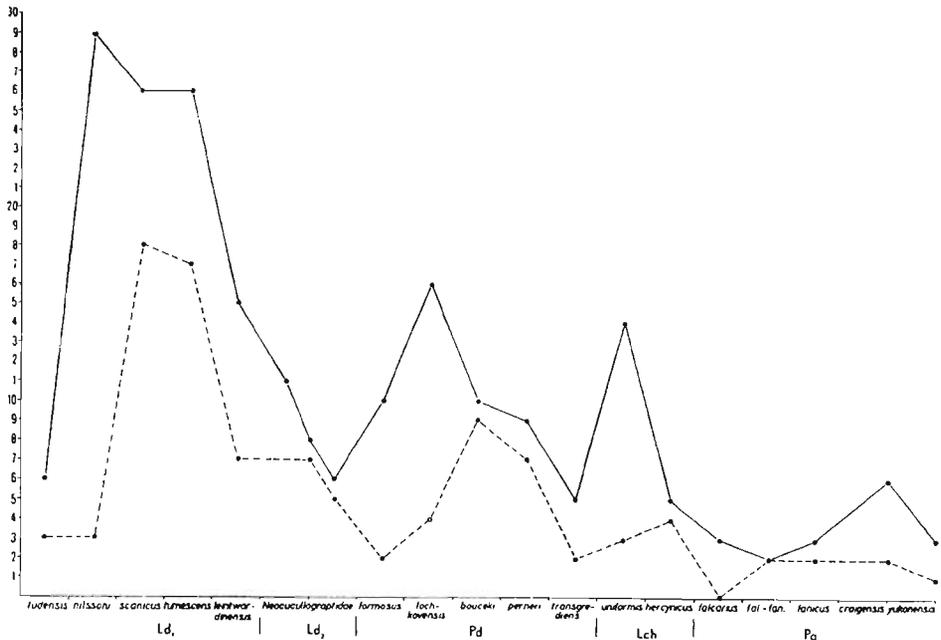


Fig. 8. Fluctuating number of late Silurian—early Devonian graptoloid species. Solid line shows the total number of species per zone; broken line—number of species surpassing zonal boundaries. Points mark the periods for which species are totalled.

of the *yukonensis* Zone in the Pragian. The subsequent periods of a maximum decrease in diversity correspond to the *kozlovski* Zone (the end of the Ludlow, the *Neocucullograptinae* horizon), to the *transgrediens* subzone (the end of the Silurian), the *fulcarius-fanicus* interzone, and to the end of the *yukonensis* Zone in the Pragian. The general regular extinction of species and decrease of their taxonomic diversity with time is described in the diagram as a successive reduction of the maximum number of species: 30 — in the early Ludlow, 16 — in the middle Pridolian, 14 — at the beginning of the Lochkovian and 6 — in the Pragian. The last ("death-phase") of monograptid evolution is distinguished by persistence in various basins of only two or three, or even one species.

The pattern of changes in the graptoloid species number in the succession of Ludlow — Pragian Zones is suggestive of the dynamics of the group evolution. The later history of graptoloids can be subdivided into three distinct phases: the Pridolian, the Lochkovian and the Pragian. Each phase displays new phylogenetic lines, extinction of earlier species and development of long-living lines.

1. The Pridolian Phase. The end of the Ludlow is marked by the extinction of a number of characteristic monograptid groups which made the core of the Ludlow assemblages. It terminates the development of the subfamilies *Cucullograptinae* and *Neocucullograptinae*, whose evolutionary divergence involved complication of the structural modifications in the thecal apertural apparatus (Urbanek 1960, 1966, 1970). The Ludlow — Pridolian boundary features a sharp change in the graptoloid fauna composition, so that towards the early Pridolian it became greatly impoverished on the superspecific level. Specific differentiation evidently increased in several monograptid phylogenetic lines. New adaptive changes are expressed in further modifications of the theca, and chiefly, of its apertural structure. Meanwhile, *Pristiograptus dubius* and *Lino-graptus posthumus* persist throughout the Pridolian time without any morphological changes.

On the whole, the shape of monograptid colonies loses some of its diversity. The ventrally curved rhabdosomes disappear, while the straight ones still persist together with those slightly dorsally curved in the proximal end or along the entire length of the colony. The stronger the dorsal curvature, the higher is the degree of thecal isolation (*M. perneri*, *M. formosus*). The thecal apertural apparatus varies in its structure. The most common are dorso-lateral hoods, with hooks similar to those of *M. priodon* occurring more rarely. Rhabdosomes having bifurcated thecae develop into a diagnostic feature (*M. transgrediens*, *M. lochkovenski*). They display lateral elevations or lobes in their proximal thecae. Various phylogenetic lines show a tendency towards a considerable elongation and overlap of the thecae in the course of the astogeny (*M. transgrediens*, *Monograptus* sp.n. 1, *Monograptus* sp.n. 2; fig. 9). In

most Pridolian monograptids the sicula is of a conventional shape which shows little variation from group to group. Some slight widening of metasicular aperture can be observed in *Monograptus willowensis*. *M. perneri* has a peculiar sicula with a sharp ventral curvature in its free subapertural part.

The species number gradually increases from six in the Upper Ludlow to ten in the *ultimus-formosus* Zone, with sixteen as the peak of diversity being reported from the *lochkovensis* Zone.¹⁾ The beginning of the Pridolian phase is associated with the appearance of new phylogenetic lines: *M. ultimus*, *M. formosus*, *M. similis* (Jaeger 1977). *M. formosus* is an example of a specialized short-living branch whose ancestral forms are unknown. It appears and gets extinct in the early Pridolian leaving no descendants. *M. ultimus* is another line of cryptogenic nature. One may assume that it is phylogenetically related with the major Ludlow *Pristiograptus* stem descending from it due to formation of paired lateral elevations on every thecal aperture in the colony. After a long interval, the *formosus* Zone yields monograptids with a dorsal or dorso-lateral thecal hood of the "*uncinatus*" type, which is to become predominant in the apertural structure during the Pridolian and further phases of the monograptid evolution. There is a distinct specific differentiation of the "hooded" monograptids within the *lochkovensis* and *bouceki* subzones. *M. similis* Bouček that appears in the *formosus* Zone may be an ancestral form of monograptids close to *M. uniformis angustidens*. The latter have been reported from the sections of Pridolian deposits in Canada and Southern Kazakhstan (Jackson and Lenz 1969, 1972; Lenz and Jackson 1971; Mikhajlova 1975). *M. birchensis* Berry et Murphy as described from the Upper Silurian of Nevada is likely to belong to the same group (Berry and Murphy 1975). They differ from the early Devonian representatives of the *M. uniformis* group by having their hoods equally developed throughout the colony and by a less significant thecal overlap (Jaeger 1976, personal communication). The tendency towards further elongation of the theca can be easily traced in some new monograptids of the Tokrau horizon (*Monograptus* sp.n. 2, fig. 5: 15), which may be related to the group *M. similis* and *M. aff. uniformis angustidens*.

Teller (1966) described peculiar monograptids of the *M. balticus* group from the boundary sections of the Ludlow-Pridolian deposits. They belong to a new phylogenetic line having an elongated theca with a hood shaped like a coiled dorsal lobe. The evolution of this group continues through the early Pridolian time. Some new species from the Tokrau

¹⁾ The present paper does not confine itself to the data on monograptid composition and distribution over the sections of Pridolian deposits in Central Europe and North America which are widely known from various publications. I also take into account the evidence obtained from the sections of the Tokrau horizon in Kazakhstan (Bandaletov 1969; Mikhajlova 1975, 1976; Koren' and Mikhajlova, in preparation).

horizon in Kazakhstan, which have not been described yet, may well have stemmed from those monograptids.

M. bouceki and *M. perneri* are well diagnosed species having a straight or gently dorsally curved rhabdosome and thecae with dorso-lateral hoods. They are confined to particular stratigraphic levels, though their relations with other monograptids are not very clear.

The Pridolian phase also features a peculiar development of biform monograptids. *M. transgrediens* may serve as an example of extreme biformity. Here belong graptoloids having a simple theca devoid of apertural additions throughout almost the entire colony. Lateral elevations can be observed in the most proximal thecae alone. Distinct thecal biformity is characteristic of monograptids of the *M. lochkovenski* type. Their paired apertural apparatuses are of a more complex structure than in *M. transgrediens*. A much larger number of proximal thecae (from 10 to over 15) have unpaired shields bifurcating in the course of growth and terminated with long paired lobes that, sometimes, have spinous processes. This group displays a distinct trend towards an unusual elongation of the thecae. This character is developed in the extreme in *Monograptus* sp.n. 1 (figs 6: 15; 9: 4) where the distal thecae are as long as 4 mm. One may assume that *M. transgrediens* and *M. lochkovenski* have a common *Pristiograptus* ancestor. This assumption makes their being referred to the *Monograptus* s.l. genus far less certain. Monograptids of this group persist up to the end of the Pridolian (*M. transgrediens*, *M. willowensis*).

Representatives of the genus *Pseudomonoclimacis* Mikhajlova, 1975 are also quite peculiar members of the Pridolian assemblages. They have straight rhabdosomes of small or medium size (figs 4: 14; 5: 14). Their thecae have a free ventral wall with a sharp genicular curve, while the simple apertures are devoid of any apertural apparatus (Mikhajlova 1975). These monograptids are very abundant making the bulk of the Pridolian assemblages at the *bouceki-perneri* subzone level in Southern Kazakhstan. The new *Pseudomonoclimacis* fauna may descend from the *Pristiograptus* stem, probably from *P. dubius*, by thecal modification due to a genicular curve.

Altogether, the Pridolian phase is distinguished by the appearance and evolution of several phylogenetic lineages associated with an intense speciation in some of them. The major evolutionary changes are of an adaptive nature being connected with modifications of thecal aperture, as well as thecal shape and proportions. No cases of appearance of new morphological structures have been recorded. All the types of apertural apparatus as observed in the Pridolian monograptids also occur, in their main features, in the Ludlow and more ancient representatives of the family. What distinguishes most of the Pridolian species is their fairly short duration. The last stage of the Pridolian phase (the *transgrediens*

subzone) displays a sudden reduction in the monograptid taxonomic diversity which is expressed in the decrease in the number of species and their subsequent disappearance. The pre-Devonian time is marked by the extinction of all typically late Silurian monograptids, including *P. dubius*, the latest representative of the long-living *Pristiograptus* stock.

2. The Lochkovian Phase. The Silurian-Devonian boundary is indicated by a wide distribution and development of the *M. uniformis* group, and by the appearance of *M. aequabilis* and *M. microdon* which belong to two new phylogenetic lineages. The *Linograptus posthumus* group persists and, at the later stages, gives rise to still more specialized genus — *Abiesgraptus*. The latter, along with the sicular cladia, acquires the ability to form numerous thecal cladia having more zooids in the colony than any other late graptoloid (Jaeger 1969). Thus, what distinguishes the Lochkovian monograptid fauna is an association of simple and specialized multiramous colonies. The Lochkovian representatives of the genus *Monograptus* have small or medium-sized rhabdosomes, straight or slightly dorsally curved. Predominant are biform monograptids, though their biformity varies strongly, from poorly developed in the *M. uniformis* group to very distinct in *M. ramstalensis* and, particularly, in *M. aequabilis aequabilis*. The latter has a fully developed hood in one to three proximal thecae alone, the remaining thecae of the colony having short dorsal processes which are hardly discernible distally. Dorsal hood of fusellar structure serves as the main type of apertural apparatus. It was also known in early Ludlow and Pridolian monograptids and, as such, may have proved to be most adaptive.

There are variations in thecal structure and proportions. They can be expressed either in the appearance of a genicular curve in the free ventral wall of some species (*M. aequabilis*, *M. ramstalensis*, *M. microdon*) or in a considerable astogenic elongation of thecae with progressive overlap (*M. uniformis*). The sicular shape and proportions remain fairly stable in the bulk of Lochkovian monograptids. *M. hercynicus* is an exception as its metasicula has a peculiar trumpet-like shape together with an undulating lateral edge of the aperture. *M. hercynicus* from the Lower Devonian of Southern Ferghana (Koren' in preparation) allows to trace the gradual development of the latter character. The lateral edge of the flared aperture is straight in the early zonal population, while in the late one it has the edge distinctly elevated and a notch at the dorsal end.

Lochkovian graptolites belong to at least four different lineages, namely: the *M. uniformis* lineage, the *M. aequabilis* lineage, the *M. microdon* lineage and the *Linograptus-Abiesgraptus* lineage.

As was mentioned above, the ancestral forms of the Devonian *M. uniformis* group evolve at the beginning of the *transgrediens* Zone (*M. aff.*

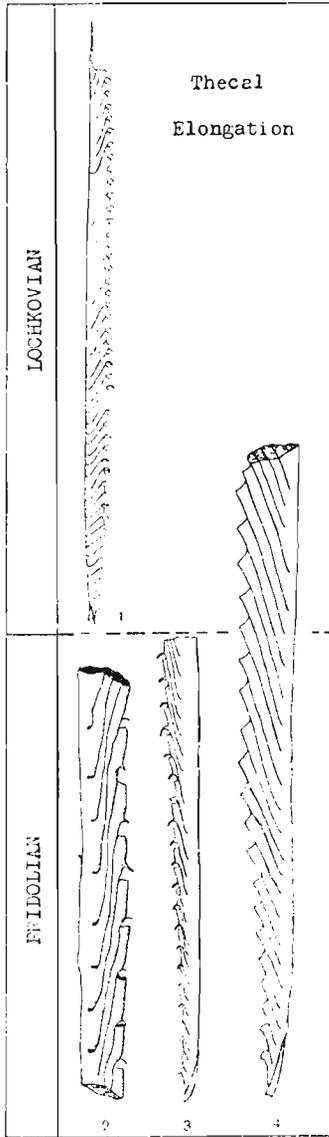


Fig. 9. Thecal elongation in the Pridolian-Lochkovian monograptids. 1 *Monograptus uniformis* Přibyl, after Jaeger 1966: fig. 1L; 2 and 3 *Monograptus* sp.n. 2, Kazakhstan: 2 collection of Bandaletov S.M., 3 collection of Mikhajlova N.F.; 4 *Monograptus* sp.n. 1, Kazakhstan, collection of Bandaletov S.M.

uniformis angustidens, *M. birchensis*) and develop throughout the Pridolian time. A fully developed apertural hood in all thecae of the colony is their only distinguishing morphological character. Typically Devonian *M. uniformis* and *M. praehercynicus* display more simplified hoods which diminish in size distally. The thecal hoods of other related species are developed in the proximal end alone, with the distal thecae lacking any apertural additions (*M. hemiodon*). Within this group variability is manifested as thecal elongation, genicular curve of the wall or weak dorsal curvature of the colonies (*M. kayseri*). The terminal members of

lineages. The morphological variation range is considerably reduced making the early Devonian graptolitic fauna more and more uniform (fig. 10). Predominant in the assemblages are monograptids of the *M. uniformis* group whose populations display greater abundance. They feature the last important speciation acme in the *uniformis* Zone (about 10 species). By the end of the *hercynicus* Zone the number diminishes again to two or three species.

3. The Pragian Phase. The Lochkovian — Pragian boundary is marked by an important evolutionary event — a complete disappearance of the last multiramous linograptid colonies. Meanwhile, the latest uniform monograptid fauna continues to develop.

The Pragian monograptids are closely related morphologically to their Lochkovian predecessors having their major character, the thecal hood structure, fully preserved. The range of variation in thecal biformity remains unaltered together with the irregular expression of this feature. At the end of the Lochkovian and throughout the Pragian there can be traced a progressive tendency to change the rhabdosome shape from straight to dorsally curved, mostly in the proximal part. The curved rhabdosomes are associated with final stages of different phylogenetic lineages (*M. kayseri*, *M. falcarius*, *M. yukonensis*). As to the size, the rhabdosomes stay within the usual proportions.

There are modifications of the sicular structure as evidenced by the change of metasicular shape and by the appearance of a long dorsal process. Almost all Pragian monograptids feature a peculiar morphological character consisting of a fully developed and smoothly curved dorsal tongue.

The beginning of the Pragian phase is remarkable for the appearance of *M. falcarius* and *M. aequabilis notoaequabilis* that continue the development of the two Lochkovian phylogenetic lineages. A gradual morphological transition from *M. hercynicus* to *M. falcarius* can follow in a series of transitional forms. Their development is associated with changes in the shape and reduction of the size of rhabdosome which is straight and fairly large in *M. hercynicus* but quite small and crescent in *M. falcarius*. Both species have a similar shape of sicular and about the same degree of thecal biformity which is revealed in the hoods being smaller and simpler distally. *Monograptus falcarius* seems to be the terminal link in the *Monograptus hercynicus* lineage since later associations do not yield species that would be morphologically related to it.

The successive appearance of *M. aequabilis notoaequabilis* and *M. falcarius* linked by morphologically continuous transitions, suggests their belonging to one and the same phylogenetic lineage. These monograptids display a distinct thecal biformity: the hoods which form an extension of dorsal walls are fully developed in the first proximal thecae alone,

whereas the subsequent thecae have no more but dorsal shields, hardly noticeable distally. The Southern Tien Shan sections of the Lower Devonian display a successive appearance and development of *M. aequabilis*, *M. a. notoaequabilis* and *M. fanicus*. They are linked by a series of transient forms which involve difficulties in discriminating them within the same sample. The development of that lineage features two successive evolutionary events, namely: 1° the appearance of *M. aequabilis notoaequabilis* with a fully developed sicular dorsal process, and 2° the transformation of *M. a. notoaequabilis* into *M. fanicus* due to a gradual change in the shape of sicula, from a narrow straight or weakly dorsally curved one into that dorsally curved and having a flared aperture. Monograptids of that phylogenetic lineage are particularly abundant, prevailing in the early Pragian graptoloid assemblages until *M. yukonensis* make their first appearance.

The appearance and development of representatives of the *M. telleri* — *M. yukonensis* phylogenetic lineage is the most notable event in the latest monograptid evolution. They make up the background of the late Pragian assemblages having abundant populations in all regions under study. Here belong: *M. telleri*, *M. craigensis*, *M. yukonensis* (with subspecies), *M. thomasi* and *M. pacificus*. Their major morphological characters are: a medium-sized rhabdosome straight or with a variable gentle dorsal curve in the proximal part, a theca having a wide dorsal or dorso-lateral hood and a straight or gently ventrally curved sicula whose dorsal process is fully developed. The hood size noticeably diminishes distally so that the thecae develop a gentle genicular curve in their free ventral wall. The Pai-Khoi and Tien-Shan sections display a successive appearance of *M. telleri*, *M. craigensis* and *M. yukonensis* (Koren' 1975).

Both the stratigraphic control and close morphological affinity of the above species linked by a series of transient forms are suggestive of their successive development. The major trend involves a regular change in the shape of the rhabdosome from a straight one in *M. telleri* through a slight dorsal curvature in the most proximal part of *M. craigensis* to sharply curved forms in *M. yukonensis*. The latter shows a high degree of variability in the rhabdosome curvature allowing to discriminate several subspecies. *M. yukonensis yukonensis* embraces those forms whose proximal part is gently curved while the representatives of *M. y. fangensis* have a sharper curvature, with the rhabdosome of the monograptids that belong to *M. n.sp. aff. yukonensis* being curved almost along its whole length (Jaeger *et al.* 1969). Though the functional meaning of the dorsal curvature does not lend itself to interpretation, the change of this feature is most probably the last attempt of the colony to preserve its viability. It should be noted that among the latest graptoloids *M. yukonensis* is the most widely distributed occurring in all early Devonian localities except Australia.

Along with *M. yukonensis* the late graptolite assemblages embrace *M. thomasi*, *M. pacificus*, and *M. atopus*. The first two species are related to the *M. telleri* — *M. yukonensis* lineage in the structure and size of their rhabdosome and in the thecal and sicular shape. *M. thomasi* can be observed both in the sections below the earliest *M. yukonensis* and in association with it. That species exhibits a thin, straight proximal part and distinctly isolated first thecae (Jaeger 1966). One can suggest two directions in the development of monograptids from the *M. telleri* — *M. yukonensis* lineage, namely: the appearance of dorsal curvature in the proximal part (*M. craigensis*, *M. yukonensis*) and the elongation of straight proximal part associated with isolation of the first thecae (*M. thomasi*). The hood structure, biformity and sicular shape of *M. pacificus* is evidence of its being related to *M. craigensis*. In contrast to it, however, a weak dorsal curvature involves the sicula alone. *M. atopus*, in turn, displays some relationship with *M. aequabilis notoequabilis* in the thecal shape and extreme biformity, differing from it by the shape of sicula distinctly flared in the aperture. Such a secondary change of the sicular shape in monograptis of the *M. aequabilis notoequabilis* lineage may be due to an attempt to modify the rhabdosome morphology at the latest stages of development.

The major trends in the Pragian monograptid evolution can be summed up as follows:

- 1° a uniform main structure of thecae and its apertural apparatus;
- 2° thecal biformity and its variability;
- 3° development of a long dorsal sicular process in most of the species belonging to different lineages;
- 4° modification of sicular shape in terminal members;
- 5° appearance of a dorsal curvature in the proximal part and its further increase to be followed by isolation of the thecae involved in the curvature.

On the whole the Pragian is the time of a phyletic monograptid evolution in the few persisting lineages. A weak speciation acme occurs at the final stage of development of the *M. yukonensis* group. The latest monograptid associations contain no more than one to three species usually represented by numerous specimens. The extinction of these monograptid species whether successive or simultaneous still remains a problem since the available stratigraphic data do not allow for an accurate time correlation of deposits yielding the latest graptoloids in various sedimentary basins.

GRAPTOLOID EXTINCTION

At the final stage of the evolution graptoloids were spread over a large basin (fig. 3). They disappear from the biological record at the time when

the evolution of other early Devonian groups knows no events as drastic in their consequences. Thus, the late monograptid extinction is a selective process which involves difficulties in establishing its true reasons. This problem has been widely discussed in literature. Jaeger (1955) and Obut (1964) believed that the group extinction was due to tectogenic processes responsible for changes in the abiotic environmental conditions which proved to be destructive for the group persistence.

There is enough evidence to confirm the effect of abiotic factors on graptoloid extinction. The Upper Silurian—Lower Devonian sections of various regions display a gradual or sharp change in lithofacies. It usually involves substitution of graptolite-bearing shale beds with shelly-carbonate, clastic or other rocks. In each particular sedimentary basin these changes are accounted for by different geological reasons. The cessation of argillaceous mud sedimentation, however, is associated everywhere with disappearance of graptoloid taphocoenoses. Regional lithofacies changes are responsible for heterochronous extinction of graptoloids in different basins. In Great Britain they disappear towards the end of the Ludlow, while in Thuringia, Barrandian, Sardinia, North Africa and Pailkoi, etc. they last until the end of the Lochkovian—the beginning of the Pragian (Jaeger 1959, 1977; Horný 1962; Alberti 1977; Koren' and Jenokjan 1970). But in spite of distinct global reduction of the early Devonian graptolite facies distribution they persisted throughout the Pragian on the territory of Alaska, Yukon, Southern Tien Shan, Thailand etc. Therefore their final extinction was not connected in these basins with any noticeable changes in the physio-geographical conditions. In his discussion of the reasons which caused extinction of the Ludlow phylogenetic lines and graptoloids as a whole, Urbanek (1970: 236—242) comes to a conclusion that the abiotic factors could not be the chief influence in those events. On the contrary, he emphasizes the importance of biotic changes, that is, "the appearance of new elements of ecosystems and biocoenosis, or an evolutionary progress of already existing ones" (*op.cit.*: 239). But, in his opinion, such a comprehensive approach to abiotic and biotic factors still would not allow a satisfactory explanation of graptolite extinction.

In fact there is no definite reason of such a selective group extinction, nor is there any known combination of factors responsible for it. In order to discuss this problem we should once again go back to the evolutionary changes which affected the graptoloids at the time preceding their extinction.

The adaptive monograptid evolution exhausted its diverse potentialities in the course of its Silurian history. This was expressed in various structural thecal modifications and, chiefly, through changes in the structure of apertural apparatus. By the early Devonian the morphological diversity is sharply reduced due to a long biological regression and may be associat-

ed with a decrease in individual adaptability. The early Devonian phase features almost no changes in the structure of the thecal apertural apparatus. This may be indicative of a loss of ecological plasticity, lack of a pronounced biotope differentiation together with late monograptids' inability to further adaptation to a varying environment. The late monograptid fauna becomes extremely monotonous. At the last stages of survival it comprises only two or three morphologically related species having fairly abundant populations and a sufficiently broad geographical extent. Further existence of monograptids may be accounted for by a complex interaction of biologically feeble organisms with the biotic and abiotic environments. In other words, their fate depended on the graptoloid position in the biogeocoenosis.

There is almost no palaeoecological or palaeontological data that would permit reconstruction of the planktonic graptoloid biocoenoses. This makes all considerations concerning possible biocoenotic relations highly speculative, though in my opinion those relations were decisive for the Hamletian "to be or not to be" of late monograptids. The analysis of the known occurrences shows that black carbonate-argillaceous shales and argillites are the main facies type of sediments bearing the most diverse and numerous graptoloid taphocoenoses. Those sediments belonging to ancient miogeosynclines occupy an intermediate position in the facies profile, between the subplatform clastic-carbonate lithofacies and eugeosynclinal volcanogenic-sedimentary formations. This part of the ancient basins was most favourable for the development of microplankton and graptoloids. It might be logical to presume that the argillaceous-mud taphotopes were fairly direct spatial projections of graptoloid biotopes. The ecological and geographical distribution of graptoloids is determined by the distribution and biomass of the phytoplankton on which they feed. The colonies of monograptids passive in their feeding habits could develop successfully in case of stability of trophic chains. Urbanek (1966: 201) points out that adaptation of certain groups to diverse modes of life, biotopes and food abundance "is expressed primarily through modifications of the feeding apparatus and feeding habits".

The uniform structure of apertural apparatus as observed in the early Devonian monograptid lineages of parallel development may result from their feeding adaptation in similar ecological milieu.

It is due to this similarity that in spite of their fairly simple thecal structure the late monograptids were probably adapted to rather a narrow range of ecological variation. This suggests that the number of niches gets reduced to one or, probably, a few, from among those they used to inhabit.

It is natural to believe that graptoloids would feed on a particular phytoplankton group which could be for instance structureless pigmented

algae. In this case, the abundance and composition of these organisms in the biotope would be of vital importance for graptoloids. A gradual decrease in the total supply of food or exhaustion of favourite food-species could result in a progressive disturbance of food balance. Throughout the geological history variations in phytoplankton productivity in the world ocean had a great effect on the planktotrophic organisms evolution, as well as on the changes in the geochemical and physical environment. According to Tappan and Loeblich (1966) the peak of phytoplankton production was reached in the Ordovician to be followed by a gradual decrease up to the late Devonian. These authors also indicate that a noticeable decrease in the phytoplankton diversity and abundance coincides with a period of the land flora expansion and marine organisms extinction. It is during the late Silurian-early Devonian time that fundamental changes occur in the flora of coastal lowlands: the early thallophytic floras are replaced with psilophytic ones which become predominant towards the beginning of the middle Devonian. This might result in considerable changes in the atmospheric and water balance of oxygen and carbon dioxide that, in turn, affected the planktonic biota (Tappan and Loeblich 1966; Tappan 1968).

The presumed feeding specialization of graptoloids would restrict their passing into other biotopes, threatening them with extinction in the presence of more successful rivals, such as pelagic dacroconarids. This group was developing successfully in the early Devonian and, probably, inhabited the same ecological niches. At least the taphocoenoses yield abundant dacroconarids — universally in association with graptoloids in both shales and limestones. Dacroconarids were associated with monograptids nearly throughout the early Devonian phase, but the Pragian features their greater diversity and abundance. If we compare adaptability of the two groups, dacroconarids have advantages over graptoloids owing to their mobility and, hence, better ability to catch food. In contrast to monograptids, the dacroconarids seemed to display a better adaptability in response to environmental changes, being capable of intruding other biotopes. Towards the middle of the early Devonian marked by the extinction of graptoloids they enter a phase of evolutionary expansion.

Much more unlikely rivals or graptoloid predators can be found in Agnatha (Thelodonti, Heterostraci) and placodermi fishes (Arthrodira). Those organisms most probably inhabited different ecological niches as their remains are almost never recorded in association with graptoloids.

Summing up the above it would be appropriate to quote Urbanek's justified conclusion that "at present, the formulation of such theory of extinction of the Graptoloidea is in fact impossible" (Urbanek 1970: 242).

Graptoloid extinction is likely to be due to a complex body of reasons. On the whole, it results from a long biological regression of the group as evidenced in the loss of adaptive plasticity ("an evolutionary hysteresis",

Urbanek 1970: 242) and in the slow deterioration of the environment associated with biotope reduction, increase in competition with better adapted organisms and, possibly, decrease of food supply.

ACKNOWLEDGEMENTS

My thanks are due to Professor O.H. Walliser and Professor A. Urbanek for the stimulating suggestions made during the period of preparing this paper. I also used a friendly exchange of opinions with Dr. R.B. Rickards to whom I express my sincere thanks. My gratitude is also due to Drs D. Kaljo, E. Kurek, V.S. Jenokjan, A.B. Ivanovskij and A.J. Berger for their helpful suggestions offered during mutual discussions. I feel deeply indebted to I. Bagaeva for her English translation of the manuscript.

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DISCUSSION

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Lithofacies and extinction of graptolites: In Yukon, *M. yukonensis*, and *M. telleri* alternate through ± 200 m of monotonous black shales. After the disappearance of these species the same type of shales (on a megascopic scale) continues in an unbroken sequence for several hundred meters more. Thus it appears that locally the paleoenvironment as based on the lithology, was unchanged.