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Early Devonian monograptids of the *telleri* biozone in the Urals-Tien Shan fold area

ABSTRACT: Morphology and stratigraphic distribution of five previously known and one new Lower Devonian monograptids of Pai-Khoi and Tien Shan areas of the USSR are described. Certain major evolutionary trends are recognized among post-hercynicus monograptids and three lineages are identified. Stratigraphic distribution of monograptids within combined section of the Lower Devonian in both areas provide new data concerning the range of taxa investigated. While the *M. telleri* biozone comprises the entire stratigraphic interval from *hercynicus* to the *yukonensis* Zone, successive appearances of other species are used to distinguished five discrete zonal subdivisions. Correlation and age of graptolite bearing beds of the Lower Devonian in both areas are discussed.

INTRODUCTION

Monograptids of the Livanov Cape and Turkparida Formations of Pai-Khoi and southern Tien Shan are indicative of these deposits being Lower Devonian within the interval of the *hercynicus-yukonensis* Zones. All representatives of the association studied with an exception of *Monograptus fanicus* n. sp. have been described elsewhere from the sections of the Lower Devonian in North America, Asia and Europe (Jackson & Lenz 1963, 1972; Jaeger & al. 1969; Churkin & al. 1970). Lack of any distinct geographic variation at the specific and subspecific level within the large areas and relative stability in the composition of their assemblages

are characteristic patterns in the distribution of this latest monograptid fauna. Palaeontological and stratigraphic data, however, are still inadequate to establish of the early Devonian graptolite development.

In the Lower Devonian of North America *Monograptus aequabilis nototaequabilis* Jaeger & Stein, *M. telleri* Lenz & Jackson and *M. craigen-sis* Jaeger are associated with *M. yukonensis* Jackson & Lenz. Beds yielding these graptolites are usually recognized as the *yukonensis* Zone, though the limits of the latter have not so far been specified due to the lack of continuous graptolite sequence. This accounts for difficulties in correlation not only with the beds on the distant areas but even within a single region.

The Lower Devonian deposits of the Urals-Tien Shan fold area represent a continuous graptolite sequence recognized in Pai-Khoi and southern Tien Shan sections. At different stratigraphic levels starting from the top of the *hercynicus* Zone the first appearance of *Monograptus falcarius* Koren, *M. aequabilis nototaequabilis* Jaeger & Stein, *M. telleri* Lenz & Jackson and *M. craigen-sis* Jaeger is recorded. *M. yukonensis* Jackson & Lenz makes its first appearance only in the upper part of the sequence studied where it is associated with all above mentioned graptolites. The completeness of the very fossiliferous sections and reliable stratigraphic control permit evolutionary trends and possible phylogenetic relationships of post-*hercynicus* monograptids to be suggested. The interval of the section comprising the *falcarius-yukonensis* Zones corresponds to the vertical occurrence of *M. telleri* Lenz & Jackson being considered in the present paper as the *telleri* biozone.

STRATIGRAPHY

The Lower Devonian sections yielding graptolites in north-western Pai-Khoi and southern Tien Shan belong to the different structure-facial zones in the limits of the Urals-Tien Shan fold area. However, they are of similar lithological composition and could be correlated on graptolite assemblages.

Pai-Khoi. The Lower Devonian section in Pai-Khoi on the coast of the Kara Sea was investigated by the author (Koren' 1969, 1971; Koren' & Jenokyan 1970) who found that the carbonate-shale deposits of the Oyu River and Livanov Cape Formations contained the *transgrediens*, *uniformis*, *hercynicus* and *falcarius* Zones (Fig. 1). The lower boundary of the *falcarius* Zone is very distinctive and can be established by disappearance of *M. hercynicus* Perner and the appearance of *M. falcarius* Koren. The thickness of the Zone is 3.5 m. The overlying strata (10.5 m thick) yield abundant *M. aequabilis nototaequabilis* and rare *M. telleri*. The beds with these graptolites are concordantly overlain by nodular limestones bearing numerous *Nowakia acuarina* (Richter) and styliolinids.

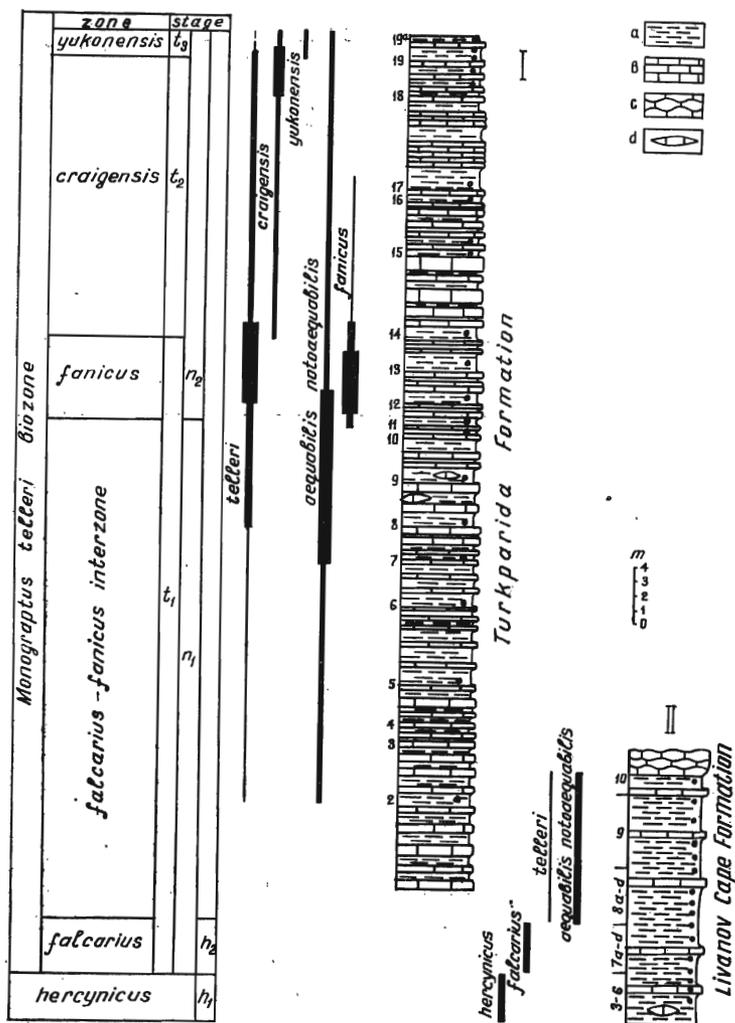


Fig. 1

Correlation of Lower Devonian sections in Zeravshano-Gissar mountain area, southern Tien Shan and in northwestern Pai-Khoi

I — section of the graptolite-bearing beds in the upper part of the Turkparida Formation in Dari-Khurd Creek, Magian district, Tadzhikistan

II — section of the Livanov Cape Formation on the shore of the Kara Sea, Arkhangelsk district

Figures from 2 to 19 and black circles mark the beds sampled for graptolites. a — graptolite shales, b — crinoidal limestones, c — nodular limestones with tentaculites, d — carbonate lenses in shales

Tien Shan. The Lower Devonian graptolite-bearing deposits of the Turkparida Formation in Zeravshan-Gissar mountain area were investigated by A. Lavrusevitch (Lavrusevitch & al. 1967, 1969). The early Devonian age of the formation is indicated by the fact that it overlies the Upper Arg subformation of the Gedinnian and underlies the Lower Magian subformation which corresponds to the beds with *Favosites regula-*

rissimus. A. Lavrusevith & V. Lavrusevitch (1973) recently published a description of one of the most complete graptolitic sections of the Turkparida Formation on the Darai-Khurd Creek. The graptolites from the above section were identified by Obut as a *yukonensis* Zone assemblage and these findings were presented by him at the Graptolite Colloquium in Novosibirsk in 1969. A paper with a description of the *yukonensis* Zone graptolites was published later (Obut 1972).

In 1970 V. Lavrusevitch, Z. Abduasimova and the author studied the sections and collected graptolites over the same territory. Detailed studies were carried out in the lower part of the strata with intercalating shales and limestones that yield abundant graptolites (section Darai-Khurd, member 8, A. Lavrusevitch & V. Lavrusevitch 1973). The material collected made it possible to establish here a sequence of distinct graptolite assemblages instead of a uniform association of the *yukonensis* Zone (Obut 1972).

Section I (Fig. 1) shows the lower part of the sequence with dark graptolite-bearing shales intercalated with crinoid detrital limestones 60 m thick (beds 2—19a in Fig. 1). Graptolites were obtained almost in every band of shale whose thickness varies from 0.2 to 1 m. Graptolites are numerous, flattened, but almost undeformed and well preserved. In addition to hundreds of specimens of each graptolite species tentaculites, crinoids, inarticulate brachiopods and orthoconic nautiloids of early Devonian age has also been noted.

The lower part of the section (beds 2—10) is characterized by *M. telleri* and *M. aequabilis notoaequabilis*. 33 m above the base of the section these two species are associated with *M. fanicus* n.sp. (bed 11); 7 m higher (bed 14) *M. craigensis* Jaeger makes its first appearance and ranges through 19 m. The overlying beds contain *M. yukonensis* Jackson & Lenz, *M. telleri*, *M. craigensis* and *M. aequabilis notoaequabilis*. Above bed 19 shale bands are thinner, the rocks are more dense, split poorly along the bedding planes and contain rare badly preserved graptolites. In the middle and the uppermost parts of the sequence (not shown in Fig. 1) single specimens of *M. cf. yukonensis* and *M. aequabilis notoaequabilis* were found.

CORRELATION AND AGE

The Lower Devonian deposits of the Pai-Khoi within the *uniformis-hercynicus* Zone could be correlated with the Lochkovian of the Barrandian. The overlying beds should be correlated with the lower part of the Pragian. The upper limit of the *hercynicus* Zone in the Barrandian is placed 4 to 4.5 m below the bottom of the Dvorce-Prokop limestones of the lower part of the Pragian (localities Čikanka, Cerna Rokle; Chlupač 1953). The overlying Pragian deposits with the exception of the beds with *M. atopus* Bouček at the top of the stage bear no graptolites which pre-

sents difficulties in correlation of the above strata with corresponding part of the section in the Pai-Khoi. The boundary of the *hercynicus-falcarius* Zones may correspond to any level of the uppermost part of Lochkovian (Dvorce-Prokop, Radotin and Kosoř facies) or the lowermost part of Pragian (Dvorce-Prokop limestone facies).

The following data are indicative, however, of the correspondence of the *falcarius* Zone to the base of the Pragian:

1. At the boundary of the *hercynicus-falcarius* Zones a change of tentaculite assemblage is taking place marked by an extinction of *Paranowakia* and appearance of *Nowakia acuaria* (Richter) and first styliolinids.

2. *M. falcarius*, *M. telleri* and *M. aequabilis nototaequabilis* unknown in the Lochkovian deposits initiate a new stage in the development of the post-*hercynicus* monograptids.

It remains unresolved, however, where in the lower part of the Pragian a stratigraphic equivalent of the top of the graptolite shales of the Livanov Formation in the Pai-Khoi should be placed (Fig. 1, section II, bed 10).

The upper member of the Turkparida Formation in southern Tien Shan (Fig. 1, section I) occupy in the whole a higher stratigraphic position as compared to the Livanov Cape Formation in Pai-Khoi (Fig. 1, section II). The beds bearing *M. aequabilis nototaequabilis* and *M. telleri* can be taken as a correlation level for the Pai-Khoi and Tien Shan sections. The above beds are at least partially of the same age. The occurrence of the monotonous graptolite assemblage comprising only two taxa in a certain stratigraphic interval in distant areas is hardly coincidental resulting from inadequate sampling or biogeographic peculiarities. Such impoverishment of the fauna is more likely to be explain by the regularities governing the monograptid evolution at that time.

The upper part of the Turkparida section with *M. telleri*, *M. craigensis*, *M. aequabilis nototaequabilis* and higher with *M. yukonensis* (Fig. 1, section I, above bed 18) can be correlated with the *yukonensis* Zone of Canada (Lenz & Jackson 1971). The latter is widely used as a stratigraphic subdivision for correlation purposes; its age, however, requiring further clarification. This circumstance makes it difficult to correlate the early Devonian graptolite facies with the deposits containing the *yukonensis* fauna elsewhere. The Lower Devonian graptolite-bearing beds in Pai-Khoi and southern Tien Shan seem to correspond to a considerable part of Pragian but they are older than the horizon with *M. atopus* in Barrandian (Bouček 1966).

SYSTEMATIC DESCRIPTION

All the graptolites described come from black clay and calcareous-clay shales. They are always flattened and preserved as silvery films. Abundant specimens of every astogenetic stages represent all taxa. Their

good preservation enables to get as full data on morphology as is available for flattened material in black shales. The Pai-Khoi graptolites are deformed, however, due to their abundance on each bedding plane it was possible to choose the least deformed material sufficient for measurements ($\beta = 40-60^\circ$). As to the Tien Shan graptolites they are flattened but almost undeformed.

The description of the following taxa will be given below:

- Monograptus falcarius* Koren
M. aequabilis notoequabilis Jaeger & Stein
M. fanicus n. sp.
M. telleri Lenz & Jackson
M. craigensis Jaeger
M. yukonensis Jackson & Lenz

Symbols and abbreviations: L — length of rhabdosome, thecae, hood and sicula; S — width of rhabdosome¹, thecae, hood and sicula aperture; N — thecal number in 10 mm; Σ — distance from top of hood of th_1 to sicula aperture; β — angle between the rhabdosome length and direction of lineation in cleaved shales. All measurements are given in mm.

The graptolite collections are housed in the Leningrad Central Geological Tshernyshev Museum; label N10145, 10505, 10875. The photographs are made by Mr. A. P. Reuss, VSEGEI.

Suborder **Monograptina** Lapworth, 1880
 Family **Monograptidae** Lapworth, 1873
 Genus **MONOGRAPTUS** Geinitz, 1852
Monograptus falcarius Koren, 1969
 (Pl. 1, Figs 3—7)

1969. *Monograptus falcarius* Koren, n. sp.; pp. 1326—1327, Figs 2, 4—8.

1970. *Monograptus falcarius* Koren; Koren' & Jenok'an, Pl. 9, Figs 8—10.

1973. *Monograptus falcarius* Koren; Koren', Pl. 7, Figs 1—10.

Topotype: specimen No. 31/10145, OGM; figured here, Pl. 1, Figs 4, 6.

Material. — 100 specimens. The description is based on measurements taken from 50 less deformed rhabdosomes.

Description. — *Rhabdosome.* Small, dorsally curved, sickle-like, from 10 up to 19 mm long having a maximum of 21 thecae. Proximal curvature ranges from 45° up to 90° , distal part being usually weakly curved or almost straight. Rhabdosome widens rapidly from 1 (0.8) mm at th_4 , a maximum width of about 1.6 (1.3) mm usually attained between th_4 and th_6 . At dorsal extremity width diminishes to 1.4 (1.2) mm.

Sicula. Short, trumpet-like, free dorsal side slightly sinuous with weak ventral curvature (Pl. 1, Figs 6—7). Flaring aperture furnished with thin virgella 0.2—0.4 mm long. Apex reaching the base of septum between th_1 and th_2 . Sicula 1.3—1.4 mm long

¹ In rhabdosome measurements the first figure indicates width at the hood level, the second, given in brackets — its width below the hood.

with aperture width up to 0.8—1 mm. Porus of th_1 close to the sicula aperture (0.1—0.15).

Thecae. Short and hooded with pronounced geniculum. Supragenicular walls short (0.5 mm), straight, parallel to the axis. Infragenicular walls and apertures form semioval excavation 0.3—0.4 mm wide with thickened edges. Hoods usually appear as a triangular structures. They grow outwards from the dorsal wall of the thecal aperture initially narrow and rapidly becoming transversally expanded. Hoods obscure thecal apertures from ventral side leaving them exposed laterally. Distally hoods become proportionately shorter, narrower, less hooked and fully expose thecal aperture. The septum between th_1 and th_2 extends almost horizontally, remaining septa being curved sinuously. Thecal number in 10 mm is 13—12.

Comparison. — *M. falcarius* has such distinctive morphologic characters as arcuate curvature of rhabdosome and short trumpet-like sicula. It is these peculiarities as well as small size of rhabdosome that make this species easily distinguishable from associated *M. telleri* Lenz & Jackson and *M. aequabilis notoaequabilis* Jaeger & Stein. We could take *M. hercynicus* Perner as the forerunner of *M. falcarius* since both show morphologic similarity and doubtlessly belong to the same phylogenetic lineage. Their affinity is displayed in such diagnostic features as shape of the sicula and structure of thecal hoods. Their morphologic disjunction at the same time can be seen in considerable gracilisation of rhabdosome as well as in the change of its shape: straight, 50 mm long in *M. hercynicus* and falcate, 19 mm long in *M. falcarius*. As to the sicula it is much shorter in *M. falcarius* than in *M. hercynicus* (1.5—1.6 and 2—2.1 mm respectively). Its apex reaches the septum base between th_1 and th_2 while in *M. hercynicus* it is at the top of th_2 hood. The sicular aperture of *M. falcarius* becomes still more expanded (0.8—1 mm as compared with 0.7—0.8 mm in *M. hercynicus*) with more pronounced flaring. Dimensions of proximal end: in *M. falcarius* rhabdosome width at th_1 is 1 (0.8) mm, while between th_1 and th_2 it equals 0.6—0.7 mm; in *M. hercynicus* the respective figures are 1.2—1.3 (0.9—1) mm and 0.9 mm. Thecae hoods for both species are of the same shape but those of *M. falcarius* are less expanded laterally.

Distribution. — Lower Devonian, Livanov Cape Formation, Pai-Khoi, the *falcarius* Zone.

Monograptus aequabilis notoaequabilis Jaeger & Stein, 1969
(Pl. 1, Fig. 1; Pl. 2, Figs 1—3; Pl. 3, Fig. 4; Pl. 4, Figs 1—2, 9;
Pl. 8, Figs 1—5)

1969. *Monograptus aequabilis notoaequabilis* n. ssp.; Jaeger & Stein, pp. 182—184, Text-fig. 1E—F; Pl. 15, Fig. A—B (see synonymy).
1969. *Monograptus aequabilis amdermaensis* ssp. n.; Koren', pp. 1327—1328, Figs 2, 9—14.
1970. *Monograptus aequabilis notoaequabilis* Jaeger et Stein; Churkin, Jaeger & Eberlein, pp. 194—195, Fig. 9C, J.
1970. *Monograptus aequabilis notoaequabilis* Jaeger et Stein; Koren' & Jenok'an, Pl. 9, Figs 1—4.
1971. *Monograptus aequabilis notoaequabilis* Jaeger et Stein; Koren', Figs 3D, 4A—C, E.
1972. *Monograptus aequabilis notoaequabilis* Jaeger et Stein; Jackson & Lenz, pp. 583—585, Text-fig. 1B.
1972. *Monograptus aequabilis notoaequabilis* Jaeger et Stein; Obut, pp. 1216—1217, Figs 2, 4—5.
1973. *Monograptus aequabilis notoaequabilis* Jaeger et Stein; Koren', Pl. 6, Figs 1—16.

Material. — Several hundreds of specimens.

Description. — *Rhabdosome*. Straight, middle-sized, normally 20 to 30 mm long, in some cases reaching a length of 40 mm and over. Proximal part straight or slightly curved ventrally at sicula and first two thecae. Some specimens have a weak dorso-ventral curvature between th_1 and th_3 (Pl. 1, Fig. 1). Width increases

from 1.1(0.9)—1.3(1) mm at th_1 to 1.5—1.9 mm at th_7 — th_{11} and then remains constant until it diminishes by 0.1—0.2 mm at extreme distal end.

Sicula. Conical, straight or slightly curved ventrally having a thin virgella 0.4—0.5 mm long and a dorsal process shaped as a scoop with a length of 0.1 to 0.5 mm. Apex of sicula reaches hood of th_2 . Dimensions: L — 1.6—2 mm; $S_{aperture}$ — 0.4—0.5 mm.

Thecae. Biform. Hoods of the first 3—8 proximal thecae are well developed triangular lobes initially narrow and rapidly becoming transversally expanded. They are arcuated, covering thecal apertures from ventral side and extending below the apertural margin. Thecal apertures are never obscured laterally. Hoods of th_5 — th_8 diminish in size and replaced with supraapertural processes 0.1 mm long. All thecae with the exception of the first two are of climacograptic appearance. Ventral walls of thecae have a sharp geniculum. The first thecae are short, rapidly narrowing towards the aperture (0.5 to 0.2 mm). Interthecal septum between th_1 and th_2 almost straight inclined towards rhabdosome axis at 50° , septa between the other thecae having a gentle S-shaped curvature. Supragenicular walls of distal thecae parallel to axis with a length of 0.7—0.8 mm. Number of thecae within the first 10 mm equals 11—10, distally 10—8. Table 1 shows measurements taken from several specimens: spec. 1 and 2 — Pai-Khoi, the *falcarius* Zone and beds with *M. aequabilis nototaequabilis* and *M. telleri*; spec. 3 and 4 — southern Tien Shan, the *fanicus* and *craigenensis* Zones.

Table 1

No.	L _{rh.}	$S_{rh.}$				N		Hooded thecae	Sicula		
		at th_1	th_1/th_2	at th_5	max.	prox.	dist.		$S_{apert.}$	L	L _{dorsal proc.}
1	22	1.3/1/	0.9	1.4/1.3/	/1.6/	11	9	5	0.45	—	0.2
2	25	1.1/0.9/	0.9	—	/1.6/	10	9	3	0.4	—	0.2
3	30	1/0.9/	0.9	1.1/0.9/	1.6/1.4/	12	10	8	0.5	1.8	0.5
4	30	1.1/0.9/	0.9	1.4/1.2/	1.6	11	9	5	0.5	1.9	0.3

The material studied indicates that the subspecies is represented by geographically dispersed populations of different age. The earliest of them, namely the Pai-Khoi population characterizes the initial stage of development (the *falcarius* Zone and the *falcarius-fanicus* Interzone). The Central Asia population corresponds to a later stage spanning the interval from the *falcarius-fanicus* Interzone to the *yukonensis* Zone.

The Pai-Khoi population represented by a bulk of several hundreds specimens does not show any important morphological or quantitative changes. Their rhabdosomes straight or slightly curved ventrally at the sicula or the first theca display distinctive thecal biformity. The first 3—4 thecae have hoods of almost similar size, whose maximum lateral width reaches 0.2—0.3 mm. Hoods of further 2—3 thecae are of smaller size while all remaining thecae have only short supraapertural processes. In most cases sicula has a short (0.1—0.2 mm) narrow (0.2 mm) dorsal tongue slightly curved towards the virgella. With some specimens it is either weakly pronounced or is lacking completely.

The Central Asia *M. aequabilis nototaequabilis* is also abundant. Alongside with the specimens whose proximal part is straight or slightly curved ventrally there occur rhabdosomes with a gentle dorso-ventral curvature at th_1 — th_7 . All thecae have apertural processes. In the bulk of specimens the hood of the first theca is larger

though some rhabdosomes have the first 6—8 thecae showing no variation in the hood size. All remaining thecae including th_{25} — th_{27} provided with short supra-apertural processes, 0.4—0.5 mm long, expanded laterally. Numerous siculae and juvenile rhabdosomes reveal the fact that the dorsal process is fully developed before the first theca budding. The width of the sicular aperture ranges from 0.4 to 0.5 mm reaching in some cases 0.6 mm.

Comparison. — Such major morphological characters as the biformity of thecae and short dorsal process of the sicula enable an accurate diagnosis of *M. aequabilis nototaequabilis* already at the initial stages of its development (the *falcarius* Zone, Pai-Khoi). Later *M. aequabilis nototaequabilis* display a reduced biformity, and namely a larger number of thecae are provided fully developed hoods. A long well developed dorsal process of the sicula becomes a permanent morphological character of the population. An acme of *M. aequabilis nototaequabilis* occurs in the upper part of the *falcarius-fanicus* Interzone and in the lower part of the *fanicus* Zone (Fig. 1, section I). At this stratigraphic level some characters display variability: the rhabdosome width, the spacing and degree of thecal biformity as well as the shape of the proximal part that changes due to the expanding of sicula aperture. Samples taken from beds 11, 12 (Fig. 1, section I) show gradual transition to a closely related species of *M. fanicus* n. sp. Their comparison will be given further in the section describing the latter.

The distribution area of *M. aequabilis nototaequabilis* embraces Australia (Victoria), Asia (Thailand, Malaya, Tadzhikistan), Europe (Barrandian, Pai-Khoi), North America (Alaska, Yukon) and possibly Africa (Morocco). The comparison of *M. aequabilis nototaequabilis* from various region is facilitated by a similar preservation of the flattened material. This subspecies described by different authors (Jaeger 1966, 1970; Jaeger & al. 1969; Lenz & Jackson 1971) displays no geographical variation. Specimens of the same sample often show more pronounced variations than those taken from different regions.

Distribution. — Lower Devonian, Pai-Khoi, the Livanov Cape Formation, the *falcarius* Zone and the *falcarius-fanicus* Interzone; southern Tien Shan, the Turkparida Formation, the *falcarius-fanicus* Interzone — *yukonensis* Zone. The accompanying assemblages are shown in Fig. 1.

Monograptus fanicus sp. n.

(Pl. 2, Figs 4—8; Pl. 3, Figs 1—3; Pl. 4, Figs 3—8; Pl. 8, Figs 6—21)

1972. *Monograptus pacificus* Jaeger; Obut, p. 1217, Figs 2, 6.

Holotype: specimen, shown in Pl. 2, Fig. 5; Pl. 8, Fig. 15, CGM, 10/10505.

Type locality: the right bank of the Darai Khurd Creek, Maglan district, Tadzhikistan.

Stratum typicum: Turkparida Formation, section I, bed 12, the *fanicus* Zone, Lower Devonian.

Derivation of the name: the species is named after the Fana Mountains.

Material. — About 360 specimens. The following description is based on the measurements of 70 specimens at all stages of development.

Diagnosis. — A straight monograptid of medium size having a sicula with the narrow upper part and trumpet-like expansion towards the aperture. A long dorsal process initially narrow and straight becomes transversally expanded and sharply curved towards the virgella. Thecae have hoods which are triangular arcuate lobes, narrow at the base and expanding transversally. They reach down below the apertural margin without covering it laterally. Towards the distal end hoods diminish in size and acquire the shape of thin processes which are dorso-ventrally extended.

Medial and dorsal thecae are of climacograptic appearance. The size of rhabdosome: L — 20—30 mm, S — 1.1—1.2 (0.8—0.9) at th_1 reaching its maximum of 2 (1.8) mm already in 10 mm from the sicula; N — in the first 10 mm 13—11, distally 11—9.

Description. — *Rhabdosome.* Straight, middle-sized, with a length of 20—30 mm sometimes up to 40 mm. The extreme proximal end due to the shape of sicula slightly curved dorsally. Virgula stretches for several millimeters beyond rhabdosome. Width rapidly increases within the first five-eight thecae and reaches its maximum at th_8 — th_{13} or in 10 mm from sicula. Width is equal to 1.1 (0.8—0.9)—1.2—1.3 (0.9—1) mm at th_1 , 1.5—1.6 (1.2—1.3) mm at th_5 reaching its maximum of 1.9 (1.7)—2.1 (1.8) mm, and being 1.7—1.8 (1.5—1.6) mm at the extreme distal end. Measurements of some specimens from beds 11—13 (Fig. 1, section I) are given in Table 2.

Table 2

No.	L	S _{rhabdosome}						
		th_1	th_1/th_2	th_2	th_3	th_4	th_5	max.
1	20	1.3/0.9/	-	1.4/1.1/	1.4/1.2/	1.5/1.2/	1.6/1.3/	1.7/1.6/
2	20	1.2/0.9/	0.9	1.2/1/	1.2/1/	-	-	1.8/1.7/
3	20	1.2/1/	1	1.2/1/	1.3/1.1/	1.5/1.2/	1.5/1.2/	1.7/1.5/
4	12	1.1/0.9/	0.9	1.1/0.9/	1.2/1/	1.3/1.1/	1.4/1.1/	-
5	18	1.2/1/	1	1.3/1/	1.2/	1.6/1.3/	1.6/1.3/	2/1.8/

Sicula. Prosicula and initial part of metasicula have the shape of a narrow cone, with metasicula sharply expanding towards aperture. Inner margin is usually straight while the outer one is gently curved dorsally which accounts for a trumpet-like shape of aperture. Apertural margins are straight having a thicker rim. Apex reaches hood of th_2 . Dorsal margin is extended as a narrow process in the shape of a scoop which gradually expands and forms symmetrical lateral lobes. This dorsal process is sharply curved towards virgella and borders from down below about one third of the sicular aperture. Dorsal process of some specimens is split, forming two narrow lobes with uneven edges separated by a slit. Such a shape of process, however, may merely result from the state of preservation. Sometimes fusselar structure can be seen along the periphery of dorsal process. In its shape and structure dorsal process resembles apertural hoods of first thecae. Virgella is shaped like a straight spine initially wide and needle-like towards the end. The collection studied includes specimens at all stages of development. Prior to budding of th_1 sicula develops a fully formed dorsal process (Pl. 4). Dimension: L — 1.7—2 mm; S_{aperture} — 0.6—0.8 mm; L_{virgella} — 0.3—0.5 mm; L_{dorsal process} — 0.5—0.7 mm, visible lateral width around the periphery reaches 0.2—0.3 mm, distance from the apertural margin to the porus of th_1 is 0.2—0.3 mm.

Thecae. The first proximal thecae short, initially wide, sharply narrowing towards the aperture (up to 2 mm). Intertheical septa placed horizontally and weakly S-curved. Free ventral walls gently convex, inclined towards virgula at 45°. Geniculum is not pronounced. Apertures of first thecae parallel to the inner margin of sicula. Thecae of medial and distal parts of rhabdosome of climacograptic appearance, 1.5 mm long and 0.5 mm wide at metatheca. Intertheical septum begins at the hood of preceding theca, curves gently and finally extends at 25—30° to axis. Free ventral walls 0.7 mm long parallel to axis. Geniculum well pronounced, supra-

and infragenicular walls almost perpendicular. Semicircular excavations about 0.4 mm deep. Apertures placed at a right angle to free ventral wall of the next theca. All thecae have arcuate apertural processes curving gently over aperture reaching its middle or ventral part. They are triangular lobes with thickened rims. As distinct from hoods of *uncinatus* type they do not cover apertures laterally. Hoods of proximal and distal thecae differ in size and shape. Hoods of the first nine to fifteen thecae are of approximately equal size. They extend down below apertural margin and are 0.3—0.5 mm long. Their lower rim is rounded and uneven, sometimes elongated laterally. In some specimens hood of th_1 forks into two narrow processes separated by a slit. This effect may very well result from a rupture of thin membranous lobe. One specimen has a thread-like lateral process 0.5 mm long at hood of th_1 . Distal hoods are thin dorsal processes 0.4—0.5 mm long overhanging apertures dorso-ventrally and extending beyond the margin for 0.2—0.3 mm. Hoods are fully developed at the early astogenetic stages (Pl. 4). Apertural margins are straight, thickened, inclined to the axis. They are exposed and well observed in flattened material. Number of thecae in first 10 mm is 13—11, distally 11—9.

Comparison. — Morphologically *M. fanicus* n. sp. is a typical representative of post-*hercynicus* monograptids. It is characterized by a well developed dorsal sicula process and astogenetic variation of thecae. Such morphological characters, however, as the shape of sicula, advanced development of hoods along the rhabdosome and thicker proximal end distinguish *M. fanicus* n. sp. from related monograptids. The material studied displays variation in some quantitative characters, degree of thecal biformity and dorsal sicula curvature. Thus, the proximal width ranges from 1.5 (1.2) mm to 1 (0.8) mm at th_1 and from 0.75 to 0.9 mm between th_1 and th_2 . Number of thecae in first 10 mm varies from 13 or 12.5 to 11, the width of sicula aperture in specimens from the same sample change from 0.55 to 0.8 mm. The whole range of variation for the above characters can be traced on a successive series of specimens taken from the same bed (Fig. 3, section I, bed 12; Pl. 8).

Along with the easily diagnosed specimens of *M. fanicus* n. sp. (Pl. 2, Figs 5—8; Pl. 8, Figs 11—21) there are rhabdosomes whose sicula has a weakly expanded aperture (0.5—0.6 mm) and hence shows only slight dorsal curvature (Pl. 8, Figs 7—9). The latter are similar to *M. aequabilis notoaequabilis*. Thus, the diagnosis of such specimens should be based on the proximal width and thecal spacing. The distinctive characters of *M. fanicus* n. sp. as opposed to *M. aequabilis notoaequabilis* are as follows:

1. trumpet-like sicula distinctly curved dorsally,
2. larger number of thecae with equally developed hoods and more pronounced apertural processes distally,
3. more closely spaced thecae in the first 10 mm,
4. wider proximal end as well as smaller rhabdosome length in the bulk of specimens.

Thus, the distinctive characters of *M. fanicus* n. sp. and *M. aequabilis notoaequabilis* are better manifested in the structure of proximal end, distal fragments being very difficult to diagnose.

Such specimens of *M. fanicus* n. sp. that have a rather thin proximal end as well as a dorsally curved sicula with an aperture weakly expanded show superficial resemblance with *M. pacificus* Jaeger. A close comparison of specimens, however, reveals distinctive morphological differences:

1. *M. fanicus* n. sp. has a less pronounced dorsal curvature of proximal end. The sicula of *M. pacificus* is fully curved dorsally at 10—45° with maximum S_{aperture} not exceeding 0.4 mm, while in *M. fanicus* n. sp. only its outer margin is dorsally curved and S_{aperture} equals 0.7—0.8 mm;

2. in *M. pacificus* all thecae are provided with hoods diminishing in size distally, while in *M. fanicus* n. sp. the hoods are distally replaced with supraapertural processes;
3. in *M. pacificus* the hoods are wider and conceal the apertures both ventrally and laterally;
4. in *M. fanicus* n. sp. the proximal end is wider and thecae show no tendency towards isolation;
5. as a whole *M. fanicus* n. sp. is characterized by a smaller number of thecae in the first 10 mm.

The above species having sicula and hoods of different shape refer to different lineages. *M. pacificus* as Jaeger (1970) postulated shows affinity to monograptids of *M. craigensis* and *M. yukonensis* type.

The main distinctive characters of monograptids under comparison are shown in Table 3.

Table 3

Character	<i>M. aequabilis</i> <i>notoaequabilis</i>	<i>M. fanicus</i>	<i>M. pacificus</i>
shape of sicula	conical, straight or slightly curved ventrally	trumpet-like, outer margin curved dorsally	conical, dorsally curved
S ^a perature of sicula	0.4-0.5 mm	0.6-0.8 mm	0.4 mm
hooded thecae	3-8	9-15	all thecae
shape of hoods	well developed triangular lobes initially narrow and rapidly becoming transversally expanded, concealing apertures ventrally		large arcuated lobes concealing apertures ventrally and laterally
N in the first 10 mm	11-10	12-11, rarely 11	13-12, rarely less than 12
S ^r habdosome at th ₁	1.1-1.3 mm	1-1.3 mm	0.9 ± 0.1 mm
S ^r habdosome th ₁ /th ₂	0.9 mm	0.7-1 mm	0.5-0.6 mm

M. fanicus n. sp. displays some similarity with *M. atopus* Bouček. Comparison of specimens, however, shows a distinction in the shape and size of sicula and in the structure of thecae.

Distribution. — Lower Devonian, southern Tien Shan, the Turkparida Formation the *fanicus* and *craigensis* Zones. *M. fanicus* n. sp. occur in the canyons of the Turkparida and Darai-Khurd Creeks, as well as near Tchashmaniat village. The assemblages of accompanying monograptids in the Darai-Khurd section are shown in Fig. 1.

Monograptus telleri Lenz & Jackson, 1972

(Pl. 5, Figs 1-3; Pl. VI, Figs 1-4; Pl. 9, Figs 1-6; Pl. 10, Fig. 1)

1971. *Monograptus telleri* Lenz et Jackson, n. sp.; p. 9, Pl. 1, Figs 11-16; Text-fig. 2G-J.
 1971. *Monograptus* aff. *thomasi* Jaeger; Koren', p. 240, Fig. 4D, F-J.
 1972. *Monograptus turkparidensis* Obut, sp. n.; p. 1218, Figs 2; 2-3.

Material. — 350 specimens from the Kara Sea shore, Pai-Khoi and from the Turkparida and Darai-Khurd Creeks, southern Tien Shan. 100 rhabdosomes were measured.

Description. — *Rhabdosome.* Straight, large-sized, average length 40–60 mm, sometimes up to 80–90 mm. Virgula extends distally for over 10 mm. In contrast to rhabdosomes having straight proximal end (Pl. 6, Fig. 3; Pl. 9, Figs 3–4) some specimens display weak dorso-ventral curvature between th_1 – th_5 (Pl. 5, Figs 1–2; Pl. 6, Fig. 2). Proximal end is thin in comparison with the rest of rhabdosome, however, there is no isolation of thecae observed. Width increases from 0.9 (0.6–0.7) \pm 0.1 mm at th_1 to 1.2–1.3 (0.9–1) mm at th_5 ; it equals 0.6–0.7 mm between th_1 and th_2 ; at a distance of 10 mm from the base of th_1 rhabdosome widens to 1.6–1.8 (1.3–1.6) mm; within the range of next 10 mm it increases rapidly up to 2.2 (2) mm, then it gradually reaches its maximum of 2.3 (2)–2.5 (2.2) mm at level of last thecae with developed hoods. At its distal extremity width does not exceed 2.2–2.3 mm. The width measurements for several specimens ($\beta = 40$ – 60°) are given in Table 4. Specimens Nos. 1, 2, 11 derive from the *falcarius-fanicus* Interzone of Middle Asia and Pai-Khoi, Nos. 3–7, 10 — from the *fanicus* Zone, Middle Asia, No. 8 — from the *craigensis* Zone, Middle Asia, No. 9 — from the *yukonensis* Zone, Middle Asia.

Table 4

No.	L	R h a b d o s o m e w i d t h						
		at th_1	th_2	th_3	th_4	th_5	in 10 mm	max.
1	60	1/0.7/	1/0.7/	1.1/0.8/	1.2/0.9/	1.3/1/	1.8/1.5/	2.2/2/
2	60	1/0.8/	1/0.8/	1.1/0.9/	-	1.2/1/	1.6/1.3/	2.7/2.5/
3	22	0.9/0.7/	1/0.7/	1.1/0.85/	1.2/0.9/	-	1.8/1.6/	-
4	35	0.8/0.6/	0.9/0.7/	1.1/0.8/	1.2/0.9/	1.3/1/	1.8/1.5/	/2.2/
5	23	0.9/0.6/	0.9/0.7/	1/0.9/	1.1/0.9/	-	-	2.1/2/
6	30	0.9/0.6/	0.8/0.6/	0.9/0.7/	-	-	-	/2.2/
7	23	0.9/0.6/	0.9/0.7/	1/0.8/	1/0.8/	1.1/0.9/	1.6/1.4/	/2/
8	60	0.8/0.6/	1/0.7/	1.1/0.8/	1.1/0.8/	1.2/1/	1.8/1.5/	-
9	40	0.9/0.6/	1/0.7/	1.1/0.8/	-	-	2/1.8/	2.5/2.2/
10	30	0.9/0.7/	0.9/0.7/	1/0.8/	1.1/0.9/	1.2/0.9/	1.7/1.5/	/2.2/
11	40	1/0.8/	1.1/0.9/	1.2/1/	1.3/1.1/	1.5/1.2/	1.9/1.6/	2.3/2/

Sicula. Straight or displaying gentle ventral curvature. Dimensions: L — 1.6–1.8 mm; $S_{aperture}$ — 0.5–0.6 mm; Σ — 1.2–1.5 mm. Apex reaches aperture of th_2 . Aperture slightly concave and furnished with virgella and dorsal process. Virgella straight, 0.5–0.7 mm long, projecting postero-ventrally. Dorsal process is strongly incurved and scoop-like, having lateral expansions. Visible lateral width of "scoop" equals 0.3 mm.

Thecae. Thecae in proximal and middle part have well developed hoods being an extension of dorsal walls. Their fusellar structure can be observed in very few cases only. Hoods are long and down-curved. They widen laterally and extend down below level of ventral and lateral margin of apertures thus obscuring them. Specimens 40–60 mm long and over have usually 16–18 hooded thecae while some rhabdosomes display 20–26 hooded thecae. The best developed are hoods of the first 10–15 thecae having lateral width of 0.3–0.4 mm and length of 0.5–0.7 mm. Thereafter hoods diminish in size and are replaced with dorsal shields 0.3–0.5 mm long that project over apertures. Some of the last thecae have no apertural processes. Ventral walls have distinct geniculum with their supra- and infragenicular parts forming a right angle. Supragenicular walls are parallel to rhabdosome axis, their

length being 0.8—1 mm. Shallow slot-like excavations can be observed distally. No interthecal septa have been traced. Thecal spacing in the first 10 mm is 11—10, in the next 10 mm it decreases to 9—8, and distally remains 8. Table 5 shows number of hooded thecae, thecal spacing and dimensions of sicula for several least deformed specimens ($\beta = 40\text{--}60^\circ$).

Table 5

No.	Hooded thecae	Thecal spacing in 10 mm			Sicula		Σ
		first 10 mm	second 10 mm	distally	S	L	
1	26	9	8	8	-	-	-
2	22	11	9	8	0.55	-	-
3	18	11	9	-	-	-	1.2
4	18	11	9	8.5-9	0.5	1.7	-
5	15	10.5-9	9	-	0.4	1.8	1.5
6	14	10.5	9	-	0.5	1.7	1.5
7	15	11	9	-	0.4	-	1.3
8	16	10.5	9	-	0.5	-	-
9	17	11	-	-	0.5	1.8	-
10	17	12	9.5	9	-	-	-
11	13	11.5	9.5	9	0.6	1.7	1.3

The following examples provide the measurements taken from strongly deformed rhabdosomes:

Specimen 3396-7, Pai-Khoi; $\beta = 80^\circ$; S_{rh} . at th_1 1.1 (0.8), at th_2 1.1 (0.9); at th_4 1.4 (1.1), at th_5 1.6 (1.6), at 10 mm 2.2 (1.9), max. = 2.6 (2.2) mm; in the first 10 mm the number of thecae equals 12, decreasing to 9 in the next 10 mm; S_{hood} 0.7 mm, L_{hood} 0.5 mm.

Specimen 3396-8, Pai-Khoi; $\beta = 10^\circ$; S_{rh} . at th_1 0.8 (0.6), at th_2 0.9 (0.6), at th_3 1 (0.7), at th_4 1.1 (0.9), at th_5 1.2 (1), at 10 mm 1.5 (1.2) mm, max. = 2 (1.8); thecae 8.5 in the first 10 mm, decreasing to 7 in the next 10 mm; S_{hood} 0.4 mm, L_{hood} 0.8 mm.

Comparison. — The major morphologic characters of *M. telleri*, such as biformity of thecae, hood structure, peculiar form and size of dorsal process — are representative for the whole group of post-hercynicus monograptids. Nevertheless, *M. telleri* differs considerably from all of them in its larger size and more pronounced distinction in the structure of proximal and distal thecae. In this respect it shows a certain similarity with some biform Lochkovian graptolites for example *Monograptus hemiodon* Jaeger (the lower part of the hercynicus Zone, Jaeger 1959). *M. telleri* can still be distinguished from *M. hemiodon*. It has a larger number of hooded thecae: no less than 20 as compared to 10 in *M. hemiodon*. Almost all distal thecae in *M. telleri* are provided with dorsal shields while some distal fragments of *M. hemiodon* display up to 30 thecae with no trace of apertural processes and finally instead of well-developed dorsal tongue *M. hemiodon* has only a short spine-like process. From the other biform Lochkovian graptolite *M. rhamstalensis* Jaeger (the uniformis Zone, Jaeger 1959) *M. telleri* varies in the larger number of hooded thecae and in a different shape of distal thecae.

Material of *M. telleri* studied comprises the Pai-Khoi and Tien Shan populations that belong to different stratigraphic levels. The oldest representatives of *M. telleri* were found in Pai-Khoi in 1968 (Koren' 1971, Fig. 4D,F—J) in the *falcarius*

Zone and in the *falcarius-fanicus* Interzone. Though morphologically they could be readily distinguished from associated monograptids their preservation and number of specimens (20) available at the time seemed to be insufficient for the establishment of a new species. They were defined and described as *M. aff. thomasi* Jaeger (Koren' 1974, Pl. 1, Figs 10—14). Later numerous monograptids of this type were collected in the Turkparida Formation, southern Tien Shan (the *falcarius-fanicus* Interzone and *fanicus-yukonensis* Zones). They were described by Obut as *Monograptus turkparidensis* n. sp. (Obut 1972, Fig. 2; 2, 3). However, the latter is no more than a younger synonym of *M. telleri* Jackson & Lenz.

The *M. telleri* biozone traced in Lower Devonian sections in Canada, Tien Shan and Pai-Khoi embraces the stratigraphic interval from the *hercynicus* to the *yukonensis* Zones. The asynchronous populations of *M. telleri* display a relative stability of their morphology in time and space. However, at a certain stratigraphic level of the Darai-Khurd section there occurs an acme of *M. telleri* (Fig. 1, section I, beds 12—14) and certain specimens distinguished by a slightly different shape of their proximal end. Specimens with a thinner proximal end and a sicula showing slight dorsal curvature (Pl. 5, Fig. 4; Pl. 6, Fig. 2; Pl. 9, Fig. 5) can be observed alongside with straight or weakly ventrally curved (Pl. 1, Fig. 2; Pl. 5, Figs 1—2; Pl. 6, Figs 1, 3). The same stratigraphic level displays the first *M. craigenis* Jaeger. The latter, not unlike *M. telleri*, has biform thecae, rhabdosome of somewhat smaller size and dorsally curved proximal end. However, its proximal part widens more gradually and the curvature ranges from slight, involving sicula and th_1 to strong, similar to *M. yukonensis*. *M. telleri* characterized by dorsally incurved sicula and *M. craigenis* with a slight curvature are very similar. These two species grade into each other which accounts for establishing their phylogenetic relationship.

Lenz & Jackson opined that *M. telleri* and *M. thomasi* Jaeger share a morphologic resemblance (Lenz & Jackson 1971, p. 18). *M. thomasi* have not been observed in Lower Devonian of Pai-Khoi and Tien Shan, however, *M. telleri* from the Turkparida Formation comprises a morphological variety similar to *M. thomasi* in having thin proximal end but showing no tendency towards isolation of thecae.

Distribution. — Lower Devonian, Pai-Khoi, the Livanov Cape Formation, the *falcarius* Zone and the *falcarius-fanicus* Interzone; southern Tien Shan, the Turkparida Formation, the Interzone *falcarius-fanicus*, the *fanicus-yukonensis* Zone (Fig. 1).

Monograptus craigenis Jaeger, 1970

(Pl. 5, Fig. 4; Pl. 6, Figs 5—6; Pl. 7, Figs 1—8; Pl. 9, Figs 7—12; Pl. 10, Figs 2—13)

1970. *Monograptus craigenis* Jaeger, n.sp.; pp. 196—202, Figs 7B, C; 8B, C; 9A, F, K; 6.
 1971. *Monograptus yukonensis* Jackson et Lenz; Lenz & Jackson, p. 18, Pl. 2, Fig. 12; Text-fig. 5D, E.
 1972. *Monograptus* cf. *craigenis* Jaeger; Jackson & Lenz, pp. 589—590, Text-fig. 4F, G, M.
 1972. *Monograptus pacificus* Jaeger; Obut, Figs 2, 9a—b.
 1972. *Monograptus avilli* Obut, sp. n.; pp. 1217—1218, Figs 2, 10, 11.
 1972. *Monograptus* cf. *craigenis* Jaeger; Obut, Figs 2, 12.

Material. — 80 specimens. Measured material: 50 specimens.

Description. — *Rhabdosome.* Middle-sized, 30—40 mm, maximum length observed 70 mm excluding free part of virgula which can reach 15 mm. Proximal end with moderate dorsal curvature of 15—30°. Curvature involves sicula and the first two or three thecae. Dorsal side is slightly curved ventrally between th_3 and th_6 , essen-

tially straight distally. Rhabdosome widens progressively in first 10 mm; at th_1 0.9—0.8 (0.7—0.6), at th_2 1—0.9 (0.8—0.7), at th_3 1.1—1 (0.9—0.8), at th_4 1.2—1.1 (0.9—0.8), at th_5 1.3—1.2 (1.1—1); at 10 mm it equals 1.9—1.6 (1.7—1.4), reaching the maximum of 2 (1.8) mm at th_{13-14} . Width between th_1 and th_2 is 0.6—0.7 mm; $\Sigma = 1.5$ mm.

Sicula. Straight, narrowly conical, 1.5—2 mm long. Dorsal side straight or weakly curved ventrally. Aperture 0.4—0.5 mm wide, furnished with thin straight virgella 0.4—0.5 mm long and dorsal process of the same length, strongly incurved and scoop-like having lateral expansions towards the end. Apex reaches hood of th_2 . Porus appears at a distance of 0.15—0.2 mm from aperture.

Thecae. Biform. The first 12—16 thecae of rhabdosomes, 35—70 mm long, furnished with hoods obscuring apertures both ventrally and laterally. Well developed hoods have lateral width of 0.25—0.3 mm, length up to 0.5 mm. At a distance of 10 mm or over hoods diminish in size and give place to dorsal shields. The extreme distal thecae bear no apertural processes. Geniculum is well pronounced, supra- and infragenicular walls being straight or slightly inclined to axis and almost normal to each other. Shallow excavation can be seen. Interthecal septa indetectable. Number of thecae in 10 mm decreases gradually: 12 in the first one, 11—10 in the second, 9.5—9 distally.

Comparison. — *M. craigensis* Jaeger was established in the *yukonensis* Zone of southeastern Alaska (Churkin, Jaeger & Eberlein 1970). This species embraces monograptids showing affinity with *M. yukonensis* Jackson & Lenz *sensu* Jaeger (1970) with a smaller dorsal curvature, however, and a wider proximal part of rhabdosome. Both species are almost identical in their thecal biformity and hood structure. As distinct from Jaeger the original authors of *M. yukonensis* treat it in a wider sense including into the species monograptids with distinct dorsal curvature. They emphasize a great range of variability in the shape of proximal end even with specimens preserved at one and the same bedding plane (Lenz & Jackson 1971). Pointing out the phylogenetic relation of *M. telleri* and *M. yukonensis*, Jackson & Lenz suggest that the transient forms should be considered as a subspecies *M. yukonensis craigensis*. The latter, however, is neither chronologically, nor geographically a variant of the above species and its establishing would contradict nomenclature rules.

In the Lower Devonian sections of Canada and Alaska monograptids under the study occur within the *yukonensis* Zone while in the southern Tien Shan sections they have been observed within a much larger stratigraphic interval namely the *telleri* biozone. The abundance of material and reliable stratigraphic control allow to draw a distinction between *M. telleri*, *M. craigensis* and *M. yukonensis* taking into account their stratigraphic position. All the three species are members of the same lineage and show the tendency towards an ever increasing curvature of proximal end. In this respect as well as by its stratigraphic position *M. craigensis* is intermediate between *M. telleri* and *M. yukonensis*. It can be especially well traced in the continuous section of the Darai-Khurd Creek where *M. craigensis* with a proximal part slightly curved dorsally makes its first appearance alongside with *M. telleri* (Figs 1 and 2, section I, bed 14). Higher up in the section monograptids acquire a stronger curvature and display a full variability range of this character (Fig. 1, section I, beds 17—18). And finally at bed 19 there appears *M. yukonensis*. At this stratigraphic level abundant *M. craigensis* is observed, predominant among them being the specimens with a stronger curvature of the proximal end. They are identical with the type specimens from the *yukonensis* Zone of Alaska (Churkin, Jaeger & Eberlein 1970). A series of specimens transient from *M. craigensis* to *M. yukonensis* can be observed in the samples from the lower part of the *yukonensis* Zone (Fig. 1, section I, bed 19; Pls 7, 10). Morphological distinction

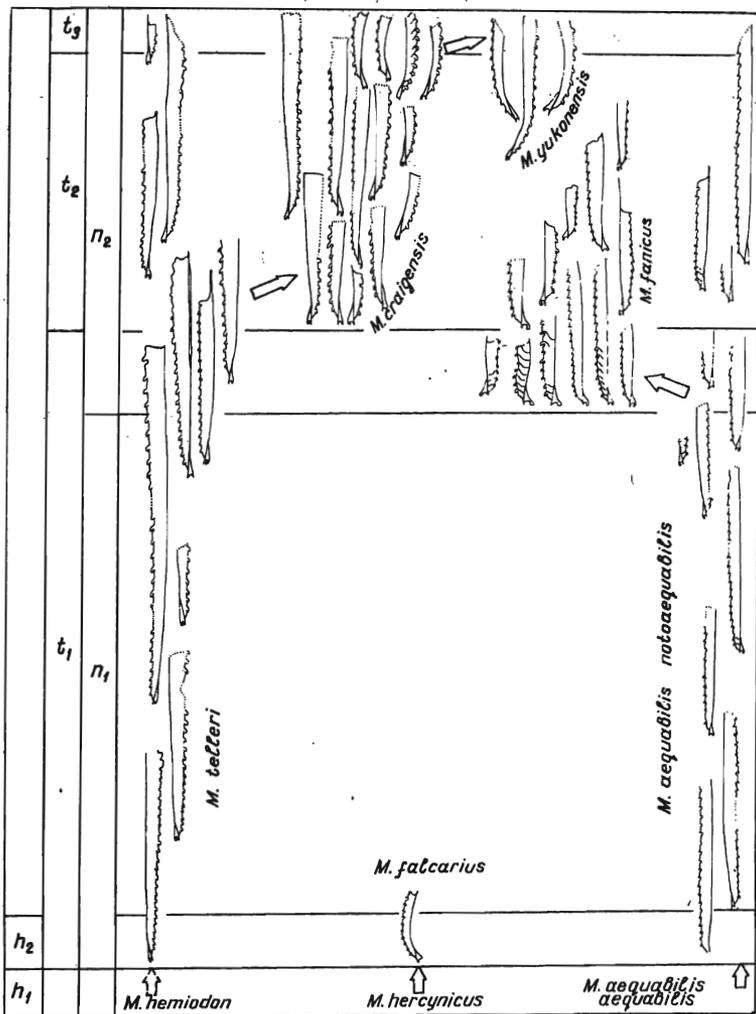


Fig. 2

Diagram of possible phylogenetic lines of post-hercynicus monograptids

Arrows mark transition from one species to another in the lineage. Horizontal lines are zonal boundaries. The stratigraphic position of graptolites shown here corresponds to the sections in Fig. 1

between the extreme forms of the above species is only slight which presents a certain problem in establishing the line between the two. *M. craigensis*, however, has a weaker dorsal curvature ($15-30^\circ$), a more pronounced decrease in the hood size distally as well as a wider rhabdosome.

Distribution. — Lower Devonian, southern Tien Shan, the Turkparida and Darai-Khurd Creeks, the Turkparida Formation, the *craigensis* and *yukonensis* Zone. The accompanying assemblages are shown in Fig. 1.

Monograptus yukonensis Jackson & Lenz, 1963

(Pl. 7, Figs 9—12; Pl. 10, Figs 14—16)

1963. *Monograptus yukonensis* Jackson et Lenz, n. sp.; Jackson & Lenz, pp. 751—753, Fig. 1a, b.
 1969. *Monograptus yukonensis* Jackson et Lenz; Jaeger, Stein & Wolfart, pp. 175—177, Figs 7D—E, 8A.
 1970. *Monograptus yukonensis* Jackson et Lenz; Berry, Fig. 2h.
 1971. *Monograptus yukonensis* Jackson et Lenz; Lenz & Jackson, pp. 17—21, Pl. 2, Figs 9—11, non 12; Text-fig. 5A—C, F, G, non 5D, E.
 1972. *Monograptus yukonensis* Jackson et Lenz; Berry & Murphy, p. 265, Fig. 5A—C.
 1972. *Monograptus yukonensis yukonensis* Jackson et Lenz; Obut, p. 1216, Fig. 2; 1.

Material. — 10 specimens.

Description. — *Rhabdosome.* Dorsally curved in proximal part (30° and over), distally straight. Dorsal curvature involves sicula and the first four thecae. Proximal part thin at th_1 — th_4 , with rhabdosome width increasing gradually. Dimensions: S at th_1 0.8 (0.5) mm, between th_1 and th_2 0.4—0.5 mm, at th_2 0.8 (0.5) mm, at th_3 0.9 (0.6) mm, at th_4 1 (0.8) mm, at th_5 1 (0.8) mm, max. at th_{10} — th_{12} 1.6 (1.4) mm; L — about 15 mm.

Sicula. Straight, conical, 2 mm long and 0.3—0.4 mm wide at aperture. Spine-like virgella 0.6 mm long and incurved dorsal process 0.4—0.5 mm long; $\Sigma = 1.5$ mm.

Thecae. With wide hoods overhanging apertures ventrally and laterally. Hoods of the first ten thecae of similar size. Interthecal septa not visible. Number of thecae in 10 mm equals 12—10.

Comparison. — In the collection studied *M. yukonensis* is represented by an insignificant number of specimens. They are for the most part the young rhabdosomes up to 15 mm long. Adult *M. yukonensis* 40—50 mm long from the Darai-Magian section are described by Obut (1972, p. 1216, Fig. 2; 1). The Tien Shan *M. yukonensis* is identical to the least dorsally curved specimens in the variability range of the species (*sensu* Jaeger 1970). Along with *M. yukonensis* in bed 19 (Fig. 1, section I) there occurs abundant *M. craigensis* displaying a full variability range from specimens close to *M. telleri* to those approaching *M. yukonensis*. We consider as *M. yukonensis* such specimens whose proximal part at th_1 — th_4 has a curvature of 30° and over. The major characters of monograptids of the *M. telleri* — *M. yukonensis* lineage are given in Table 6.

M. yukonensis from the Turkparida Formation shows a greater similarity with the Canadian representatives of the species (Lenz & Jackson 1971, Text-fig.

Table 6

Character	<i>M. telleri</i>	<i>M. craigensis</i>	<i>M. yukonensis</i>
Rhabdosome: L	40—90 mm	30—70 mm	15—50 mm
S at th_1	0.9/0.6—0.7/0.4	0.9—0.8/0.7—0.6/	0.8/0.5/
S between th_1 and th_2	0.6—0.7	0.6	0.4—0.5
S max.	2.3/2/—2.5/2.2/	2/1.8/	1.6—/1.4/
shape of proximal end	straight	curved dorsally at sicula and th_1 — th_3 /10—15°/	curved dorsally within the first four thecae and over /30° and more/
Thecae: hooded thecae	13—26	12—16	12 and over
N proxin.	11—10	12	12—10
N distal.	9—8	9.5—9	9

5A, B, C; Pl. 2, Fig. 10). They differ from *M. yukonensis* of Lower Devonian sections in the Thailand and Alaska by a weaker curvature and bigger width of the proximal part.

Distribution. — Lower Devonian, southern Tien Shan, the Turkparida Formation, the *yukonensis* Zone. The assemblage of accompanying monograptids in the Darai-Khurd section is given in Fig. 1.

MORPHOLOGY AND PHYLOGENY

Detailed observations of monograptids morphology are restricted by their preservation as silvery films on the bedding surface of block shales. We can observe only such characters as the shape of rhabdosome, sicula, thecae and thecal hoods. These limitations are partly made up for by the abundance of specimens.

A number of common morphological characters are indicative of the *telleri* biozone monograptids. They are astogenetic variability of thecae, the presence of thecal hoods which are extensions of the dorsal walls as well as a dorsal sicular process. The combination of such characters accounts for a specific appearance of the latest monograptid fauna. It must have shown the best adaptability to the environments during the possible reduction of ecological niches suitable for graptolite habitation. Impoverished composition and lack of significant morphologic changes testify to the attenuation of the monograptid evolution rate at this later stage of their development. Thus, less significant morphological characters should be chosen for diagnosis of early Devonian monograptids as distinct from Silurian species of the family. To these diagnostic features belong the degree of thecal biformity, the hood shape and the size of proximal end. The most important of all, however, is the gradual change in the shape of proximal part, namely, the appearance and increase of dorsal curvature. Such an approach to taxonomic problem facilitates the application of early Devonian monograptids for stratigraphic subdivision and correlation.

Taxonomic evaluation and establishing intraspecies variation of early Devonian monograptids under study proved to be difficult. The representatives of populations within single sample as well as throughout the section allows to trace a number of transient forms between related taxa. Thus, considerable difficulty has been experienced in distinguishing between *M. aequabilis notoequabilis* and *M. fanicus* n. sp. from the same sample (Fig. 1, section I, beds 11—13). The same is true for *M. telleri*, *M. craigensis* and *M. yukonensis* which appear in a sequence and are closely related morphologically.

Three groups of monograptids can be recognized on the basis of their hood structure, sicular shape, proximal end curvature and degree of thecal biformity. The first group involves *M. telleri*, *M. craigensis* and *M. yukonensis*, the second — *M. aequabilis notoequabilis* and *M. fanicus*

n. sp., while the third group comprises *M. hercynicus* and *M. falcarius*. Subsequent appearance of the species within one group as well as morphologic transitions between them are indicative of their belonging to the same lineage.

Already in the lower boundary of the *telleri* biozone we can identify three lineages, namely, appearance of *M. telleri*, further development of *M. aequabilis* and termination of the *M. hercynicus* line. The lineage consisting of three subsequent members: *M. telleri*, *M. craigensis* and *M. yukonensis* is the most progressive among monograptids of the *telleri* biozone. The main trend of their development lies in gradual change of the shape of proximal end from straight in *M. telleri*, slightly curved dorsally in *M. craigensis* to strongly in *M. yukonensis*. The whole variation range for proximal end curvature can be traced in the upper part of the *telleri* biozone (Pl. 10). Difficulties in discrimination between synchronous populations of the above species in the *yukonensis* Zone give rise to different taxonomic evaluation (Jaeger 1970, Lenz & Jackson 1971). Such discrimination is more accurate when we have a chance to observe a gradual increase in the degree of the proximal end curvature within the stratigraphic interval below the *yukonensis* Zone. Alongside with this feature the transition from *M. telleri* to *M. yukonensis* is expressed by a slight decrease of rhabdosome size and more distinct thecal biformity. Sicular shape and hood structure undergo no change. Monograptids of the *M. telleri* — *M. yukonensis* lineage dominate quantitatively in the upper part of the *telleri* Zone (Figs 1—2, *t*₃). Table 7 illustrates proportions of various monograptids in the Darai-Khurd section.

The main trend of phylogeny of the *M. aequabilis* — *M. fanicus* n. sp. lineage consist in the change of sicular shape from straight and narrow or slightly curved ventrally in *M. aequabilis notoequabilis* to curved dorsally and expanding trumpet-like in *M. fanicus* n. sp. The stru-

Table 7

Species \ No. of bed	No. of bed																		
	3	4	5	6	7	8	10	11	12	13	14	14a	15	16	17	18	19	19a	
<i>M. aequabilis notoequabilis</i>	1	17	2	10	40	8	6	75	17	85	1	6	1	5	1	2	2		
<i>M. fanicus</i> n. sp.	-	-	-	-	-	-	-	50	185	30	10	29	6	8	3	-	-	-	
<i>M. telleri</i>	-	1	-	10	6	4	13	55	25	52	13	30	1	2	19	3	-		
<i>M. craigensis</i>	-	-	-	-	-	-	-	-	-	-	2	3	3	1	-	20	14	4	
<i>M. yukonensis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	3	

cture of the apertural hoods undergoes no changes, the number of hooded thecae, however, increases with time. *M. aequabilis notoequabilis* builds up the major portion of the graptolite assemblage in the lower part of the *telleri* biozone. The acme of *M. aequabilis notoequabilis* and *M. fanicus*

n. sp. is observed in the middle part of the Zone while by the end of this interval proliferation of the members of this lineage seems to loose in its intensity and they are no more predominant in the *craigensis-yukonensis* time.

The development of the *M. hercynicus* — *M. fanicus* lineage is characterized by the change in the rhabdosome shape and the decrease in its size from straight and large in *M. hercynicus* to arcuate and small in *M. fanicus* n. sp. They get extinct in the lowermost part of the *telleri* biozone and no morphologically similar forms with trumpet-like sicula are observed later.

Thus, the major trends of evolution of all monograptids of the *telleri* biozone can be summed up as follows:

1. appearance of a dorsal sicular process and its further presence as a permanent character in all members of monograptid assemblage,
2. appearance of a dorsal curvature at the proximal end of the rhabdosome and further increase in its degree, traced in all the lineages,
3. change in the sicular shape in one of the lineages,
4. decrease in the degree of thecal biformity and rhabdosome size,
5. proximal introduction of the main morphological changes.

STRATIGRAPHIC SIGNIFICANCE

Investigations of stratigraphic distribution of graptolites in the sections of the Livanov Cape and Turkparida formations provided new data concerning the range of post-*hercynicus* monograptids and their assemblages. *M. aequabilis notosaequabilis* and *M. telleri* have the widest biozones. The first appearance of *M. aequabilis notosaequabilis* above the top of the *hercynicus* Zone in Pai-Khoi and the occurrence of rare *M. aequabilis* within the top of Pragian (Bouček 1966, Jaeger 1969) seem to indicate that its range fits into the Pragian stage. Comparison of the data on the distribution of *M. telleri* in the type sections of the Lower Devonian of north-western Canada (lower part of the *yukonensis* Zone; Lenz & Jackson 1971) and in the sections of Pai-Khoi and South Tien Shan indicates that the given biozone comprises the sequence from the top of the *hercynicus* Zone to the lower part of the *yukonensis* Zone inclusively. This is why both above mentioned monograptids in spite of the common occurrence and distinct specific characters are of no use for the purpose of detailed subdivision. In the lower part of the sequence studied both species are associated with *M. falcarius* (Fig. 1, section II, bed 7), then with *M. fanicus* n. sp. (Fig. 1, section I, beds 12—13). Within this interval monograptids of the *M. aequabilis* — *M. fanicus* n. sp. lineage are predominant. Above it

monograptid assemblages are enriched by successive appearance of *M. craigensis* (Fig. 1, section I, bed 14) and *M. yukonensis* (bed 19). The upper part of the *telleri* biozone is characterized by abundance of monograptids from the *M. telleri* — *M. yukonensis* lineage. It should be noted that in Lower Devonian sections of northwestern Canada only rare *M. aequabilis notoequabilis* are observed on the background of *M. yukonensis* and *M. telleri*.

Development of monograptids within the three lineages was used as the basis for the subdivision of the section investigated. Monograptids of the *telleri* biozone constitute five successive assemblages. The zonal delimitations are based on the first appearance of the index-species. Thus, the limits of the zone are determined by the appearance of two consecutive species of the same lineage ("consecutive lineage-segment-zones" *sensu* Hedberg, 1972). The zones introduced therefore, cannot be considered as range zones with the only exception of the *falcarius* Zone as their upper limits do not coincide with the disappearance of the zonal taxa.

In the combined section of the Lower Devonian of Pai-Khoi and southern Tien Shan the following stratigraphic subdivisions can be traced:

1. the *falcarius* Zone,
2. the *falcarius-fanicus* Interzone,
3. the *fanicus* Zone,
4. the *craigensis* Zone,
5. the *yukonensis* Zone.

The subdivision suggested could be used as the basis for correlation within the Urals-Tien Shan folded area and may supply data for interregional correlation.

Acknowledgements. My thanks are due to Dr Z. M. Abduasimova, Dr A. I. Kim and V. I. Lavrusevitch for making possible my study of the Lower Devonian sections in South Tien Shan. I am indebted to Prof. A. Urbanek for reading and criticising the manuscript. I should like to express my gratitude to Dr H. Jaeger, Dr D. Jackson and Prof. A. Lenz for the helpful discussions while looking through graptolite collections. Thanks are also due to Mrs. I. Bagaeva for translation of the manuscript into English.

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**DOLNODEWOŃSKIE MONOGRAPTIDY BIOZONY *TELLERI* Z OBSZARÓW
PAJ-CHOJU I TIEN-SZANU**

(Streszczenie)

W pracy przedstawiono morfologię oraz zasięgi stratygraficzne pięciu znanych gatunków dolnodewońskich monograptidów z obszarów Paj-Choju i Tien-szanu (ZSRR) oraz ustanowiono jeden nowy. Ustalono główne kierunki rozwojowe post-hercyńskich monograptidów, wydzielając trzy linie ewolucyjne. Rozprzestrzenienie stratygraficzne monograptidów w obrębie analizowanych profili dostarcza nowych danych odnośnie zasięgów badanych taksonów. Wydzielona Biozona *M. telleri* obejmuje interwał stratygraficzny od zony *M. hercynicus* aż po *M. yukonensis* włącznie, a równoległe występowanie w jej obrębie innych gatunków umożliwia ponadto wyróżnienie pięciu odrębnych Zon. Omówiono także korelację i wiek dolnodewońskich osadów z graptolitami z obu regionów.

DESCRIPTION OF PLATES 1—10

PL. 1

Monograptids of the *falcarius* Zone, Fig. 1, section II, bed 7, Livanov Cape Formation, the shore of the Kara Sea near the Amderma village, Pai-Khoi

- 1 — *Monograptus aequabilis notoaequabilis* Jaeger & Stein, CGM, 1/10505, $\times 5$.
- 2 — *Monograptus telleri* Lenz & Jackson, CGM, 21/10145, $\times 7$.
- 3-7 — *Monograptus falcarius* Koren. Figs 3-5 — CGM, 30/10145, 31/10145, 2/10505, $\times 7$; Figs 6-7 — CGM, 31/10145, 6/10145, $\times 30$.

PL. 2

Monograptids of the *fanicus-craigensis* Zones, Fig. 1, section I, Turkparida Formation, southern Tien Shan

- 1-3 — *Monograptus aequabilis notoaequabilis* Jaeger & Stein. Fig. 1 — CGM, 3/10505, $\times 8$, *craigensis* Zone, bed 14; Fig. 2 — CGM, 4/10505, $\times 10$, *fanicus* Zone, bed 12; Fig. 3 — CGM, 5/10505, $\times 10$, *fanicus* Zone, bed 12.
- 4-8 — *Monograptus fanicus* n. sp. Bed 12. Fig. 4 — 6/10505, $\times 10$; Fig. 5 — holotype, CGM, 7/10505, $\times 10$; Fig. 6 — CGM, 18/10875, $\times 8$; Fig. 7 — CGM, 8/10505, $\times 10$.

PL. 3

Monograptids of the *fanicus* Zone, Fig. 1, section I, beds 12—13, Turkparida Formation, southern Tien Shan

- 1-3 — *Monograptus fanicus* n. sp., $\times 10$. These specimens can be considered as transitional to *M. aequabilis notoaequabilis* Jaeger & Stein on account of the shape of the sicula. Fig. 1 — CGM, 13/10875; Fig. 2 — CGM, 9/10505; Fig. 3 — CGM, 10/10505.
- 4 — *Monograptus aequabilis notoaequabilis* Jaeger & Stein vel *Monograptus fanicus* n. sp., CGM, 11/10505, $\times 10$.

PL. 4

Successive stages of development of juvenile rhabdosomes *Monograptus aequabilis notoaequabilis* Jaeger & Stein and *M. fanicus* n. sp., *fanicus* Zone, Fig. 1, section I, beds 11—12, Turkparida Formation, southern Tien Shan

- 1-2, 9 — *Monograptus aequabilis notoaequabilis* Jaeger & Stein. CGM, 27/10875, 28/10875, 14/10505, $\times 25$.
- 3-8 — *Monograptus fanicus* n. sp. CGM, 34/10875, 33/10875, 35/10875, 12/10505, 36/10875, 13/10505, $\times 25$.

PL. 5

Morphological transition from *Monograptus telleri* Lenz & Jackson to *Monograptus craigensis* Jaeger indicated in the shape of the proximal end. Southern Tien Shan, Turkparida Formation, Fig. 1

- 1-2 — *Monograptus telleri* Lenz & Jackson. Fig. 1 — CGM, 1/10875, $\times 10$, *fanicus* Zone, bed 13; Fig. 2 — CGM, 15/10505, $\times 10$, *fanicus* Zone, bed 12.
- 3 — *Monograptus telleri* Lenz & Jackson. This specimen can be considered as transitional to *M. craigensis* on account of the shape of the proximal end, *fanicus* Zone, bed 13, CGM, 5/10875, $\times 10$.
- 4 — *Monograptus craigensis* Jaeger. CGM, 9/10875, $\times 10$, *yukonensis* Zone, bed 19.

PL. 6

Morphological transition from the straight rhabdosomes of *Monograptus telleri* Lenz & Jackson to *M. craigensis* Jaeger with the proximal end weakly curved dorsally.

Southern Tien Shan, Turkparida Formation, Fig. 1, section I

- 1-4 — *Monograptus telleri* Lenz & Jackson. Figs 1-2 — juvenile rhabdosomes, CGM, 16/10505, *fanicus* Zone, 44/10875, *craigensis* Zone, $\times 25$; Figs 3-4 — proximal ends of adult rhabdosomes, CGM, 4/10875, *craigensis* Zone, CGM, 3/10875, *falcarius-fanicus* Interzone, $\times 25$.
- 5-6 — *Monograptus craigensis* Jaeger. The proximal ends of adult rhabdosomes, CGM, 6/10875, $\times 25$, *craigensis* Zone, CGM, 10/10875, $\times 25$, *craigensis* Zone

PL. 7

Monograptids of the *craigensis* and *yukonensis* Zones, southern Tien Shan, Turkparida Formation, Fig. 1, section I, beds 18—19

- 1-8 — *Monograptus craigensis* Jaeger. CGM, 17/10505, $\times 3$; 18/10505, $\times 2$; 19/10505, $\times 5$; 9/10875, $\times 3$; 8/10875, $\times 5$; 20/10505, $\times 3$; 21/10505, $\times 5$; 22/10505, $\times 3$.
- 9-12 — *Monograptus yukonensis* Jackson & Lenz. Figs 9-10 — CGM, 47/10875, $\times 5$, $\times 25$; Fig. 11 — CGM, 12/10875, $\times 10$; Fig. 12 — CGM, 10/10875, $\times 5$.

PL. 8

Monograptids of *M. aequabilis* — *M. fanicus* lineage. The gradual morphological transition from *M. aequabilis notoequabilis* to *M. fanicus* n. sp. and variability in the shape of sicula in *M. fanicus* n. sp. traced in one and the same sample, section I, bed 12

- 1-5 — *Monograptus aequabilis notoequabilis* Jaeger & Stein, CGM, 23/10505, $\times 3$; 24/10505, $\times 4$; 5/10505, $\times 4$; 4/10505, $\times 4$; 25/10505, $\times 4$.
- 6-21 — *Monograptus fanicus* n. sp. Figs 6-10 — specimens close to *M. aequabilis notoequabilis* on account of the sicula shape; CGM, 26/10505, $\times 4$; 27/10505, $\times 5$; 28/10505, $\times 4$; 29/10505, $\times 5$; 30/10505, $\times 5$. Figs 11-21 — specimens with the trumpet-like sicula, CGM, 31/10505, $\times 4$; 10/10505, $\times 4$; 13/10505, $\times 5$; 6/10505, $\times 4$; 7/10505, $\times 4$, holotype; 32/10505, $\times 5$; 33/10505, $\times 4$; 34/10505, $\times 5$; 18/10875, $\times 4$; 35/10505, $\times 5$; 17/10505, $\times 5$.

PL. 9

Gradual morphological transition from *Monograptus telleri* Lenz & Jackson to *M. craigensis* Jaeger, traced in samples from beds 14—15, *craigensis* Zone, Turkparida Formation, Fig. 1

- 1-6 — *Monograptus telleri* Lenz & Jackson, CGM, 36/10505, 37/10505, 4/10875, 38/10505, 5/10875, 44/10875, $\times 5$.
- 7-12 — *Monograptus craigensis* Jaeger, CGM, 39/10505, 46/10875, 4/10505, 40/10505, 41/10505, $\times 5$; 42/10505, $\times 4$.

PL. 10

Monograptids of the *M. telleri* — *M. craigensis* — *M. yukonensis* lineage, Turkparida Formation, *yukonensis* Zone, Fig. 1, bed 19

- 1 — *Monograptus telleri* Lenz & Jackson, CGM, 43/10505, $\times 5$.
- 2-13 — *Monograptus craigensis* Jaeger, CGM, 44/10505, $\times 5$; 45/10505, $\times 5$; 46/10505, $\times 5$; 47/10505, $\times 5$; 8/10875, $\times 5$; 9/10875, $\times 3$; 19/10505, $\times 5$; 9a/10875, $\times 5$; 8/10875, $\times 5$; 48/10505, $\times 5$; 21/10505, $\times 5$; 22/10505, $\times 3$.
- 14-16 — *Monograptus yukonensis* Jackson & Lenz, CGM, 12/10875, $\times 4$; 47/10875, $\times 5$.

