

Early Llandovery monograptids from Bornholm and the southern Urals: taxonomy and evolution

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The most complete Lower Llandovery succession of mudrocks yielding graptolites within the *ascensus*, *acuminatus* and *vesiculosus* Biozones was studied in the Billegrav-1 core, South Bornholm. Special attention is given to the taxonomy and stratigraphical ranges of monograptids found in the *vesiculosus* Biozone in the core and nearby exposures in Øle Å. Monograptids of the *ascensus-acuminatus* and *vesiculosus* Biozones were also discovered in condensed carbonaceous shale sequences of the Sakmara Formation in the southern Urals. Monograptids from Bornholm and the southern Urals are described, and referred to 5 genera and 17 species (4 new and 4 in open nomenclature). The new genus *Huttagraptus* (type species *H. praestrachani*) is erected. Based on the present taxonomical studies the main morphological trends, phylogenetical relationships and diversity dynamics of the earliest monograptids are discussed.

Key words: Graptoloids, monograptids, Early Silurian, taxonomy, biostratigraphy, evolution, phylogeny, Bornholm, Denmark, southern Urals, Russia.

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The lack of detailed knowledge of the taxonomy, stratigraphical ranges and phylogenetic relationships of the earliest Llandovery monograptids results from a global rarity of well preserved specimens from the *acuminatus* and *vesiculosus* Biozones. The monograptids have been most extensively studied in the British sections (Hutt 1968, 1974, 1974–1975; Hutt & Rickards 1970; Hutt et al. 1970; Rickards 1974, 1976; Rickards & Hutt 1970; Rickards & Rushton 1968; Rickards et al. 1977). More recently they have been found and partly described from Bohemia (Štorch 1986, 1988, 1994), Canadian Arctic Islands (Melchin 1989; Lukasiak & Melchin 1994) and China (Chen 1984, 1986; Chen & Lin 1978; Fang et al. 1990; Li et al. 1990).

A project to examine the earliest monograptids from Bornholm, Denmark and the southern Urals, Kazakhstan was initiated in 1993, the main goal of which was a comparative analysis of their taxonomic composition and morphology in different sedimentary environments. Some of the early Llandovery monograptids from the Øle Å locality, South Bornholm had

previously been described by Bjerreskov (1975). Early Llandovery monograptids had been collected from the southern Urals since the early 1950s to mid 1970s, but no taxonomical studies had been undertaken. The present paper analyses the taxonomy, morphology and diversity dynamics of monograptids, in the early Llandovery *acuminatus* and *vesiculosus* Biozones in both regions.

Geological setting and depositional environments

Bornholm is located within the Sorgenfrei-Tornquist Zone (*sensu* EUGENO-S working group 1988; Vejrbæk et al. 1994), which forms the boundary between the relatively stable Fennoscandian/East European Platform to the northeast and the northwest European sedimentary basins to the southwest. The Llandovery and Wenlock graptolite-bearing mudstones, approximately 110 m thick, are exposed in the rivulet Øle Å, South

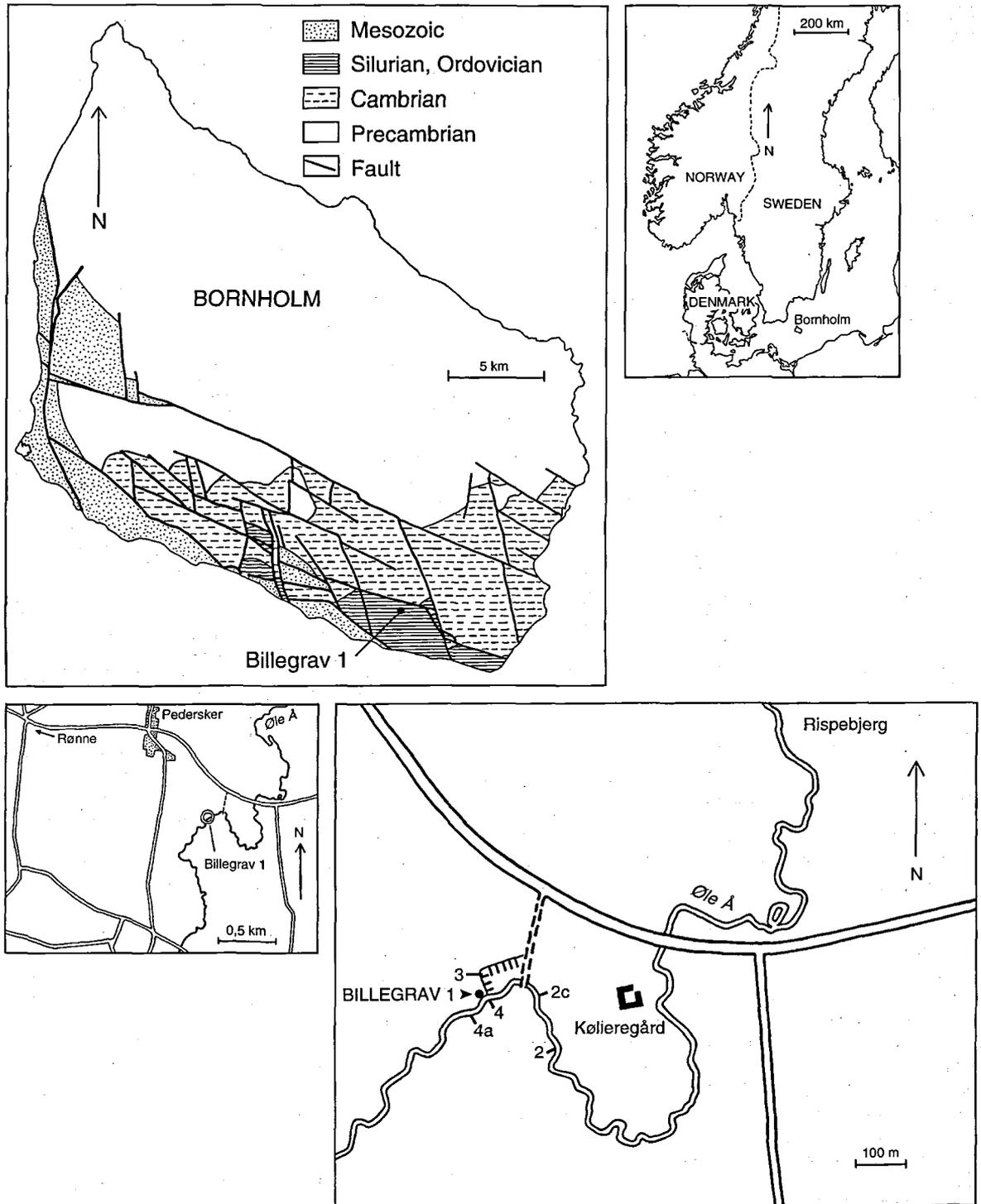


Fig. 1. Schematic geographical map showing the graptolite localities and Billegrav-1 core in South Bornholm, modified after Bjerreskov (1975) and Pedersen (1989).

Øle Å exposures revised from Bjerreskov (1975)

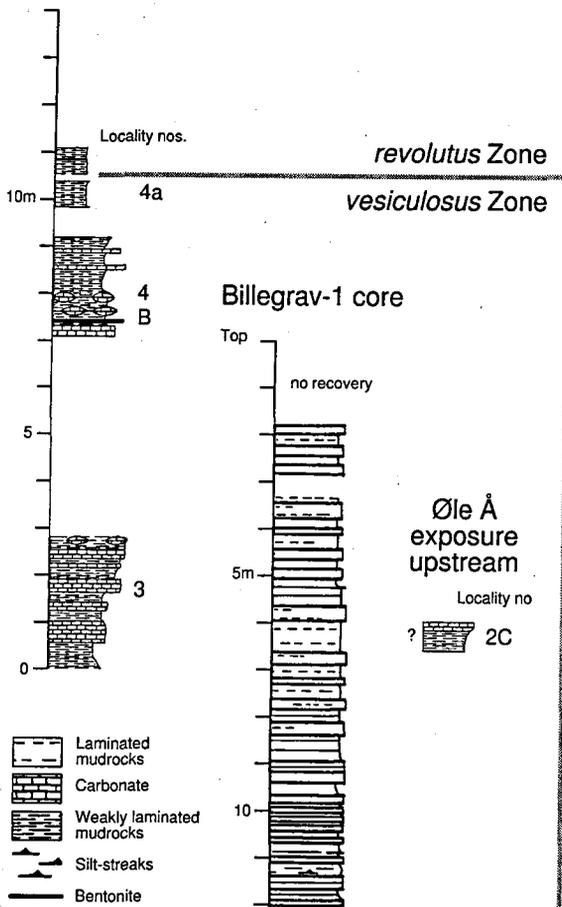


Fig. 2. Stratigraphical position of the Øle Å localities (partly after Bjerreskov 1975) and the upper part of the Billegrav-1 core sequence (after Pedersen 1989).

Bornholm (Fig. 1). They occur in a number of small fault blocks tilted at low angles and are only accessible along small streams (Bjerreskov & Stouge 1985).

For the present study new well preserved graptolites of the *vesiculosus* Biozone (= *acinaces* Biozone, Bjerreskov 1975) have been collected from the bottom of the rivulet from the exposures 4a and 2c (Figs 1, 2). The well-preserved pyritized graptolites (exp. 4a) occur in finely laminated light grey to dark grey siltshales. The dark grey laminated mudstones (exp. 2c) yield numerous flattened specimens. However, in all localities studied the lowermost Silurian strata below the *vesiculosus* Biozone are not exposed.

The complete sequence of stratigraphically well dated graptolite assemblages of the *persculptus*, *ascensus*, *acuminatus* and *vesiculosus* Biozones was discovered in the shallow drill-hole Billegrav-1 in the valley of Øle Å close to exposure 4 (Fig. 1). System-

atic search for graptolites in the core material resulted in a very comprehensive graptolite collection.

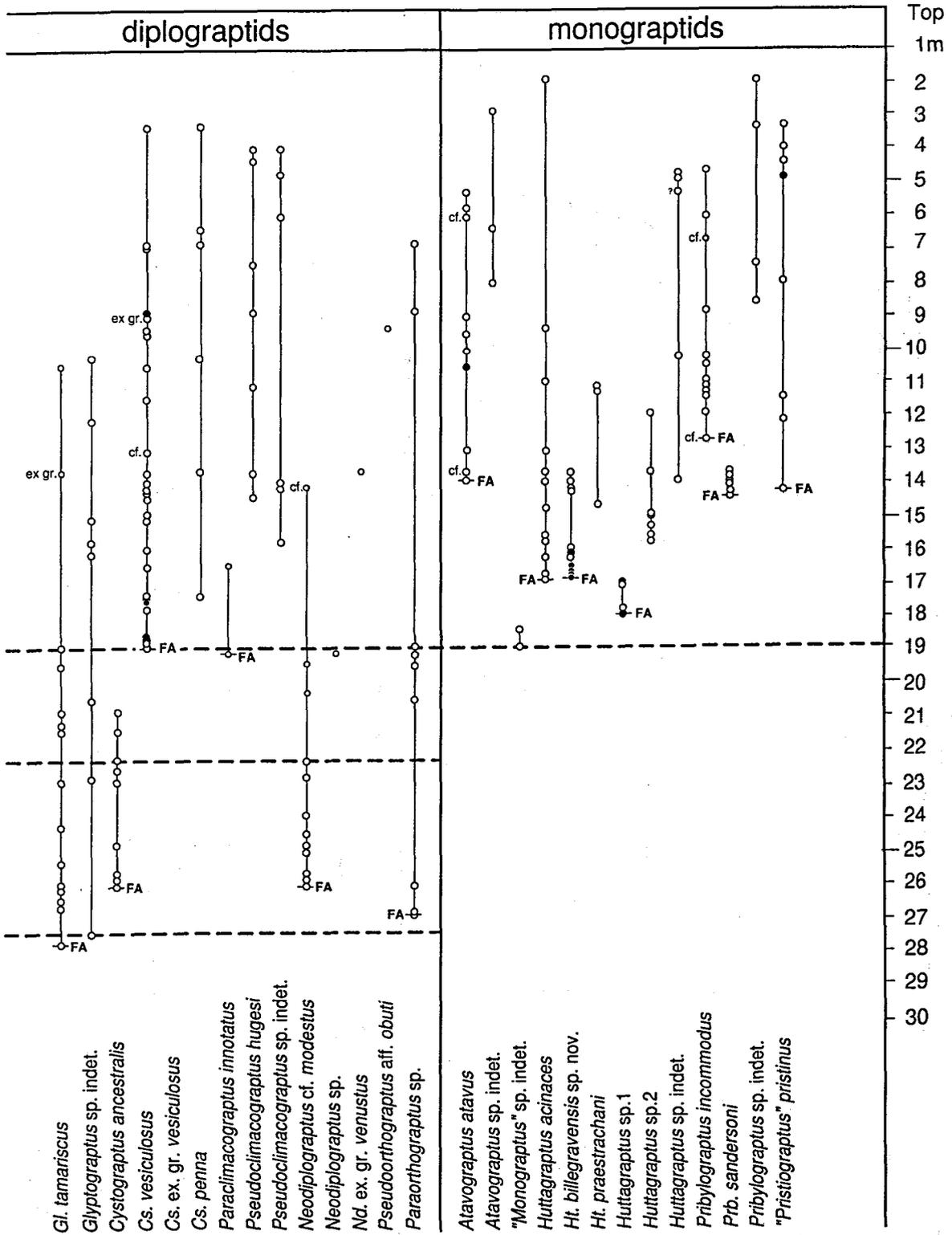
The Bornholm graptolite-bearing mudrocks were formed in the outer part of the epicontinental sea covering a comparatively stable Baltoscandian platform which was situated in subtropical to moderately low palaeolatitudes in Late Ordovician to Early Silurian time. A depositional model for the Lower Palaeozoic mudshales, alternating with greyish mudstones and silt-streaked shales was discussed in detail by Pedersen (1989), based on the core material from Billegrav-1. They were interpreted as being deposited below the wave base in a low energy, anoxic environment with short periods of better ventilation and higher energy hydrodynamics. The average or background sedimentation was represented by the black and dark grey laminated and organic rich mudshales and siltshales yielding numerous graptolites. The sediments were not significantly bioturbated, suggesting that habitability by benthic faunas was very restricted.

The deposition may have been rapid by comparison with the Ordovician strata (Lindström 1971) and sediments may have been deposited below the wave base. An average rate of deposition could be about 1 mm per 10 years (Pedersen 1995, personal communication). Pale silty laminae sometimes show graded bedding which may be a sign of rapid settling from suspension and represent short duration events resulting in formation of very distal turbidite or storm layers.

The second region of this study is the Mugodzhary Range within the Kazakhstan part of the southern Urals (Fig. 3). The graptolite-bearing strata are represented here by the condensed sequence of carbonaceous, silicified shales and cherts of the Sakmara Formation. Continuous sequences within the Sakmara Formation are rarely preserved in extensive stratigraphical ex-



Fig. 3. Schematic geographical map showing the Kos-Istek Region of the southern Urals, Western Kazakhstan (from Koren' & Rickards 1996).



posures caused by the very complicated geological structure. The rocks are strongly deformed, frequently overthrust and usually exposed within different nappes or in chaotically arranged tectonic slabs. In general, they form a linear belt directed from north to south which is called the Sakmara Zone and are interpreted as the marginal Sakmara allochthon which is differentiated in the southern part of the Uralian collisional fold belt (Ruzhentsev & Samygin 1969).

A relatively detailed plate-tectonic pattern of the southern Urals development was summarized by Zonenshein et al. (1990). This interpretation was adopted and further developed within a broad Eurasian plate-tectonic scenario by Sengör et al. (1993). This latest model shows that the lower Silurian terrigenous-volcanogenic rocks of the Sakmara Formation could have been formed in the paleoequatorial latitudes within the Sakmara-Magnitogorsk marginal sea to the east of East-European plate. The Sakmara trough continued to expand in Early Silurian time and this restricted the supply of terrigenous material to the central parts of the trough. Sedimentation mainly involved the accumulation of the cherty shales of the Sakmara Formation. These are comparable with the bathyal sediments of marginal basins and the island arc complexes. There are no traces of a bottom fauna, and the single preserved biological components of the pelagic ecosystems are numerous graptolites and radiolarians.

Biostratigraphy

Bornholm

The complete succession of the *persculptus*, *ascensus*, *acuminatus* and *vesiculosus* Biozones has been established through a 30 m thick interval from high-resolution sampling in the Billegrav-1 core (Fig. 4). The investigated part of the core comprises the finely laminated grey to dark-grey shales alternating in some intervals with limestone beds.

The lower part, about 11 m thick, is characterized by a diplograptid fauna. The long-ranging species of *Normalograptus* usually dominate. Graptolites, preserved as flattened specimens, are most frequent in the dark grey mudshales. In the upper part of the *persculptus* Biozone numerous specimens of the index-species are preserved in relief, being infilled with pyrite. This part of the core was thoroughly sampled and X-rayed to find the earliest monograptids, although no specimens were detected.

Based on the first appearances of the zonal species the successive biozones, e.g. the *ascensus* and *acuminatus* Biozones are well defined (Fig. 4). The taxonomic composition of associated diplograptids is similar for both units. It includes long-ranging species and those confined to this interval such as *Normalograptus*

trifilis (Manck) and *Cystograptus ancestralis* Storch. Rare specimens of *Akidograptus ascensus* Davies occur within the whole range of *Parakidograptus acuminatus* (Nicholson).

The base of the *vesiculosus* Biozone is defined by the first occurrence of the zonal species in association with the earliest *Huttagraptus* sp. indet. From this level upwards in the section monograptids increase in numbers and diversity. In the interval studied, nine species of monograptids have been identified, belonging to the genera *Atavograptus*, *Huttagraptus* gen. nov., "*Pristiograptus*", *Lagarograptus* and *Pribylograptus*. The diagnostic species of *Dimorphograptus*, *Rhaphidograptus* and other diplograptids are associated with monograptids through the whole zonal sequence and give a good stratigraphic control. Three species are left in open nomenclature because of incomplete preservation (Fig. 4).

Graptolites are much more abundant in the lower part of the *vesiculosus* Biozone (depth 18–13 m), where the mudrocks dominate.

The upper part of the *vesiculosus* Biozone, 10 m thick, comprises alternating dark grey mudstones and medium grey limestone beds (5–10 cm). Graptolites occurring in the mudstone layers below the lime rich part of the core are less frequent and fragmentary.

Numerous and well-preserved graptolites of the upper part of the *vesiculosus* Biozone (= *acinaces* Biozone, Bjerreskov 1975) have been found in the dark grey mudshales exposed at the bottom of the rivulet Øle Å (exp. 4a and 2c; Fig. 2).

In exposure 2c numerous monograptids are represented by specimens of *Atavograptus atavus* (Jones) and "*Pristiograptus*" *pristinus* (Hutt). Among the associated diplograptids, *Normalograptus normalis* (Lapworth) and *Cystograptus vesiculosus* (Nicholson) are dominant. The graptolites are flattened and on some bedding surfaces they show distinct preferred orientation.

Finely laminated light grey to dark grey mudshales yielding numerous pyritized graptolites are exposed in the locality 4a (Fig. 2). New, more extensive collections were made for the present study. This locality yields the most complete monograptid assemblage of the upper part of the *vesiculosus* Biozone. It includes *At. atavus*, *Huttagraptus acinaces* (Törnquist), "*Pr.*" *pristinus*, *Pribylograptus incommodus* (Törnquist) and *Lagarograptus* sp. in association with the most important diagnostic diplograptids. In some layers graptolites occur together with very peculiar, but enigmatic structures of organic origin. These organisms show meandering structures, sometimes bifurcating or have regular sinuosity. All these peculiar features are well seen in the X-ray pictures made from the samples (Fig. 5D, E, F). In the opinion of Dr. R. Bromley (1995, pers. communication) some of these structures can be interpreted as trace fossils preserved *in situ*; others look more like epipelagic tube-like colonial organisms of an uncertain systematic position.

Table 1. Zonal associations of the southern Urals graptolites.

BIOZONE	GRAPTOLITE ASSEMBLAGE
<i>cyphus</i>	<i>Gl. tamariscus nikolaevi</i> , <i>N. normalis</i> , <i>N. rectangularis</i> , <i>Prc. innotatus</i> , <i>Pseudorthograptus inopinatus</i> , <i>Dittograptus inconstans</i> *, <i>Dt. physophora</i> , <i>Dimorphograptus swastsoni</i> , <i>Rhaphidograptus toernquisti</i> , <i>Metaclimacograptus hughesi</i> , <i>Mt. undulatus</i> , <i>Monograptus a. austerus</i> , <i>M. revolutus</i> , <i>Ht. ninae sp. nov.</i> , <i>Ht. strachani</i> , <i>Prb. incommodus</i> , <i>Prb. sandersoni</i> , <i>Lg. inexpeditus</i> , <i>Lg. karaensis sp. nov.</i>
<i>vesiculosus</i>	<i>Gl. bulbosus</i> *, <i>Cs. vesiculosus</i> , <i>N. normalis</i> , <i>Prc. innotatus</i> , <i>D. erectus</i> , <i>Mt. undulatus</i> , <i>A. atavus</i> , <i>Ht. incurvus sp. nov.</i> , <i>Ht. ninae sp. nov.</i> , <i>Ht. praestrachani</i> , <i>Prb. cf. Prb. sandersoni</i> , <i>Prb. incommodus</i>
<i>acuminatus-ascensus</i>	<i>Neodiplograptus sp.</i> , <i>N. cf. N. balticus</i> , <i>N. cf. N. mirnyensis</i> , <i>N. trifilis</i> , <i>Hirsutograptus longispinus</i> *, <i>Prk. acuminatus</i> , <i>Ak. ascensus</i> , <i>A. primitivus</i>

* - new species described by Koren and Rickards (1996)

In exposure 4a the lower boundary of the overlying *revolutus* Biozone is established by a distinctive change in the taxonomic composition of graptolites (Bjerreskov 1975). It is recognized by the appearance of *Monograptus revolutus* Kurck and *Coronograptus cyphus* (Lapworth).

Southern Urals

The lower Silurian carbonaceous silicified shales and cherts yielding graptolites are included in the lower part of the Sakmara Formation, which is widely distributed in the Mugodzhary Range of the southern Urals. Continuous sequences within the Sakmara Formation are rarely preserved in extensive stratigraphic exposures. The rocks are deformed and usually exposed within different nappes and tectonic slices, and the real stratigraphic and biostratigraphic sequence can be reconstructed only by using graptolites. The graptolites derive from numerous localities in the Kos-Istek region between rivers Or' and Ilek (Fig. 3; Leonenok 1955; Koren' 1964, 1967, 1986; Rickards & Koren' 1974; Urbanek et al. 1982; Koren' & Rickards 1996). The graptolite-bearing strata usually occur as loose *in situ* blocks on low, flat hills and alongside small creeks. Therefore, it is impossible to measure continuous sections, but still all the individual collections occur in stratigraphic succession. The collections were made during mapping projects, led by many regional geologists, in which one of the authors (TNK) participated.

The graptolite assemblages of the *ascensus-acuminatus*, *vesiculosus* and *cyphus* Biozones have been established along the Kara-Dzhilga Valley in the Kos-Istek Region (Table 1). The monograptid species found

in this stratigraphic interval are described in the present paper. The associated diplograptid fauna was recently monographed by Koren' & Rickards (1996).

Comparison of the taxonomic composition of contemporaneous early Llandovery monograptid assemblages in Bornholm and the southern Urals shows the following:

1. *Atavograptus primitivus* (Li), the single *ascensus-acuminatus* Biozone monograptid species, was recognized only in the deep-water biofacies in the southern Urals and not in the epicratonic, shallower-water biofacies on Bornholm. Previously it was recorded from China and the Canadian Arctic (Li 1990; Lukasik & Melchin 1994).
2. The *vesiculosus* Biozone monograptid assemblage in both regions includes several common species of *Atavograptus*, *Huttagraptus* and *Pribylograptus*. Among them are *A. atavus*, *Huttagraptus praestrachani* (Hutt & Rickards), *Pribylograptus sandersoni* (Lapworth) and *Prb. incommodus*. All these species are known also from Great Britain, China and the Canadian Arctic. They can be considered as pandemic taxa characteristic of epicratonic and deep-water facies. Yet some new huttagraptids described herein are now known only in one of the studied regions. *Ht. acinaces*, well represented in the British (*acinaces* Biozone) and Scandinavian sequences (*acinaces* Biozone, Bjerreskov 1975; the late *vesiculosus* Biozone in the present paper) was not recognized in the southern Urals and elsewhere.
4. *Lagarograptus inexpeditus* (Obut & Sobolevskaya), first described from the *triangulatus* Biozone in the northern part of Siberia (Obut et al. 1968) is discovered in the *cyphus* Biozone of the southern Urals. Besides these two regions the spe-

cies is known only from Canadian Arctic (Melchin 1989).

5. In general, the *vesiculosus* Biozone monograptids are much more numerically abundant in the epicratonic biofacies as it is shown by the Bornholm sequences. However, they are not a dominant part of the *vesiculosus* Biozone assemblage in the deep-water biofacies of the southern Urals.

Preservation and terminology of graptolites

The preservation of graptolites collected from finely laminated grey to dark-grey mudshales at the localities 2c and 4a in Øle Å varies from flattened specimens to those preserved in three dimensions infilled with pyrite (Bjerreskov 1975, 1991). The 3-D specimens were investigated by X-ray (Fig. 5) and some of them were isolated from the sediments. The new collections from the Billegrav-1 core are represented by flattened rhabdosomes with the periderm replaced by a silvery carbonaceous film. This is often partly flaked off and only thin impressions of the rhabdosomes are seen on the bedding planes. In some bed units graptolites are quite numerous but seldom complete due to the 3.2 cm diameter of the core. The Uralian graptolites are preserved as flattened rhabdosomes in the carbonaceous silicified shales and cherts. The periderm is not strongly carbonized and in many cases, especially on the weathered surfaces, fuselli and apertural thecal structures are clearly seen. As there is no tectonic deformation of graptolites in any collection studied, accurate measurements of morphological features such as proximal thecae and sicula length can be made. These dimensions are critical for taxonomic differentiation of the early Llandovery monograptids, especially in view of the limited number of diagnostic morphological characters and the extremely narrow proximal part of the rhabdosome.

In the following systematic description the terminology is used in the sense described by Bulman (1970). Some additional terms for morphological characters, introduced by Rickards (1974, 1976) and Hutt (1975) are used. In measuring graptolites the present authors followed the standard practice. Thecal spacing was calculated in the traditional way which is the number of thecae in 5 or 10 mm. The range of values for dorso-ventral width of the rhabdosome are given in brackets. The only abbreviation used is "th1, 2, 3 etc." for thecae. Bar scales are 1 mm unless otherwise stated.

Repository

The described and figured specimens are in the type collection of the Geological Museum of the University of Copenhagen (prefix MGUH).

Table 2. Systematic list of described graptolites.

Family Monograptidae Lapworth, 1873
 Genus *Atavograptus* Rickards, 1974, emended herein
Atavograptus atavus (Jones, 1909)
Atavograptus primitivus (Li, 1983)
 Genus *Huttagraptus* gen. nov.
Huttagraptus praestrachani (Hutt & Rickards, 1977) in Rickards et al. 1977
Huttagraptus acinaces (Törnquist, 1899)
Huttagraptus billegravensis sp. nov.
Huttagraptus incurvus sp. nov.
Huttagraptus ninae sp. nov.
Huttagraptus strachani (Hutt & Rickards, 1970)
Huttagraptus sp. 1
Huttagraptus sp. 2
Huttagraptus sp. 3
 Genus *Pristiograptus* Jaekel, 1889
 "Pristiograptus" *pristinus* Hutt, 1975
 Genus *Pribylograptus* Obut & Sobolevskaya, 1966
Pribylograptus incommodus (Törnquist, 1899)
Pribylograptus sandersoni (Lapworth, 1876)
 ?*Pribylograptus* sp.
 Genus *Lagarograptus* Obut & Sobolevskaya, 1968 in Obut et al. 1968
Lagarograptus inexpeditus Obut & Sobolevskaya, 1968
Lagarograptus karaensis sp. nov.

Systematic palaeontology

Family Monograptidae Lapworth, 1873
 Genus *Atavograptus* Rickards, 1974

Type species. – *Monograptus atavus* Jones, 1909.

Horizon. – Llandovery, Rhuddanian to lower Aeronian, the *persculptus* Biozone to the *argenteus* Biozone inclusive.

Diagnosis (emended from Rickards 1974). – Rhabdosome long (at least 300 mm), slender (0.2–1 mm) and gently dorsally curved, becoming straight distally. Sicula about 1.3–1.4 mm long with low position for the origin of th1 and with apex reaching to about the aperture of th1. Thecae with slightly everted apertures,

Fig. 5. X-ray photos of pyritized graptolites from exposure 4a in Øle Å. A, B, *Atavograptus atavus* (Jones, 1909); *revolutus* Biozone; A, MGUH 24162, fragments of distal parts MGUH 24163; B, MGUH 24164, a proximal fragment with sicula preserved; C, MGUH 24165 "*Pristiograptus*" *pristinus* Hutt, 1975; *vesiculosus* Biozone; D-F, *Huttagraptus acinaces* (Törnquist, 1899); *vesiculosus* Biozone; D, MGUH 24166, proximal fragment with sicula preserved; E, MGUH 24167; F, MGUH 24168, fragments of distal parts. Arrows in D-F show problematic trace fossils; D, MGUH 24169; E, MGUH 24169; F, MGUH 24170. All figures are $\times 10$.

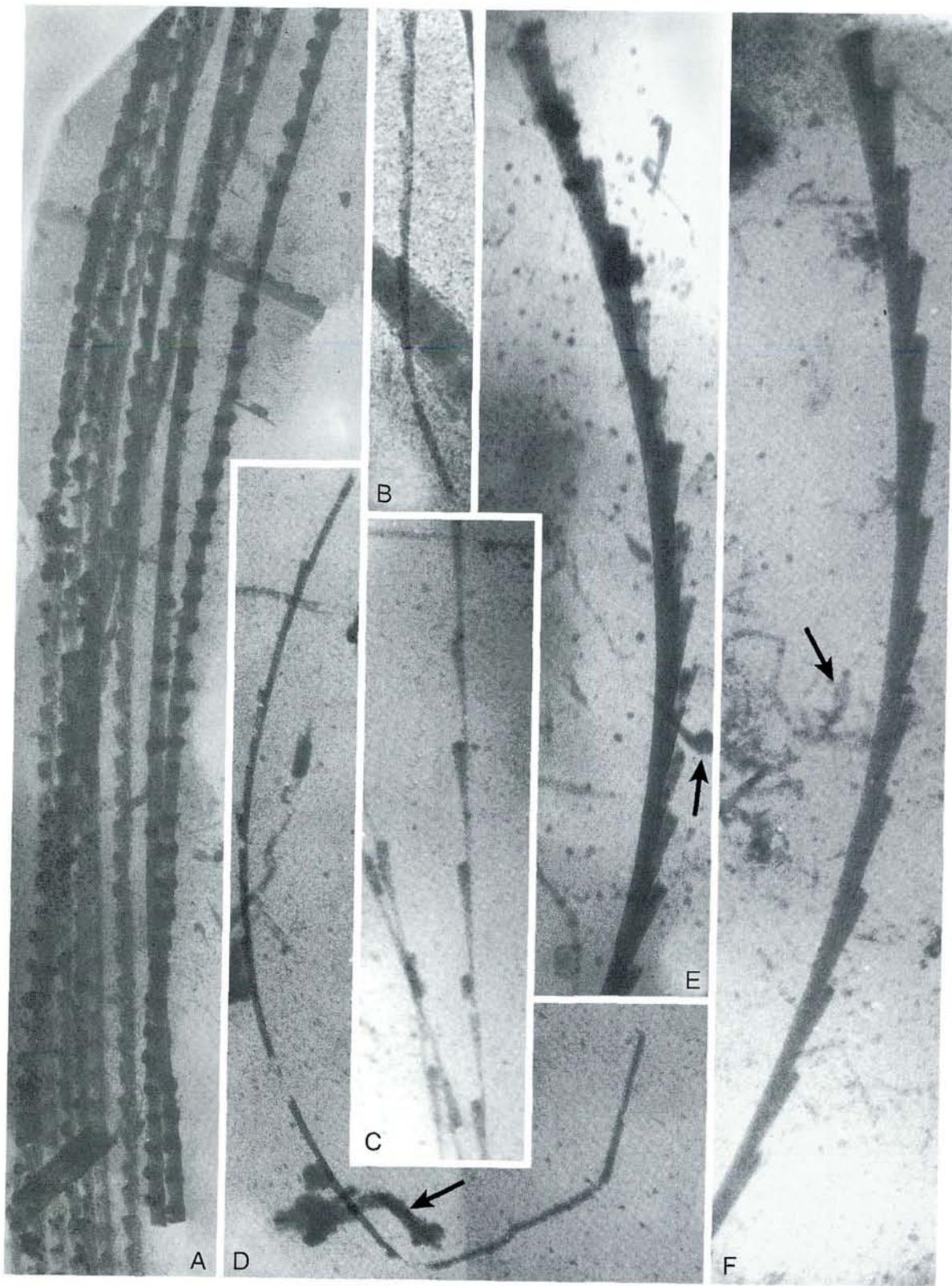


Table 3. Monograptid dimensions

	thecal spacing in 10 mm		length of sicula	rhab. width		thecal overlap		thecal length	
	p.	d.		p.	d.	p.	d.	p.	d.
<i>Atavograptus</i>									
<i>A. atavus</i>	6-7	9-10		0.2-0.3	1.2-1.4	1/5	1/2		2
<i>A. primitivus</i>	9-9.5	7-8	1.7-1.75	0.25-0.3	0.36-0.4	1/5	1/3	1.4-1.8	1.6-1.7
<i>Huttagraptus</i>									
<i>Ht. praestrachani</i>	9-10	7-8	2.4	1.5-0.2	0.8		1/3-1/2		1.7-2.0
<i>Ht. acinaces</i>	4-5	6-7	7	0.2-0.25	1.35-1.45	1/2	2/3		
<i>Ht. billegravensis</i> n. sp.	6.5-7.5	8.5	3.5-3.7	0.25	0.8	1/5	1/4	2.2-2	
<i>Ht. incurvus</i> n. sp.	10		2?	0.25	0.45	1/3	1/2		
<i>Ht. ninae</i> n. sp.	9		3.7-3.8	0.2	0.3-0.4	1/3		1.7-1.8	1.35
<i>Ht. strachani</i>	7-8		>3	0.3	0.5	1/5	1/3	1.6-1.7	
<i>Huttagraptus</i> sp. 1	5.5/5	8.5-9		0.2	0.6-0.7				
<i>Huttagraptus</i> sp. 2	6.5-7.5	5.5-6.5	2.1-2.2	0.24	0.6-0.7		1/4		2.1-2.2
<i>Huttagraptus</i> sp. 3	6-7	8	2	0.28	0.55	1/5	1/3	2	1.8-2
<i>Pribylograptus</i>									
<i>Prb. incommodus</i>	7	8		0.5	0.65	<1/2	2-3		
<i>Prb. sandersoni</i>	6.5	7.5-8.5	1.8-2.0	0.14	0.6	1/8	1/3	2.0	1.6
? <i>Pribylograptus</i> sp.		8-9	1.0	0.15	0.3	1/2			2.5
<i>Lagarograptus</i>									
<i>Lg. inexpeditus</i>	8		>4	0.35-0.4	0.5-0.55	>1/3			
<i>Lg. karaensis</i> n. sp.	8		1.9	0.48	0.65	>1/3	1.6 (th1)		
<i>Pristiograptus</i>									
" <i>P.</i> " <i>pristinus</i>	6	5.5-6	>0.9	0.15	0.23	1/10-1/12		1.9	1.9-2.0

p. = proximal; d. = distal; rhab. = rhabdosome; all dimensions are in mm.

gently convex free ventral walls or flowing geniculum.

Remarks. – The taxonomy and evolutionary relationships of the early monograptids advance were considered by the significant investigations of Hutt and R.B. Rickards (Hutt 1968; Hutt & Rickards 1970, Rickards & Hutt 1970; Rickards 1974, 1976; Rickards et al. 1977). Since then, localities yielding some new species have been discovered in China (Chen & Lin 1978; Li 1990; Ye 1994) and recently in Bornholm and the southern Urals. Present knowledge of morphology and stratigraphic distribution shows that within the *Atavograptus plexus* (sensu Rickards 1974) two distinctive species groups can be recognized. The first, included within *Atavograptus* s.s., are *At. ceryx*, *At. primitivus* and *At. atavus*, species which have glyptograptid thecal style, and comparatively short siculae and thecae. The second group is characterized by the proximal introduction of strongly geniculated thecae with genicular rims and/or well developed genicular flanges. It embraces the stratigraphically younger species from the *vesiculosus* Biozone which are assigned to *Huttagraptus* gen. nov. Among them are *Ht. praestrachani* (type species), *Ht. acinaces*, *Ht. billegravensis* sp. nov., *Ht. strachani*, *Huttagraptus*

sp. 1, and *Huttagraptus* sp. 2., *Huttagraptus* sp. 3., described herein.

Atavograptus atavus (Jones, 1909)

Figs 5A, B; 6, 7A-D, F

1909 *Monograptus atavus* sp. nov.; Jones, p. 531, text-fig. 18a-d.

1975 *Monograptus atavus* Jones; Bjerreskov, p. 44, pl. 6, figs G-H (see synonymy).

1975 *Atavograptus atavus* (Jones); Hutt, p. 62-63, pl. 11, fig. 1; pl. 12, figs 5, 9, 10.

1986 *Atavograptus atavus* (Jones); Štorch, pl. 6, figs 1-4.

1988 *Atavograptus atavus* (Jones); Štorch, p. 12-13, pl. 1, figs 1, 2, 3; text-fig. 2A.

Type. – Lectotype, by subsequent designation by Přibyl & Spasov (1955), p. 195, figured by Jones (1909), text-fig. 18b; GSM 23710; from the Llandoverly of the Rheidol Gorge, Mid-Wales.

Material. – About 100 specimens, both flattened and preserved in relief from the exposures 2c, 4 and 4a, in Øle Å, more than 20 flattened fragments from the Billegrav-1 core, depth 5.40 m-14.00 m, Bornholm;

and a few specimens from the Kos-Istek region, the southern Urals.

Description. – Rhabdosome more than 100 mm long, proximally with gentle dorsal curvature becoming straight distally. The maximum dorso-ventral width is 1.2–1.4 mm. The most proximal fragments are 0.4–0.5 mm wide, in the mesial part of the rhabdosome the dorso-ventral width increases to 0.2 mm within a distance of about 40 mm. However, the extreme distal fragments, 30 mm long, have uniform width.

Thecae are simple tubes which increasing overlap from 1/5 proximally to 1/2 distally. The straight thecal apertures are everted throughout. The proximal thecae have a smooth geniculum, which becomes slightly more pronounced in mesial and distal parts of the rhabdosome. The angle of thecal inclination increases from 5° to 10°–15° towards the distal end. The maximum length of the distal thecae is 2 mm, the width of apertures is 0.5–0.6 mm. The thecal count increases from 6–7 to 9–10 in 10 mm distally.

Remarks. – The thecae and dimensions of the present specimens agree well with material described from Wales and Lake District (Hutt 1975), although they lack the extreme proximal end. We found only one specimen with a sicula despite extensive X-ray analysis of samples yielding abundant fragments of *At. atavus* from the exposure 4a in Øle Å (Fig. 5B).

Atavograptus primitivus (Li, 1983).
Figs 7E, G; 8, 9

1983 *Pristiograptus primitivus* sp. nov.; Li (in Yang et al. 1983), p. 499–500, pl. 173, figs 12, 13.

1990 *Atavograptus primitivus* (Li); Li, p. 210, pl. 1, figs 12, 13; text-fig. 1g.

1990 *Pristiograptus antiquatus* sp. nov.; Li, p. 215–216, pl. 1, figs 8–11, text-fig. 1e–f.

1994 *Atavograptus primitivus* (Li); Lukasik & Melchin, p. 1160–1162, figs 1, 3, 4.

Type. – Not designated.

Material. – More than 35 flattened but well preserved rhabdosomes at different astogenetic stages from exposures 671/1, 671/2 and 671/8 in the Kos-Istek region, the southern Urals.

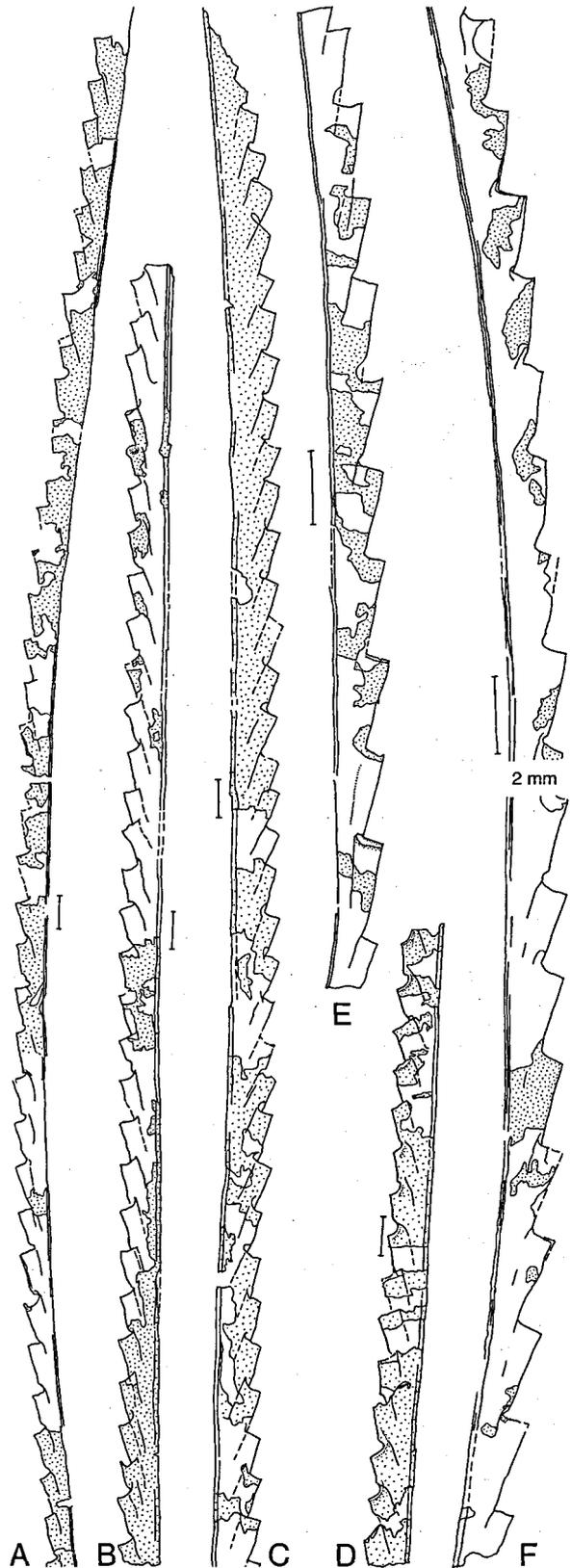
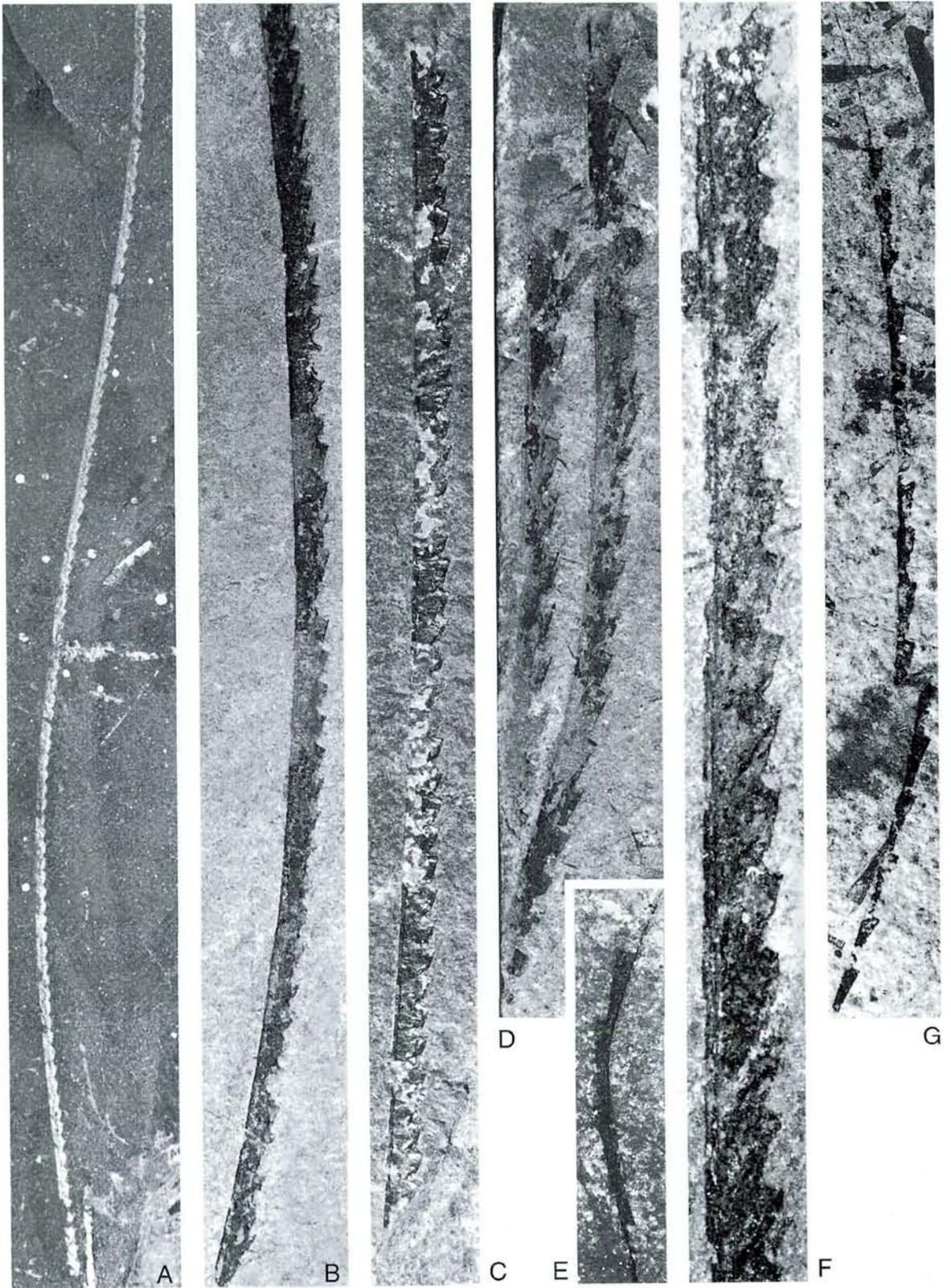


Fig. 6. A–D, F, *Atavograptus atavus* (Jones, 1909), fragments of different parts of rhabdosomes, *vesiculosus* Biozone, Øle Å, Bornholm; A, MGUH 24172, sample 5; B, MGUH 24173, exp. 2c; C, MGUH 24174; D, MGUH 24175, exp. 2c; E–F, Billegrav-1 core, depth 14.00 m; E, MGUH 24176; F, MGUH 24177.



Description. – The rhabdosome with a gentle dorsal curvature, more than 20 mm long. The dorso-ventral width at th1 is 0.25–0.30 mm and the maximum of 0.36–0.4 mm is attained between th3 and th5. A long (more than 5 mm) thread-like nema is characteristic of the early astogenetic stages (Figs 8, 9).

The thecae have horizontal to slightly everted apertures with thickened apertural rims. A flowing geniculum is present, but not always seen in the flattened material. The free ventral walls are almost straight throughout the most of their length and are inclined at 6°–8° to the rhabdosome axis proximally and at 10° distally. The thecal overlap increases from 1/5 to less than 1/3 towards the distal end. The distal thecae are 1.6–1.7 mm long and 0.2 mm wide at the aperture. The thecal count is 9–9.5 in 10 mm proximally and 7–8 distally.

The sicula is 1.7–1.75 mm in length of which about 0.4 mm comprises the prosicula. The sicula aperture is in general 0.2 mm wide, in some cases it attains 0.3 mm. In many specimens a thread-like virgella, 3 mm long, is present. The sicula apex is usually situated below the th1 aperture, sometimes it is very close to the aperture. Th1 originates at a distance of 0.4 mm (0.6 mm) above the sicula aperture and attains a length of 1.4–1.8 mm.

Remarks. – The rhabdosome structure, dimensions and thecal shape of the present specimens leave no doubt that they can be assigned to *At. primitivus*. The Uralian form shows a distinct variation in the position of th1 bud and the th1 length, which results in a slightly different position of the sicular apex respectively to the th1 aperture. This variation shows that the Uralian form embraces the diagnostic features of two species, *At. primitivus* and "*Pristiograptus*" *antiquatus* Li, described from the local *Parakidograptus primarius* Biozone of China. This supports the conclusions made by Lukasik and Melchin (1994) that *At. antiquatus* is a junior synonym of *At. primitivus*. The latter resembles the earliest monograptid, *Atavograptus ceryx* Hutt & Richards especially in the size of the sicula, the length of th1 and the dorso-ventral width of the rhabdosome. It differs, however, in having longer and more widely spaced thecae with everted apertures, a less distinct geniculum, a higher position of th1 bud, a lower position of sicular apex and extremely long

virgella. *Atavograptus primitivus* can be compared with the proximal part of the rhabdosome of *At. atavus*. *Atavograptus primitivus* has straighter thecae, longer sicula (1.7–1.75 mm as to compare with 1.2–1.4 mm) and its dorso-ventral width does not exceed 0.4 mm at a distance of 20 mm from the sicula.

Genus *Huttagraptus* gen. nov.

Derivation of name. – In honour of Dr. J. E. Hutt, who made significant contributions to the studies of the early Llandovery monograptids.

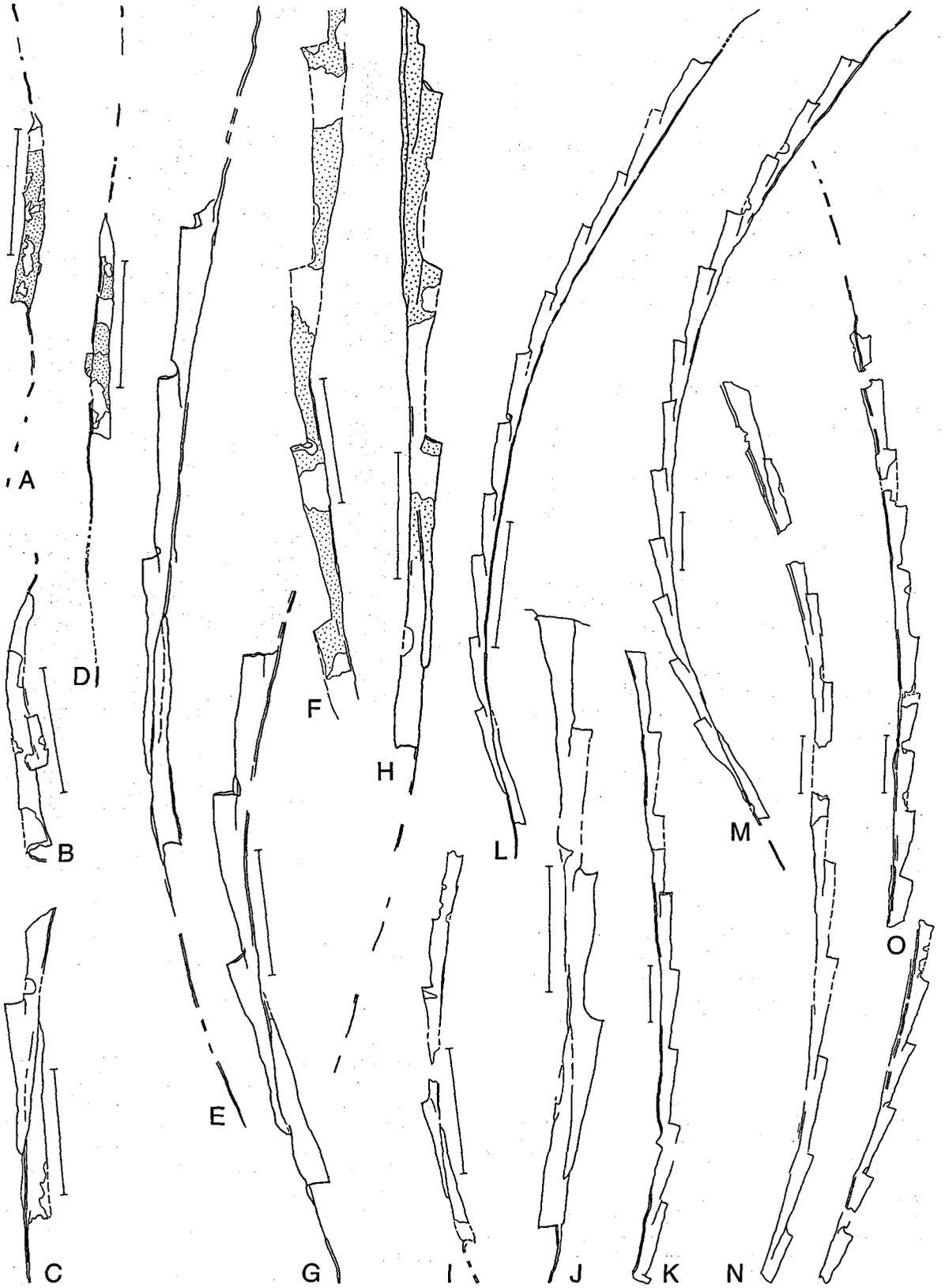
Type species. – *Atavograptus praestrachani* Hutt and Rickards, 1970 in Rickards et al. 1977.

Horizon. – Llandovery, Rhuddanian, the *vesiculosus* to *cyphus* Biozones.

Diagnosis. – Species possessing a long and slender rhabdosome with strong to slight dorsal curvature. Thecae geniculate in proximal or mesial parts of the rhabdosome, in some species throughout the whole rhabdosome. Pronounced geniculum may have genicular flanges overhanging apertures. Proximal thecae with straight horizontal apertures, semicircular or slit-like excavations; metathecal ventral walls are parallel or slightly inclined to the dorsal side of the rhabdosome. Gradual changes such as lessening of geniculum, increase in thecal inclination (up to 5°–10°) and inversion of thecal apertures take place towards the distal end. Sicula usually long (more than 3 mm) with high position for the origin of th1.

Remarks. – The arbitrary inclusion of species such as "*Monograptus*" *strachani* in *Atavograptus* and not into *Monoclimacis* was discussed by Rickards (1974). The present extensive collection of so-called atavograptids from the *vesiculosus* Biozone in the Billegrav-I core and in the southern Urals provided more knowledge about the morphology of previously known and some new species described herein. They constitute a morphologically separate group of species and it seems to be justifiable to group them into a new genus *Huttagraptus*. They have geniculated thecae with thickened rim and flanges within the main part of the rhabdosome and share a tendency to a distinctive lessening of the geniculum towards the distal end. The characteristic monoclimacid-like thecal shape combined with the long sicula and the high position for the origin of th1 are enough to exclude such species as *gracilis*, *praestrachani* and *strachani* from *Atavograptus* and to assign them to this new genus *Huttagraptus*. This genus embraces as well the following taxa: *Ht. acinaces*, *Ht. billegravensis* sp. nov., *Ht. incurvus* sp. nov., *Huttagraptus* sp. 1, *Huttagraptus* sp. 2 and *Huttagraptus* sp. 3. The species assigned to *Huttagraptus* differ in thecal spacing and overlap, length

Fig. 7. A–D, F, *Atavograptus atavus* (Jones, 1909), distal fragments; *vesiculosus* Biozone; A, MGUH 24178; B, MGUH 24179; C, MGUH 24180; D, MGUH 24181; F, MGUH 24183; A–C, exp. 2c, Øle Å, × 2.5; B–D, exp. 4, Øle Å, × 5; F, MGUH 24183, exp. 671/8, Kara-Dzhilga, the southern Urals, × 10; E–G: *Atavograptus primitivus* (Li, 1983), proximal and distal fragments, exp. 671/8, Kara-Dzhilga; *ascensus-acuminatus* Biozone; E, MGUH 24282; G, MGUH 24184, × 10.



of sricula and th1 as well as in the position of the origin of th1. Thus, the specific differentiation requires well preserved and complete material as far as the proximal part of the rhabdosome is concerned. The distal parts of the rhabdosomes referred to *Huttagraptus* sp., *Ht. billegravensis*, *Ht. praestrachani* and *Ht. strachani* are difficult to differentiate. From its thecal style *Huttagraptus* gen. nov. can be considered as a morphologically transient genus between *Atavograptus* and *Lagarograptus*. The latter develops distinct genicular flanges, slightly expanded apertures, often in combination with ventral processes. *Huttagraptus* gen. nov. is distinguished from *Monoclimacis* by the elongated extreme proximal part of the rhabdosome and less geniculate distal thecae.

Huttagraptus praestrachani (Hutt & Rickards 1977) in Rickards et al. 1977
Figs 10A–I, 16A–E

1970 *Monograptus* sp. 1; Hutt & Rickards, p. 75–76, fig. 3c, d.

1977 *Atavograptus praestrachani* sp. nov.; Rickards et al., p. 102–103, fig. 17, p. 37.

Type. – Holotype figured by Hutt & Rickards (1970), fig. 3c, N A 60415, SM from Keisley (National Grid ref. NY 71382379), the *atavus* Biozone.

Material. – 12 fragmentary specimens preserved as flattened from the Billegrav-1 core, depth 15.20–14.70 m; 17 flattened specimens, mostly proximal and mesial parts of rhabdosomes from the southern Urals, Kos-Istek region, localities 477, 671/1, 671/8, 671/9, 1500/47 and 1643, the *vesiculosus* Biozone.

Description. – The fragments are 10–20 mm long, with variable dorsal curvature in the proximal part. The dorso-ventral width increases slowly from 0.15–0.2 mm at th1 to 0.25–0.30 mm at th5, the most distal fragments are 0.8 mm wide.

The thecae are distinctly geniculate, the feature is emphasized by the presence of genicular rims. The horizontal or slightly everted apertures open into slit-like excavations, which occupy 1/3 or even 1/2 of the dorso-ventral rhabdosome width. Apertural margins



Fig. 9. *Atavograptus primitivus* (Li, 1983); *ascensus-acuminatus* Biozone, exp. 671/8, Kara-Dzhilga. A–C, specimens showing early astogenetic stages; D, distal fragment. A, MGUH 24200; B, MGUH 24201; C, MGUH 24202; D, MGUH 24203; A, D, $\times 40$; B, C, $\times 20$.

←
Fig. 8. *Atavograptus primitivus* (Li, 1983); *ascensus-acuminatus* Biozone, exp. 671/8–74, Kara-Dzhilga, the southern Urals. A–E, G, early astogenetic stages; A, MGUH 24185; B, MGUH 24186; C, MGUH 24187; D, MGUH 24188; E, MGUH 24189; F, MGUH 24190; G, MGUH 24191; H, I, J, proximal fragments; H, MGUH 24192; I, MGUH 24193; J, MGUH 24194; K, N, O, fragments with no sricula; K, MGUH 24195; N, MGUH 24198; O, MGUH 24199; L, M, complete rhabdosomes; L, MGUH 24196; M, MGUH 24197.

are usually thickened, which is especially well seen in the Uralian specimens. The supragenicular walls are straight and almost parallel to the dorsal side of the rhabdosome, distally they are inclined at no more than 5°. The most distal thecae are 1.7–2.0 mm long, 0.2 mm wide at the apertures and overlap 1/3 to 1/2 of their length. They show weaker geniculum, more open aperture and no traces of genicular flanges. Thecal count is 9–10 in 10 mm proximally and 7–8 in 10 mm distally.

Sricula is up to 2.4 mm long and 0.2 mm wide at the

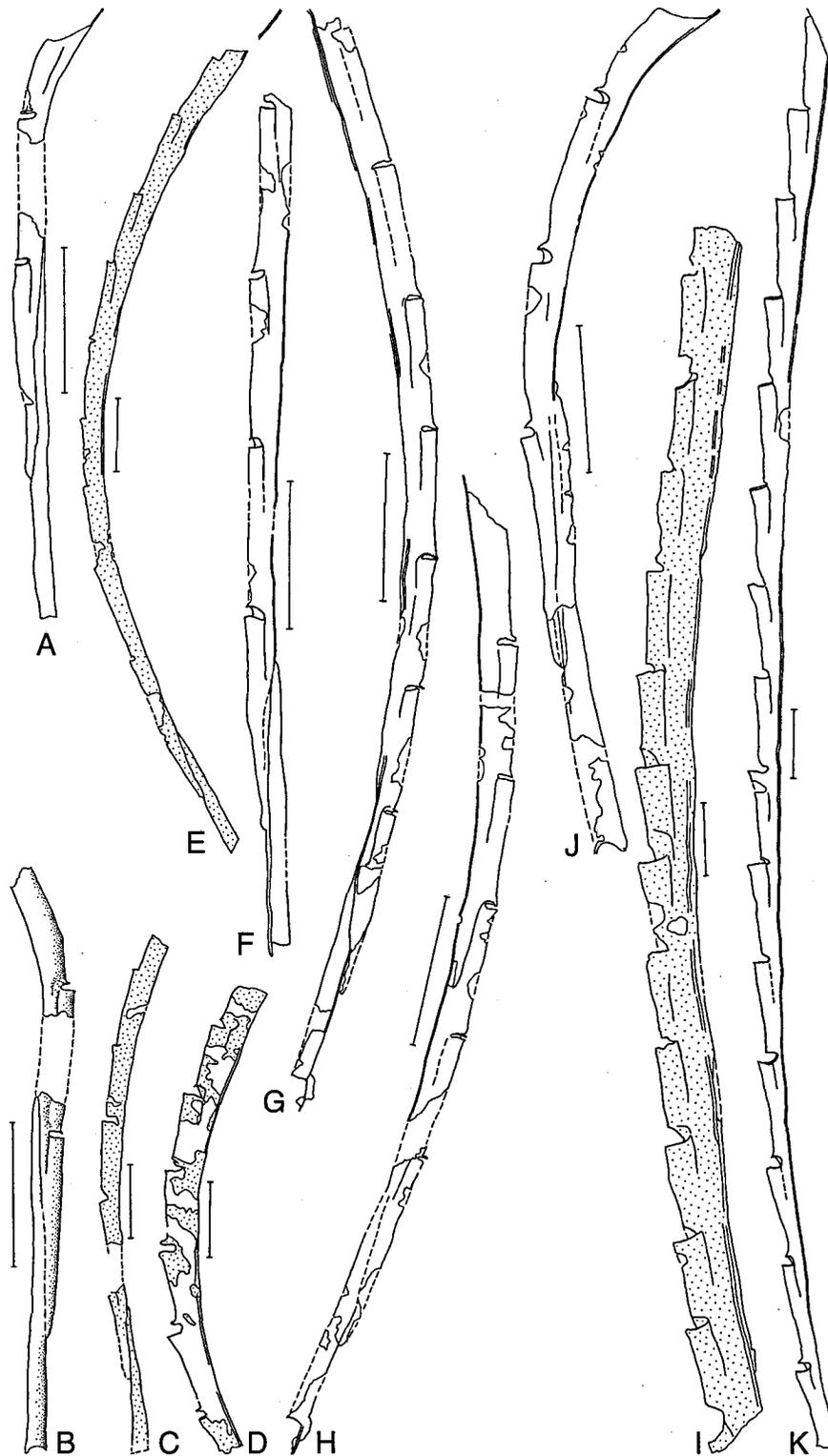


Fig. 10. A–I, *Huttagraptus praestrachani* (Hutt & Rickards, 1977), *vesiculosus* Biozone. A–C, F, proximal fragments; A, MGUH 24204; B, MGUH 24205, exp. 477, Kos-Istek region; C, MGUH 24206, exp. 671/8, Kara-Dzhilga; F, MGUH 24209, Billegrav-1 core, sp. 1, depth 15.20 m; D, I, rhabdosome fragments; D, MGUH 24207, depth 11.20–11.35 m; I, MGUH 24212, exp. 671/8; E, G, H, complete rhabdosomes; E, MGUH 24208, exp. 671/8, Kara-Dzhilga; G, MGUH 24210, exp. 1643, Kos-Istek region; H, MGUH 24211, exp. 1643; J, K, *Huttagraptus strachani* (Hutt & Rickards, 1970), *cyphus* Biozone, exp. 671/8, Kara-Dzhilga, the southern Urals; J, MGUH 24213; K, MGUH 24214.

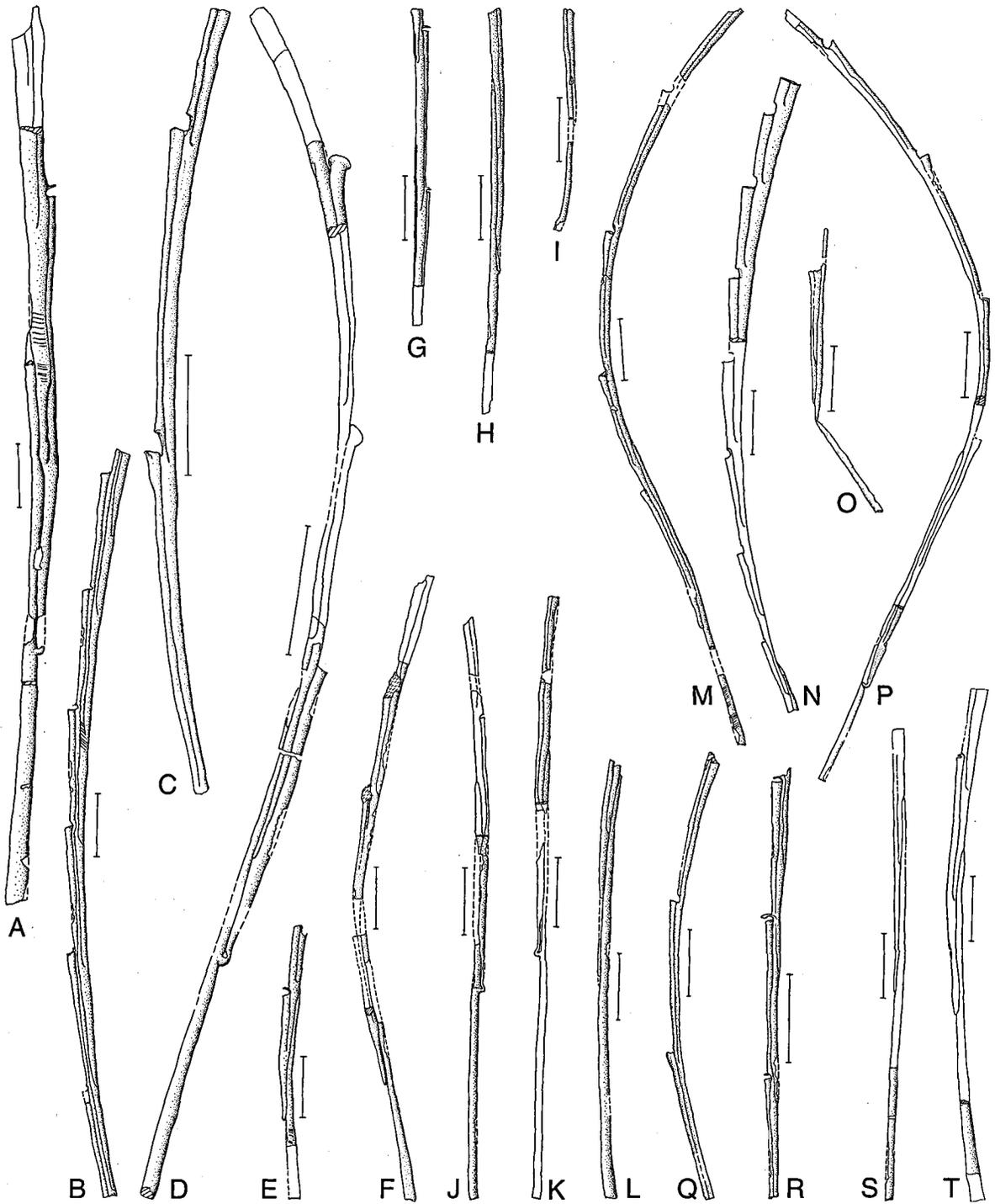


Fig. 11. *Huttagraptus acinaces* (Törnquist, 1899), A–S, proximal fragments, upper part of the *vesiculosus* Biozone, Øle Å, exp. 4a; A, MGUH 24215; B, MGUH 24216; C, MGUH 24217; D, MGUH 24218; E, MGUH 24219; F, MGUH 24220; G, MGUH 24221; H, MGUH 24222; I, MGUH 24223; J, MGUH 24224 a; K, MGUH 24224 b; L, MGUH 24225; M, MGUH 24226; N, MGUH 24227; O, MGUH 24228; P, MGUH 24229; Q, MGUH 24230; R, MGUH 24231; S, MGUH 24232; T, LO, sp. 1436T, Törnquist, 1899, pl. 1, figs 7, 8.

aperture. The position of the apex varies from a level slightly below to slightly above the th1 aperture. Th1 originates at a distance about 0.65–0.75 mm above the sicula aperture and it attains a length of 1.35–1.55 mm.

Remarks. – The thecal structure of the current specimens resemble closely *Ht. strachani*, as does the shape of the rhabdosome and the attenuated extreme proximal end. The distinct change of the thecal count from 10 to 7 in 10 mm towards the distal end agrees well with that mentioned in the original description (Rickards et al. 1977). However, the sicula preserved in the few specimens studied does not reach 3 mm in length, typical for *Ht. strachani*.

Huttagraptus acinaces (Törnquist 1899)
Figs 5D, E, F; 11, 12, 13

1899 *Monograptus acinaces* n. sp.; Törnquist, p. 5, pl. 1, figs 7, 8.

1970 *Monograptus acinaces* Törnquist; Hutt & Rickards, p. 76, text-fig. 3i–j.

1975 *Monograptus acinaces* Törnquist; Bjerreskov, p. 45–46, fig. 14C, pl. 6, fig. 1.

1975 *Lagarograptus acinaces* (Törnquist); Hutt, p. 69, pl. 13, figs 5–6; text-fig. 16, figs 1–3.

Type. – Holotype figured by Törnquist (1899), pl. 1, figs 7, 8; LO 1436t and refigured herein, Figs 11T, 12H; from the Llandoverly of Röstånga, Scania.

Material. – More than 100 well preserved specimens, pyritized in 3d and in low relief at all astogenetic stages; exp. 4, (Bjerreskov 1975) and 4a in Øle Å; 25 flattened specimens, mostly mesial and distal fragments treated as *Ht. cf. Ht. acinaces* from the Billegrav-1 core, depth 2.10–16.75 m.

Description. – The rhabdosome is more than 50 mm long, broadly dorsally curved proximally and becoming more straight distally. The proximal end and the first 5–10 thecae are extremely narrow. Successive measurements of dorso-ventral width are as follows: at th1 0.2–0.25 mm (0.16 mm; 0.3 mm), 2 mm (0.28 mm), th3 0.2–0.24 mm (0.34 mm) and th4 0.27 mm (0.37 mm), between th10 and th15 0.6–0.8 mm. The rhabdosome attains the maximum dorso-ventral width of 1.35–1.45 mm at the distal end.

The proximal thecae are long and slender, overlapping one half of their length. Distinct variation in thecal overlap within the rhabdosome is present. In the majority of specimens a horizontal line at the level of the th1–th2 apertures crosses one septum, and further on, in the mesial part of the rhabdosome it crosses two septa. There are, however, specimens in which a horizontal line drawn across the level of a thecal aperture in the proximal part crosses no intertheatal septa.

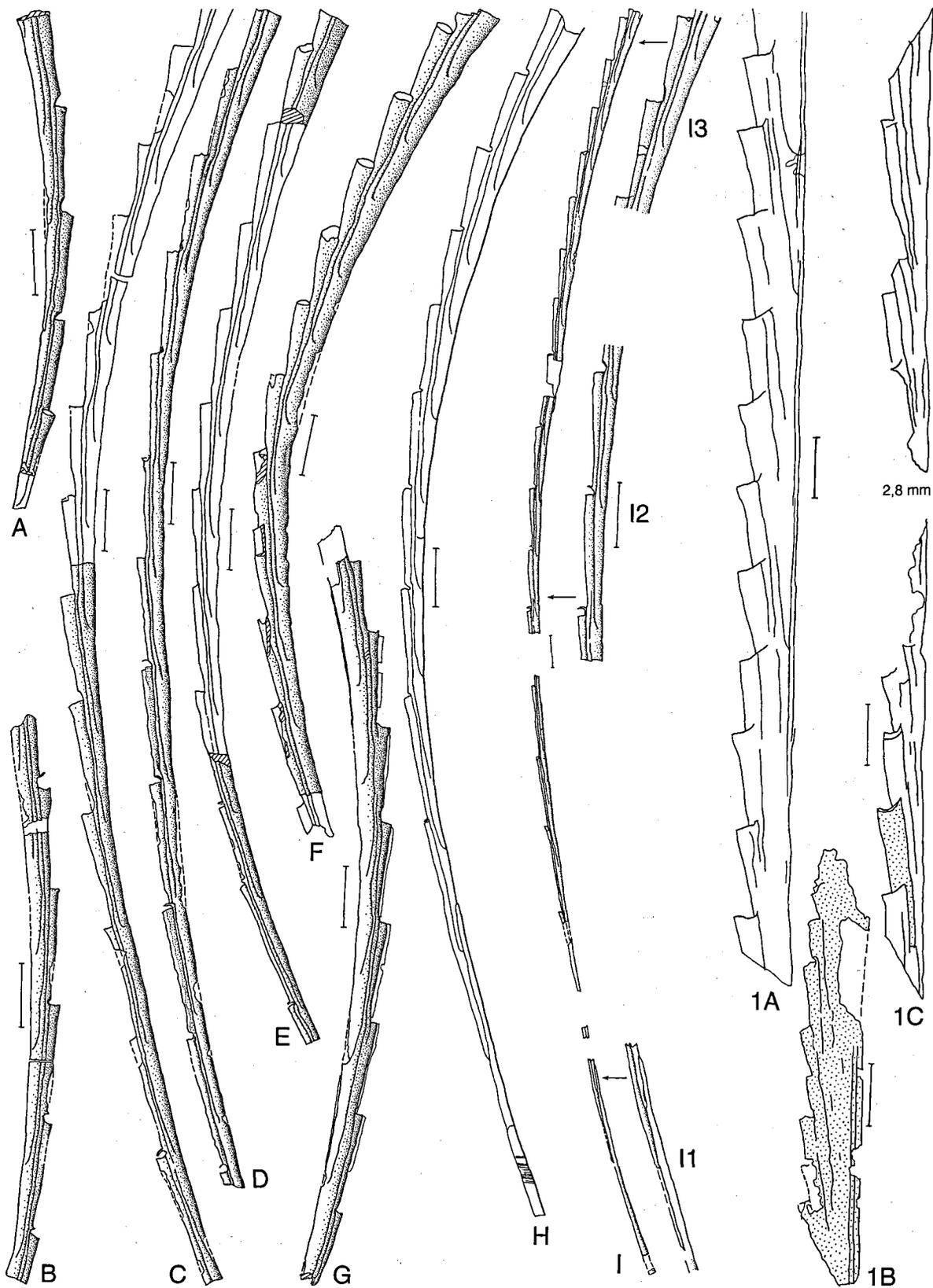
The proximal and mesial thecae have slightly expanded and everted apertures, straight supragenicular walls except for the small but distinct geniculum which occasionally gives rise to a genicular flange, 0.01 mm long (Figs 11A, B, R; 12C, D, I). In general the thecal overlap increases up to 2/3 within the first 15–20 mm of the rhabdosome length. The thecae slowly increase in width from 0.12 mm at the prothecal aperture to the subapertural part of the metatheca where a width of 0.23–0.24 mm is suddenly reached. Intertheatal septa are almost parallel to each other, though straight ventral walls are inclined at 5° in the proximal part and up to 10° distally. The proximal and mesial thecae show broad and open excavations. In the most distal fragments there is only a slight suggestion of a weak geniculum and the thecae are generally straight tubes overlapping for about 2/3 of their length, with distinctly everted and straight apertures. The thecal count increases from 4–5 in 10 mm proximally to 6–7 in 10 mm distally.

The extremely long and narrow sicula attains a maximum length of more than 7 mm, the apertural width reaches 0.23–0.24 mm. Th1 originates at a distance of 3 mm above the aperture of the sicula. A short horizontal component of initial growth of th1 is well seen in some pyritized specimens preserved in full relief (Fig. 11A, D, J, K). The same feature, unusual for monograptids, is present in the earliest huttagraptids, such as *Ht. billegravensis*. The sicula is more than 7 mm long. The apex does not reach the th1 aperture and it is usually slightly below or above the base of the septum between th1 and th2. The protheca of th1 and the apical part of sicula overlap at a distance of 3–4 mm (2.1–2.3 mm).

Remarks. – “*Monograptus*” *acinaces* Törnquist was assigned by Hutt (1975) and Rickards (1976) to *Lagarograptus* after the discovery of ventral processes at a single distal fragment of *Monograptus rheidolensis* Jones from Wales, considered by them to be a synonym of “*M.*” *acinaces* (Hutt & Rickards 1970, text-fig. 3j). The present authors studied the type material of Törnquist (1899), housed in the Geological Institute in Lund, of which some specimens are refigured

Fig. 12. *Huttagraptus acinaces* (Törnquist, 1899), *vesiculosus* Biozone, Øle Å, exp. 4a. A–G, distal fragments with strongly overlapping thecae; A, MGUH 24233; B, MGUH 24234; C, MGUH 24235; D, MGUH 24236; E, MGUH 24237; F, MGUH 24238; G, MGUH 24239; H, I, adult rhabdosomes; H, LO 1436T, 1437T, Törnquist, 1899, pl. 1, figs 7, 8; I, MGUH 24240, I1, I2 and I3 details of proximal end and thecal structure of the same specimen.

Fig. 12/1. *Huttagraptus cf. acinaces* (Törnquist, 1899), distal fragments, Billegrav-1 core, *vesiculosus* Biozone; A, MGUH 24241, depth 16.75 m; B, MGUH 24242, depth 16.90 m; C, MGUH 24243, depth 16.75 m.



herein (Figs 11T, 12H). However, we failed to detect any ventral structures in flattened, but well preserved specimens. These structures are not present in the numerous specimens of *Ht. acinaces* from Bornholm, some of which are in low or full relief. The ventral processes have not been discovered during the extensive X-ray analysis of the pyritized specimens in relief from exposure 4 in Øle Å (Fig. 5). Some of them have been isolated and no other apertural structures except for the occasional small genicular flanges were shown. Similar observations were made by Storch (1988) who described *Ht. acinaces* (i.e. *Lg. aff. acinaces*) from Bohemia which lacks the ventral processes. In this case their absence is difficult to ascribe to poor preservation, because specimens of *Lagarograptus tenuis* in the same type of preservation show well developed triangular ventral structures (Hutt 1968, Storch 1988, text-fig. 5B–D). In addition numerous specimens of *Ht. acinaces* from Arctic Canada do not reveal these structures (Melchin 1995, personal communication). The present authors consider the development of the ventral processes as an important diagnostic feature of the *Lagarograptus* genus as it was postulated in the original description (Obut et al. 1968). For the above reason the species *acinaces* is excluded from *Lagarograptus* and assigned to *Huttagraptus* gen. nov.

The complete and well preserved material of *Ht. acinaces* from Øle Å allows a detailed study of the morphology and proportions of rhabdosome, thecae and sicula, as well as of their variation in size. Hutt (1975) mentioned a variation in the position of the sicular apex in the specimens studied from the *acinaces* Biozone of Lake District. Original material from the Llandovery of Sweden (Törnquist 1899) as well as the Bornholm collections, previously described by Bjerreskov (1975) and those studied by the present authors also show this variation, though the sicular apex does not reach the th1 aperture. In addition other characters such as the position for the origin of th1, the degree of overlap of th1 and the apical part of the sicula, the length of th1, as well as the degree of overlap of interthecal septa were found to be variable. The dorso-ventral width of the rhabdosome within the first 5–7 thecae is variable as is their length which results in variations in the thecal count in the first 10 mm.

Huttagraptus billegravensis sp. nov.
Fig. 14

Derivation of name. – After the Billegrav-1 core.

Type. – Holotype, Fig. 14A, specimen 3, MGUH 24251, the Billegrav-1 core, depth 16.75 m.

Horizon. – Rhuddanian, the *vesiculosus* Biozone.

Material. – About 50 fragments of flattened rhab-

dosomes, including extreme proximal parts with well preserved siculae; the Billegrav-1 core, depth 13.75–16.75 m.

Diagnosis. – More than 30 mm long slender rhabdosome, often with broad dorsal curvature, minimum dorso-ventral width 0.25 mm, maximum 0.8 mm. Biform thecae, strongly geniculate proximally with flowing geniculum distally, widely spaced, numbering 6.5 proximally to 7.5–8.5 distally in 10 mm. Sicula more than 3.7 mm long.

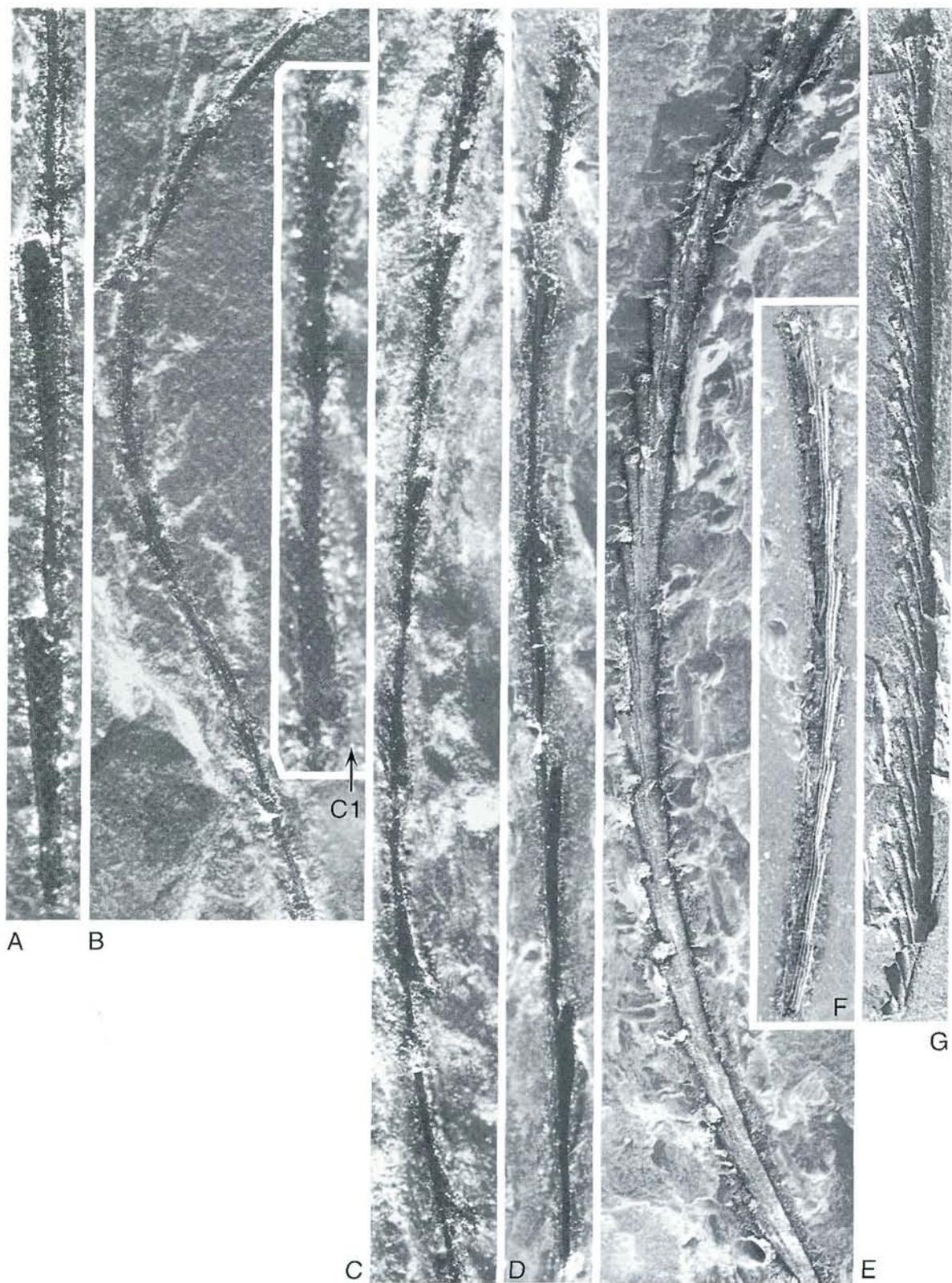
Description. – The rhabdosome is more than 30 mm long, broadly dorsally curved and slowly increasing in width up to 0.5–0.6 mm, a few fragments are 0.8 mm wide. Proximally the rhabdosome widens from 0.25–0.35 mm at th1 to 0.35–0.5 mm at th5 and 0.40–0.55 mm at th 10. Distally the dorso-ventral width increases at about 0.1 mm within a distance of 25 mm.

The thecae are geniculate, the feature is especially well expressed in the proximal part of the rhabdosome. The geniculate margin is thickened and some thecae show small genicular flanges. Apertural excavations occupy 1/2 to 1/3 of the dorso-ventral width. The straight apertures are horizontal, free ventral walls are almost parallel to the rhabdosome axis. The distal thecae show only a slight suggestion of geniculum and become almost pristiograptid-like. Their ventral walls are inclined at 8°–10° and apertures are slightly everted. However, the thecal morphology cannot be fully understood in specimens preserved flattened. The thecae overlap from 1/5 to 1/4 of their length, and they number 6.5–7.5 in 10 mm, in some cases 8.5 in 10 mm distally.

The sicula is 3.5–3.7 mm long and 0.24–0.26 mm wide at the aperture. Th1 is 2.2–2 mm long and originates about 1.5 mm above the sicula aperture. The sicula apex reaches the level of th1 aperture, the virgella is 2 mm long.

Remarks. – The species has close affinities with *Ht. praestrachani* in general shape of the rhabdosome the morphology and proportions of thecae. It differs, however, in having longer sicula and more widely and evenly spaced thecae within both proximal and distal part of the rhabdosome. The free ventral walls of the distal thecae are more straight than those in *Ht. praestrachani*. It can be distinguished from *Huttagraptus gracilis* (Hutt) in having more robust proximal end and more widely spaced thecae.

Fig. 13. A, C, D, *Pristiograptus pristinus*, Hutt, 1975, upper *vesiculosus* Biozone, Øle Å, exposure 4a; A, MGUH 24244 × 30; C, MGUH 24246; C1 enlargement of C; D, MGUH 24247 × 20; B, E–G, *Huttagraptus acinaces*, upper *vesiculosus* Biozone, Øle Å, exp. 4a; B, MGUH 24245, proximal part, × 15; E, MGUH 24248 × 10; F, MGUH 24249, × 5; G, MGUH 24250.



Huttagraptus incurvus sp. nov.

Figs 15, 16E–G

Derivation of name. – Latin “incurvus” meaning curved.

Type. – Holotype, Figs 15C, 16F, MGUH 24269 specimen 1643–19, the southern Urals, Kos-Istek region, the Sakmara Formation, the *vesiculosus* Biozone.

Material. – 20 flattened specimens, some of which are well preserved from the same exposure as the holotype as well as from localities 477 and 1500/47 from the same region; the combined *vesiculosus-cyphus* Biozones.

Diagnosis. – Rhabdosome sickle-like, dorsally curved, reaching 0.45 mm in the dorso-ventral width. Thecae are strongly geniculated, the feature which is accentuated by the well developed genicular flanges. Supragenicular walls are almost parallel to the rhabdosome axis. Small excavations are distinct. Thecae number 10 in 10. Sicular apex does not reach the th1 aperture.

Description. – The rhabdosome is up to 10 mm long, strongly dorsally curved. The dorso-ventral width increases slowly from 0.25 mm to the maximum of 0.45 mm within th5–th7.

Uniformly geniculated thecae have pronounced genicular flanges overhanging the horizontal or slightly everted thecal apertures. Excavations are small compared to the thecal length. The supragenicular walls are almost straight and parallel to the dorsal wall. Thecae overlap 1/3 to 1/2 of their length and number 10 in 10 mm.

Sicula is not complete in the subapertural portion, but its estimated length could be 2 mm. The apex does not reach the th1 aperture. Th1 is about 0.85 mm long.

Remarks. – From all known huttagraptids *Ht. incurvus* differs in having a sickle-like, fairly strong dorsally curved rhabdosome, well developed genicular flanges and the distinctly shorter th1. Compared to the other huttagraptids it has a shorter sicula, but this could be due to incomplete preservation of the metasicular part. Nevertheless, the above-mentioned differences are important, which make a generic assignment of this species to some extent arbitrary. The thecal style shows some distinct similarity with *Monoclimacis*, however the thecae have most probably genicular flanges and not dorsal hoods. The rhabdosomal size and thecal count of *Ht. incurvus* is similar to that of “*Monoclimacis*” *lunata* (Chen & Lin) described from the same stratigraphical level in China (Chen & Lin 1978). However, the Chinese species has very high position of the sicular apex, situated at about mid-way between th2 and th3 apertures.

Huttagraptus ninae sp. nov.

Figs 25A, C, D; 26A–C

Derivation of name. – In honour of the late Dr. Nina I. Leonenok, who was one of the first to study graptolite biostratigraphy in the southern Urals.

Type. – Holotype, figs 25C, 26B, MGUH 25353, exp. 1909 (spec. 1) from the *vesiculosus-cyphus* Biozone of the Kos-Istek region, the southern Urals.

Material. – 10 flattened fragments of the proximal part with sicula from the localities 671/8 and 1909, the same region and horizon as for holotype.

Diagnosis. – Broadly dorsally curved rhabdosome, 15 mm long and 0.4 mm wide. Geniculate thecae have well developed hoods, inclined supragenicular walls and slightly everted apertures. Long sicula and high position for the origin of th1.

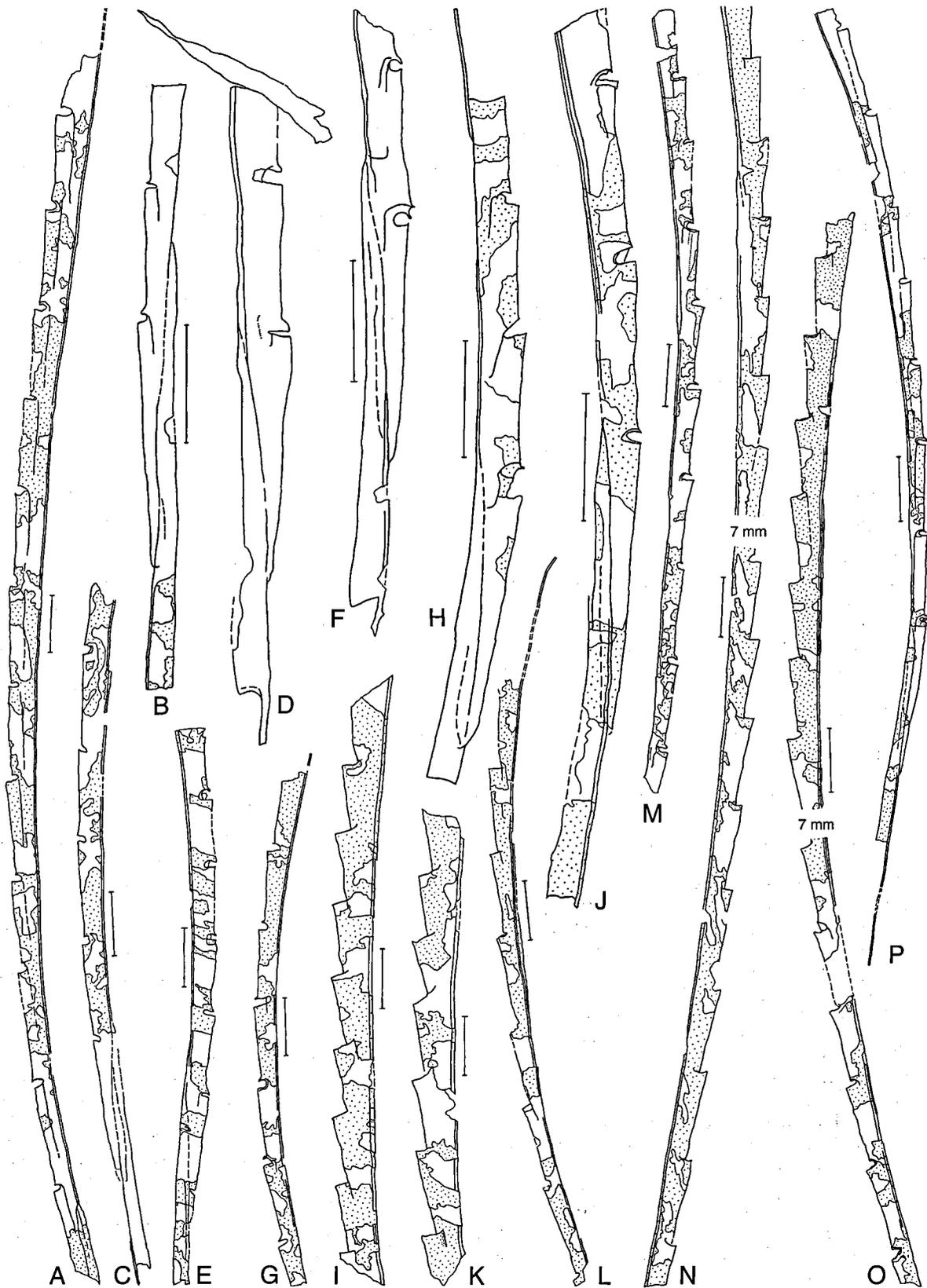
Description. – Rhabdosome, 15 mm long, with an open dorsal curvature. The dorso-ventral width is 0.2 mm at th1, the maximum of 0.3–0.4 mm is attained between th4 and th5.

The strongly geniculate thecae have well developed genicular hoods, 0.1 mm long, completely overhanging the straight slightly everted apertures and slit-like excavations. Some of the thecae (Figs 25A, 26B; th3 and th4) show a tendency to an expansion of the ventral apertural margin. The most distal thecae are 1.35 mm long and 0.15 mm wide at the apertures. They overlap 1/3 of their length and are inclined at 5°–7° to the rhabdosome axis. Thecal count can be estimated as 9 in 10 mm.

Sicula is up to 3.7–3.8 mm long and approximately 0.2 mm wide at the aperture. Its apex is about the level of th1 aperture. Th1 is 1.7–1.8 mm long and originates at a distance of 1.6–1.7 mm above the sicular aperture.

Remarks. – The new species has longer genicular hoods compared with the other species of *Huttagraptus*. By the rhabdosomal shape and dimensions it is similar to *Ht. strachani* from which it can be distin-

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Fig. 14. *Huttagraptus billegravensis* sp. nov.; fragments of rhabdosomes at different astogenetic stages, Billegrav-1 core, *vesiculosus* Biozone; A, MGUH 24251, holotype, depth 16.75 m; B, MGUH 24252, depth 13.85 m; C, MGUH 24253, depth 16.75 m; D, MGUH 24254, depth 16.25 m; E, MGUH 24255, depth 16.25 m; F, MGUH 24256, depth 16.75 m; G, MGUH 24257, depth 14.00 m; H, MGUH 24258, depth 16.75; I, MGUH 24259, depth 14.35 m; J, MGUH 24260, depth 16.75; K, MGUH 24261, depth 14.35 m; L, MGUH 24262, depth 15.05 m; M, MGUH 24263, 14.00 m; N, MGUH 24264, depth 16.40–16.60 m; O, MGUH 24265, depth 14.20 m; P, MGUH 24266.



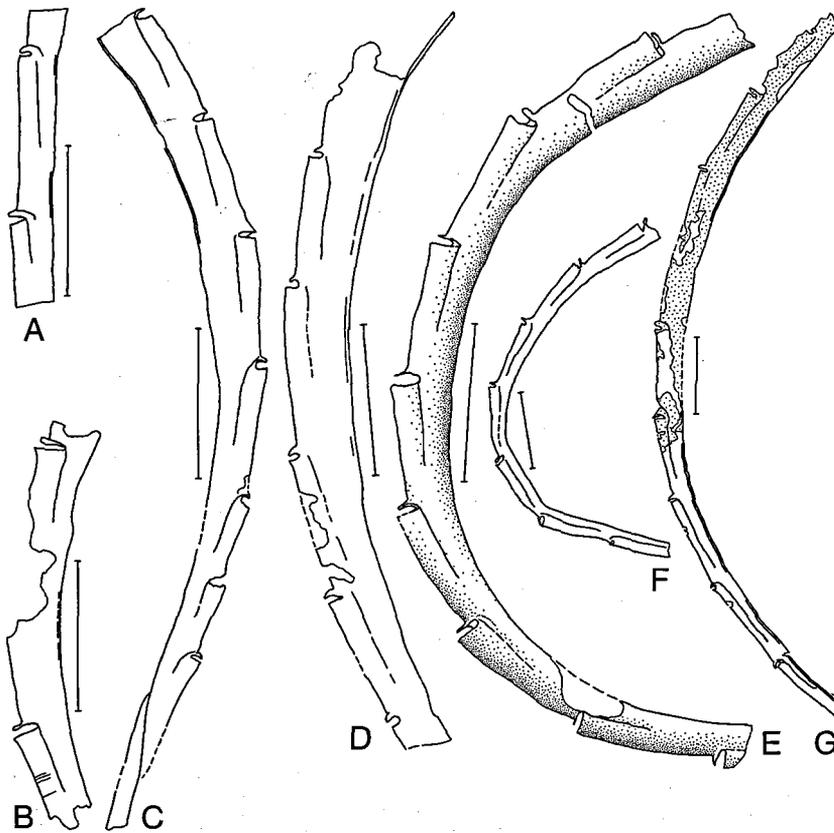


Fig. 15. *Huttagraptus incurvus* sp. nov., *vesiculosus* Biozone, Kos-Istek region, the southern Urals. A, B, fragments showing thecal structures; A, MGUH 24267, exp. 1643; B, MGUH 24268, exp. 1643; C, MGUH 24269, holotype, exp. 1643; D, MGUH 24270, exp. 1643; E, MGUH 24271, exp. 477; F, MGUH 24272, exp. 1500; G, MGUH 24273, exp. 1643.

guish by the more closely spaced and strongly overlapping thecae (Table 3).

Huttagraptus strachani (Hutt & Rickards 1970)
Figs 10J, K; 20A, B

1910 *Monograptus incommodus* Törnquist; Elles & Wood, p. 406, pl. 40, fig. 1a-e, text-fig. 272a-e.

1970 *Monograptus strachani* sp. nov.; Hutt & Rickards, p. 75, text-fig. 3g-h.

1970 *Atavograptus strachani* (Hutt & Rickards 1970 in Rickards 1970); p. 65-66, text-fig. 14, fig. 29; text-fig. 16, figs 14, 15; text-fig. 18, fig. 7 (see synonymy).

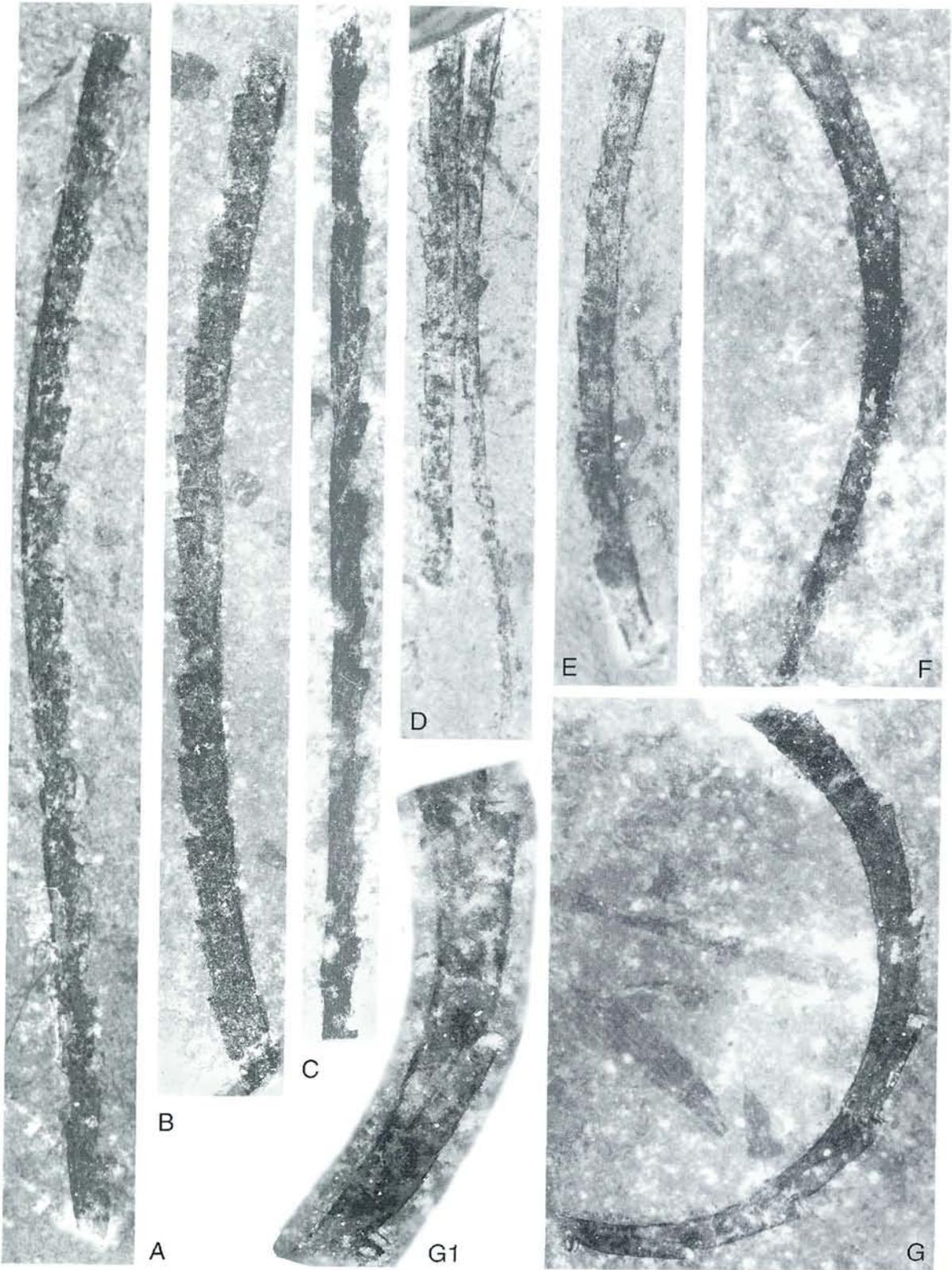
Type. - Holotype figured by Elles & Wood 1911, text-fig. 272a; SM A21030; from the Birkhill Shales, *cyphus* Biozone, Dobb's Linn, Scotland.

Material. - 4 flattened, but well preserved fragments of proximal and mesial parts of the rhabdosome from exposure 671/8, Kos-Istek region, the southern Urals, *cyphus* Biozone.

Description. - The rhabdosome is 20 mm long with a gentle dorsal curvature throughout its length. The dorso-ventral width increases slowly from 0.3 mm at th1 to 0.5 mm of about 20 mm from the sicula.

The distinctly geniculate thecae predominate in astogeny. They have semicircular excavations, almost horizontal apertures and well developed genicular rims; sometimes there is a suggestion of genicular flanges. Towards the distal end geniculation decreases and most thecae have a small flowing geniculum. The supragenicular walls are almost parallel to the rhabdosome axis in the proximal part and show a tendency to be slightly inclined distally. Thecal overlap in-

Fig. 16. A-E, *Huttagraptus praestrachani* (Hutt & Rickards, 1977), *vesiculosus* Biozone. A, MGUH 24274; B, MGUH 24275; C, MGUH 24276; E, MGUH 24278; A-C, E, distal fragments; D, MGUH 24278 proximal and distal fragments, probably belonging to the same colony; exp. 671/8 and 671/1, Kara-Dzhilga, the southern Urals. All $\times 10$; E-G: *Huttagraptus incurvus* sp. nov., *vesiculosus* Biozone; E, MGUH 24278; F, holotype, MGUH 24269, exp. 1643, Kos-Istek region, southern Urals; G, MGUH 24279 exp. 477, the same region; G1, detail of the thecal structure; F, G, $\times 20$; G1, $\times 40$.



creases from 1/5 to more than 1/3 distally. Thecal count is 7–8 in 10 mm.

The sicula is more than 3 mm long, and 0.25 mm wide at the aperture. The virgella is usually uncomplete. Th1, 1.6–1.7 mm long, originates at a distance 1.3 mm above the sicular aperture. The sicular apex is slightly above the th1 aperture.

Remarks. – The dimensions and thecal structure of these specimens agree well with the previous descriptions of *Ht. strachani*. The species can be distinguished from *Ht. praestrachani* by the more widely set proximal thecae and more constantly developed genicular rims and small flanges.

Huttagraptus sp. 1
Fig. 17F–K

Material. – 10 flattened fragments without sicula; the Billegrav-1 core, depth 16.75–18.15 m, *vesiculosus* Biozone.

Description. – The rhabdosome is broadly dorsally curved with a tendency to be less so distally. The longest fragments reach about 20 mm and have 20–22 thecae, although the fragmentary material suggests that the rhabdosome could have been longer. No proximal ends with sicula have been seen. The dorso-ventral width increases from 0.2 mm to 0.6–0.7 mm.

The thecae are geniculate with straight supragenicular walls inclined at 2°–5° to the rhabdosomal axis. Horizontal apertures open into slit-like excavations occupying 1/3 to 1/2 of the dorso-ventral width. Some thecae show thickened genicular rims. Distal thecae appear to become less geniculate and almost pristiograptid-like with the ventral walls inclined at 6°–8°. The thecal length and overlap could not be measured due to the heavily carbonized nature of the periderm. Thecae number 9–10 in 10 mm, in a few specimens up to 5.5 in 5 mm proximally and 8.5–9 in 10 mm in the most distal fragments.

Remarks. – The present form shows typical huttagraptid affinities in having distinctly geniculate thecae with genicular rims and excavations. However, the proximal end with sicula has not been found. *Huttagraptus* sp. 1 appears in the core slightly earlier than other species of *Huttagraptus*. It differs from *Ht. billegravensis* sp. nov. in having more strongly geniculate and closely set thecae and can be distinguished from *Ht. gracilis* by the more pronounced geniculum throughout the whole rhabdosome length. Compared with *Ht. praestrachani* the present form has more closely spaced thecae with no tendency to form genicular rims and it attains its maximum dorso-ventral width more quickly.

The rhabdosomal shape and size as well as the the-

cal outline in *Huttagraptus* sp. 1 are almost identical to those in the uniserial part of *Di. elongatus*. In the Billegrav-1 core both forms occur together at a depth of 16.75–17.80 m, which makes specific assignment of many specimens difficult dealing with fragmentary material (Fig. 17). The only observed differences between the two forms are the less strongly curved rhabdosome and slightly more rapid increase in the dorso-ventral width in the uniserial portion of *Di. elongatus*. The difference in number of thecae, which is 9–10 in 10 mm in *Huttagraptus* sp. 1 and 7.5–9 in the uniserial portion of *D. elongatus* does not seem to be significant.

Huttagraptus sp. 2
Fig. 18

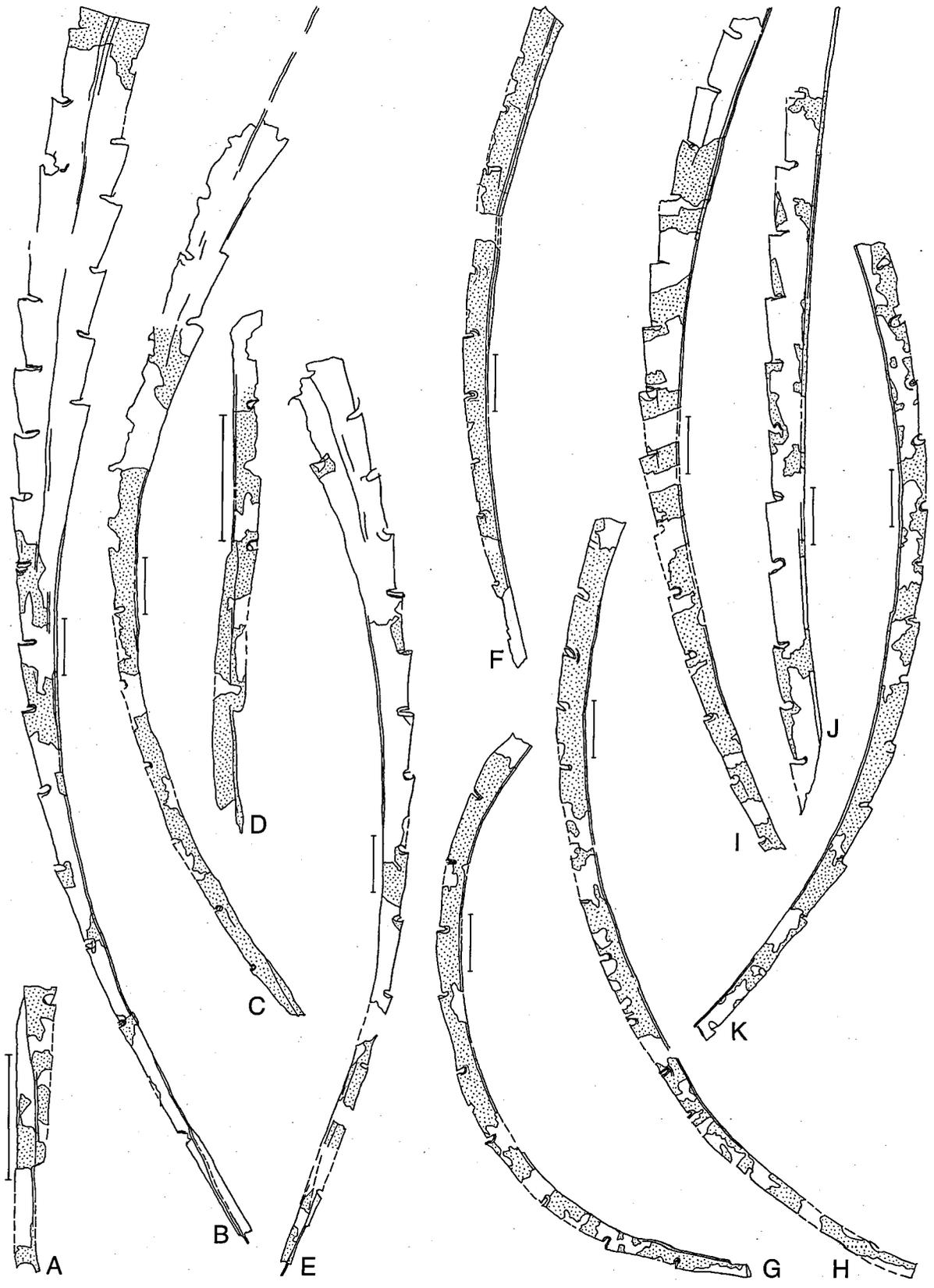
Material. – The fragmentary material comprises 15 flattened fragments of the mesial and distal parts of rhabdosomes from the Billegrav-1 core, depth 12.00–15.80 m, *vesiculosus* Biozone.

Description. – The rhabdosome is more than 50 mm long, slender and broadly dorsally curved becoming almost straight distally. The slowly increasing dorso-ventral width is 0.24–0.26 mm at th1, 0.24–0.27 mm at th2, 0.3 mm at th3, 0.33 mm at th4 and 0.35 mm at th5. The rhabdosome widens generally to 0.1–0.2 mm at a distance of about 20 mm and reaches 0.6–0.7 mm in the most distal fragments.

The proximal 10 to 15 thecae are strongly geniculate, with well developed genicular rims, and their supragenicular walls are almost parallel to the dorsal side of the rhabdosome. A geniculum is less pronounced in the distal thecae, which have slightly everted apertures and ventral walls inclined at 5°–8°. The distal thecae are 2.1–2.2 mm long and 0.3–0.4 mm wide. They overlap at about 1/4 of their length and number 6.5–7 in 10 mm proximally and 5.5–6.5 in 10 mm distally.

Only two short fragments have a sicula and a few proximal thecae. The sicula is 2.1–2.2 mm long and

Fig. 17. A–E, *Dimorphograptus elongatus* Törnquist, 1899, lower part of the *vesiculosus* Biozone, Billegrav-1 core; A, MGUH 24280, a juvenile rhabdosome with th2 starting to grow, depth 17.10; D, MGUH 24283, a fragment of a uniserial part of a rhabdosome with sicula showing the high position for the th1 origin, depth 17.10 m; B, C, E, adult uni-biserial rhabdosomes; B, MGUH 24281, depth 17.20 m; C, MGUH 24282, depth 17.30 m; E, MGUH 24284, depth 17.20 m; F–K, *Huttagraptus* sp. 1, fragments of different parts of rhabdosomes with no sicula, lower *vesiculosus* Biozone, Billegrav-1 core; F, MGUH 24285, depth 18.15 m; G, MGUH 24286, depth 16.75 m; H, MGUH 24287, depth 17.95 m; I, MGUH 24288, depth 17.10 m; J, MGUH 24289, depth 17.10 m; K, MGUH 24290.



0.3 mm wide at the aperture. The apex reaches the level at the base of the th1 and th2 septum, which is well below the th1 aperture. The virgella is incomplete. Th1, about 2 mm long, originates 0.6 mm above the sicular aperture.

Remarks. – The broad dorsal curvature, the long, slender rhabdosome and geniculate proximal and mesial thecae are the main features which make an assignment of the present form to *Huttagraptus*. *Huttagraptus* sp. 2 can be distinguished from the other species of the genus in having either very widely set thecae (contrary to *Ht. gracilis*) or more slender proximal end (as compared with *Ht. billegravensis*). The sicula seen in a few short specimens is not more than 2 mm long with th1 bud situated close to its aperture (0.55 mm), both features are not typical for the huttagraptids studied. However, the proximal fragments found may not belong to the same species, thus the present form is described in open nomenclature until more complete material is found.

Huttagraptus sp. 3
Fig. 25E

Material. – One flattened specimen from exp. 4a in Øle Å, Bornholm, the upper part of *vesiculosus* Biozone.

Description. – The rhabdosome, 18 mm long, with an open dorsal curvature. The dorso-ventral width slowly increases from 0.28 mm at th1 to 0.4 mm at th5 and the maximum of 0.5–0.55 mm is attained at th10.

The geniculate thecae have well developed genicular hoods, 0.10–0.15 mm long. They overhang horizontal or slightly everted apertures and shallow excavations. The proximal thecae are strongly elongated and overlap approximately 1/5 of their length. The distal thecae, 1.8–2 mm long, overlap 1/3 of their length. The angle of inclination of the ventral walls increases from 5°–6° proximally to 10°–12° distally. The thecal count is 6–7 in the first 10 mm and it increases distally to 8 in 10 mm.

Sicula is approximately 2 mm long and 0.2 mm wide at the aperture. Th1 originates at about 1.0 mm above the sicular aperture and attains 2 mm in length. The sicular apex reaches only a half way of the th1 length.

Remarks. – The dorsally curved rhabdosome with elongated and geniculated thecae, genicular rims or hoods is characteristic of several huttagraptid species described herein from the *vesiculosus* Biozone. The present form has more strongly developed genicular hoods, which are of the size, typical for lagarograptids. However, it has no indication of the ventral apertural processes. From *Ht. ninae* sp. nov. it differs in having shorter sicula, more widely spaced thecae and lower position of sicular apex. The preservation of the sin-

gle specimen is not enough to describe it as a new species.

Pristiograptus Jaekel 1889

Type species. – *Pristiograptus frequens* Jaekel, 1889, by the original designation.

“*Pristiograptus*” *pristinus* Hutt 1975
Figs 5C, 13A–D, 19

1975. *Pristiograptus fragilis pristinus* subsp. nov.; Hutt, p. 60, text-fig. 14, figs 8–9.

Type. – Holotype figured by Hutt 1975 SM A83992; text-fig. 14, fig. 8; SM A83992; *acinaces* Biozone of Yewdale Beck, Lake District.

Material. – More than 100 specimens in different state of preservation, flattened, in low relief and in 3-D from exp. 4 (Bjerreskov 1975) and exp. 4a in Øle Å; about 50 flattened fragments from the Billegrav-1 core, depth 3.40–14.35 m, *vesiculosus* Biozone.

Description. – Fragments of the extremely slender flexed rhabdosome are more than 30 mm long with a dorso-ventral width of 0.15–0.23 mm at the thecal aperture.

The thecae are 2 mm long, overlapping each other at about 1/10–1/12 of their length. They mostly consist of slowly widening prothecae, the metathecae being exceptionally short (no more than 0.1–0.16 mm) and slightly flaring. The apertures are straight and distinctly everted. The width at the base of metatheca is 0.03 mm in specimens in 3D and 0.05–0.08 mm in flattened rhabdosomes. The free ventral walls are straight, 1.65–1.8 mm long, and inclined at 2°–3° to the rhabdosome axis. The thecal count is 6 in 10 mm proximally to 5.5–6 in 10 mm distally.

One fragment of the extreme proximal part of the rhabdosome have at least partly preserved metasacula, 0.9 mm long (Fig. 19A). Th1 possibly originates at a

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Fig. 18. *Huttagraptus* sp. 2, fragments of rhabdosomes at different astogenetic stages; *vesiculosus* Biozone, Billegrav-1 core. A, MGUH 24291, depth 15.10 m; B, MGUH 24292, depth 15.05 m; C, MGUH 24293, 15.05 m; D, MGUH 24294, depth 15.05 m; E, MGUH 24295, depth 15.70 m; F, MGUH 24296, depth 14.70–14.75 m; G, MGUH 24297, depth 15.10 m; H, MGUH 24298, depth 15.20 m; I, MGUH 24299, depth 15.80 m; J, MGUH 24300, depth 15.05 m; K, MGUH 24301, depth 5.67–5.90 m; L, MGUH 24302, depth 15.34 m; M, MGUH 24303, depth 8.47–8.65 m; N, MGUH 24304, depth 9.49–9.58 m; O, MGUH 24305, depth 15.80 m; P, MGUH 24306, depth 9.65–9.75 m.



distance of 0.8 mm from the aperture of the sicula and attains 1.9 mm in length.

In the material studied several bipolar rhabdosomes have been found (Figs 5C, 19K, L), which shows a distinct example of formation of a regeneration branch, 25 mm long, growing in the opposite direction to that of the primary branch. The regenerating branch, called pseudocladium (Urbanek 1963, 1973), is 25 mm long, shows some irregularities in the thecal formation at the level of th4 and th5. Metatheca of th4 is abnormally long contrary to th5, which is very short, and attains a comparatively large width at the aperture. This case could be interpreted as regeneration after damage at the level of th5.

Remarks. – The present specimens agree well with “*Pr.*” *fragilis pristinus*, known from the Lake District (Hutt 1975). Originally this form was described as a subspecies, although the distinct thecal shape and proportions justify full species rank. In Bornholm “*Pr.*” *pristinus* occurs within the upper part of the *vesiculosus* Biozone which is much earlier than any other pristiograptid species. In some beds it is found in masses as shown by the X-Ray investigations (Fig. 5C). Generic assignation of “*Pr.*” *pristinus* is uncertain as it differs from the oldest known Aeronian representatives of *Pristiograptus* (*Pr. concinnus*) in having: (1) strongly elongated thecae, (2) extremely short metathecae with a tendency to some isolation in its subapertural part and (2) the high position of the th1 bud. However, with a better knowledge of the possible derivation of “*Pr.*” *pristinus*, the species could be considered as the probable progenitor of the Silurian pristiograptid stock.

Genus *Pribylograptus* Obut & Sobolevskaya 1966

Type species. – *Monograptus incommodus* Törnquist, 1899; by original designation.

Pribylograptus incommodus (Törnquist, 1899)
Figs 20C–D, 21

- 1899 *Monograptus incommodus* n. sp.; Törnquist, p. 11, pl. 2, figs 1–5.
1966 *Pribylograptus incommodus* (Törnquist); Obut & Sobolevskaya, p. 34, pl. 6, fig. 9, ?text-fig. 25.
1968 *Monograptus incommodus* Törnquist; Rickards & Rushton, p. 272, fig. 4 a–d.
1968 *Pribylograptus incommodus* (Törnquist); Obut, Sobolevskaya (& Merkurjeva), p. 88, pl. 16, fig. 8, pl. 17, figs 4–5, non figs 1–3.
1970 *Monograptus incommodus* Törnquist; Hutt & Rickards, p. 69, text-fig. 2c.
1975 *Pribylograptus incommodus* (Törnquist); Hutt, p. 71–72, pl. 16, 6, 8, 10; text-fig. 16, fig. 6.

1975 *Monograptus incommodus* Törnquist; Bjerreskov, p. 50, fig. 16F, pl. 7, D.

Type. – Lectotype figured by Törnquist 1899, pl. 2, fig. 1; LO 1456t; by subsequent designation by Přibyl 1948, p. 79; refigured Hutt & Rickards 1970, text-fig. 2c. Figured herein, fig. 21A.

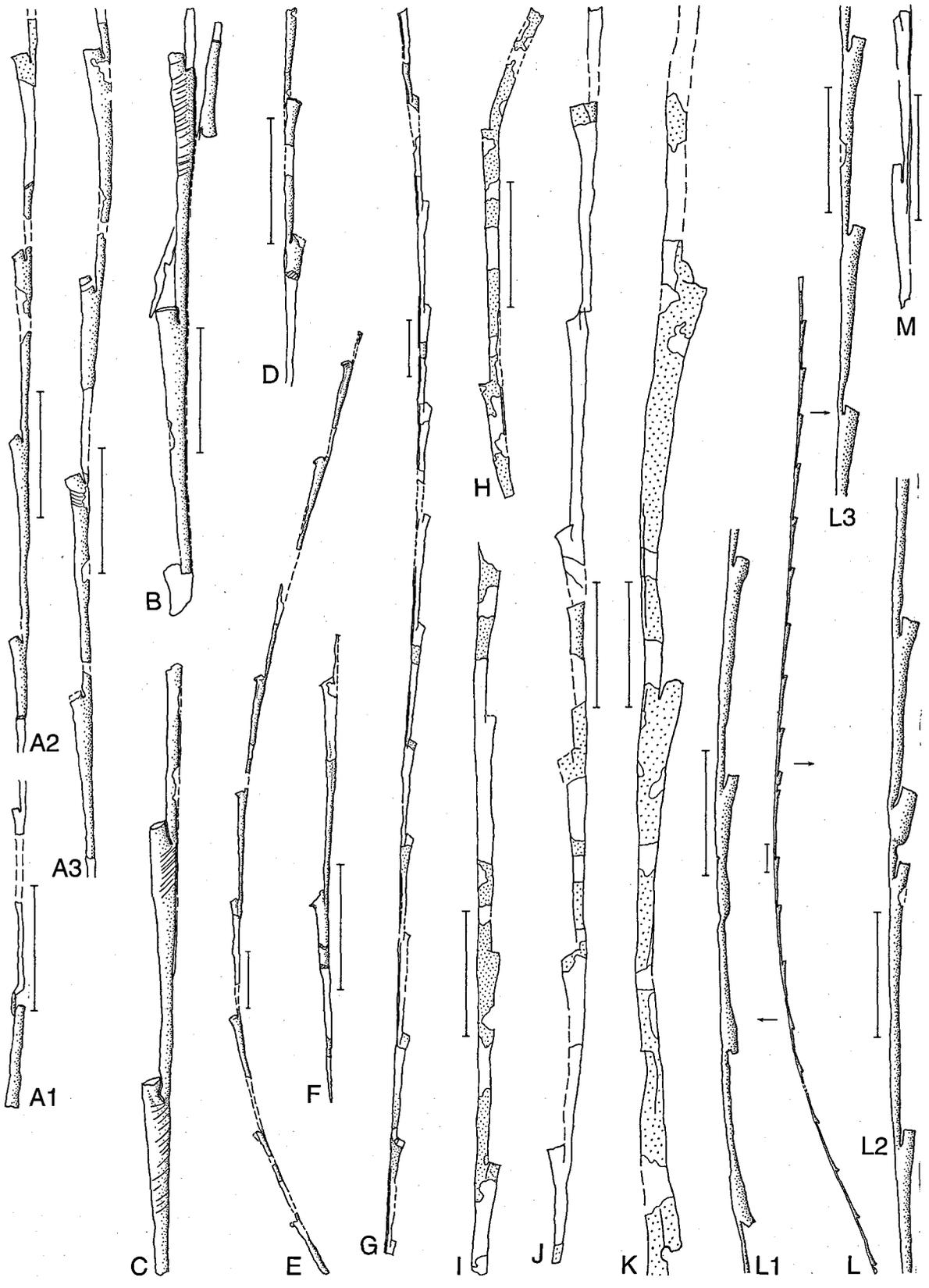
Material. – More than 100 specimens which are fragments of mesial and distal parts of rhabdosomes, preserved as flattened, in low and full relief, the Billegrav-1 core, depth 3.40–12.80 m and in exp. 4, 4a in Øle Å; upper *vesiculosus* Biozone; 6 flattened specimens from the localities 1909-2, 671/8–308, the combined *vesiculosus-cyphus* Biozone, Kara-Dzhilga, Kos-Istek region; 5 fragments, consisting of several thecae isolated from limestones, exposure 1011, Orenburg district, River Dergaish, the Masovo Village, the southern Urals, *vesiculosus* Biozone.

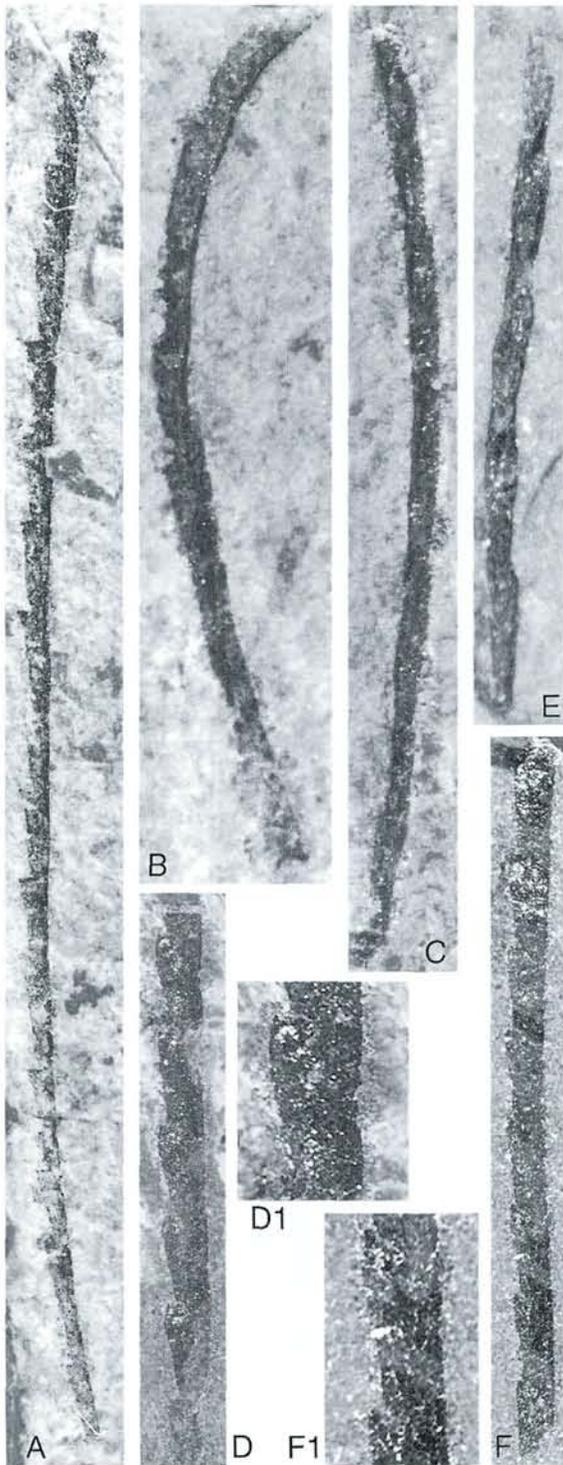
Description. – Rhabdosome flexed, more than 30 mm long, with the maximum dorso-ventral width varying from 0.5 mm to 0.65 mm. The proximal end with sicula has not been found.

The most distal thecae are 2–3 mm long and 0.15–0.25 mm wide in the metathecal part. Their angle of inclination is less than 10° and the overlap does not reach 1/2 of the thecal length. The ventral and dorsal walls of the thecae are parallel to the rhabdosome axis, except for a geniculum with well pronounced genicular rim. The apertures are transversally expanded and elaborated in the form of a pair of lateral lappets, 0.2 mm long and 0.18 mm high. The lappets are adpressed to the dorso-lateral sides of the rhabdosome. Thecae number 7–8 in 10 mm.

Remarks. – The type material of *Prb. incommodus* has been studied and refigured herein (Fig. 21A). The thecal morphology and dimensions leave no doubt that the fragmentary rhabdosomes, found in Bornholm, and in the southern Urals belong to *Prb. incommodus*.

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Fig. 19. “*Pristiograptus*” *pristinus* Hutt, 1975, upper *vesiculosus* Biozone; A1–A3, fragments of a pyritized specimen with partly preserved sicula, MGUH 24307, exp. 4; B, C, D, short fragments of pyritized specimens, showing thecal structure, exp. 4a; B, MGUH 24308; C, MGUH 24244; D, MGUH 24309; E, F, G, fragments of pyritized specimens, exp. 4a; E, MGUH 24310; F, MGUH 24311; G, MGUH 24312; H, I, fragments of flattened rhabdosomes, Billegrav-1 core, depth 14.35 m; H, MGUH 24313; I, MGUH 24314; J, MGUH 24315, exp. 4a; K, MGUH 24316, fragment of a bipolar rhabdosome, Billegrav-1 core, depth 14.35 m; L, MGUH 24317, a pyritized rhabdosome showing primary and regenerating branches, exp. 4a; L1, detail showing the place of regeneration; L2, detail showing irregularities in thecae formation; L3, details of thecal structure; M, MGUH 24318, Billegrav-1 core, depth 4.75 m.





From *Prb. sandersoni* the present species differs in having stronger introversion of thecal apertures with well developed lateral structures. However, this feature is not always evident in the flattened specimens.

Pribylograptus sandersoni (Lapworth, 1876)
Figs 20E, F; 22A–G

- 1876 *Monograptus sandersoni* sp. nov.; Lapworth, p. 310, pl. 11, fig. 2a–e.
1968 *Pribylograptus sandersoni* (Lapworth); Obut, Sobolevskaya (& Merkurjeva), p. 89–90, pl. 17, figs 6, 77, pl. 18, figs 1, 3, ?2.
1970 *Pribylograptus sandersoni* (Lapworth); Rickards, p. 66–67, text-fig. 14, fig. 25.
1975 *Monograptus sandersoni* Lapworth; Bjerreskov, p. 49–50, fig. 16D.

Type. – Lectotype figured by Lapworth 1876, pl. 11, fig. 2a; subsequently designated by Přibyl 1948, p. 79; from the Birkhill Shales, Dobbs Linn, Scotland.

Material. – 12 poorly preserved flattened fragments, the Billegrav-1 core, depth 13.80 m–15.00 m; 10 fragments of flattened rhabdosomes including the extreme proximal ends with sicula from the localities 399/4–2, 671/1–400, 671/8–280, 671/8–288, 671/8–308; the Kos-Istek region, the southern Urals, *vesiculosus* Biozone.

Description. – The rhabdosome fragments observed in the present material are 10–15 mm long and usually almost straight. The dorso-ventral width measured at th1 aperture is 0.14–0.16 mm, it reaches 0.6 mm in the most distal fragments.

The thecae have straight or slightly sigmoidally curved ventral walls, inclined at 5°–10° to the rhabdosome axis. Their apertures are introverted and have

Fig. 20. A–B: *Huttagraptus strachani* (Hutt & Rickards, 1970), Kara-Dzhilga, the southern Urals, *cyphus* Biozone; A, MGUH 24319, a distal fragment, exp. 671/8a, × 10; B, MGUH 24320, a proximal fragment with sicula preserved, exp. 671/8, × 20; C, D: *Pribylograptus incommodus* (Törnquist, 1899); C, MGUH 24321, a proximal fragment with sicula, preserved, MGUH 24321, exp. 1643, combined *vesiculosus-cyphus* Biozone, Kos-Istek region, the southern Urals, × 20; D, MGUH 24322, a distal fragment, the Billegrav-1 core, *vesiculosus* Biozone, × 10; D1, detail of the thecal structure of the same specimen, × 20; E, F, *Pribylograptus sandersoni* (Lapworth 1876); E, MGUH 24323, exp. 399–4, combined *vesiculosus-cyphus* Biozone, Kos-Istek region, the southern Urals, × 20; F, MGUH 24324, *vesiculosus* Biozone, the Billegrav-1 core, × 10; F1 detail of the thecal structure of the same specimen, × 20.

a tendency to be addressed to the lateral side of the rhabdosome. Distal thecae show slight apertural expansion. Thecal overlap increases from 1/8 seen in the extreme proximal end to 1/3 in the most distal fragments, where thecae are 1.5–1.6 mm long. Thecae number 6–6,5 in 10 mm proximally and 7.5–8.5 in 10 mm distally.

Sicula is 1.8–2.0 mm long and 0.1 mm wide at the aperture with the apex reaching about half of the th1 length. Th1 originates at approximately 1.0 mm above the sicular aperture and attains the length of 2.00 mm.

Remarks. – In spite of the fragmentary material the diagnostic features of *Prb. sandersoni*, such as the introversion and adpression of slightly expanded thecal apertures, are well seen in the material studied. For the first time the thread-like extreme proximal end with sicula and widely spaced thecae has been observed in the Uralian collection from the *vesiculosus* Biozone. *Prb. sandersoni* can be distinguished from the succeeding *Prb. incommodus* in having simpler apertural structures with no signs of lateral lappets.

?Pribylograptus sp.

Fig. 22K–M

Material. – 1 specimen in 3D from the exp. 4a (sp. 884) in Øle Å, Bornholm; 3 fragments of flattened rhabdosome including the extreme proximal part with sicula from the localities 399/4–2 and 1643–37, Kos-Istek region, the southern Urals, the *vesiculosus* Biozone.

Description. – Rhabdosome is more than 40 mm long with the dorso-lateral width being 0.15 mm at th1, 0.17 mm at th5 and 0.25–0.3 mm in the most distal fragments.

Thecae, up to 2.5 mm long, are strongly geniculate with distinctive rims and small excavations. Their apertures show a slight tendency to introversion. The supragenicular walls are straight, sometimes slightly convex in the subapertural part. Thecae overlap about 1/2 of their length and number 8–9 in 10 mm.

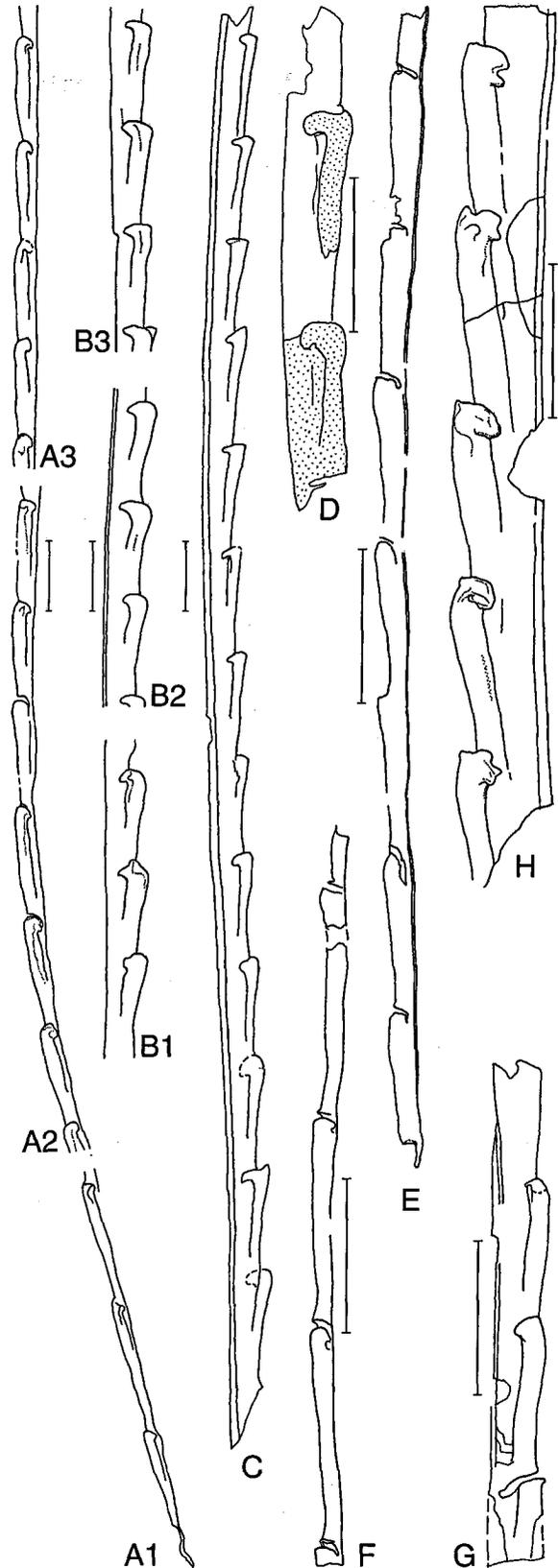


Fig. 21. *Pribylograptus incommodus* (Törnquist, 1899); A, holotype, fragment showing thecal structure, LO 14567, Törnquist, 1899, pl. II, fig. 1; B, LO 14571, Törnquist, 1899, pl. II, fig. 2, details of thecal structure; C, LO 1460T, Törnquist, 1899, pl. II, fig. 5, distal fragment; D, MGUH 24325, a distal fragment, upper part of *vesiculosus* Biozone, depth 8.47–8.66 m; E, F, fragments showing proximal thecae structure; E, MGUH 24326, exp. 671/8-308, Kara-Dzhilga; F, MGUH 24327, exp. 1909/2, Kos-Istek region; combined *vesiculosus-cyphus* Biozone, the southern Urals; G, H, fragments showing distal thecae structure; G, MGUH 24328, exp. 671/8–280, Kara-Dzhilga; H, MGUH 24329, Billegrav-1 core, 1, depth 8.80–8.95 m.

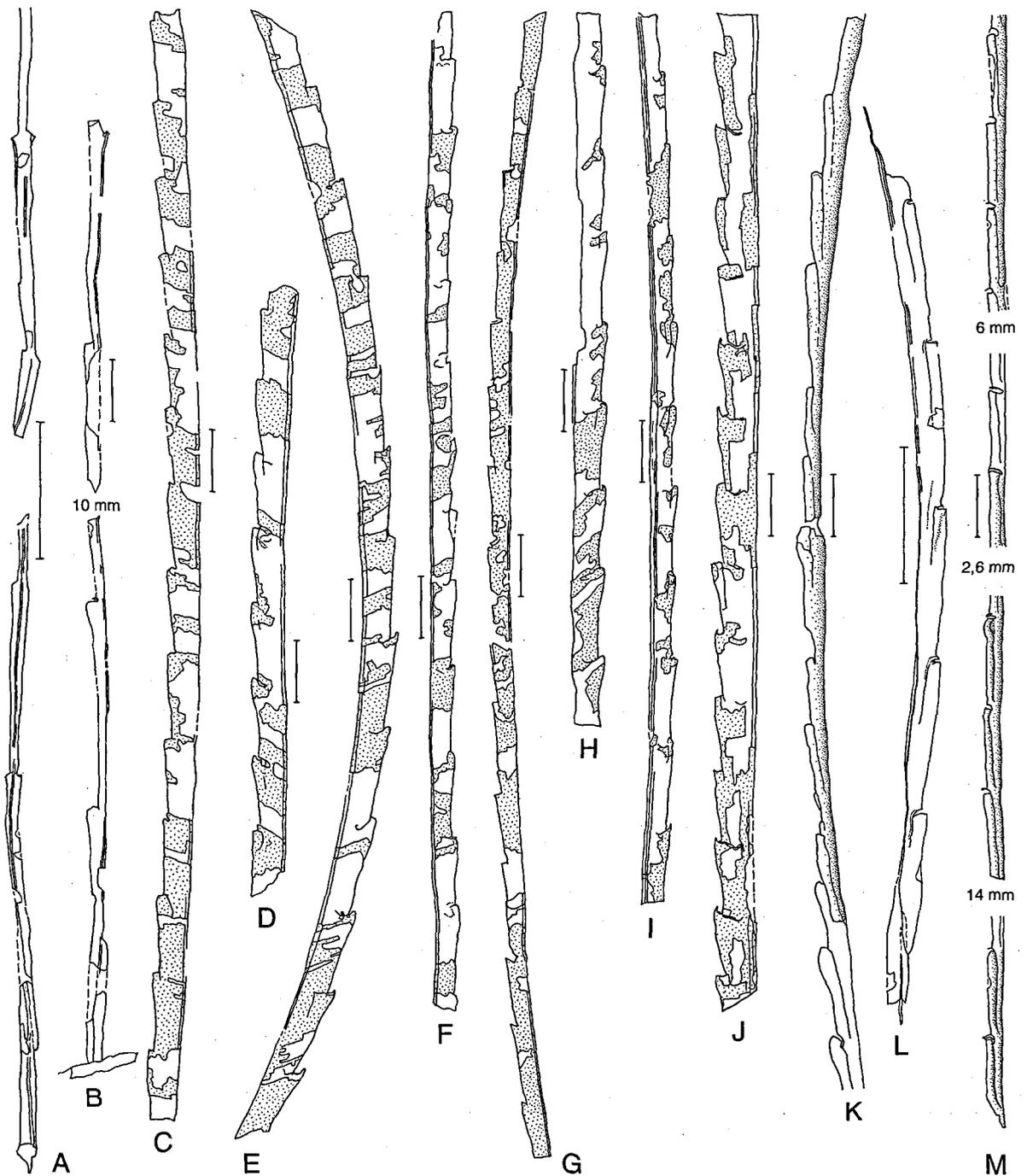


Fig. 22. A–G: *Pribylograptus sandersoni* (Lapworth, 1876), proximal fragments, *vesiculosus* Biozone, the southern Urals; A, MGUH 24330, exp. 671/8; B, MGUH 24331, exp. 671/8–288; C–J, mesial and distal fragments, *vesiculosus* Biozone, Billegrav-1 core; C, MGUH 24332, depth 14.05 m; D, MGUH 24333, 11.35–11.45 m; E, MGUH 24334, depth 11.35–11.45 m; F, MGUH 24335, depth 14.05 m; F, G, MGUH 24336, depth 14.05 m; H, MGUH 24337, depth 14.05 m; I, MGUH 24338, depth 14.00; J, MGUH 24339, depth 14.35 m; K–M, ?*Pribylograptus* sp., *vesiculosus* Biozone; K, M, MGUH 24340, fragments of the same rhabdosome, Øle Å, exp. 4; L, MGUH 24341, a proximal fragment, Kos-Istek region, exp. 1643/50–37.

Sicula is about 1 mm long and 0.13 mm wide at the aperture. Its apex reaches the level of the half way of the th1 length. Th1, 1 mm long, originates at the distance of 0.4 mm above the sicular aperture.

Remarks. – The specimens studied are preserved as fragments of different parts of rhabdosomes making a complete description of this species impossible. The longest fragment from Øle Å is strongly limonitized which results in incomplete preservation of the thecal apertures (Fig. 22K, M). This might be the reason for an almost undistinguishable thecal introversion. The well developed genicular rims and small slit-like apertural excavations give an impression that the specimen has huttagraptid affinities. The Uralian material is too fragmentary, although the extreme proximal end is quite well preserved (Fig. 22L). From *Prb. sandersoni* the present form differs in having much shorter sicula and less introverted thecae.

Genus *Lagarograptus* Obut & Sobolevskaya 1968 in Obut et al. 1968.

Type species. – *Lagarograptus inexpeditus* Obut & Sobolevskaya 1968, by original designation.

Horizon. – Llandovery, *vesiculosus* to *sedgwickii* Biozones.

Diagnosis. – Rhabdosome with moderate dorsal curvature, relatively slim with tendency to be parallel-sided. Sicula long, with metasicula occupying most of its length, apex reaching the level around the th1 aperture and with high origin of th1 bud. Long slender thecae overlap about 1/2 of their length; slit-like or semicircular apertural excavations and overhanging pronounced geniculum which may have well developed genicular flanges; a triangular shaped ventral apertural process is present in all thecae.

Remarks. – *Lagarograptus* was originally defined as a monospecific genus, based on *Lg. inexpeditus*, the type species from the lower *triangulatus* Biozone (Obut et al. 1968). Later, it was emended by Rickards (1976), who emphasized that the main diagnostic features of the genus are the parallel-sided rhabdosome,

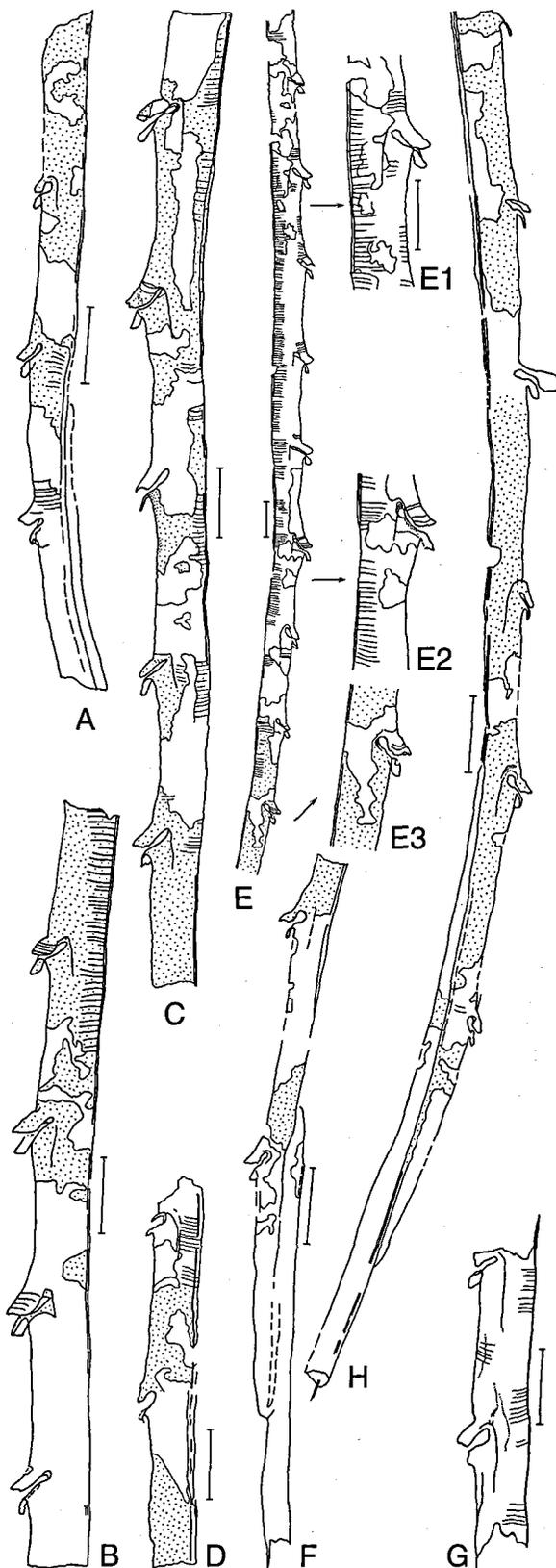


Fig. 23. *Lagarograptus inexpeditus* Obut & Sobolevskaya, 1968, *cyphus* Biozone, Kos-Istek region, the southern Urals. A–E, fragments of the distal part of the rhabdosomes; A, MGUH 24342, exp. 399/4–30; B, MGUH 24343, sp. exp. 408–501; C, D, MGUH 24344, fragments of the same specimen, exp. 399–4–31; E, MGUH 24345, exp. 399–4–10, E1, E2, E3, details of thecal structure; F, MGUH 24345, a proximal part of a rhabdosome with sicula, same specimen as E; G, MGUH 24347, exp. 408–501a; H, MGUH 24347, exp. 408–501a.

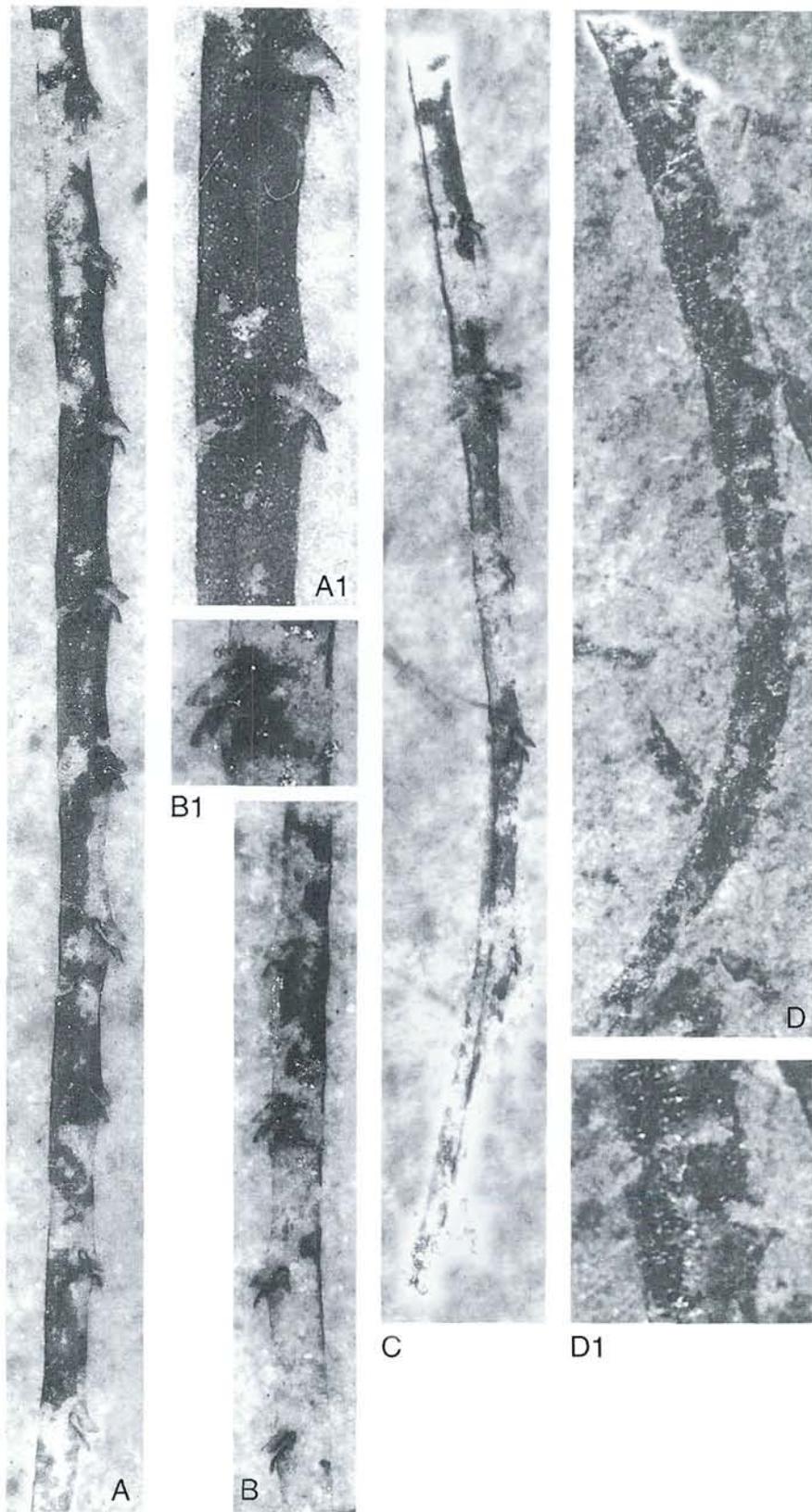


Fig. 24. A-C:
Lagaragraptus
inexpeditus Obut &
 Sobolevskaya, 1968;
 upper part of the
vesiculosus to *cyphus*
 Biozone, exp. 399-4, the
 Kos-Istek Region. A, B,
 distal fragments, $\times 20$; A1,
 B1, enlarged parts of the
 same rhabdosomes
 showing thecal hoods and
 ventral outgrowths; A,
 MGUH 24348; B, MGUH
 24349, $\times 40$; C, MGUH
 24350 proximal part of the
 rhabdosome with well
 preserved long sicula, \times
 20; D, MGUH 24351,
Lagaragraptus karaensis
 sp. nov., holotype, *cyphus*
 Biozone, exp. 671/8,
 Kara-Dzhilga, $\times 20$; D1,
 a detail of the apertural part
 of a theca, showing hood
 and a small ventral
 outgrowth, $\times 40$.

the long sicula, the elongated and strongly overlapping thecae which may have genicular hoods and ventral apertural processes. In the emended generic diagnosis "*Monograptus tenuis* Portlock was included in *Lagarograptus* because of the presence of the ventral apertural outgrowths (Hutt 1968) which resemble those of *Lg. inexpeditus*.

Significantly shorter ventral structures have been discovered in *Lagarograptus karaensis* sp. nov. from the *cyphus* Biozone of the southern Urals but, contrary to *Lg. inexpeditus* and *Lg. tenuis*, *Lg. karaensis* possesses a much shorter sicula and it does not show the thecal elongation. At the same time some species described from the *convolutus* Biozone of Bohemia (Storch 1988) have been assigned to *Lagarograptus*, though all of them lack both the ventral apertural processes and genicular hoods. This somewhat arbitrary assignment was mainly based on their shared general common features such as dorsally curved rhabdosome, long sicula, geniculate thecae with slightly expanded and everted aperture. Several taxa possessing ventral apertural processes are with reservations assigned to the genus *Lagarograptus*. More studies are needed to elucidate the taxonomic value of the ventral apertural processes, as their appearance in different lineages cannot be excluded. Variation both of sicula size, and in the degree of thecal elongation in different species possessing genicular flanges and ventral processes, are additional characters that have to be evaluated for better understanding of their evolutionary relationships.

Lagarograptus inexpeditus Obut & Sobolevskaya
1968 in Obut et al. 1968
Figs 23; 24A–C

1968 *Lagarograptus inexpeditus* sp. nov.; Obut et al.,
p. 91–92, pl. 18, figs 4–6; pl. 19, figs 1–6.

Type. – Holotype figured Obut et al. 1968, pl. 18, fig. 4, CGM 14/976, lower *triangulatus* Biozone, Norilsk region, IM24, depth 316.4–320.4 m, North Siberia.

Material. – 10 fragmentary, but well preserved specimens showing different parts of rhabdosomes, including extreme proximal ends. The fusellar structure is well seen due to a special kind of preservation with not strongly carbonized periderm in the weathered silicious rocks. Exp. 399–4, upper combined *vesiculosus*

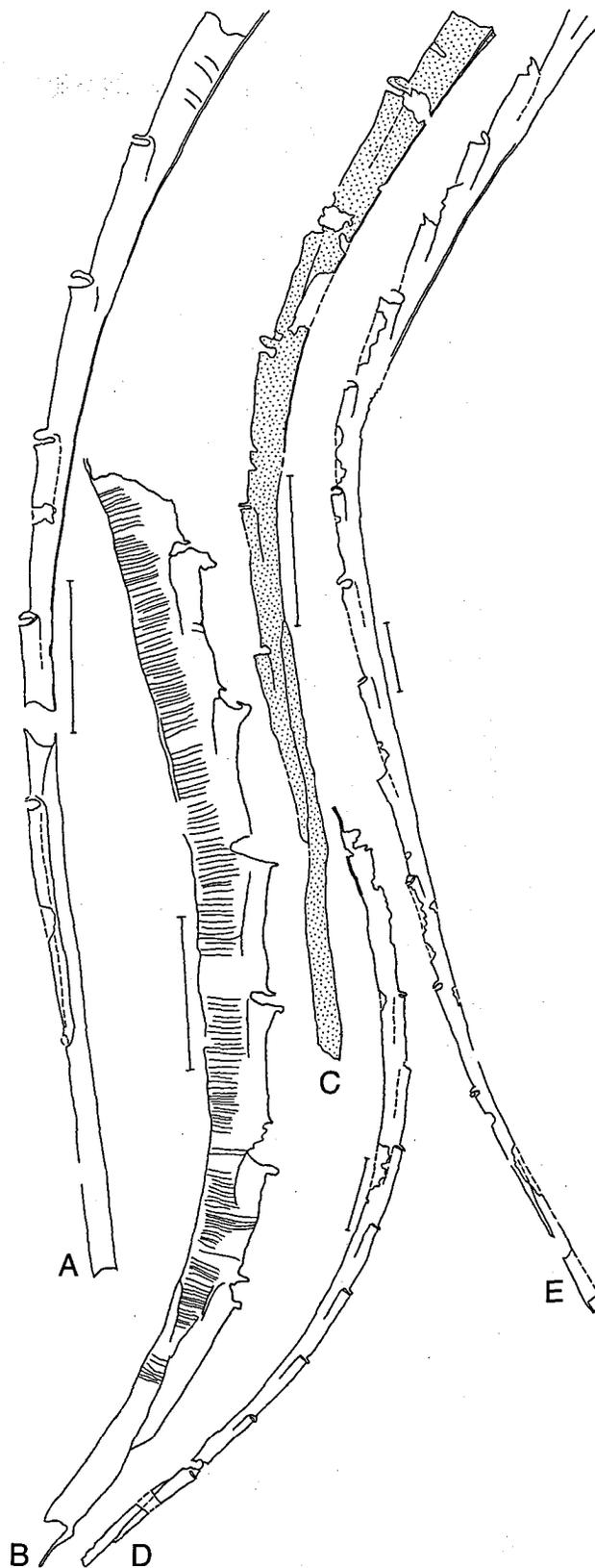


Fig. 25. A, C, D, *Huttagraptus ninae* sp. nov., combined *vesiculosus-cyphus* Biozone; A, MGUH 24352, exp. 1909–1; Kos-Istek region; B, *Lagaragraptus karaensis* MGUH 24351, holotype, exp. 671/8–267, Kara-Dzhilga; C, holotype, MGUH 24353; D, MGUH 24354, exp. 671/8–11a, Kara-Dzhilga; E, *Huttagraptus* sp. 3, MGUH 24355, Øle Å, exp. 4a, *vesiculosus* Biozone.



sus-cyphus Biozone, Kos-Istek region, the southern Urals.

Description. – The gently dorsally curved rhabdosome is more than 15 mm long with an open dorsal curvature. The dorso-ventral width increases from 0.35–0.4 mm at th1 to the maximum of 0.5–0.55 mm within the first 10 mm.

Uniform thecae possess a strong geniculum and shovel-like genicular hoods overhanging the whole aperture. The hoods are 0.25 mm long and 0.15 mm wide at their margins. The present material clearly displays the irregular microfusellar structure of the hood. The supragenicular walls are straight or slightly concave and parallel to the rhabdosome axis throughout the rhabdosome, except at the extreme proximal end where thecae are inclined at 5°. The apertures are straight and strongly everted. Triangular ventral processes grow outwards from the ventral margin of the thecal apertures. Initially narrow they become rapidly transversally expanded. There is a suggestion of their convex shape. They are 0.16 mm long and 0.10 mm wide at the margin. Intertheal septa are indistinct, although they appear to overlap slightly more than at 1/3 of their length in the distal part of the rhabdosome. Thecae number 8 in 10 mm.

The slightly dorsally curved sicula, is more than 4.00 mm long and 0.2 mm wide in the aperture, with a very narrow apical part and an apex reaching the level above the th2 aperture. Th1 originates at a distance of 0.8 mm from the base of sicula. Initially it grows shortly in a horizontal direction (Fig. 23F), further on, after a sharp knee-like bend it grows upwards parallel to the sicula at a distance of 1.8–1.9 mm.

Remarks. – The present specimens agree well with the original description of *Lg. inexpeditus* (Obut et al. 1968). The slightly lower position of the sicular apex and higher origination of th1 in the Uralian form (0.75–0.8 mm as compared with 0.4–0.5 mm in the Siberian specimens) are the only differences. *Lg. inexpeditus* is similar to *Lg. tenuis* (Portlock), known from the *sedgwickii* Biozone, in shape of thecae having ventral processes at their apertures. The absence of dorsal hoods in *Lg. tenuis*, so well developed in *Lg. inexpeditus* is an important difference between two species. *Lg. inexpeditus* has as well slightly shorter sicula, the wider extreme proximal end and its maximum dorso-ventral width does not exceed 0.55 mm.

Fig. 26. A–C, *Huttagraptus ninae* sp. nov., *vesiculosus* to *cyphus* Biozones, southern Urals; A, MGUH 24357; C, MGUH 24353; C1, details of apertural structure of thecae; exp. 671/8, Kara-Dzhilga; B, MGUH 24353, holotype, exp. 1909, Kos-Istek region. A–C, × 20; C1, × 40.

Lagarograptus karaensis sp. nov.
Figs 24A–C; 25B

Type. – Holotype, Figs 24D, 25B, MGUH 24351 (Specimen 267), exp. 671/8, the Kara-Dzhilga, *cyphus* Biozone, the southern Urals, Kazakhstan.

Derivation of name. – From the geographical name Kara-Dzhilga Valley.

Material. – One well preserved specimen.

Description. – The rhabdosome is slightly dorsally curved, 10 mm long, widening rapidly within the first 10 mm. The dorso-ventral width is 0.48 mm at th1 and th2, 0.6 mm at th5 and the maximum of 0.65 mm is attained at th15.

The geniculate thecae have short genicular hoods (0.1 mm) and ventral processes (0.1 mm). Slightly concave free ventral walls are inclined at about 5° to the rhabdosome axis. Thecae overlap more than 1/3 of their length and number about 8 in 10 mm.

The sicula is 1.9 mm long and 0.2 mm wide at the aperture. Th1, 1.6 mm long, originates at the level about half-way of the sicula length. The sicular apex reaches the th1 aperture.

Remarks. – The present species differs from *Lg. inexpectatus* and *Lg. tenuis* in having significantly shorter sicula and less developed ventral apertural processes. From the former species *Lg. karaensis* can be as well distinguished by the much less developed genicular hoods and more inclined free ventral walls of thecae.

Morphology and phylogeny

Rickards and Hutt (1970) postulated the origin of the first monograptid species, *Atavograptus ceryx* (in the *persculptus* Biozone) from glyptograptid stock. Recently, the idea of the akidograptid origin for the first monograptid colony was forwarded by Li (1990) and supported by Melchin (pers. comm. 1996). This new suggestion is based on the much closer similarity between akidograptids and *Atavograptus ceryx* in having early upward growth of the first theca and late differentiation of th1². Therefore, the transition from akidograptid to monograptid requires a less radical transformation of the early astogeny than a direct evolution from a glyptograptid or normalograptid.

The earliest monograptids studied from the *ascensus*, *acuminatus* and *vesiculosus* biozones share extremely long and slender rhabdosomes. The growth of the colonies continued beyond the average length of contemporaneous biserial graptolites and their length is similar to that of the late Ordovician nema-graptids.

The long slender rhabdosomes typical for these early monograptids partly explain the rarity of the extreme proximal end fragments. At an early stage in their evolution, however, monograptids with different thecal morphology were able to regenerate their rhabdosomes after breakage. Occurrences of bipolar uniserial rhabdosomes in the *vesiculosus* Biozone have been recorded by Rickards (1973). In the material studied here several well preserved specimens of "*Pristiograptus*" *pristinus* show a regenerating branch (Fig. 19).

Variable dorsal curvature, expressed mostly in the proximal part of the rhabdosome was typical for the majority of earliest monograptid species. By the end of the *vesiculosus* Biozone and beginning of the *cyphus* Biozone the dorsal curvature became more rigid (*Coronograptus*, *Lagarograptus*). This feature was shared also by the contemporaneous dimorphograptids with a long uniserial proximal part. The numerous specimens from the Billegrav-1 core, depth 18.15–16.75 m, show striking similarity between monograptids, assigned to *Huttagraptus* sp. 1 and uniserial parts of *Di. elongatus*. They closely resemble each other in having dorsally curved rhabdosomes, and similar thecal size and geniculation, making it difficult to distinguish between them (Fig. 17). Among the observed differences only less strong rhabdosomal curvature and slightly more rapid increase in the dorsoventral width in the uniserial portion of *Di. elongatus* can be mentioned.

In general, the taxonomic differentiation of the early Llandovery monograptids at generic and species level is based on three main morphological criteria as far as theca and proximal end structure are concerned.

The first is the degree of thecal geniculation, resulting in the glyptograptid or "monoclimacid" thecae. This feature is used to differentiate two genera, e.g. *Atavograptus* Rickards and *Huttagraptus* gen. nov.

Simple, weakly geniculated thecae with horizontal or slightly everted, undifferentiated apertures are common for *Atavograptus*. This feature, combined with the short sicula, was retained from the assumed biserial ancestral stock. The first monograptids, e.g. *A. ceryx* and *A. primitivus* represent the generalized or standard *Atavograptus* morphotype, which did not undergo noticeable changes during *ascensus-acuminatus* time. Recent data (Li 1983; Lukasik & Melchin 1994) and the present material show that the *Atavograptus* line consists of three successive chronological species such as *At. ceryx* (in the *persculptus* Biozone), *At. primitivus* (in the *ascensus-acuminatus* Biozone) and *At. atavus* (in the *vesiculosus-gregarius* biozones), which share the same shape of thecae. The elongation of sicula and thecae with no increasing thecal overlap are the only changes which could have easily bridged the transition between *At. atavus* and *At. primitivus* (Fig. 27). Further morphological changes within the *Atavograptus* line, expressed in *A. atavus* are an increase in length and dorso-ventral width of the colony, attenuation

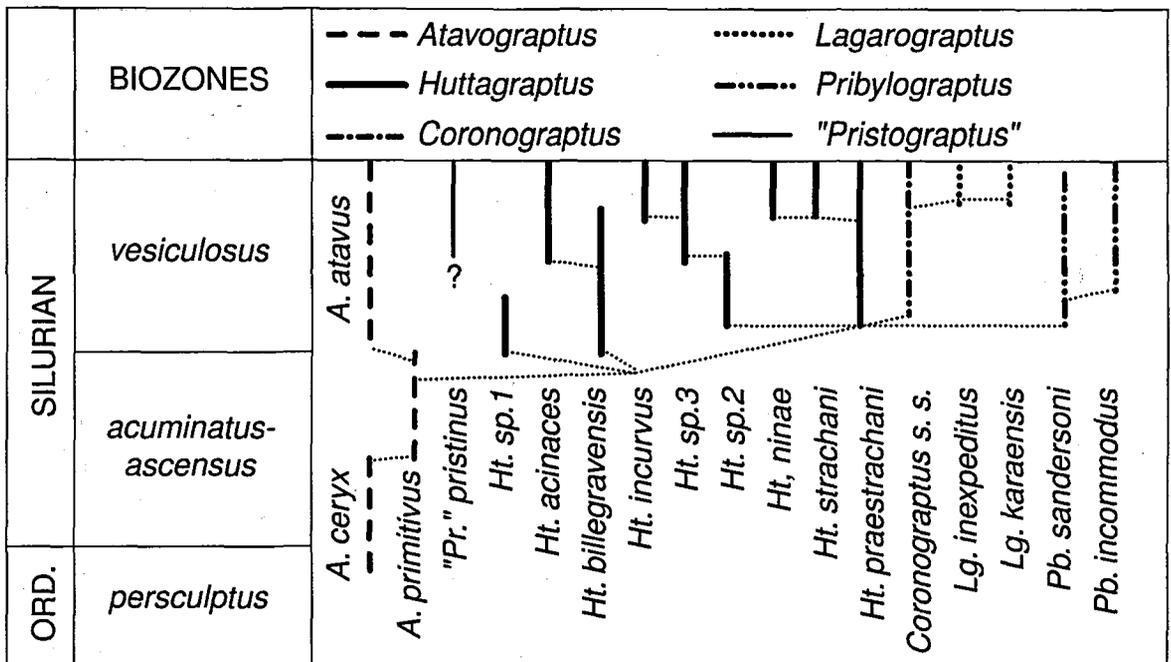


Table 4. Suggested phylogenetic relationships of the species described.

of the extreme proximal part and elongation of thecae resulting in more widely spaced thecae.

The *Atavograptus* stem line continued as a conservative group and at the same time it could have played an important role in the monograptid diversification, first in the *vesiculosus* Biozone and later, during Aeronian-early Telychian time. For example it could have been the source of lineages with simple thecal morphology, as seen in "*Pristograptus*" *pristinus*. The further development of this species towards early Aeronian robust *Pristograptus* s.s. (*Pr. concinnus*) seems likely (Rickards et al. 1977, Fig. 30). The evolutionary potential of *Atavograptus* as the source of new progressive lineages can be compared with the standard morphotypes presented by the *Normalograptus* group among contemporaneous biserial graptolites (Koren' & Rickards 1996) and with the *Pristograptus dubius* stock during the Late Wenlock recovery from the *lundgreni* extinction event (Koren' & Urbanek 1994).

Strongly geniculate weakly hooded thecae are typical for *Huttagraptus* gen. nov., *Pribylograptus* and *Lagarograptus*. This character is first seen in *Huttagraptus* sp. 1, *Ht. billegravensis* sp. nov. and *Ht. praestrachani* which derive from *At. pristinus* at the beginning of the *vesiculosus* Biozone. Geniculate thecae are retained in pribylograptids and in lagarograptids which evolve most probably from *Ht. praestrachani* during *vesiculosus* time (Fig. 27).

The second important diagnostic feature of the *vesiculosus* Biozone monograptids is the presence of

variable genicular rims, flanges or hoods, ventral apertural processes and/or lateral apertural expansions. A differentiation of the genera *Huttagraptus* gen. nov., *Pribylograptus* and *Lagarograptus* are based on different combinations of these features. Strongly geniculate thecae with genicular flanges and hoods place huttagraptids morphologically apart from the *Atavograptus* stock. The various size and astogenetic penetrance of these structures are used for the species differentiation in *Huttagraptus* gen. nov. The specialized *Pribylograptus* morphotype appears close to the beginning of the *vesiculosus* Biozone (Fig. 27). Together with genicular flanges it possesses characteristic lateral apertural expansions which, in flattened material, give an impression of the introverted appearance of the thecal aperture. The long slender rhabdosome lacks any elongation of thecae and proximal end. Based on the present material, it is suggested that *Ht. praestrachani* is the probable ancestor of the first pribylograptids (Fig. 27).

The new *Lagarograptus* morphotype possesses the peculiar ventral apertural outgrowths and, at the same time it retains the main huttagraptid features such as a long sicula and strongly geniculated thecae with more elaborated genicular hoods. This can be taken as an example of the extreme morphological specialization. *Lagarograptus* could have derived from *Huttagraptus* stem via early coronograptids, which first show a tendency to flaring thecal aperture (Fig. 27).

The proximal end structure of the early monograptids, e.g. the size and proportions of the sicula, posi-

tion of the origin of th1, length and overlap of the proximal thecae is the third key morphological feature critical for species differentiation in *Atavograptus*, *Huttagraptus* and *Lagarograptus*.

The elongation of the sicula and extreme proximal end also the high position of the origin of th1 are first seen in some biserial (*Akidograptus* and *Parakidograptus*) and uniserial graptolites (*At. primitivus*) in the *ascensus* and *acuminatus* biozones. Since the beginning of the *vesiculosus* Biozone this is shared by some early huttagraptids, e.g. *Ht. billegravensis* and *Huttagraptus* sp. 2 and dimorphograptids with a long uniserial part. An extreme value of the sicular length and the high position for the th1 bud is reached in *Ht. acinaces* in late *vesiculosus* time (Fig. 27). This character is interpreted here as an important morphological novelty introduced independently in several lineages first in the *ascensus* and *acuminatus* biozones, then in the *vesiculosus* Biozone.

The other important feature with respect to taxonomy is the proportions of prothecal and metathecal parts, expressed in thecal elongation and degree of their overlap. They are well represented in different lineages as it is seen in *Ht. acinaces* (Figs 11, 12) and "*Pr.*" *pristinus* (Fig. 19). The former displays an extreme and progressive elongation of metathecae during astogeny, whereas in the latter species thecae consist mostly of the prothecal part and do not show any noticeable increase in overlap during astogeny.

A number of morphological characters such as inclination of thecae to the rhabdosome axis, thecal overlap, degree of geniculation, presence or absence of genicular hoods are subject to astogenetic variation. Most of the species studied are characterized by gradual modification of successive thecae in the colony (*Lagarograptus*, *Pribylograptus*). Huttagraptids, in particular, such as *Ht. billegravensis* sp. nov., *Ht. praestrachani* and *Huttagraptus* sp. 2 show well pronounced thecal biformity beginning in the lower *vesiculosus* Biozone. Their proximal and mesial thecae are distinctly geniculated, while those in the distal part have almost straight free ventral walls, even allowing for the effects of preservation. In some cases, however, e.g. *H. strachani* the monoclimal thecae are spread almost through the whole colony.

The overall pattern of the *vesiculosus* Biozone diversification among monograptids is marked by the appearance of several kinds of derived thecal structures based on the *Atavograptus* stem line. Some of them were susceptible to further progressive changes (Rickards et al. 1977). However, the unsatisfactory preservation of present material and incompleteness of data on stratigraphical ranges of particular species makes the reconstruction of the individual lineages difficult.

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The illustrations were prepared with the help of T. Bredsdorff (Geological Museum of the University of Copenhagen). The X-Ray photographs were done by J. Aagaard in the Geological Institute of the University of Copenhagen. The light photography of the graptolites was undertaken by B. S. Pogrebov in the Department of Palaeontology of the University of St. Petersburg and by S. L. Jakobsen in the Geological Museum of the University of Copenhagen. A. K. Brantsen helped correcting the manuscript. The authors direct their thanks to the above mentioned persons.

Dansk sammendrag

Der er foretaget undersøgelser af monograptider (enkeltradede graptoloider) i den komplette lagserie af nedre Llandovery graptolitskifre fra Billegrav-1 boringen ved Øle Å på Sydbornholm. De taxonomiske studier er især koncentreret omkring monograptidfaunaen i *vesiculosus* Biozonen i de nærliggende blottede lag i Øle Å. Yderligere er der til sammenligning undersøgt monograptider fra en kondenseret serie af dybbassin-aflejringer bestående af carbonatholdige skifre fra *vesiculosus* Biozonen i Sakmara Formationen i Syd Ural. Aflejringsmiljøerne og biostratigrafien i de to områder er kort beskrevet, og der er foretaget en sammenligning af de to faunaer, som tilsammen kan henføres til 5 slægter og 17 arter, hvoraf 4 er nye og 4 er i åben nomenklatur. Der er beskrevet en ny slægt *Huttagraptus* med typeart *Ht. praestrachani*.

På grundlag af de taxonomiske studier af monograptider er phylogenen og diversitetsdynamikken diskuteret.

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