

NEW LATE SILURIAN MONOGRAPTIDS FROM KAZAKHSTAN

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ABSTRACT. Some new and previously unrecorded graptolites are described from sections through the Tokrau horizon in the north-east Balkhash area of Kazakhstan, USSR. They include *Monograptus anerosus* sp. nov., *M. balaensis* sp. nov., *M. beatus* sp. nov., *M. microdon aksajensis* subsp. nov., *M. mironovi* sp. nov., *M. nimius* sp. nov., *M. prognatus* sp. nov., *M. supinus* sp. nov., *M. willowensis* (Berry and Murphy), and *Neocucullograptus kozlowskii* Urbanek. These species were collected through approximately 750 m of section referable to the *lochkovensis*, *bouceki*, and *perneri* zones. A local zone of *M. microdon aksajensis* is established for the first time in the uppermost Silurian of Kazakhstan. The successive zonal associations contain almost all species known in the Přídolí beds of the Barrandian area. The new graptolite fauna includes monograptids having uniform or biform thecae with apertural additions of differing structures. Most of the apertural apparatuses are unusual for the Přídolí stage of graptolite evolution, although they are not new but are partly homeomorphs of those known in the Ludlow Series. The variety of thecal structures discovered in the Kazakhstan collections suggests that the Přídolí monograptid faunas are less monotonous than previously suggested.

UNTIL comparatively recently our knowledge of late Silurian (post-Ludlow) graptolites was limited to the results of investigations of Central European sections, and mainly of the Přídolí sequence of Bohemia. The first zonal subdivision established by Přibyl (1940, 1941) on the basis of the stratigraphical distribution of seven or eight species in the Přídolí sections proved to be essentially correct. It now has broad usage for subdivision and correlation of post-Ludlow deposits in different continents, with certain amendments. In the 1960s active international research began within this stratigraphical interval, and evidence of new occurrences of Přídolí monograptids has been published recently by, among others, Abduazimova (1970), Biske and Rinenberg (1973), Jackson and Lenz (1969), Jaeger (1967, 1975), Koren' (1973, 1978, 1979), Mikhajlova (1971, 1975, 1976), Paškevičius (1979), and Teller (1964, 1969). These papers mostly refer to the distribution of graptolites in sections, with systematic descriptions rarely being given. Until recently, data on the composition and morphology of Přídolí monograptids were scarce, and graptoloid associations in this stratigraphical interval were considered to be quite monotonous. Incompleteness of knowledge of Přídolí-age monograptids was clearly demonstrated by the unexpected discoveries of new monograptids ('*Saetograptus pilosus* Jackson and Lenz, 1972 and '*S.*' *willowensis* Berry and Murphy, 1975) with unique apertural structures, in Yukon and central Nevada. More varied monograptid faunas were described from the lowermost Přídolí sections of the south-west Ukraine as a result of studies of drill cores (Tsegel'nik 1976).

Study of the monograptid fauna of the upper Silurian Tokrau horizon in Kazakhstan has shown it to be the most complete and diverse of all known Přídolí graptoloid associations. It comprises not only almost all the monograptids reported from the Přídolí beds of the Barrandian, but also taxa similar or identical to those which occur in North America. In addition, there are some new monograptids important for phylogenetic reconstructions, which fill some gaps in previously suggested lineages and show more diverse trends of development and dynamics of evolution within late Silurian monograptid populations.

PREVIOUS STUDIES AND BIOSTRATIGRAPHY

The Tokrau horizon (Regional Stage of Soviet usage) is the uppermost subdivision of the Silurian in Kazakhstan (Bandaletov and Mikhajlova 1968; Bandaletov 1969). In the type area it is represented

by a continuous sequence of sandstones, 750 m thick, yielding numerous graptolites at several successive stratigraphical levels. Benthic faunas (brachiopods, corals, trilobites, crinoids, and ostracodes) occur in terrigenous rocks and occasionally in lenses of organo-detrital limestones.

The age and boundaries of the Tokrau horizon were defined on the basis of graptolites first found in 1965 in the course of geological mapping. Later, beginning in 1968, they were collected and studied by Dr. N. F. Mikhajlova, and in 1974 the present author was invited to study the graptolites and the Tokrau sections. Field work in 1975 and 1978 was carried out jointly with Drs. S. M. Bandaletov and Mikhajlova as well as with other colleagues from Kazakhstan. The collections were first studied jointly with Dr. Mikhajlova in 1975-1976. However, from the outset I came to conclusions as to the age of the assemblages which were substantially different from those drawn previously by Dr. Mikhajlova (1971, 1975, 1976), mainly because of differing views on the scope and taxonomic interpretation of species important for correlation. These differences of interpretation necessitate publication of the results.

Stage	Graptolite zonal standard	Bandaletov et al. 1968 ; Bandaletov 1969	Mikhajlova 1971	Mikhajlova 1976	Bandaletov & Koren' 1976-1980	Horizon	Stage			
LOCHKOV	<i>N. uniformis</i>	AJNASU <i>N. kazachstanensis</i>	AJNASU <i>N. kazachstanensis</i>	AJNASU beds with <i>N. kazachstanensis</i>	graptolites not yet discovered	?	LOCHKOV			
PŘÍDOLÍ	<i>M. transgrediens</i>	TOKRAU <i>F. bandaletovi</i>	TOKRAU <i>F. bandaletovi</i> (local zone)	TOKRAU <i>F. bandaletovi</i>	TOKRAU <i>F. bandaletovi</i>	TOKRAU <i>F. bandaletovi</i>	TOKRAU PŘÍDOLÍ			
	<i>M. permieri</i>							Subzones: <i>M. transgrediens</i>	upper part	<i>M. microdon akaajensis</i>
	<i>M. boučeki</i>							<i>M. permieri</i>	lower part	<i>M. permieri kazachstanensis</i>
	<i>M. lozhkoviensis</i>							<i>C. J. chekmanova</i>	<i>C. J. chekmanova</i>	<i>M. lozhkoviensis</i>
	<i>M. ulianovi</i>							<i>M. formosus</i>	<i>M. formosus</i>	<i>M. formosus</i>
LUDLOW	Neocucullograptinae	AKKAN	AKKAN	AKKAN beds with Neocucullograptinae	AKKAN beds with <i>N. kazlowiki</i> beds with <i>B. bohannoni tenuis</i> and <i>B. kusovienensis</i>	AKKAN	LUDLOW			

TEXT-FIG. 1. Different interpretations of the zonal subdivision and correlation of the Tokrau horizon.

Text-fig. 1 shows different interpretations of the scope, boundaries, and age of Silurian stratigraphical units based on successive studies of the composition and distribution of graptolites in the sections in north-east Balkhash. In the upper part of the section, assigned to the boundary beds of the Tokrau and Ajnasu horizons, two graptolite zones, *Pseudomonoclimacis bandaletovi* and *Monograptus kazachstanensis* have been established (Bandaletov and Mikhajlova 1968; Mikhajlova 1971). The index species were described later by Mikhajlova (1975). Among the graptolites characteristic of the *M. kazachstanensis* Zone, *Monograptus uniformis uniformis*, *M. u. angustidens* and *M. aequabilis* were identified by Dr. Mikhajlova, and these occurrences were taken as evidence for assignment of the *M. kazachstanensis* Zone to the Lower Devonian. The Silurian-Devonian boundary in Kazakhstan was placed at the base of this graptolite zone (Resheniya . . . 1976). Later, on the basis of occurrences of *M. transgrediens* in the assemblage, the *M. kazachstanensis* Zone was correlated

with two standard zones, *M. transgrediens* and *M. uniformis*. Thus, the correlation of the Silurian-Devonian boundary in Kazakhstan became less definite (Mikhajlova 1976).

Since 1974 more detailed biostratigraphical research has been carried out in north-east Balkhash. Bed by bed sampling was carried out in the stratotype section of the Tokrau horizon in the Kokbajtal Mountains, as well as in other sections including a new area near the Aksaj and Sarybiik mountains. The major aim of this work was the study of graptolites in the upper part of the section in connection with the problem of the Silurian-Devonian boundary in Kazakhstan. As a result, extensive and diagnostic collections were made, mostly from numerous artificial trenches. The graptolites are preserved better on fresh bedding planes. During this period a re-study was also made of graptolites collected before 1973 and housed in the Palaeontological Museum of the Central Kazakhstan Geological Survey and in the Central Geological Tschernyshev Museum (Karaganda and Leningrad respectively). The main results of my palaeontological and stratigraphical studies can be summarized as follows (see also text-fig. 2).

1. The Tokrau succession begins with the *formosus* Zone. In the underlying sequence of the Akkan horizon the presence of the *Neodiversograptus kozlowskii* Zone is established for the first time. *Monograptus ultimus*, previously identified from these sections (Mikhajlova 1976, p. 100), together with *M. parultimus* Jaeger, which is characteristic of the base of the Přídolí, were not confirmed in the boundary beds of the *kozlowskii*-*formosus* zones in Kazakhstan.

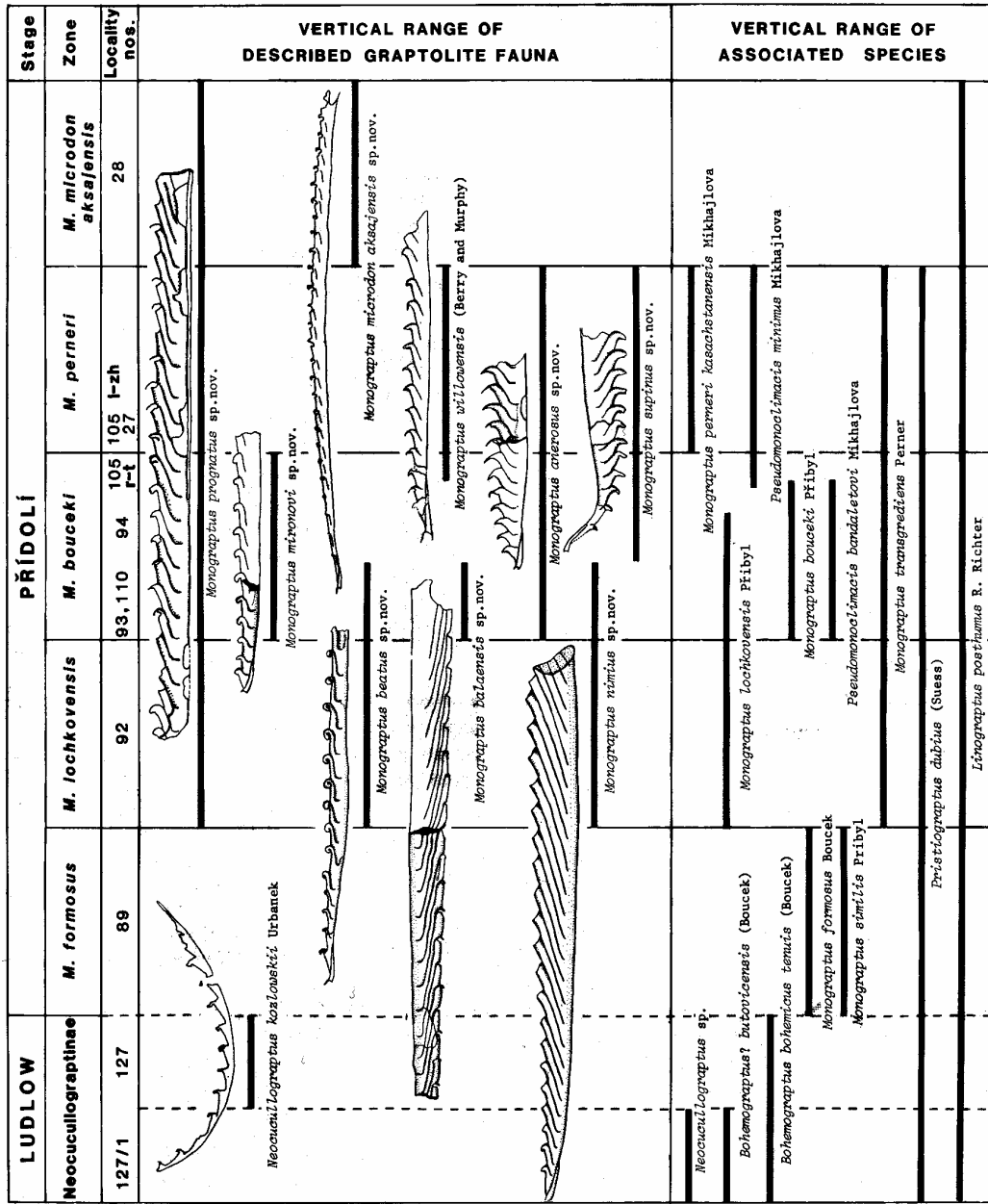
2. Strata above the last occurrences of *M. formosus* Bouček (loc. 92 in the stratotype section) are assigned to the *M. lochkovensis* Zone. This is characterized by the zonal species in association with numerous and diverse monograptids, including *M. transgrediens* Přibyl. The latter was previously identified as *M. chelmiensis* Teller and strata bearing it were considered as the *chelmiensis* Zone (text-fig. 1).

3. The local zone of *Pseudomonoclimacis bandaletovi* (locs. 110, 94) corresponds to the *bouceki* Zone of the standard scale. It contains numerous specimens of *M. bouceki* Přibyl in several sections within the region.

4. *M. kasachstanensis* Mikhajlova, as noted in the original description of the species, is 'identical in rhabdosome shape and size' to *M. perneri* Bouček (Mikhajlova 1975, p. 155). Difficulties in distinguishing these forms are increased by the inadequate preservation. The Barrandian specimens are mostly flattened compared with the Kazakhstan material, which is beautifully preserved in full to low relief. With the help of Dr. H. Jaeger, who kindly provided type material, photographs, and detailed measurements of the Bohemian *M. perneri*, I have concluded that it is most probably identical to *M. kasachstanensis*. However, in adopting caution and bearing in mind the different preservation of the taxa under comparison, the Kazakhstan form is referred to here as a geographical variant *M. perneri kasachstanensis*. The strata bearing it correlate with the *perneri* Zone of the graptolite standard. This correlation is supported by the stratigraphical position in the Tokrau section above the *bouceki* Zone, as well as by the presence in the assemblage of *M. willowensis* (Berry and Murphy) and species closely similar morphologically to *M. pilosus* (Jackson and Lenz). Both these North American monograptids are characteristic of the middle Přídolí (Berry and Murphy 1975; Jackson and Lenz 1969).

5. The presence of *M. uniformis uniformis* Přibyl, *M. uniformis angustidens* Přibyl, and *M. aequabilis* Přibyl mentioned by Mikhajlova (1975) in the upper part of the section has not been confirmed. The specimens described as these species (CGM Leningrad N10290) have different apertural structures and belong to the new species *M. anerosus*, *M. mironovi*, and *M. prognatus* (see synonymies). The latter is closely similar to *M. uniformis angustidens* and *M. praehercynicus* Jaeger. It differs in having uniformly developed hoods, a thinner proximal extremity, and greater overlap of interthecal septae in the distal part of the rhabdosome.

6. The Přídolí graptolite-bearing succession terminates with the new local zone of *M. microdon aksajensis*. Among the impoverished zonal assemblage, *M. transgrediens* does not occur. A similar situation is known in the Upper Silurian-Lower Devonian sections of central Nevada (Berry and



TEXT-FIG. 2. Stratigraphical distribution of monograptids in the Tokrau horizon of the north-east Balkhash area. Locality numbers in the third column are the numbers of exposures in the stratotype section of the Tokrau horizon at Kokbajtal Mountain (127-105) and those of the section near Aksaj Mountain (27, 28).

Murphy 1975). Here the local *M. birchensis* Zone is recognized in strata immediately underlying beds with the first appearance of *M. uniformis*. Within this topmost Silurian zone, *M. transgrediens* is not found. As in Kazakhstan, *M. microdon* R. Richter is the most common species in the zonal assemblage.

MORPHOLOGY

The morphology of the Tokrau monograptids can be determined only from specimens preserved in the rock. Nevertheless, the collections are represented by numerous specimens of different astogenetic stages, well preserved in relief or flattened. Many specimens studied give a general idea of the apertural structures, though investigation of some morphological problems awaits the recovery of isolated material.

The new Tokrau monograptids and some previously known Přidolí species can be classified into morphological groups on the basis of shape and degree of development of the apertural structures. There is not enough data to judge whether the morphological similarity reflects phylogenetic affinities or whether it exemplifies convergent evolution. No doubt both took place, and some of these groups unite monograptids belonging to different lineages.

Monograptus similis group. In the assemblages studied, monograptids possessing uniformly developed hoods of *M. uncinatus* type are most common. They span the complete stratigraphical interval from the *formosus* Zone to the *microdon aksajensis* Zone (inclusive). A maximum of development is observed in the *lochkovensis*–*boučeki* zones. *M. similis* Bouček is the oldest member of the group. The other members appear successively as follows: *M. prognatus* sp. nov., *M. beatus* sp. nov., *M. mironovi* sp. nov., and *M. balaensis* sp. nov. These species belong to at least two lineages. The first consists of *M. similis* and *M. prognatus*, connected by gradual morphological transition observed at the *formosus*–*lochkovensis* boundary. To this group probably belongs *M. birchensis* Berry and Murphy. These species most probably represent the Přidolí links in the lineage ancestral to the early Devonian *M. uniformis* group. Their Ludlow forerunners are still unknown. The morphological gap between the last Silurian and early Devonian monograptids having thecae of *M. uncinatus* type is not significant and it is expressed in the degree of development of hoods within the colony. *M. mironovi* and *M. balaensis* apparently represent short-lived offshoots. The second lineage includes *M. beatus* and *M. microdon aksajensis* and probably derives from *M. kallimorphus* Kraatz (late Ludlow). The morphological gap between the latter and *M. beatus* is possibly to be filled by an intermediate link.

Monograptus anerosus sp. nov. group. In the *boučeki* and *perneri* zones there occur the peculiar spiny monograptids *M. anerosus* sp. nov. and *M. supinus* sp. nov., closely similar to *M. pilosus* (Jackson and Lenz) from the Přidolí sequence of Canada. They have uniform apertural structures developed initially as dorso-lateral hoods, becoming later folded or separated by a mesial slit. In the last stage they terminate in long, paired apertural processes as *M. supinus*, a possible descendant of *M. anerosus*. The morphological changes at the transition are insignificantly small, manifested only in gracilization and dorsal curvature of the proximal end of the rhabdosome. There are intermediate specimens in the collections studied (Pl. 49, fig. 2; text-fig. 3f). The origin of the *M. anerosus* group is unclear but one can assume a relationship with the *M. lochkovensis* group, as well as affinities with *M. boučeki*.

M. transgrediens–*M. lochkovensis* group. Among the graptolite associations of the *lochkovensis* and *boučeki* zones there occur numerous biform graptolites like *M. lochkovensis* Bouček, *M. transgrediens* Perner and *M. nimius* sp. nov. *M. willowensis* occurs in the *M. perneri kasachstanensis* Zone. These species are characterized by similar apertural structures of the proximal thecae. The structures are distinct in detail and in the degree of penetrance within the colony. *M. nimius* has small lateral elevations at the first theca and in this respect it is closely similar to *M. transgrediens*. The other species, *M. willowensis*, is closer to the *M. lochkovensis* group and probably evolved from it. It inherits

well-developed apertural structures at about thecae ten-twelve, which terminate with paired lateral spines. Distal thecae are simple tubes in both species.

Some common tendencies are characteristic of the different morphological groups. One of the strangest trends is the thecal elongation developing towards the distal end. *M. nimius*, *M. balaensis*, and *M. microdon aksajensis* display this feature in different Přídolí time intervals. In extreme cases the thecae became more than 5 mm long, greatly overlapping each other. The elongation of thecae does not correlate with changes in their shape. The elongated thecae can be straight (*M. nimius*), distinctly undulating (*M. balaensis*), or sigmoidally curved (*M. microdon aksajensis*).

There are also some other morphological types which are not considered in this paper. The peculiar monograptids with climacograptid-like thecae devoid of any apertural additions are worth mentioning. They have been discovered in the *bouceki-perneri kasachstanensis* level and were assigned to *Pseudomonoclimacis* Mikhajlova, 1975. They are not known outside Kazakhstan within the Přídolí.

The new late Přídolí monograptids are associated with long-lived *P. dubius* (Suess) (*formosus* to *perneri kasachstanensis* zones inclusive) and *Linograptus posthumus* R. Richter (throughout the sequence studied).

All the species described in this paper with hoods (*M. similis* group), those with lateral lobes (*M. transgrediens* group), and those having more complicated intermediate structures (*M. lochkovens* and *M. anerosus* groups) are considered within the scope of the genus *Monograptus s.l.* (Bulman and Rickards 1970). The affinities of the apertural structures in some of the newly discovered Přídolí monograptids with early Ludlow saetograptids can be considered a clear example of homeomorphy. They do not serve as an evolutionary basis for discussing the Přídolí monograptids. More detailed knowledge of morphology, affinities, and biozonation of Přídolí monograptids is necessary before creating new genera which would have more value than mere technical validity.

SYSTEMATIC PALAEOLOGY

Material. Well-preserved graptolites in the collections are in greenish-grey siltstone and sandstone lithologies. They are preserved either as flattened, undeformed specimens or in low to full relief infilled with limonite. Abundant specimens of successive astogenetic stages represent most taxa. The material was collected by S. M. Bandaletov, A. I. Mironov, L. M. Paletz, M. A. Olenicheva, N. F. Mikhajlova, and the author, and is housed in the Central Geological Tschernyshev Museum, Leningrad (CGM), under accession number 10876. The photographs are by Mr. B. S. Pogrebov, Leningrad University, and A. P. Reuss, VSEGEL; drawings were prepared by the author.

Symbols and abbreviations. L—length of rhabdosome, thecae, sicula, etc.; S—width of rhabdosome, thecae, etc.; Σ —distance from the top of the hood to the sicular aperture; th^1 , th^2 . . . the first, second . . . thecae. All measurements are given in mm. Dimensions included in brackets after the figures for rhabdosome width in some species give the dorso-ventral width across the aperture excluding the thecal hoods.

Suborder MONOGRAPTINA Lapworth, 1880

Family MONOGRAPTIDAE Lapworth, 1873

Genus MONOGRAPTUS Geinitz, 1852

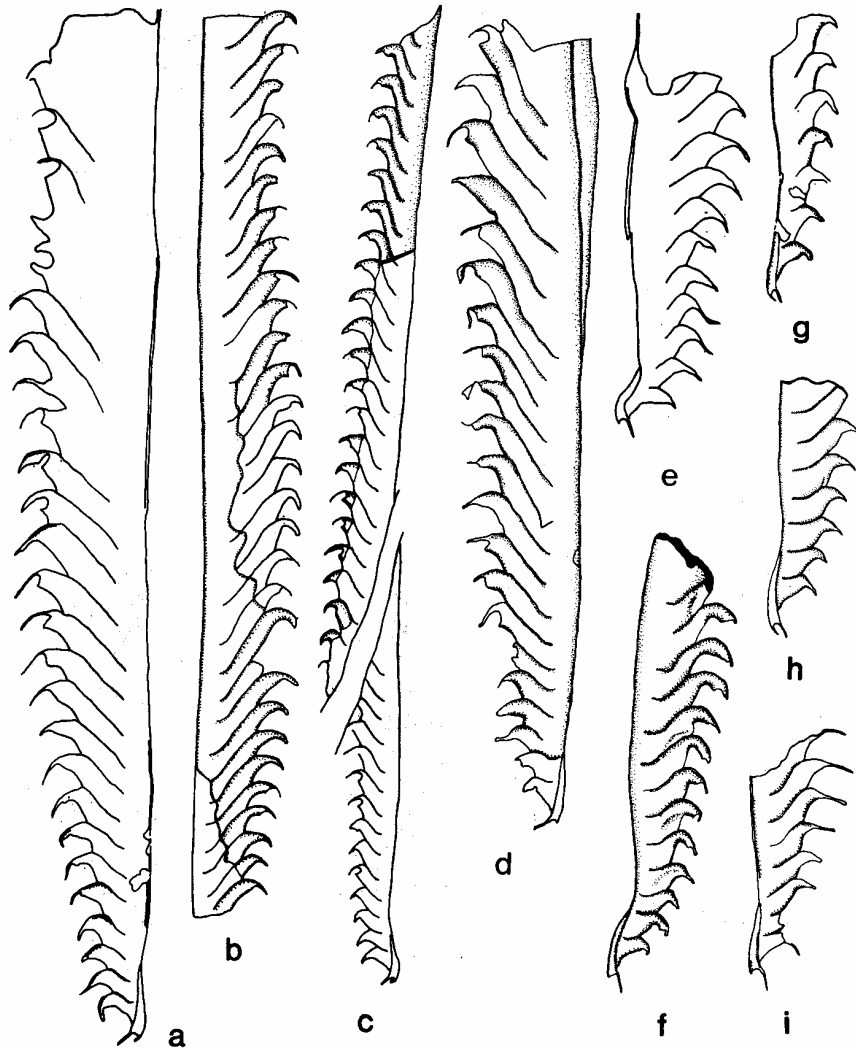
Monograptus anerosus sp. nov.

Plate 49, figs. 1–5; text-fig. 3

- 1975 *Monograptus uniformis*; Mikhajlova, p. 153, pl. 37, figs. 4–6.
 1975 *Monograptus angustidens*; Mikhajlova (*pars*), p. 154, pl. 37, fig. 1, *non* figs. 2, 3.
 1976 *Monograptus* aff. *uniformis*; Mikhajlova, pl. 2, fig. 19.
 1976 *Monograptus* cf. *uniformis*; Mikhajlova, pl. 3, fig. 5.

Derivation of name. Latin *anerosus*, meaning fat.

Holotype. CGM 1/10876; Pl. 49, fig. 1, text-fig. 3a; *bouceki* Zone, Tokrau horizon, from the Bala well.



TEXT-FIG. 3. *Monograptus anerosus* sp. nov.; a, holotype, 1/10876, $\times 6$; b, distal part of rhabdosome, 5/10290, $\times 4$; c, 1/10290, $\times 4$; d, rhabdosome in low relief, 6/10876, $\times 6$, loc. 94/1; e, flattened young rhabdosome, 7/10876, $\times 6$, loc. 35; f, g, rhabdosomes in full and low relief, transitional to *M. supinus* sp. nov. on account of the curvature of the proximal end, 8/10876, 2/10876, $\times 6$, loc. 105; h, i, 9/10876, loc. 68, 10/10876, loc. 105, $\times 6$.

Description. Rhabdosome straight, large, more than 35 mm long, with comparatively thin extreme proximal end at th^{1-2} . Dorsal edge displays slight dorsal curvature between th^{3-5} with sicula becoming distinctly curved ventrally. Width across the aperture (including hood and lobe structures but excluding spines) at th^1 0.75-0.95, above the aperture of th^1 0.5-0.7, at th^2 1.0-1.2, th^3 1.2-1.5, th^4 1.3-1.6, th^5 1.45-1.75, at 5 mm 1.8-2.3, at 10 mm 2.0-2.5; maximum width 2.5-3.0, sometimes 2.1-2.2 in rhabdosomes 35 mm long.

Long (up to 3.5 mm), straight thecae parallel-sided (0.4-0.5 mm), inclined towards virgula at 50-60° at the extreme proximal end and 35-45° distally. They end with distinctive apertural structures that are beak-like in profile and uniform within the rhabdosome. The degree of thecal overlap increases from $\frac{1}{2}$ proximally to $\frac{3}{4}$ and $\frac{2}{3}$

distally. At the proximal end interthecal septae are slightly curved, lying almost normal to the axis. At 5 mm a horizontal line at the aperture level crosses one septum, distally—not more than two. Subapertural part of thecae is isolated and projected in ventral direction, while the free ventral wall lies at low angle to the axis. Although numerous specimens are available, details of the apertural structure are unclear, since the preservation in rock gives no possibility of observing these features in ventral view. Judging from specimens in relief, one can assume that in the initial stages the short shield was under construction as a result of the subsequent development of both dorsal and lateral thecal walls. Later the mesial slit appears, and paired curved lateral lobes are formed. The latter terminate in stout spines projecting ventrally. The apertural structures described are similar to those in *M. lochkovensis*. The length of the isolated subapertural part of the thecae and that of the lobes is about 0.5–0.85; length of apertural processes is equal in all thecae, 0.3–0.5. Thecal spacing 7.5–8.0 in 5 mm proximally, 9–10 in 10 mm distally.

Sicula curved distinctly ventrally, with apex reaching the upper edge of the apertural structure of th^2 . Dimensions, L 1.3–1.6, sometimes 1.8, S aperture 0.15–0.2. Stout virgella 0.6–0.7 mm long is directed ventrally downward. There is a short (0.15 mm) curved dorsal process. The first theca is very short (0.7–0.75), Σ 0.8–1.05.

Discussion. The long, straight thecae at a gentle angle to the axis and the robust nature of the rhabdosome distinguish *M. anerosus* from other Pridoli monograptids. The complicated dorso-lateral apertural structures are unusual for late Silurian graptoloids, and their reconstruction given in the description above is not the only possibility. It could have been an undivided, hood-like structure with a deep fold but no slit in the middle, and terminating with long, paired processes situated dorso-laterally—a structure similar to that described by Tsegel'nyuk (1976) for '*Acanthograptus*' *spineus* and '*A.*' *aculeatus*. From the first growth stages the paired lateral lobes terminating with long spines could be formed—a structure homeomorphic to that of *Saetograptus*. This second possibility is less probable, but isolated material is needed for a more detailed analysis of morphology. In the shape of its apertural structures as seen in lateral view *M. anerosus* is similar to '*Saetograptus*' *pilosus*, described from post-Ludlow beds in the Yukon (Jackson and Lenz 1972). The structure is interpreted by those authors as paired lateral lobes. However, the real nature of the apertural additions cannot be reconstructed from the material preserved as silver-coloured films in shales. Thus, the assignment of this species to *Saetograptus* cannot be proved even on a morphological basis, to say nothing of phylogenetic criteria. This case seems to serve as a good example of convergent evolution, with the homologous thecal structure appearing independently. Comparison with some specimens of '*S.*' *pilosus* kindly provided by Professor A. Lenz shows that the new species differs in its larger size of rhabdosome, especially in its width. Further differences are in the straighter proximal extremity and in the closer thecal spacing, 7.5–8 in the first 5 mm as compared to 5–6 in the Yukon material. *M. anerosus* differs from *M. bouceki* in having paired apertural processes and larger rhabdosome size. Comparison with *M. supinus* sp. nov., which is closely similar morphologically and probably phylogenetically, is given in the description of the latter.

Distribution. Tokrau horizon, *M. bouceki*–*M. perneri kasachstanensis* zones, north-east Balkhash.

Material. More than fifty specimens well preserved as limonitic moulds in full to low relief, also flattened; Kokbajtal Mountains, locs. 93/1, 93/2, 255, 94, 105, 65, 41, 69; Kiikbaj Mountains, loc. 35; Bala well, loc. 209; Ashchi–Azek, loc. 47; Sarybiik Mountains, loc. 23.

EXPLANATION OF PLATE 49

Tokrau horizon, *M. bouceki* (locs. 209, 20, 92, 94) and *M. perneri* (loc. 105) zones.

Figs. 1–5. *Monograptus anerosus* sp. nov. 1, holotype, 1/10876, $\times 5$, loc. 209. 2–5, paratypes. 2, 2/10876, loc. 105, $\times 10$. 3, 3/10876, loc. 105, $\times 5$. 4, 4/10876, loc. 209, $\times 10$. 5, 5/10876, loc. 105, $\times 5$.

Fig. 6. *Monograptus balaensis* sp. nov., holotype, 11/10876, loc. 20, $\times 10$.

Figs. 7–10. *Monograptus beatus* sp. nov. 7, 7a, holotype, 12/10876, loc. 20, $\times 5$, $\times 10$. 8–10, paratypes. 8, 9, early growth stages, locs. 92, 110, $\times 20$. 10, 15/10876, loc. 94/3, $\times 10$.



KOREN', *Monograptus*

Monograptus balaensis sp. nov.

Plate 49, fig. 6; text-fig. 4a

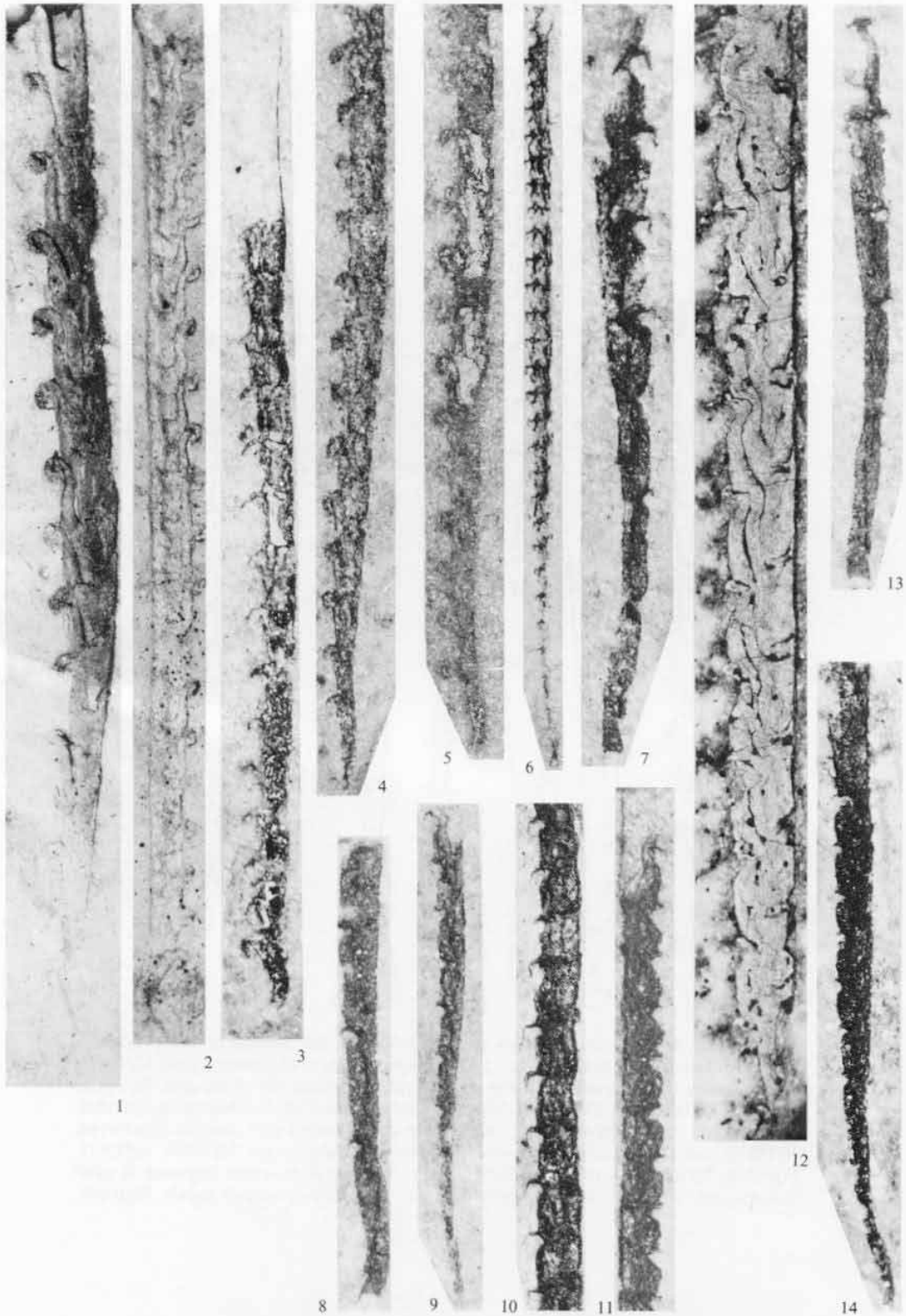
Derivation of name. After the Bala well, north-east Balkhash.*Holotype.* CGM 11/10876; Pl. 49, fig. 6, text-fig. 4a; 2.3 km south-west of the Sarybiik Mountains, loc. 20, Tokrau horizon, *bouceki* Zone.*Description.* A large, straight monograptid, 35–40 mm long with proximal end weakly curved dorsally between th^{1-6} . Width increasing gradually: at th^1 0.75(0.6), th^2 0.8–0.9(0.65–0.7), th^3 0.8–1.0(0.7–0.8), th^4 0.9–1.1(0.8), th^5 1.15(0.9), at 10 mm 1.2(1.0)–1.5(1.2), at 15 mm 1.45(1.2)–1.7(1.45) and maximum width at 20 mm 1.65(1.45)–2.0(1.65).Thecae long and narrow, strongly overlapping. The most distinctive feature is the strong, progressive elongation of thecae, from th^1 being 1 mm long to the distal thecae up to 4.5–5.5 mm long. Distally the thecal width to length ratio is 1:10. The thecal overlap reaches $\frac{1}{3}$ their length distally. Intertheal septa are straight and overlap strongly distally. A horizontal line at 10 mm from the sicular aperture crosses one septum, at 15 mm one septum and the base of the second, and further on distally it crosses two to three septa. Free ventral walls of the thecae are almost parallel to the axis. Metathecae strongly curved sigmoidally, displaying a sharp geniculum and shallow, semicircular apertural excavations. Thecal apertures 0.15–0.2 mm wide, and lie horizontally or are slightly everted. Thecae are furnished with short, down-curved hoods hanging closely above the apertures. They occur at a rate of 6 in 5 mm and 11.5–12.0 in 10 mm proximally, and 10–11 in 10 mm distally.Sicula curved weakly ventrally, with the apex almost reaching the aperture of th^2 . Dimensions, L 1.5–1.75, S aperture 0.15–0.2, Σ 1.25.*Discussion.* This species is distinct from any previously reported Pridoli monograptids in having long and extremely narrow thecae that overlap each other strongly in the middle and distal part of the rhabdosome.*Distribution.* Tokrau horizon, middle part, *lochkovensis*–*bouceki* zones, north-east Balkhash.*Material.* Ten specimens in full to low relief, Bala well, locs. 209, 201; Sarybiik Mountain, loc. 20.*Monograptus beatus* sp. nov.

Plate 49, figs. 7–10; Plate 50, figs. 1–5; text-fig. 4b–g

1975 *Monograptus* n. sp. aff. *microdon* R. Richter; Jaeger, p. 115, pl. 2, figs. 1, 2, text-fig. 5d.1975 *Monograptus aequabilis* Přibyl; Mikhajlova (*pars*), pl. 38, fig. 6.*Derivation of name.* Latin *beatus* meaning beautiful.*Holotype.* CGM 12/10876; Pl. 49, fig. 7, text-fig. 4b; 2.3 km south-west of Sarybiik Mountain, loc. 20, *bouceki* Zone.*Description.* Rhabdosome narrow, straight, 20–25 mm long. Dorsal edge displays slight dorsal curvature between th^{2-4} whereas the proximal extremity at th^1 and sicula are curved ventrally. At th^{1-2} the rhabdosome is of equal width, which is characteristic of the species. The width increases gradually between th^3-10 ; thereafter it may remain constant or show a slight decrease distally. Width at th^1 0.55–0.65, above the th^1 hood 0.3–0.35, at

EXPLANATION OF PLATE 50

Figs. 1–5. *Monograptus beatus* sp. nov., Tokrau horizon, *M. lochkovensis* (loc. 92) and *M. bouceki* (locs. 15, 20, 110, 94) zones, paratypes. 1, 16/10876, loc. 20, $\times 10$. 2, 17/10876, loc. 15a, $\times 10$. 3, 18/10876, loc. 94/1, $\times 10$. 4, 19/10876, loc. 110, $\times 10$. 5, 20/10876, loc. 110, $\times 10$.Figs. 6–14. *Monograptus microdon aksajensis* subsp. nov., Tokrau horizon, eponymous zone, loc. 28. 6, holotype, 26/10876, $\times 5$. 7–14, paratypes. 7, 8, 27/10876, 28/10876, $\times 20$. 9, 29/10876, $\times 10$. 10, 11, 30/10876, 31/10876, $\times 10$. 12, rhabdosome in relief, distal fragment, 32/10876, $\times 20$. 13, 33/10876, $\times 20$. 14, 34/10876, $\times 10$.



KOREN', *Monograptus*



TEXT-FIG. 4. *a*, *Monograptus balaensis*, sp. nov., holotype, rhabdosome in relief, 11/10876, $\times 6$; *b-g*, *Monograptus beatus* sp. nov.; *b*, holotype, fragment of proximal part, 12/10876; *c-e*, *g*, young rhabdosomes with the characteristic shape of the distal end, 21/10876, 22/10876, 23/10876, 25/10876, locs. 20, 15; *f*, distal fragment of rhabdosome in full relief, 24/10876, loc. 15; *h-q*, *Monograptus microdon aksajensis* subsp. nov., loc. 28; *h*, holotype, 26/10876, $\times 4$; *i-o*, young rhabdosomes at different growth stages, 35/10876, 36/10876, 27/10876, 33/10876, 28/10876, 37/10876, 38/10876, $\times 10$; *p*, proximal fragment of adult rhabdosome, 34/10876, $\times 10$; *q*, distal fragment with well-developed hoods, 39/10876, $\times 10$.

th² 0.55-0.75, th³ 0.65-0.75, th⁴ 0.65-0.8, at 5 mm 0.8-0.85, at 10 mm 0.85-0.95, with a maximum of 0.85-1.0 across the hood and 0.7-0.75 above it. A prominent, free nema is commonly thin.

Thecae long, narrowing to the aperture and strongly curved sigmoidally, displaying a sharp geniculum. The ventral walls are parallel to the axis. Dimensions, L 1.5-1.7, S aperture 0.1-0.15. Thecae overlap half of the succeeding thecae, the base of the interthecal septum is at the level of the hood of the preceding theca. Apertural structures develop as dorso-lateral hoods, which are down-curved, extending ventrally and obscuring the apertures both ventrally and laterally; beginning with th²⁻³ they are retroverted to face and almost to touch the ventral edge of the aperture. Their dorso-ventral width accounts for $\frac{1}{2}$ to $\frac{3}{4}$ the total width of the rhabdosome. Thecae occur at a rate of 6-7 in 5 mm and 11.5-12.0 in 10 mm proximally, and 10.5-11.0 in 10 mm distally.

Prosicula very narrow and short (0.3 mm), metasicula weakly or distinctly curved ventrally, more strongly so in the subapertural part with the aperture facing down ventrally. Dimensions, L 1.4-1.5, S aperture 0.17-0.2. The sicula carries a stout virgella 0.55-0.65 mm long, and a narrow, weakly curved dorsal tongue (0.15 mm). Apex extends to a level between the hoods of th¹⁻², Σ 1.25-1.4. The ventral wall of th¹ at 1 mm length is 0.2-0.25 mm above the aperture.

Discussion. *M. beatus* differs from *M. kallimorphus* Kraatz and *M. balticus* Teller (the latter being possibly a junior synonym of the former) in having a comparatively straight proximal end and larger rhabdosome. It can also be distinguished by its longer thecae and lesser degree of thecal hood retroversion. Compared with *M. cf. balticus* Teller from the Road River Formation of the Yukon (Jackson and Lenz 1972) the Kazakhstan species differs in having a thinner proximal extremity and a greater thecal count. The long, retroverted hoods and short thecae separate this species from late Přidolí-Lochkov monograptids such as *M. microdon*. One can suggest that *M. kallimorphus* (late Ludlow), *M. beatus* (middle Přidolí) and *M. microdon* (which are all similar morphologically) belong to one lineage with some unknown links within the Ludlow-Lochkov interval.

Distribution. Tokrau horizon, middle part, *lochkovensis-bouceki* zones, north-east Balkhash.

Material. Eighty-six specimens at various growth stages, well preserved in low to full relief or flattened; Kokbajtal Mountains, locs. 92, 110, 93/1-4; Sarybiik Mountains, locs. 15a, 20a; Aksaj Mountains, loc. 75.

Monograptus microdon aksajensis subsp. nov.

Plate 50, figs. 6-14; text-fig. 4h-q

Derivation of name. After the Aksaj Mountains of north-east Balkhash.

Holotype. CGM 26/10876; Pl. 50, fig. 6, text-fig. 4h; Aksaj Mountains, loc. 28, the eponymous zone in the upper part of the Tokrau horizon.

Description. Rhabdosome straight, thin, reaching 30 mm in length. The proximal end between th¹⁻⁵ varies from straight to weakly curved dorsally, while the sicula has a ventral curvature. The width increases imperceptibly up to a maximum of 0.7-0.95 (0.55-0.8) mm at a distance of 10 mm from the first theca, thereafter being constant. Successive increase in width, at th¹ 0.25(0.2), th² 0.3(0.22-0.25), th³ 0.3-0.4(0.25-0.35), th⁴ 0.4-0.45(0.3-0.4), th⁵ 0.45-0.5(0.4-0.45), at 10 mm 0.7-0.95(0.55-0.8).

Uniform thecae are strongly curved near the apertures of preceding thecae, forming a sharp geniculum. They overlap significantly, with the interthecal septae noticeably undulating. Thecae have short dorso-lateral hoods 0.15-0.3 mm long and 0.05-0.1 mm high hanging above the apertures, with their edges extending beyond the ventral walls of thecae at 0.1-0.2 mm. Straight apertures of proximal thecae are exposed laterally. Distal hoods are more strongly developed laterally and obscure the thecal apertures. The middle part of the hood resembles a weakly down-curved shield. Protheca expanded, bottle-like at the base, narrowing sharply to the aperture. At the base of the lateral side of the protheca a distinct wrinkle can be observed (Pl. 50, fig. 12), directed ventrally downwards from the nema. Metathecae are of equal width over most of their length, narrowing sharply towards the aperture. The free part of the metatheca is convex, with the subapertural part introverted. Thus, hoods grow first dorsally, then they turn upwards ventrally. Most of the hood is under the geniculum of the succeeding theca. This distinctive outline of the subapertural part of the thecae is well seen at the growing end of the rhabdosome (Pl. 50, figs. 9, 11, 13). Towards the dorsal end the thecae have a strong tendency to elongation, which is expressed in a greater degree of thecal overlap. Dimensions of distal thecae, L 2.1-2.15 (metatheca occupies $\frac{3}{4}$ the whole length), S metatheca from 0.25-0.27 above geniculum to 0.1 near the aperture. The base of the interthecal septum of thⁿ and thⁿ⁺¹ almost reaches the upper edge of the thⁿ⁻² hood. A horizontal line across the hood

distally crosses not more than one septum. The thecal count ranges from 6·0–6·5 in 5 mm and 12·5–13·0 in 10 mm proximally, to 12·0–12·5 in 10 mm distally.

The extreme proximal end is very thin. The sicula is short with its apex reaching the level of the th^1 aperture. The base of th^1 is at 0·17–0·22 mm above the sicular aperture. The sicula is provided with a virgella 0·3–0·5 mm long and with a short dorsal tongue. Dimensions of sicula, L 1·0–1·2, S aperture 0·12–0·15(0·2), Σ 1·3–1·4.

Discussion. Numerous well-preserved specimens both in low relief and flattened allow details of the distinctive thecal structure to be studied for the first time. Previous knowledge of the morphology of *M. microdon* was based on studies of flattened and often deformed material preserved mainly as silver films in black shales. A thin rhabdosome and small, barely noticeable hoods are considered to be diagnostic features of this species. Differentiation of subspecies is based on the shape of the proximal end—straight, curved dorsally, or curved ventrally (*M. m. microdon* R. Richter; *M. m. silesicus* Jaeger). In my material it is possible to see the extensive range of variation in the curvature of the proximal end, from straight to distinctly curved dorsally. On the same bedding planes there are straight rhabdosomes similar to *M. m. microdon* and dorsally curved forms typical of *M. m. silesicus*, with all transitions. This therefore casts doubt on the possibility of using the shape of thin, flexible proximal extremities as a reliable taxonomic criterion. The new Kazakhstan subspecies differs from *M. m. microdon* in having a thinner proximal end at the level of th^{1-5} and a lesser maximum width not exceeding 1 mm. It also has more closely spaced thecae, 13–12 in 10 mm as compared with 10·5–8·5 characteristic of the type subspecies from the uppermost Silurian and Lower Devonian (Thuringia, Urals, central Nevada).

From monograptids of the *M. similis* group, with uniform thecae having hoods of the *M. uncinatus* type, this subspecies can be distinguished by its longer and thinner thecae with sigmoidal curvature, by its smaller hoods, and its thinner proximal end; also, the maximum rhabdosome width is lower. Comparison with *M. beatus* sp. nov., to which it is probably related, is given in the description of the latter species.

Distribution. Uppermost part of the Tokrau horizon, the eponymous local zone, north-east Balkhash. This local zone terminates the continuous Silurian succession of terrigenous rocks. The level of the Silurian–Devonian boundary is not proved biostratigraphically since graptolites are not found in the overlying strata, but one would predict the appearance of *M. uniformis* close to this level.

Material. Eighty specimens at various growth stages preserved both flattened and sometimes as limonitic moulds in full relief; Aksaj Mountain, loc. 28.

Monograptus mironovi sp. nov.

Plate 51, figs. 1–3; text-fig. 5a–e

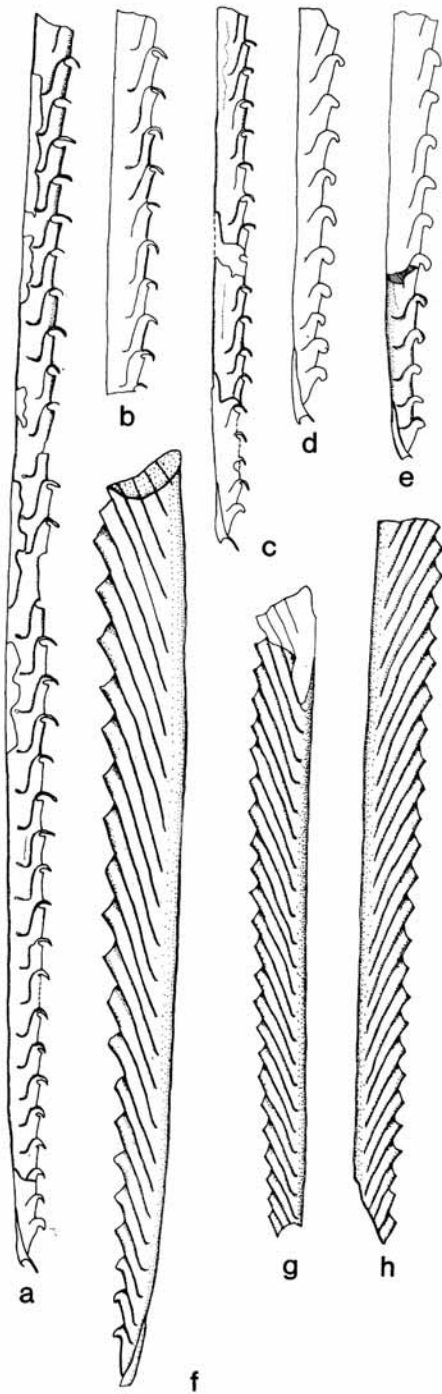
1975 *Monograptus aequabilis*; Mikhajlova (*pars*), pl. 38, figs. 1, 2.

Derivation of name. In honour of the Kazakhstan geologist A. I. Mironov.

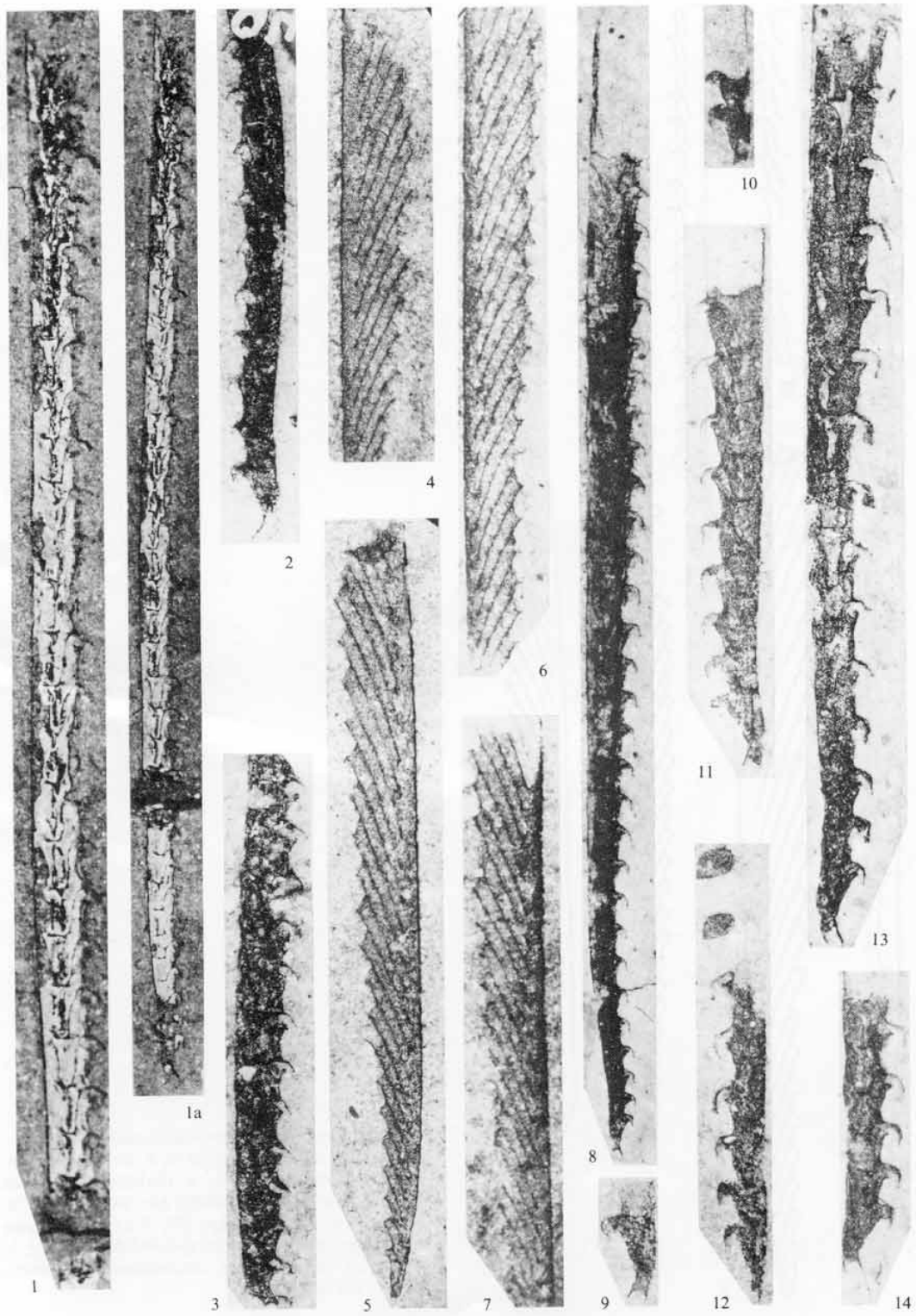
Holotype. CGM 40/10876; Pl. 51, fig. 1, text-fig. 5a; Kokbajtal Mountains, loc. 94/1, Tokrau horizon, *bouceki* Zone.

EXPLANATION OF PLATE 51

- Figs. 1–3. *Monograptus mironovi* sp. nov., Tokrau horizon, *M. bouceki* Zone, loc. 94/1. 1, 1a, holotype, 40/10876, $\times 10$, $\times 5$. 2, 3, paratypes, 41/10876, 42/10876, $\times 10$.
 Figs. 4–7. *Monograptus nimius* sp. nov., Tokrau horizon, *M. bouceki* Zone, loc. 44. 4, paratype, 47/10876, $\times 5$. 5, holotype, 48/10876, $\times 5$. 6, 7, 49/10876, 50/10876, $\times 5$.
 Figs. 8–14. *Monograptus prognatus* sp. nov., Tokrau horizon, *M. microdon aksajensis* local Zone, loc. 28. 8, holotype, 51/10876, $\times 5$. 9, 10, early growth stages, 52/10876, 53/10876, $\times 10$. 11, 13, paratypes, 54/10876, 56/10876, $\times 10$. 12, 14, 55/10876, 57/10876, $\times 10$.



TEXT-FIG. 5. *a-e*, *Monograptus mironovi* sp. nov., $\times 6$; *a*, holotype, 40/10876; *b*, distal fragment, 43/10876, loc. 94/1; *c-e*, rhabdosomes in full and low relief, 44/10876, loc. 94/1, 45/10876, loc. 15, 46/10876, loc. 75; *f-h*, *Monograptus nimius* sp. nov.; *f*, holotype, 48/10876, $\times 6$; *g, h*, distal fragments of rhabdosomes in relief, 50/10876, $\times 4$.



KOREN', *Monograptus*

Description. Rhabdosome straight, medium sized, 20–30 mm long. The dorsal edge between th^{2-4} is weakly curved dorsally, the ventral edge is straight. A slight increase of width within the rhabdosome is characteristic of the species. Successive width measurements, at th^1 0.75–0.8(0.5–0.65), above the hood of th^1 0.55, at th^2 0.65–0.8(0.5–0.6), th^3 0.75–0.85(0.6–0.75), th^4 0.75–0.85(0.55–0.75), th^5 0.8–0.9(0.65–0.75), maximum width 0.8(0.6)–1.0(0.8) between th^{6-8} , sometimes reaching 1.25(1.0) and thereafter constant.

Thecae comparatively short (1.8–1.9), slightly curved sigmoidally, overlapping for half of their length. The ventral walls and interthecal septa are parallel or inclined slightly to the axis. In the middle and distal parts of the rhabdosome the bases of the interthecal septa are at the level of the preceding thecal hood. Dorsal apertural hoods hang over the aperture and extend down slightly below its ventral edge. The hood of th^1 is slightly larger than the others and its length corresponds to one-third of the whole dorso-ventral width of the rhabdosome. Thecal hoods are equally developed along the rhabdosome, including the extreme dorsal end; they are 0.3–0.35 mm long and 0.35–0.4 mm high. Thecae number 6.5–7.5 in 5 mm and 13–14 in 10 mm proximally, and 10.5–12.0 in 10 mm distally.

The extreme proximal end is not thin in comparison to the small size of the rhabdosome. Sicula straight or slightly curved ventrally. The first theca is short and broad at its base, originating at 0.15 mm above the sicular aperture. The sicula terminates with a stout virgella 0.5–0.6 mm long and a short dorsal tongue; the apex extends to the level of the th^2 aperture. Dimensions of sicula, L 1.3–1.6, S aperture 0.2–0.25, Σ 1–1.2.

Discussion. This species is comparable to *M. similis* Přibyl in general structure and rhabdosome shape. It differs, however, in being narrower at th^1 and in the distal part of the rhabdosome. Its maximum width is 1.0(0.8) as compared with 1.2–1.5(1.0–1.2) in *M. similis*. It can also be distinguished from *M. similis* by its shorter thecae, shorter sicula, and larger size of hoods projecting considerably and uniformly beyond the free ventral wall. It has close affinities with *M. beatus* sp. nov. but it can be distinguished by: 1, shorter hoods that are not retroverted at the edges; 2, greater width of the extreme proximal end (0.55 above th^1 hood as compared with 0.3–0.35 mm); 3, straight extreme proximal end including the sicula itself; and 4, more closely packed thecae. It differs from *M. prognatus* sp. nov. in having a smaller rhabdosome, a slight increase in width within the rhabdosome, and in having the free ventral walls of the thecae lying parallel to the axis.

Distribution. Middle part of the Tokrau horizon, *bouceki* Zone, north-east Balkhash.

Material. Forty-eight well-preserved specimens, both flattened and in low relief; Kokbajtal Mountains, locs. 94/1–3; Bala well, loc. 75; Sarybiik Mountains, locs. 15a, 20.

Monograptus nimius sp. nov.

Plate 51, figs. 4–7; text-fig. 5f–h

Derivation of name. Latin *nimius* meaning extraordinary.

Holotype. CGM 48/10876; Pl. 51, fig. 5, text-fig. 5f; Ashchi–Azek, loc. 44, Tokrau horizon, *bouceki* Zone.

Description. Rhabdosome large, 25–35 mm long. The extreme proximal end between th^{5-6} is slightly curved ventrally. Width increases rapidly within the first 10 mm, thereafter more slowly up to the distal end. Width measurements, at th^1 0.75–0.85, th^2 0.85–1.0, th^3 0.95–1.1, th^4 1.1–1.2, th^5 1.15–1.3, at 5 mm 1.2–1.4, at 10 mm 1.6–1.65, at 15 mm 1.75–2.1, maximum width 2.25–2.65 (specimens in relief) and 2.85 (flattened) for rhabdosomes more than 20 mm long. The extreme proximal end appears to taper in comparison with the remainder of the rhabdosome.

Thecae biform, the first three to four provided with paired lateral lobes, each small and rounded; remaining thecae are simple tubes with even, retroverted apertures. Thecae long and slender, parallel-sided over most of their length and distinctly widening towards the apertures. The progressive astogenetic elongation of thecae accompanied by development of thecal overlap is the most characteristic morphological feature. Length of successive thecae, th^1 1.25, th^5 2.25, th^{10} 3.5, th^{15} 4.5, and th^{20} 5.5. Average size of distal thecae: L 5.0, S aperture of protheca 0.4, S aperture of metatheca 0.5; S : L more than 1 : 10. Overlap increases from $\frac{1}{4}$ proximally to $\frac{2}{3}$ of the succeeding thecae distally. A horizontal line across the thecal aperture at 5 mm from the sicula crosses two interthecal septa, at 10 mm it crosses two and the base of the third, at 20 mm and thereafter not less than three. Angle of thecal inclination 18–23°. Thecae number 5.5–6.5 in 5 mm and 10.5–11.5 in 10 mm proximally, 8–9 in 10 mm distally.

Sicula slightly curved ventrally, with apex reaching a level between the apertures of th^1 and th^2 . Dimensions of sicula, L 1.75, S aperture 0.25–0.3, Σ 1.5.

Discussion. *M. nimius* differs from closely similar biform monograptids such as *M. transgrediens* Perner and *M. lochkovens* Bouček in having extremely long and strongly overlapping thecae with a small angle of inclination to the axis. In both *M. lochkovens* and *M. transgrediens* a horizontal line across the thecal aperture crosses two intertheal septa at the most. A ratio of thecal width to length of 1:10 is unknown among previously recorded Příklad monograptids, except for *M. balaensis* sp. nov. described herein. *M. lochkovens* is most similar to *M. nimius*, but the latter is distinguished by having a lower number of proximal thecae provided with paired lateral additions that are smaller and have no processes.

Distribution. Middle part of the Tokrau horizon, *lochkovens*–*bouceki* zones, north-east Balkhash.

Material. Thirty well-preserved specimens both in relief and flattened; Kokbajtal Mountains, locs. 92, 110, 93/4, 94/1; Sarybiik Mountains, loc. 15a; Ashchi–Azek, loc. 44.

Monograptus prognatus sp. nov.

Plate 51, figs. 8–14; Plate 52, figs. 1–5, 8–10; text-fig. 6

1975 *Monograptus angustidens*; Mikhajlova (*pars*), p. 154, pl. 37, figs. 2, 3.

1976 *Monograptus angustidens*; Mikhajlova, pl. 1, fig. 21.

1969 ?*Monograptus* aff. *angustidens*; Jackson and Lenz, p. 21, pl. 3, figs. 6–9, pl. 5, fig. 7.

1978 ?*Monograptus* aff. *angustidens*; Jackson, Lenz and Pedder, p. 21, pl. 3, figs. 4, 11.

Derivation of name. Latin *prognatus* meaning deriving from somebody.

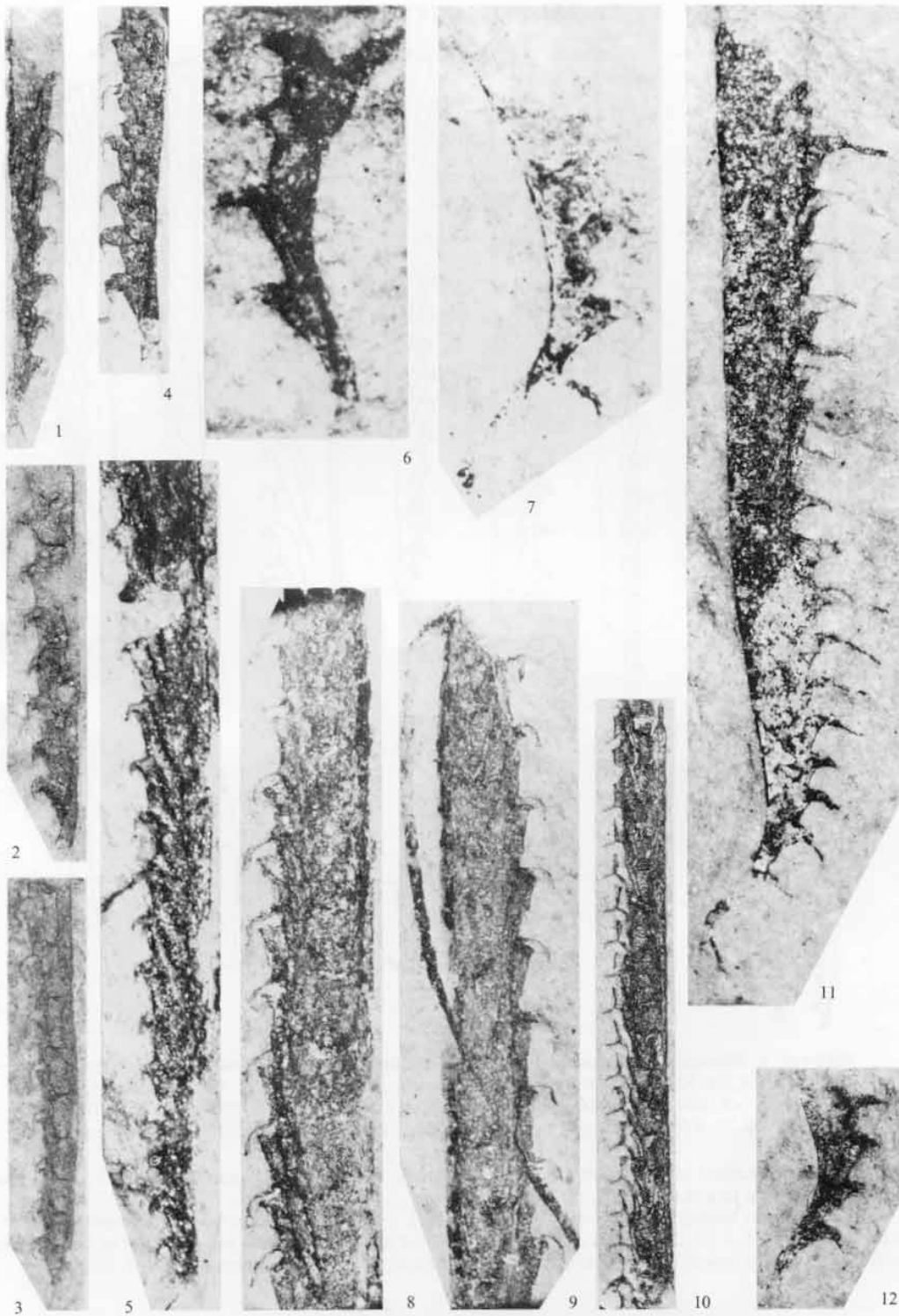
Holotype. CGM 51/10876; Pl. 51, fig. 8; from the *microdon aksajensis* Zone, uppermost part of the Tokrau horizon, Aksaj Mountains, loc. 28.

Description. Rhabdosome straight, large, 30–40 mm or up to 50–60 mm long. The extreme proximal end is very thin, dorsal edge displays slight dorsal curvature between th^3 – 5 . A stout, free nema continues beyond the distal thecae for more than 10 mm. Width at th^1 0.6–0.85(0.45–0.65), above th^1 hood 0.35–0.55, at th^2 0.65–0.95(0.5–0.75), th^3 0.7–1.0(0.6–0.8), th^4 0.75–1.0(0.6–0.85), th^5 0.8–1.1(0.6–0.85), at 5 mm 0.95–1.25(0.75–1.15), at 10 mm 1.35–1.65(1.1–1.4), maximum width in specimens 20–50 mm long is 1.6–2.0(1.3–1.75), in those up to 60 mm long is 2.0–2.3(1.75–1.8). The noticeable variation in dorso-ventral width can be explained partly by different states of preservation. Thecae are weakly curved sigmoidally and have long dorsal hoods. They project 0.3 mm beyond the ventral edge of the rhabdosome and extend down below the aperture for 0.2–0.3 mm; they are 0.5–0.75 mm long and 0.2–0.3 mm high. Hoods are well developed and uniform within the whole rhabdosome, being 0.75 mm long on the extreme distal thecae (Pl. 52, figs. 8–10). Apertures are clearly visible in ventral view beginning with th^3 – 4 . Proximally the hoods occupy $\frac{1}{3}$ and distally $\frac{1}{4}$ to $\frac{1}{5}$ of the dorso-ventral width of the rhabdosome, and they have small excavations 0.15–0.2 mm long and 0.25–0.3 mm wide. The overlap of intertheal septa increases distally. At 5 mm from the sicula the septum between th^n and th^{n+1} reaches the level of the th^{n-1} hood, and a horizontal line across the aperture does not cut any septum; at 10 mm it crosses the base of one septum, at 15–20 mm it cuts one septum and sometimes the base of another, and at the extreme distal end it cuts two septa. Thecal overlap increases from $\frac{1}{4}$ to $\frac{3}{4}$ of their length. The distal thecae are 3.0–3.5 mm long, 0.25–0.35 mm wide; the angle of inclination to the axis reaches 10–15°, sometimes 20°. Free ventral walls

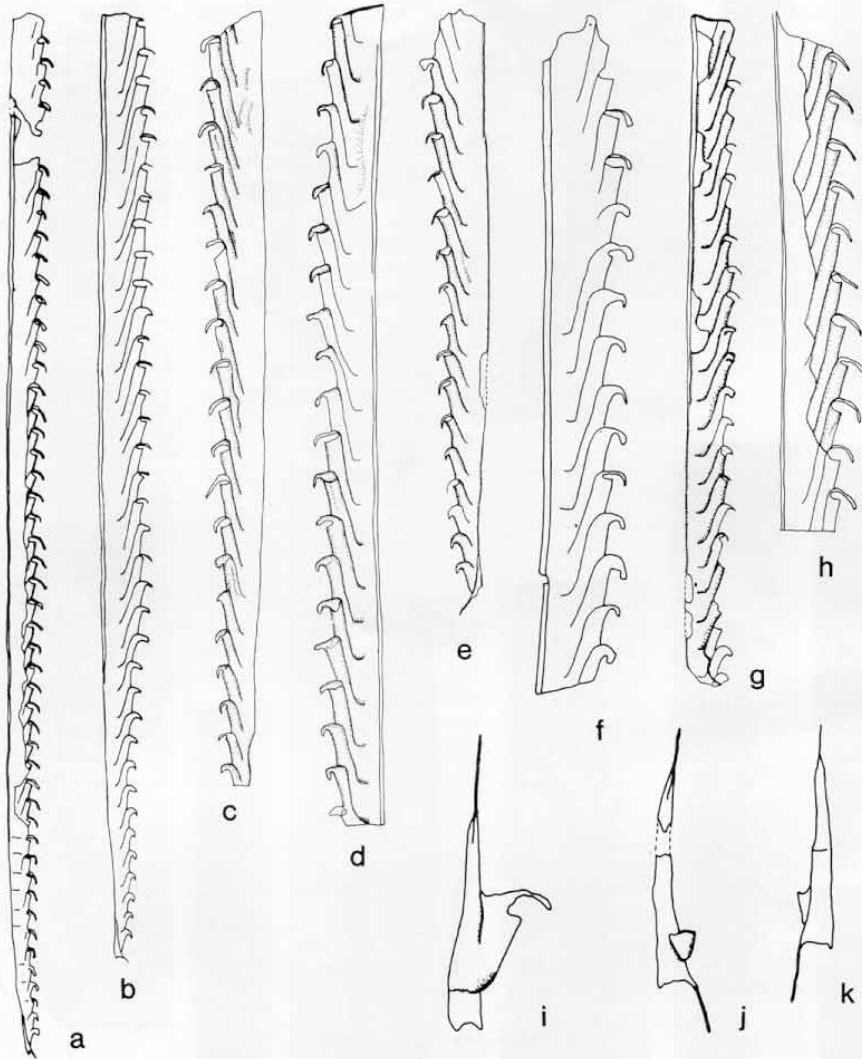
EXPLANATION OF PLATE 52

Figs. 1–5, 8–10. *Monograptus prognatus* sp. nov., Tokrau horizon, *M. lochkovens* (loc. 92), *M. bouceki* (locs. 15, 20) and *M. microdon aksajensis* (loc. 28) zones. 1, 58/10876, loc. 28, $\times 10$. 2, 59/10876, loc. 20, $\times 10$. 3, 60/10876, loc. 15a, $\times 10$. 4, 61/10876, loc. 28, $\times 10$. 5, paratype, 62/10876, loc. 92, $\times 10$. 8–10, distal fragments of adult rhabdosomes with well-developed hoods, 63/10876, 64/10876, loc. 28, $\times 10$; 65/10876, loc. 92, $\times 5$.

Figs. 6, 7, 11, 12. *Monograptus supinus* sp. nov., Tokrau horizon, *M. bouceki* Zone, loc. 94/1. 6, 7, 12, young rhabdosomes, 75/10876, 76/10876, $\times 20$; 78/10876, $\times 10$. 11, holotype, 77/10876, $\times 10$.



KOREN', *Monograptus*



TEXT-FIG. 6. *Monograptus prognatus* sp. nov.; a, b, adult rhabdosomes, 66/10876, $\times 3$, loc. 28, 67/10876, $\times 4$, loc. 92; c, d, distal rhabdosome fragments, 68/10876, loc. 92, 69/10876, loc. 15, $\times 6$; e, 62/10876, $\times 6$, loc. 92; f-h, distal fragments of adult rhabdosomes, 70/10876, loc. 15, 2/10290, 71/10876, loc. 77, $\times 6$; i-k, early stages of development, 72/10876, 73/10876, 74/10876, $\times 20$, loc. 28.

are straight and inclined at 10° to the nema. The thecal count is 6.0-6.5 in 5 mm and 11.0-12.5 in 10 mm proximally, 9-10 in 10 mm distally.

Sicula straight or weakly curved ventrally. Dimensions, L 1.35-1.8, S aperture 0.2-0.3, L virgella 0.5-0.65, L dorsal tongue 0.1, Σ 1.1-1.35. Apex reaches the level of the base of the septum between th^{2-3} or between the hoods of th^{1-2} . The base of th^1 is 0.2 mm above the sicula aperture, its length being about 0.85-1.05 mm.

Discussion. *M. prognatus* is fairly close to *M. uniformis angustidens* Přibyl, *M. praehercynicus* Jaeger and *M. birchensis* Berry and Murphy in thecal shape and hood structure. From all these species it differs, however, in one important feature, namely in the uniform development of hoods within the whole rhabdosome. This feature is more or less typical of Přidolí monograptids, as opposed to the *M. uniformis* group and others displaying a distinct decrease of hoods distally. From *M. u. angustidens* and *M. praehercynicus* it also differs in having a thinner proximal extremity and greater overlap of thecae distally. From the latter, *M. prognatus* can be distinguished by its lower distal width, more closely packed proximal thecae, smaller sicula, and shorter distance between sicular aperture and the upper edge of th¹ hood. From *M. birchensis* it differs in having a thinner and commonly straight proximal end within the first 10 mm, as well as having a narrower sicular aperture and shorter distance to the hood of th¹. In contrast to *M. birchensis* the new species displays a lower thecal inclination to the axis (28–33° in *M. birchensis*) and a greater overlap of distal intertheal septae. *M. prognatus* is comparable with *M. uncinatus* Tullberg in having hoods developed equally within the rhabdosome. It differs, however, in having smaller hoods and less strongly curved thecae with free ventral walls inclined to the axis. The length of thecae and their overlap are markedly greater than in *M. uncinatus*. The well-developed hoods on the distal thecae, slender proximal extremity, very gradual increase in rhabdosome width, lesser thecal overlap and angle of inclination separates *M. prognatus* from *M. u. uniformis* Přibyl. It also differs in having more closely spaced thecae and a shorter sicula that never reaches 2 mm. The larger rhabdosome and the longer thecae displaying stronger overlap distinguish *M. prognatus* from *M. similis* Přibyl. The material studied makes it possible to trace a morphological transition between *M. similis* and *M. prognatus*, expressed in increase in rhabdosome size together with thecal elongation and stronger thecal overlap. Stratigraphically, the new species succeed *M. similis*, appearing just above its last occurrences at the top of the *formosus* Zone and occurring thereafter through the whole Přidolí sequence. It can be assumed that *M. prognatus* is a precursor of the Lower Devonian monograptids of the *M. uniformis* group. *M. similis*, *M. prognatus* and *M. uniformis* could have been successive members of the same lineage developing within Přidolí–Lochkov times. The representatives of this lineage were conservative in the general morphology of their thecae, possessing similar hoods that are homeomorphs of those in *M. uncinatus* throughout the whole time span. They underwent insignificant morphological modification, namely a change of thecal size and proportions, appearance of thecal bioformity expressed in distal decrease and then complete reduction of hoods, and in a small variation in rhabdosome size.

Distribution. Tokrau horizon, *lochkovens*, *bouceki*, *perneri*, *kasachstanensis* and *microdon aksajensis* zones, north-east Balkhash, most abundant in the uppermost local zone where it occurs with *M. microdon aksajensis*, and *Linograptus posthumus*. The marked impoverishment of the graptolite association suggests an immediate stratigraphical proximity to the *M. uniformis* level.

Material. More than 170 specimens of different astogenetic stages, well preserved, mainly flattened and sometimes in low relief; Kokbajtal Mountains, locs. 92, 110, 93/1, 105, 65, 69, 30, 41; Kiikbaj Mountains, loc. 7a; Aksaj Mountains, locs. 27, 28; Sarybiik Mountains, locs. 15a, 20, 22; Ashchi–Azek, loc. 47.

Monograptus supinus sp. nov.

Plate 52, figs. 6, 7, 11, 12; text-fig. 7

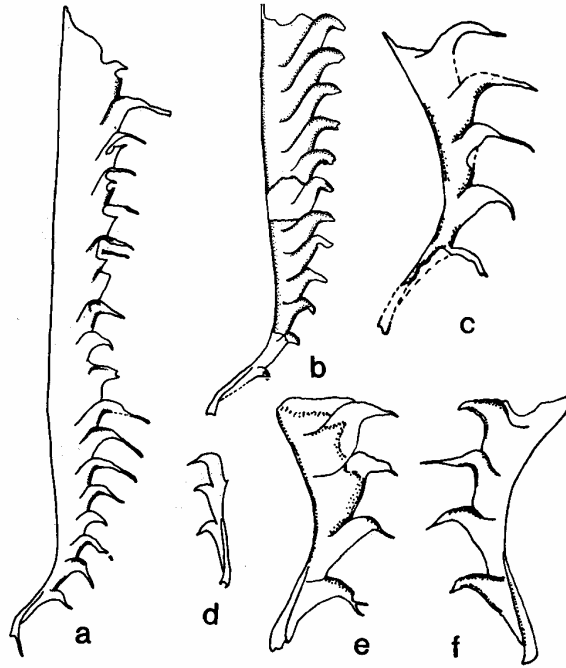
1976 *Monograptus* sp.; Mikhajlova, pl. 2, fig. 15.

Derivation of name. Latin *supinus* meaning curved dorsally (back).

Holotype. CGM 77/10876; Pl. 52, fig. 11, text-fig. 7a; Kokbajtal Mountains, loc. 94/1, middle part of Tokrau horizon, *bouceki* Zone.

Description. Rhabdosome of medium-size with slender proximal end, sharply curved dorsally (45°) within the first three to five thecae. Dimensions of adult rhabdosomes, L 20–40, S maximum 2.0–2.25. Successive measurements of width, at th¹ 0.6, above the th¹ aperture 0.3, at th² 0.7–0.8, th³ 1.0–1.1, th⁴ 1.3, th⁵ 1.4, at 5 mm 1.5–1.6, at 10 mm 1.7–1.9, maximum width attained distally.

Thecae have uniform apertural additions identical to those of *M. anerosus*. The proportions of the thecae and their inclination to the axis change within the rhabdosome due to the marked curvature of the proximal end. The first three or four thecae have long prothecal sections and overlap for not more than $\frac{1}{4}$ of their length. Distally the thecal overlap increases to $\frac{2}{3}$ of the length. The angle of inclination to the axis changes from 50° to $30\text{--}35^\circ$ distally. A horizontal line across the thecal aperture proximally does not meet any septum; distally it crosses two septa.

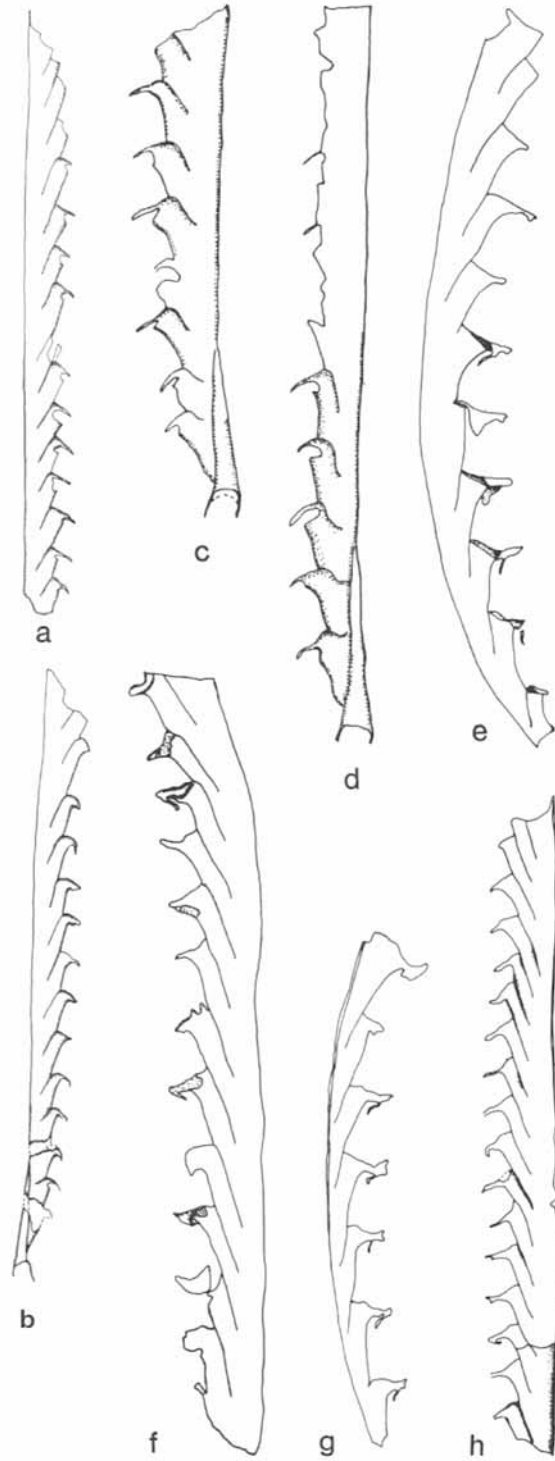


TEXT-FIG. 7. *Monograptus supinus* sp. nov.; a, holotype, 77/10876, $\times 6$; b, rhabdosome in relief, 79/10876, $\times 6$, loc. 22; c-f, young rhabdosomes, 76/10876, $\times 12$, 80/10876, $\times 6$, 78/10876, $\times 12$, 75/10876, $\times 12$, loc. 94/1.

The beak-like apertural structures project ventrally, terminating in straight processes 0.8–1.0 mm long and 0.1–0.2 mm thick at the base. Sometimes a bifurcation of processes can be observed and their ends are connected by membranes. Details of apertural spine structures are not clear in the material studied. They are probably similar to monofusellar processes, with edges folded together into a tube, as described previously as a characteristic feature of *Saetograptus chimaera* (Urbanek 1958). Thecae are spaced at 7 in 5 mm and 13–14 in 10 mm proximally, and at 11–12 in the distal 10 mm.

Sicula weakly curved ventrally with apex reaching the level of the th¹ aperture or slightly above. Dimensions, L 1.15–1.2, S aperture 0.15–0.2, L virgella 0.25–0.35, Σ 1.4–1.5.

Discussion. Although possessing the general form of the thecal structures of *M. anerosus*, this species is distinct in having a markedly thinner proximal end and in its stronger dorsal curvature. Some specimens transient from *M. anerosus* to *M. supinus* are present in the collections studied. They display an intermediate degree of proximal end width and curvature (Pl. 49, fig. 2; text-fig. 3f). *M. supinus* has obvious affinities in thecal structure with '*Saetograptus pilosus* Jackson and Lenz. However, besides the distinction already mentioned it has more fully developed apertural processes, more closely spaced proximal thecae, and a larger rhabdosome. All three species (*M. anerosus*, *M. supinus*, '*S. pilosus*') are considered to be closely similar and phylogenetically related. They



TEXT-FIG. 8. *a-d*, *Monograptus willowensis* (Berry and Murphy), loc. 105; *a*, *b*, distal and proximal fragments of adult rhabdosomes, 84/10876, 87/10876, $\times 6$; *d*, proximal fragments of rhabdosomes in relief, 81/10876, 82/10876, $\times 12$; *e-h*, *Neocucullograptus kozlowskii* Urbanek, loc. 127; *e*, 95/10876, $\times 10$; *f*, *g*, 96/10876, 97/10876, $\times 10$; *h*, 98/10876, $\times 6$.

possess distinctive spinose thecal structures that are not known otherwise beyond the end of the early Ludlow.

Distribution. Tokrau horizon, *bouceki* and *perneri kasachstanensis* zones, north-east Balkhash.

Material. Fifteen specimens at different stages of development, preserved both in half relief and flattened; Kokbajtal Mountains, locs. 94, 94/1, 105p; Sarybiik Mountains, loc. 22.

Monograptus willowensis (Berry and Murphy, 1975)

Plate 53, figs. 1-6; text-fig. 8a-d

1975 *Saetograptus willowensis* Berry and Murphy, p. 79, pl. 7, fig. 7, text-fig. 18d.

Holotype. University of California at Riverside 6043/1, upper part of the Roberts Mountain Formation, Pridoli, Willow Creek, Nevada, USA.

Description. Rhabdosome straight, medium sized, 35-50 mm long. Dorsal margin between th^{1-5} weakly curved dorsally. Rhabdosome widens rapidly in the first 5 mm, thereafter width increases more slowly to a maximum in the distal part. Successive width measurements (exclusive of apertural processes), at th^1 0.75-0.85, above the aperture 0.45-0.55, at th^2 0.8-0.95, th^3 0.95-1.0, th^4 1.0-1.1, th^5 1.0-1.1, at 5 mm 1.05-1.25, at 20 mm 1.2-1.6, maximum 1.4-1.75, sometimes 1.85.

Thecae are distinctly biform. The proximal 12-14 thecae have distinctive apertural structures similar to those described in *M. anerosus*. Distal thecae are simple tubes with extroverted, even apertures. In lateral view the apertural additions of proximal thecae appear as beak-like structures terminating in paired spines. Details of thecal morphology are not clear as the specimens studied are preserved in rock. The apertural structures could have been formed either as paired, completely separate lateral lobes or as more complicated dorso-lateral additions. They are 0.6-0.65 mm long at the most (including spines), decreasing distally where they become less visible, giving place first to small lateral additions and then disappearing. Their overlap increases distally from $\frac{1}{4}$ to $\frac{3}{4}$ of their length, and the angle of inclination also increases. The base of the intertheical septum in the distal part of the rhabdosome reaches to the middle of the free ventral wall of the succeeding theca. A horizontal line crosses not more than one septum. Dimensions of thecae, L 2.5-3.0, S 0.35-0.45, S:L 1:6, inclination 20-25°. Thecae spaced at 6.0-6.5 in 5 mm and 11-12 in 10 mm proximally, and at 9-10 in 10 mm distally.

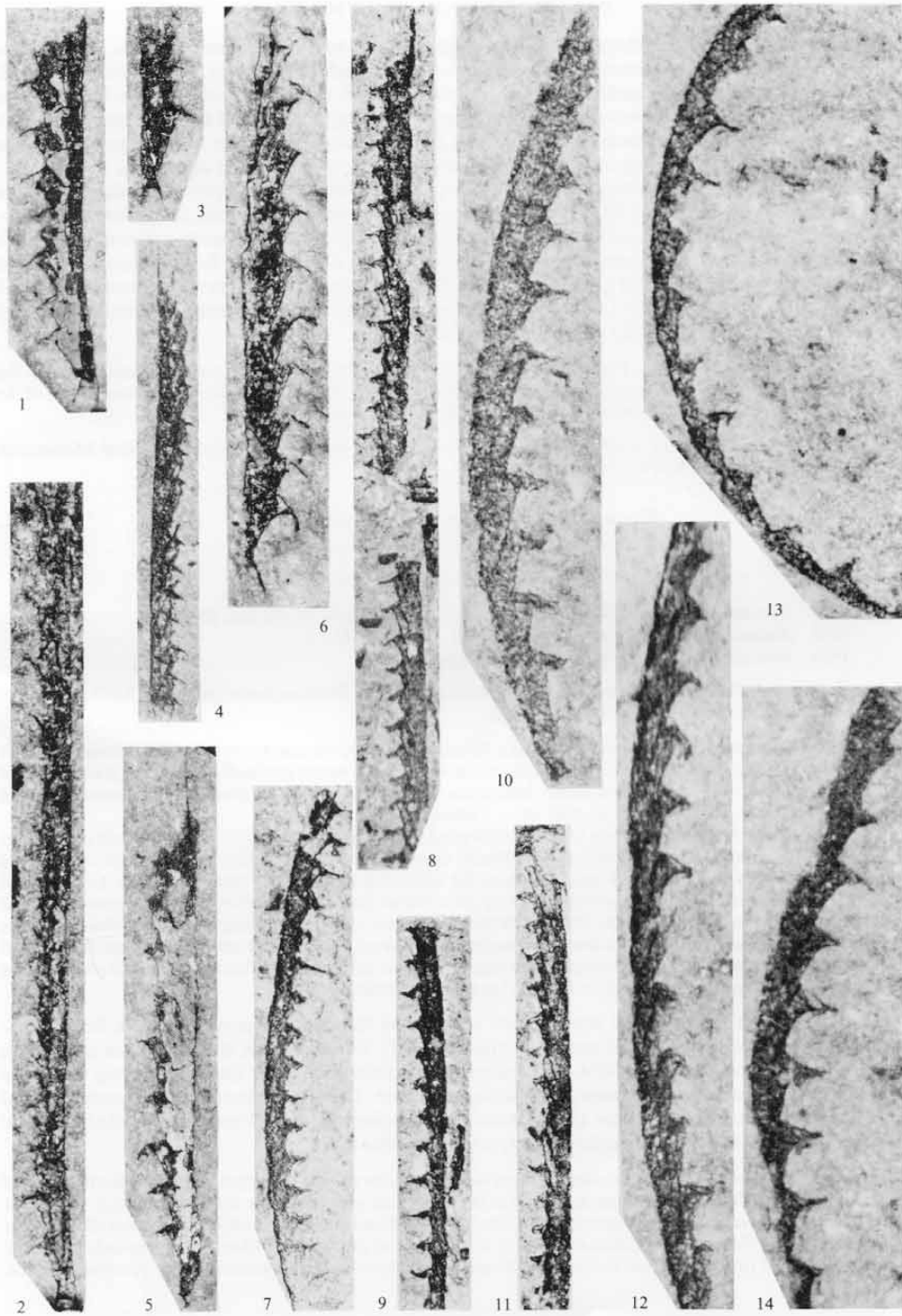
Sicula large, thin apically and widening markedly, almost flaring, at the aperture. A 0.25 mm long dorsal tongue is strongly incurved and well developed. Dimensions of sicula, L 2.0-2.1, S aperture 0.35, L virgella 0.5-0.55. Apex lies between the apertures of th^{2-3} , the base of th^1 is 0.2-0.25 mm above the sicular aperture, E 1.25-1.4.

Discussion. The distinctive biformity of the thecae, and the proximal apertural structures make the assignment of specimens to *M. willowensis* quite evident. Only slight variations in rhabdosome size were discovered when comparing the Kazakhstan specimens with typical material from Nevada (Willow Creek section), kindly provided by Dr. H. Jaeger. They differ insignificantly in their lower rhabdosomal width and more closely spaced thecae having a lower angle of inclination to the axis. The sicular aperture of the Kazakhstan form is less flared and the feature itself can be observed only in some specimens. These differences are probably due to the different preservations—flattened specimens from central Nevada and in full to low relief in Kazakhstan.

EXPLANATION OF PLATE 53

Figs. 1-6. *Monograptus willowensis* (Berry and Murphy), Tokrau horizon, *M. perneri kasachstanensis* Zone, loc. 105. 1, 81/10876, $\times 10$. 2, 82/10876, $\times 10$. 3, young rhabdosome, 83/10876, $\times 10$. 4, distal fragment, 84/10876, $\times 5$. 5, 6, rhabdosomes in half relief, 85/10876, 86/10876, $\times 10$.

Figs. 7-14. *Neocucullograptus kozlowskii* Urbaneek, Akkan horizon, eponymous zone, loc. 127. 7, 8, 9, 11, distal fragments, 88/10876, 89/10876, 90/10876, 92/10876, $\times 5$. 10, 12, 14, fragments of middle parts of rhabdosomes, 91/10876, 93/10876, 95/10876, $\times 10$. 13, proximal part of rhabdosome with no sicula, 94/10876, $\times 10$.



KOREN', *Monograptus*, *Neocucullograptus*

As discussed above, the thecal structure is not unique to Přidolí monograptids, but similar apertural additions are characteristic of synchronous species belonging to the *M. lochkovensis* and *M. anerosus* groups. From the closely similar *M. lochkovensis*, *M. willowensis* differs in having a smaller rhabdosome and thecae, a lower degree of septal overlap distally, and in its sicular shape. Although having apertural processes similar to those of the *M. anerosus* group, it can be distinguished by the well-expressed thecal biformity and the different shape of the proximal end and sicula.

The original assignment of this species to *Saetograptus* (Berry and Murphy 1975) does not seem to be justified. It was based on the apertural structures of the proximal thecae, reminiscent of *Saetograptus fritschi linearis*. Even now it seems premature to determine the generic assignment of such species as *M. willowensis*, *M. anerosus*, *M. lochkovensis*, and other similar forms because details of their thecal morphology are not clear. Neither the *M. lochkovensis* nor *M. anerosus* groups are linked phylogenetically with the lower Ludlow saetograptids. One can suggest instead that similar apertural structures appear independently at later stages of evolution.

Distribution. Roberts Mountain Formation of central Nevada, the eponymous zone corresponding to the middle part of the Přidolí. In Kazakhstan it occurs at approximately the same level in the uppermost part of the *bouceki* Zone (rare) and in the *perneri kasachstanensis* Zone (common).

Material. Thirty-six specimens at different stages of development, preserved in relief; Kokbajtal Mountains, locs. 105, 69, 30, 13a, 41; Kiikbaj Mountains, loc. 35.

Genus NEOCUCULLOGRAPTUS Urbanek, 1970

Neocucullograptus kozlowskii Urbanek, 1970

Plate 53, figs. 7-14; text-fig. 8e-h

1970 *Neocucullograptus kozlowskii* n. sp. Urbanek, p. 348, pls. 37-39, figs. 18-20.

1976 *Neocucullograptus kozlowskii*; Tsegelnjuk, pl. 41, fig. 11.

1976 *Neocucullograptus* sp. n. Mikhajlova, pl. 1, figs. 4-7.

Holotype. Urbanek 1970, text-fig. 20A-B, Palaeozoological Institute, Warsaw; lower part of the Siedlce Beds, the eponymous zone, Melnik borehole (873.40-854.60).

Description. Fragmentary rhabdosomes more than 30 mm long with no proximal extremities preserved. They are straight distally and broadly arcuate proximally (up to 130°). They widen gradually within the greater part of their length, distally they are parallel-sided. Maximum width of the observed proximal fragments measured across the aperture 0.4, above it 0.2, distally 1.0-1.2 and 0.9-1.0 respectively.

Thecae are slender tubes, 2.0-2.2 mm long, parallel-sided in the metathecal part. Free ventral walls are straight and inclined to the axis at 15-20°. Overlap of the thecae increases from $\frac{1}{3}$ to $\frac{1}{2}$ distally. Thecal count ranges from 9.0 to 10.5. The straight intertheatal septa begin at the level of the succeeding thecal aperture. Only general features of the apertural apparatus structure can be observed in specimens preserved in rock. From the lateral lobes characteristic of this species only left hypertrofied structures 0.8-0.85 mm long are usually observed in the material studied. These have a well-developed tongue-like ventral process that conceals the aperture almost completely. In some cases one can distinguish the edges of a short gular process. Prominent rostral processes are usually clearly visible; these are straight, 0.5 mm long and projected ventrally.

Discussion. The structure of the lateral lobes is taken as the main diagnostic feature for the discrimination of neocucullograptid species (Urbanek 1970). Details of this structure were studied on the material isolated from the matrix. *N. kozlowskii* is distinct from other species in having strikingly asymmetrical lateral lobes of a more complicated structure. The left apertural lobe possesses ventral and long rostral processes. These characteristic morphological details are distinguishable in the Kazakhstan material and thus confirm the specific identification.

Distribution. *N. kozlowskii* was first described from the eponymous zone in the upper part of the Siedlce Beds of Poland. Later it was found in the uppermost part of the Kopanina beds below the first occurrence of *M. ultimus* in the Barrandian area, as well as in synchronous deposits of Lithuania and the south-west Ukraine (Paškevičius 1979; Tsegelnjuk 1976). In Kazakhstan it occurs in the uppermost part of the Akkan horizon in beds above the last occurrences of ?*Bohemograptus butovicensis* Bouček and below the first appearance of *M. formosus* Bouček.

In its known localities the vertical range of *N. kozlowskii* does not overlap with the ranges of *M. ultimus* and *M. formosus*.

Material. More than sixty specimens in low to full relief preserved in coarse-grained sandstones; Kokbajtal Mountains, loc. 127.

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