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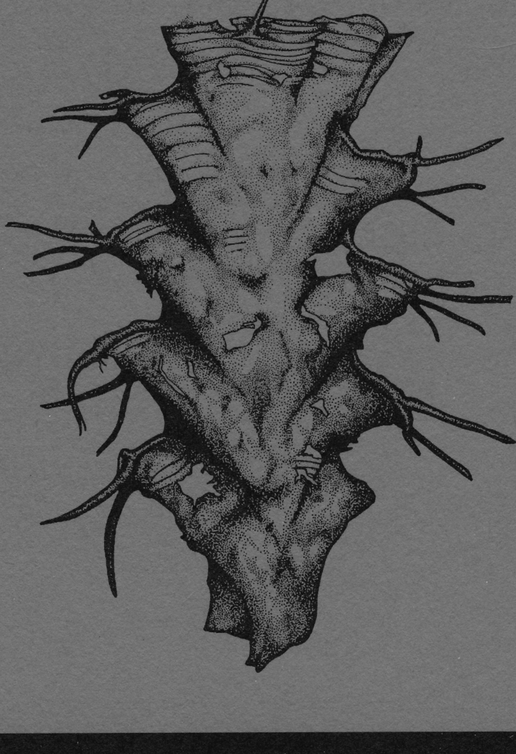
Taxonomy and evolution of Llandovery biserial graptoloids from the southern Urals, western Kazakhstan



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SPECIAL PAPERS IN PALAEONTOLOGY NO. 54

TAXONOMY AND EVOLUTION OF LLANDOVERY BISERIAL GRAPTOLOIDS FROM THE SOUTHERN URALS, WESTERN KAZAKHSTAN

BY

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with 14 plates, 2 tables and 23 text-figures

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ABSTRACT. The well preserved Llandovery biserial and uni-biserial graptoloid fauna of the Mugodzhary Range of the Kos-Istek region of western Kazakhstan gives an unusual insight into the biodiversity of Llandovery assemblages. Sixty-three taxa are described, of which twenty-one are left in open nomenclature, assigned to the families Glyptograptidae, Akidograptidae, Dimorphograptidae and Metaclimacograptidae fam. nov. There are thirteen new species: *Glyptograptus bulbus*, *Neodiplograptus korinevskii*, *Hirsutograptus longispinus*, *H. villosus*, *Victorograptus morosus*, *Parapetalolithus dignus*, *Rivagraptus inconstans*, *R. rozmanae*, *R. sentus*, *Corbograptus enigmatica*, *Metaclimacograptus khabakovi*, *Me. khvorovi* and *Me. orcus*. Five new genera and a new subgenus are erected on the basis of Uralian material: *Hirsutograptus*, *Victorograptus*, *Parapetalolithus*, *Rivagraptus*, *Corbograptus*, and the subgenus *Pseudorthograptus* (*Dimorphograptoides*). Two other new genera are erected, *Persculptograptus* and *Sudburigraptus*, based on material from Wales and Alaska respectively. The type material of the genera *Comograptus* and *Dittograptus*, from Norilsk, Siberia, is redescribed. The diverse graptolite assemblages of the Kos-Istek region have enabled accurate attribution of faunas to biozones of Rhuddanian to early Telychian age.

The multispinose biserial graptoloids evolved in three main lineages: (1), *Normalograptus* to *Hirsutograptus*; (2), *Pseudorthograptus* (*Pseudorthograptus*) *mutabilis* to *P.* (*Dimorphograptoides*) and to *P.* (*P.*) *obuti*, *P.* (*P.*) *insectiformis* and *P.* (*P.*) *inopinatus*; *P.* (*P.*) *obuti* to *Corbograptus*, *Dittograptus* and *Victorograptus*; *P.* (*P.*) *mutabilis*/*obuti* to *Petalolithus*; (3), *Sudburigraptus* to *Rivagraptus cyperoides*, *R. rozmanae*, *R. sentus*, *R. inconstans* and *R. bellulus*; and *Rivagraptus* to *Agetograptus*.

LOWER Silurian graptolite-bearing strata are widely distributed in the Mugodzhary Range of the southern Urals. They are especially well known in numerous localities in the Kos-Istek region between the rivers Or' and Ilek (Pavlinov 1937; Leonenok 1955; Text-fig. 1) and the graptolites collected from this region form the basis of this paper. A sequence of black, carbonaceous, silicified shales and cherts, about 300 m thick, has been assigned to the Sakmara Formation.

Exposures usually occur on low, flat hills and alongside small creeks. All the graptolite collections were made in the 1970s during mapping projects, led by many regional geologists, and in which one of the authors (TNK) participated. In some cases, small trenches were dug specially to collect graptolites, though the best preserved examples come from weathered shales or cherts. The graptolite assemblages encompass the Rhuddanian, Aeronian and part of the lower Telychian. In this paper we concentrate on new discoveries among the biserial component of the faunas.

Long, continuous sequences are difficult to find, because of generally poor exposure. In addition, complicated tectonic structures are characteristic of the region. The Sakmara Formation is involved in several nappes and tectonic slices, and the stratigraphy can be reconstructed only by using graptolite assemblages.

No other fossils, except radiolarians and algae, have been found in these deposits, which are typical deep-water hemipelagic sediments.

The following assemblages have been established, from the base upwards:

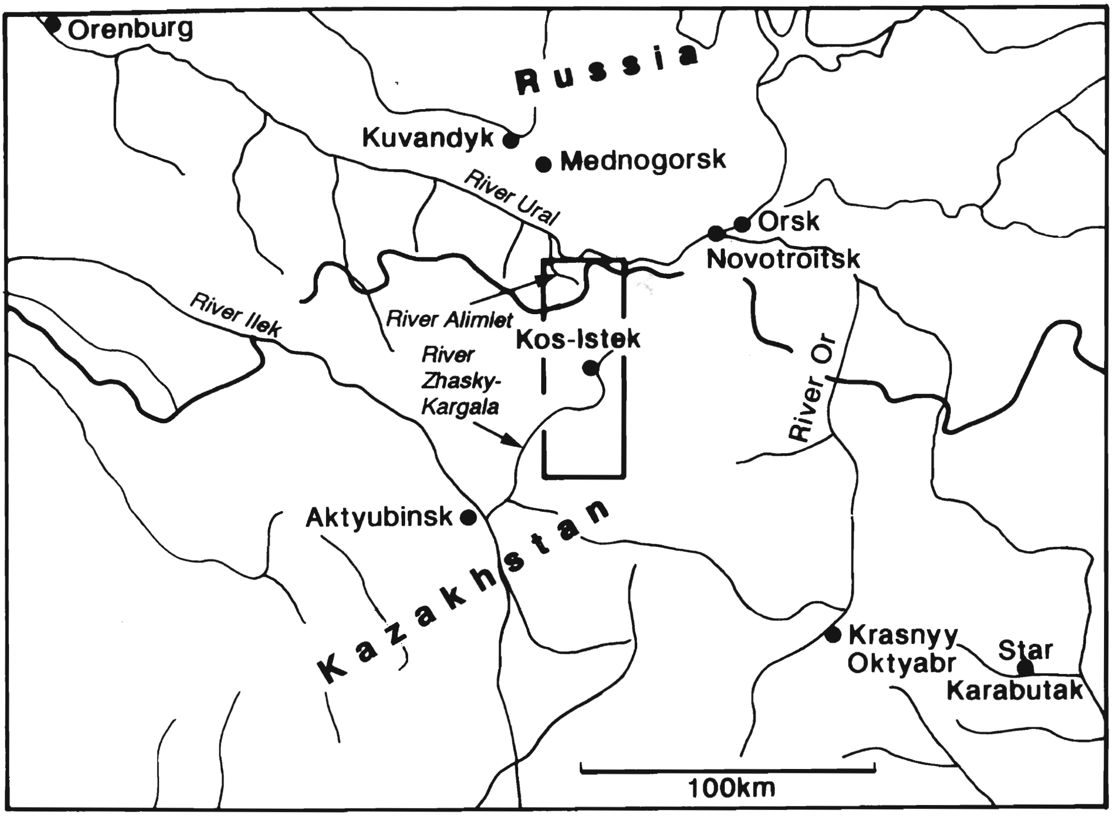
The ascensus-acuminatus *Biozone*

Neodiplograptus sp., *Normalograptus* cf. *balticus* (Pedersen), *N.* cf. *mirnyensis* (Obut and Sobolevskaya; Pl. 5, fig. 1), *N. trifilis* (Manck), *Hirsutograptus longispinosus* gen. et sp. nov., *H. villosus* gen. et sp. nov., *Parakidograptus acuminatus* (Nicholson) and *Akidograptus ascensus* Davies.

In addition to both zonal species occurring together, *ascensus* being the more common, the most peculiar feature of the assemblage is the presence of numerous and very characteristic spiny diplograptaceans assigned to *Hirsutograptus* gen. nov.

The vesiculosus *Biozone*

Glyptograptus bulbus sp. nov., *Cystograptus vesiculosus* (Nicholson), *Normalograptus normalis* (Lapworth; Pl. 5, figs 2–3, 6), *Paraclimacograptus innotatus* (Nicholson), *Dimorphograptus erectus* (Elles and Wood), *Metaclimacograptus undulatus* (Kurck) and *Atavograptus* ex. gr. *atavus* (Jones).



TEXT-FIG. 1. Geographical location of the southern Urals locality. The Mugodzhary Range is on the Russia/Kazakhstan border between the rivers Alimlet and Zhaksy-Kargala.

Among these species *Cy. vesiculosus* is most common and represented by specimens at various astogenetic stages. Atavograptids, common elsewhere at this stratigraphical level (e.g. *atavus* Biozone of Great Britain), are not well preserved and are uncommon. The other diagnostic feature of the biozone is the incoming of *D. erectus* and *Me. undulatus*.

The cyphus *Biozone*

Glyptograptus aff. *elegans* Packham, *G. tamariscus nikolayevi* Obut, *Normalograptus normalis* (Lapworth), *N. rectangularis* (McCoy; Pl. 5, figs 4–5, 7–8), *Paraclimacograptus innotatus* (Nicholson), *Pseudorthograptus* (*Pseudorthograptus*) *inopinatus* Bouček, *P.* (*P.*?) sp. C, *P.* (*P.*) sp. D; *P.* (*P.*) sp. F, *Rivagraptus inconstans* gen. et sp. nov., *P.* (*Dimorphograptoides*) *physophora* (Nicholson), *Corbograptus enigmatica* gen. et sp. nov., *Dimorphograptus confertus swanstoni* Lapworth, *Rhaphidograptus toernquisti* (Elles and Wood), *Metaclimacograptus hughesi* (Nicholson), *Me. undulatus* (Kurck), *Monograptus revolutus* Kurck and numerous badly preserved atavograptids.

This assemblage is much more diverse than those of earlier biozones because of evolutionary radiations in some phylogenetic stocks. Especially noticeable is a radiation within the glyptograptids, as well as in the new pseudorthograptid and rivagraptid lineages. Monograptids are more diverse but are still not very common.

The gregarius *Biozone*

Glyptograptus cf. *enodis enodis* Packham, *G. incertus* Elles and Wood, *G.* aff. *serratus* Elles and Wood, *G.* cf. *serratus* Elles and Wood, *G. tamariscus distans* Packham, *G. t. linearis* Perner, *G. tamariscus tamariscus* Nicholson, *Pseudoglyptograptus* sp., *Normalograptus medius* (Törnquist), *N. miserabilis* (Elles and Wood), *N. normalis* (Lapworth), *N. rectangularis* (McCoy), *Petalolithus folium* (Hisinger), *Pe. minor* (Elles), *Pe. wuxiensis* Ye, *Pe.* sp. A, *Pe.* sp. B, *Parapetalolithus* cf. *kurcki* (Rickards), *Pa.* sp. A, *Rivagraptus rozmanae* gen. et sp. nov., *R. sentus* gen. et sp. nov., *Agetograptus primus* (Obut and Sobolevskaya), *Pseudorthograptus* (*Pseudorthograptus*) *obuti* (Rickards and Koren'), *P.* (*P.*) *inopinatus* (Bouček), *P.* (*P.*) sp. B, *P.* (*P.*) sp. C, *P.* (*P.*) sp. D, *P.* (*P.*) sp. F, *Metaclimacograptus hughesi* (Nicholson), *Me. khabakovi* sp. nov., *Monograptus argenteus* (Nicholson), *M. communis* Lapworth, *M. difformis* Törnquist, *M. elegans* (Koren'), *M. limatulus* Törnquist, *M. lobiferus* (McCoy), *M. millepeda* (McCoy), *M. pectinatus* Richter, *M. toernquisti sensu* Sudbury, *M. triangulatus triangulatus* (Harkness), *Coronograptus gregarius* (Lapworth), *Lagarograptus inexpeditus* Obut and Sobolevskaya, '*Pristiograptus*' *fragilis* (Rickards), *Rastrites longispinus* Perner and *Ra. peregrinus* Barrande. In the upper part of the biozone *Victorograptus morosus* gen. et sp. nov., *P.* (*P.*) *insectiformis minutus* (Churkin and Carter), *R. bellulus* (Törnquist) and *P.* (*P.*) sp. A are also found.

The *gregarius* Biozone assemblage is the highest in diversity in the Llandovery in the southern Urals, as in many other regions. This is partly because it is an extensive stratigraphical interval which, in the present state of knowledge in the Urals, cannot yet be subdivided. Radiations in several lineages are responsible for the great diversity of diplograptaceans possessing thecal and sicular spinosity, including pseudancora, meshwork and connected membraneous structures. Among them, pseudorthograptids and petalolithids are the most important. Those with a simple virgella, but well developed thecal apertural spines, are represented by several species of the new genus *Rivagraptus* together with *Agetograptus*. Another typical feature of the assemblage is the sudden diversification of the metaclimacograptids; the sudden incoming of a much more diverse monograptid fauna is a well-known, diagnostic feature of this part of graptolitic sequences everywhere.

The convolutus *Biozone*

Glyptograptus ex. gr. *tamariscus* Lapworth, *Normalograptus medius* (Törnquist)?, *N. normalis* (Lapworth)?, *N. rectangularis* (McCoy), *Petalolithus folium* Hisinger, *Pe. minor* Elles, *Cephalograptus cometa extrema* Bouček and Přibyl, *C. tubulariformis* (Nicholson), *Parapetalolithus* ex gr. *palmeus* (Barrande), *Pseudorthograptus* (*Pseudorthograptus*) sp. A, *P.* (*P.*) sp. G, *M. communis* Lapworth, *M. convolutus* (Hisinger), *M. decipiens* Törnquist, *M. denticulatus* Törnquist, *M. elegans* (Koren'), *M. lobiferus* McCoy, *M. toernquisti sensu* Sudbury, *M. undulatus* Elles and Wood, *Rastrites approximatus* Lapworth and *Ra. phleoides* Törnquist.

In this assemblage diplograptaceans are represented by less morphologically diverse taxa and mostly by those known in the preceding biozone. Parapetalolithids possessing a simple virgella, with no pseudancora, are an exception, but they are quite rare. In fact, this assemblage is more distinguishable by its rich, new, monograptid fauna. Some speciation takes place in petalolithid stocks, such as in the *Pe. folium* line, resulting in the appearance of several species of *Cephalograptus* during the late *convolutus* Biozone.

The sedgwickii *Biozone*

The *sedgwickii* Biozone has been recognized within the area by the occurrence of the eponymous species; no other graptolites were found.

TABLE 1. Classification of Silurian graptoloids. * = described; 0 = figured only; x = neither described nor figured.

	Diplograptacea Lapworth, 1873, emend.
	Glyptograptidae Mitchell, 1987 (*normalis* [H] and *tamariscus* [I] development)
	Glyptograptus Lapworth, 1873, emend.
*	*auritus* Bjerreskov, 1975
*	*bulbus* sp. nov.
*	aff. *elegans* Packham, 1962
*	cf. *enodis enodis* Packham, 1962
*	*incertus* Elles and Wood, 1907
*	cf. *serratus* Elles and Wood, 1907
*	aff. *serratus* Elles and Wood, 1907
*	*t. tamariscus* (Nicholson, 1868)
*	*t. distans* Packham, 1962
*	*t. linearis* Perner, 1897
*	*t. nikolayevi* Obut, 1965
	Pseudoglyptograptus Bulman and Rickards, 1968
*	sp.
	Comograptus Obut and Sobolevskaya, 1968
	Persculptograptus gen. nov.
	Cystograptus Hundt, 1942
*	*vesiculosus* (Nicholson, 1868)
	Neodiplograptus Legrand, 1987
*	*korinevskii* sp. nov.
*	sp.
	Normalograptus Legrand, 1987
*	cf. *balticus* (Pedersen, 1922)
x	*medius* (Törnquist, 1897)
x	*miserabilis* (Elles and Wood, 1906)
o	cf. *mirnyensis* (Obut and Sobolevskaya, 1967)
o	*normalis* (Lapworth, 1877)
o	*rectangularis* (McCoy, 1850)
*	*trifilis* (Manck, 1923)
	Hirsutograptus gen. nov.
*	*villosus* sp. nov.
*	*longispinosus* sp. nov.
	Victorograptus gen. nov.
*	*morosus* sp. nov.
	Sudburigraptus gen. nov.
*	sp. A
	Paraclimacograptus Přibyl, 1947
*	*innotatus* (Nicholson, 1869)
	Petalolithus Suess, 1851
*	*folium* (Hisinger, 1837)
*	*minor* (Elles, 1897)
*	*ovatoelongatus* (Kurck, 1882)
*	*wuxiensis* Ye, 1978
*	sp. A
	Cephalograptus Hopkinson, 1869
*	*cometa extrema* Bouček and Přibyl, 1941
x	*tubulariformis* (Nicholson)
	Parapetalolithus gen. nov.
*	*dignus* sp. nov.
*	cf. *kurcki* (Rickards, 1970)
*	ex gr. *palmeus* (Barrande, 1850)
*	sp. A

TABLE 1. (*Cont.*)

	Rivagraptus gen. nov.
*	*bellulus* (Törnquist, 1890)
*	*cyperoides* (Törnquist, 1897)
*	*inconstans* sp. nov.
*	*rozmanae* sp. nov.
*	*sentus* sp. nov.
	Agetograptus Obut and Sobolevskaya, 1968
*	*primus* Obut and Sobolevskaya, 1968
	Pseudorthograptus (*Pseudorthograptus*) Legrand, 1987
*	*obuti* (Rickards and Koren', 1974)
*	*insectiformis minutus* (Churkin and Carter, 1970)
*	*inopinatus* (Bouček, 1944)
*	*mutabilis* (Elles and Wood, 1907)
*	spp. A–G
	Pseudorthograptus (*Dimorphograptoides*) subgen. nov.
*	*physophora* (Nicholson, 1868)
*	cf. *physophora* (Nicholson, 1868)
	Dittograptus Obut and Sobolevskaya, 1968
	Corbograptus gen. nov.
*	*enigmatica* sp. nov.
	Akidograptidae Li and Ge, 1981 (*ascensus* [J] development)
	Akidograptus Davies, 1929
*	*ascensus* Davies, 1929
	Parakidograptus Li and Ge, 1981
*	cf. *acuminatus* (Nicholson, 1867)
	Dimorphograptidae Elles and Wood, 1908
	Dimorphograptus Lapworth, 1876
*	*erectus* Elles and Wood, 1908
*	*confertus swanstoni* Lapworth, 1876
	Rhaphidograptus Bulman, 1936
*	*toernquisti* (Elles and Wood, 1906)
*	*extenuatus* (Elles and Wood, 1908)
	Metaclimacograptidae fam. nov. (*normalis* [H], ? *tamariscus* [I] development)
	Metaclimacograptus Bulman and Rickards, 1968
*	*hughesi* (Nicholson, 1869)
*	*khabakovi* sp. nov.
*	*khvorovi* sp. nov.
*	*orcus* sp. nov.
*	*undulatus* (Kurck, 1882)
	Retiolitidae Lapworth, 1873 (none described in this paper)
	Monograptacea Lapworth, 1873 (none described in this paper)
	Monograptidae (see New Classification section)

The guerichi (*formerly* minor) –turriculatus *Biozone*

Glyptograptus auritus Bjerreskov, *Parapetalolithus dignus*, gen. et sp. nov., *Petalolithus ovato-elongatus* (Kurck), *Pseudoplegmatograptus obesus* (Lapworth), *Monograptus halli* (Barrande), *Monograptus guerichi* (Loydell, Štorch and Melchin), *M. turriculatus* among other monograptids.

Diplograptaceans are not well known from this stratigraphical level in this area. Among them are several last appearances of glyptograptids, parapetalolithids, and petalolithids. The recognition of the *guerichi* and *turriculatus* biozones is based mostly on the diagnostic biozonal species.

A NEW CLASSIFICATION OF LLANDOVERY BISERIAL GRAPTOLOIDS

Few workers dispute Fortey and Cooper's (1986) definition of the Suborder Virgellina, or their emendation of Lapworth's (1873) superfamily Diplograptacea. In this paper we accept these definitions as our starting point for a revision of Silurian biserials. The extensive analysis of the Diplograptacea by Mitchell (1987) is, in our view, largely applicable to the Ordovician biserials, but hardly touches upon problems raised by Silurian biserials which evolved for the most part in the early Llandovery re-establishment of a diverse graptoloid plankton. Thus Mitchell places Silurian biserials in only two of his pattern groupings, namely H and I; although subsequently Melchin and Mitchell (1991) paid more attention to Silurian diversification, introducing two further categories of proximal development, namely J and M for dimorphograptids and monograptids respectively. The general attribution of these patterns is supported by ourselves (Table 1), but it is important to recognize that details of development are still known in relatively few species, and that the Silurian diversification described in this paper hinges on many more varied morphological features than the necessarily simple proximal development displayed in categories H–J and M.

The developmental categories can be defined as follows:

Category/Pattern H (Mitchell 1987; emend. Melchin and Mitchell 1991). $Th1^2$ foramen on $th1^1$ protheca; early fuselli growing on this foramen meld later with $th1^2$ dorsal flange developed on $th2^1$ (e.g. *Normalograptus normalis* (Lapworth)).

Category/Pattern I (Mitchell 1987; emend. Melchin and Mitchell 1991). Differs from H only in that the downgrowing part of $th1^1$ is usually relatively short and positioned near the sicular aperture and there is no foramen of $th1^2$ in the same sense as in H; and point of origin of $th1^2$ is higher (e.g. *Glyptograptus tamariscus* (Nicholson)).

Category/Pattern J (Melchin and Mitchell 1991). Downward growing portion of $th1^1$ even shorter and $th1^1$ more upward growing and closer to rhabdosomal axis (e.g. *Akidograptus ascensus* Davies).

Category/Pattern M (Melchin and Mitchell 1991). $Th1^1$ upward growing, probably in all species (e.g. *Atavograptus ceryx* (Rickards and Hutt, 1970)).

The use of letters to designate developmental types is perhaps not a good idea, simply from the point of view of ease of communication: it has the same drawbacks as numerical notation systems in stratigraphical nomenclature (Rickards 1995). For that reason we suggest that the H–J and M patterns should be entitled after species typical of the pattern, as follows: H = *normalis* Pattern; I = *tamariscus* Pattern; J = *ascensus* Pattern; M = *ceryx* Pattern. (We note that Melchin and Mitchell's (1991) statement concerning their fig. 2.12 illustration of *Atavograptus ceryx* that it is reconstructed after Rickards and Hutt, 1970 is misleading: fig. 2.12 is, in fact, a copy of the Rickards and Hutt fig. 1*b* with some distal thecae added, possibly hypothetically).

The *normalis* Pattern originated in the Ordovician and, indeed, most of the forms listed by Mitchell (1987) are Ordovician species of *Climacograptus*, *Glyptograptus* and *Diplograptus*. *N. normalis* itself appears late in the Ordovician and persists well into the Silurian, possibly as high as the *convolutus* Biozone. In the text below, the family Metaclimacograptidae is referred to the *normalis* Pattern (H, *sensu* Mitchell 1987).

The *tamariscus*, *ascensus* and *ceryx* patterns are almost entirely Silurian, the first two probably being restricted to the Llandovery and early Wenlock in the sense that the development patterns for the later Wenlock and Ludlow retiolitids are uncertain in the Mitchell (1987) scheme of things. The *ascensus* Pattern includes biserials and uni-biserials and the *ceryx* Pattern only uniserials. There is, therefore, a gradual shift in developmental style from biserial to uni-biserial to uniserial form, but the overall change is necessarily small simply because few morphological options are open, at least in terms of developmental detail. The changes are of an order of magnitude less than the change from styles A to G of Mitchell (1987). Our feeling is that on present information about Silurian developmental details the concepts of developmental styles H–J and M are not all that useful. In particular, there is certainly considerable variation in such morphological factors (listed by Mitchell 1987) as sicular length, and whether or not the sicular aperture possesses only a virgella or has additional processes (see Systematic Palaeontology below).

An area where there is more disquiet concerns Mitchell's (1987) redefinition of the Monograptidae to include H–J pattern biserials. This seems to us to place an unnecessary burden on interpreting past or present literature, especially with regard to biostratigraphical discussions. For example, the monograptids have been a very clear indicator of very latest Ordovician to Devonian strata based on their characteristically uniserial scandent stipes. To include biserials and uniserials, of both Ordovician and Silurian age, seems to us to risk great confusion in biostratigraphical analyses. We do not dispute his cladistical analysis and the deduced conclusions on broad phylogenetic relationships, but for very practical reasons recommend retaining the family Monograptidae in its long-used sense (see Bulman 1970) and follow Loydell (1992) in placing this family in the Monograptacea. This necessarily means that our concept of the Diplograptidae differs from that of Mitchell (1987) and Melchin and Mitchell (1991). We would place the subfamily Eoglyptograptinae in the Diplograptidae (that is, taken out of the Monograptidae *sensu* Mitchell 1987; Melchin and Mitchell 1991), and raise the subfamilies Akidograptinae, Dimorphograptinae, Retiolitinae and Monograptinae to familial status (see Table 1). The remaining Silurian genera, including our new genera, are placed in the Glyptograptidae (including some biserials such as *Petalolithus* placed in the Retiolitinae by Mitchell 1987, fig. 16). Our view is that this reflects better the essentially Silurian origin and diversification of the great majority of glyptograptids, dimorphograptids, retiolitids, and monograptids. It does not detract in any way from the suggested phylogenetic relationships suggested by Mitchell's (1987) analysis. In addition we recognize the Akidograptidae and Metaclimacograptidae simply because of the spectacular morphological changes that have taken place in their evolutionary lineages (despite little change in the *developmental* style). Štorch and Serpagli (1993) erected the family Normalograptidae to encompass the genera *Normalograptus*, *Neodiplograptus* and *Cystograptus*. Further revision of Silurian diplograptids may show this to be practicable, but for the present we are reluctant to use Normalograptidae.

Table 1 summarizes our proposed classification and the fauna described in the Systematic Palaeontology section, where full definitions are given when emendation has taken place. It should be noted that the Glyptograptidae embraces 20 genera and subgenera, a diversification comparable with that of the Ordovician biserials which are represented by no less than 11 striking developmental patterns (A, A^1–G, J–K) as compared with four weakly differentiated ones in the Silurian. Our views on the generic and specific relationships disclosed by the Uralian fauna are discussed in the evolution section.

Our classification reflects at least a broad phylogeny although we have been only partially successful in defining individual species lineages: the reasons for this are discussed at appropriate points in the evolutionary section. The main features used in the classification are as follows:

1. Thecal form. In many instances much more subtle aspects of thecal form can be recognized than hitherto, such as the distinctions between the 'orthograptid' thecae of *Rivagraptus* and *Dittograptus*.
2. Absence, presence and nature of thecal and sicular apertural *and other* spines. Again, a new and surprising diversity of forms is revealed by this fauna.
3. Whether the sicula is virgellate (only), ancorate or pseudancorate: the last feature in particular is much more widely recognized, and more variable, than hitherto supposed.
4. Presence and nature of rhabdosomal membranes.
5. Presence of unusual extrathecal meshworks and pseudo-retiotilid meshworks (e.g. *Corbograptus* gen. nov.).

The Uralian fauna is at present unique in that, in addition to the usual common Llandovery species, which enable precise dating and correlation of the strata, there is a suite of spectacular forms such as *Hirsutograptus* gen. nov., *Victorograptus* gen. nov. and *Rivagraptus* gen. nov.: only glimpses of these rhabdosomal types have so far been detected in other regions, and it seems unlikely that their recognition in the Urals is due solely to exceptional preservation.

TABLE 2. Distribution of rhabdosomal spines and pseudancora in diplograptacean genera.

Non-spinose	Virgellate	*Sudburigraptus*
		Parapetalolithus
	Pseudancorate	*Akidograptus*
		Petalolithus
Sicular spinosity	—	*Glyptograptus* (*pars*)
		Pseudoglyptograptus (*pars*)
		Comograptus
		Hirsutograptus
Thecal spinosity (genicular)	Virgellate	*Hirsutograptus*
		Comograptus
	Pseudancorate	*Dittograptus*
		Victorograptus
Thecal spinosity or mucrosity	Virgellate	*Rivagraptus*
(ventral or ventro-lateral)	Pseudancorate	*Pseudorthograptus*
		Dittograptus
Thecal spinosity (lateral)	Virgellate	*Agetograptus*

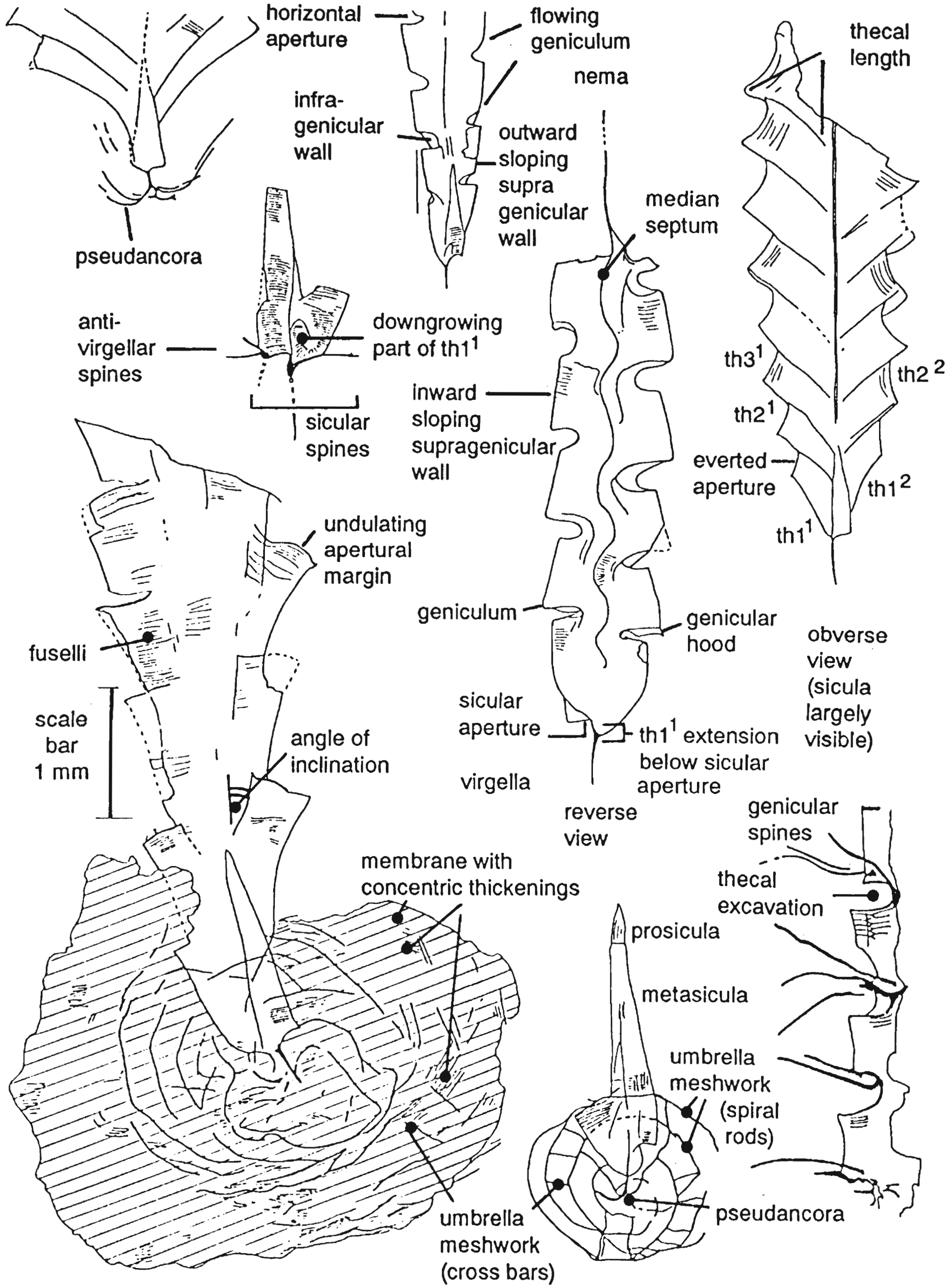
MORPHOLOGICAL NOVELTIES

The extent of sicular and rhabdosomal spinosity and meshworks/membranes in Silurian biserial graptoloids has not been fully appreciated previously (but see Chen and Lin 1978; Bates and Kirk 1992). Although virgellar division, usually simple bifurcations, had been known for many years it was not until the work of Hutt *et al.* (1970) that virgellar meshworks were identified. Rickards and Koren' (1974) described such structures in *Orthograptus insectiformis* (Nicholson) and *O. obuti* (Rickards and Koren'), as well as extensive sicular apertural spinosity in *Pseudoglyptograptus* spp.: whether the latter involved virgellar divisions or apertural spines was uncertain, although in some specimens a robust virgella seemed undivided. The Urals collections show that such structures are widespread and are important in taxonomy.

Virgellar division appears in the *ascensus-acuminatus* Biozone, at the very base of the Silurian, and some of our specimens of *Akidograptus* suggest at least rudimentary meshwork systems rather than merely dichotomous divisions. In the succeeding *vesiculosus* Biozone (= *atavus* Biozone of Britain) virgellar meshworks and the first membranes were well established in *Pseudorthograptus* (*Pseudorthograptus*) *mutabilis* (Elles and Wood) and *P.* (*Dimorphograptoides*) *physophora* (Nicholson). In the lower *gregarius* Biozone there was considerable diversification (Text-fig. 3) resulting in *Dittograptus*, *Corbograptus* and the first *Petalolithus* spp. with virgellar divisions. These are referred to throughout this text as pseudoancorae, although it should be borne in mind that the structures may be homologous with the ancorae of retiolitids (see Mitchell 1987 for a summary of the observations, arguments and implications).

Of other rhabdosomal spines we are aware only of sicular and thecal spines in *Hirsutograptus* and *Normalograptus trifilis* (Manck) from the *ascensus-acuminatus* Biozone: after that they appear in several lineages in the *gregarius* Biozone, notably in the genera *Rivagraptus*, *Agetograptus*, *Victorograptus* and *P.* (*Pseudorthograptus*). Pseudorthograptids prior to the *gregarius* Biozone have blunt apertural process but seemingly lack spines.

Table 2 summarizes the types of rhabdosomal spines and the taxonomic distribution of these in virgellate and pseudancorate rhabdosomes. On present information, thecal spinosity is rare in other groups, but does occur in *Glyptograptus serratus barbatus* Elles and Wood (*sedgwickii* Biozone) and *Comograptus comatus* Obut and Sobolevskaya (*triangulatus* Biozone): we comment on the former in our definition of *Comograptus*. Spinosity specific to the sicula occurs in *Hirsutograptus* and *Normalograptus trifilis* (Manck) in the *ascensus-acuminatus* Biozone but thereafter is absent until the



TEXT-FIG. 2. Morphological terms used in this paper. For additional definitions, see section on morphological novelties.

triangulatus Biozone (*Pseudoglyptograptus rhayaderensis* Rickards and *P. tabukensis* Rickards and Koren'). *G. serratus barbatus* also has sicular spines, as does *Co. comatus*. In most of these groups sicular spinosity seems to be useful in characterizing taxa at species level, but no higher, whereas thecal spinosity, virgellar membranes and virgellar meshworks seem to be of value at generic level even though having species-specific features (Text-fig. 3).

Text-figure 2 summarizes the morphological terms used in this work. Thecal spacing is given in measurements of the number of thecae in a unit length, 5 mm or 10 mm in most cases. In some cases where a more precise measure of spacing change is needed, we use the method advocated by Packham (1962) where one or two thecae are measured and this figure is 'translated' to a thecae per 10 mm figure. Both systems are clear in context; and both are easily comparable with earlier literature, which uses one or other as a rule. However, we do not like the 2TRD method suggested by Howe (1983) since it does not, in our view, convey a ready picture of the thecal size and spacing, is not readily comparable with most previous literature figures, and does not improve on the Packham (1962) method of registering small changes.

The term *pseudancora* we use to describe rapid and multiple divisions of the virgella resulting in an upward-growing *umbrella* around the proximal part of the rhabdosome, and which resembles, but may not be homologous with, the *ancora* in some retiolitids. The *meshwork* is a combination of concentric and radial rods (or cross bars) which derive certainly from the earlier stages of the pseudancora, and which often support a *membrane*. The *membrane* is of unknown nature, roughly resembling thin periderm, occasionally with faint striations visible upon it.

It is difficult to judge how widespread are the ancorate structures described in this paper: certainly, exceptional preservation is needed for them to be visible. The same argument can be used with respect to delicate and/or small spinose structures such as those described in *Rivagraptus* gen. nov. Our opinion is that these structures do not represent a local biofacies of Kazakhstan but that they will, eventually, be found to be widespread: for example, RBR (unpublished data) has identified *Rivagraptus* (*Rivagraptus*) cf. *sentus* sp. nov. and *Pseudorthograptus* (*Pseudorthograptus*) *inopinatus* Bouček in Victoria, Australia. It is usually possible to decide whether the virgella of a particular species is a single spike, or whether it is divided. Even a slightly divided virgella, as seen in some akidograptids, must indicate the potential for ancorate basketworks.

EVOLUTION OF THE LLANDOVERY BISERIAL GRAPTOLOIDS

Text-figure 3 depicts our interpretation of the evolution of the spinose biserial genera and species, and their relationships to some of the non-spinose genera. Many of the forms are new, and the result is an overall picture not seen before, because most sections show only a few of these species, and then they are not always well preserved (for example, the pseudancora and thecal spinosity in such forms as *Pseudorthograptus* (*P.*) *insectiformis* may be absent or uninterpretable).

The earliest genus is *Hirsutograptus*, restricted to the *ascensus-acuminatus* Biozone at the base of the Silurian. Two species have been distinguished: *H. longispinosus* gen. et sp. nov. and *H. villosus* gen. et sp. nov. In essence *Hirsutograptus* is a tiny normalograptid with an abundance of genicular and other spines, notably proximal sicular and thecal spines. The development pattern is not clear, but may be of *normalis* or *tamariscus* type. If the spines are ignored, the rhabdosome is tiny, septate, closely resembling that of *Normalograptus* species, such as *N. mirnyensis* (Obut and Sobolevskaya) and *N. acceptus* (Koren' and Mikhaylova; see also Koren' *et al.* 1983), with close thecal spacing and relatively long supragenicular walls. It seems almost certain that one of these late Ordovician/early Silurian normalograptids is the ancestor of the *Hirsutograptus* species, although there is a slight resemblance of the supragenicular wall to some small forms of *Paraclimacograptus*: *Par. innotatus exquisitus* (Rickards, 1970) has similar small dimensions, but this form has not been recorded below the *atavus* Biozone.

Victorograptus morosus gen. et sp. nov., from high in the *gregarius* Biozone, has a superficial resemblance to *Hirsutograptus* (especially *H. longispinosus*) in having pronounced genicular spines and, possibly, 'climacograptid' thecae. However, it seems unlikely that they are directly related, partly because of the as yet unbridged time gap of three biozones, but also because the pseudancora and meshwork of *Victorograptus* may link *V. morosus* more closely to the coeval *Dittograptus* which may have some genicular spines. The main difference between the two genera is that *Dittograptus* has pseudorthograptid thecae and *Victorograptus* possibly 'climacograptid' thecae (see further comments on this in the systematic descriptions). There are, therefore, two reasonable options for the derivation of *Victorograptus*, of which we favour *Dittograptus* or a pseudorthograptid.

As is the case in so many Llandovery groups, the pseudorthograptids show two major phases of evolution: the earliest Llandovery phase, part of the post-glacial recuperation of plankton; and a phase beginning in the *triangulatus* Biozone. With the genus *Pseudorthograptus* the second is the more spectacular.

In the *atavus* to *cyphus* biozones *P.* (*Pseudorthograptus*) *mutabilis*, *P.* (*P.*) *obuti* and *P.* (*Dimorphograptoides*) *physophora* are similar forms (the specific differences being described carefully in the systematic section). It seems likely that the third derived from *P.* (*P.*) *mutabilis* by development of a 'uniserial' portion, thus paralleling similar evolution in other lineages. In this case the 'uniserial' portion is achieved by the excessive length of $th1^2$ which opens above the aperture of $th2^1$, as in *Agetograptus* (see below). *P.* (*P.*) *obuti* is a *cyphus* Biozone derivative of the earlier *P.* (*P.*) *mutabilis*: the thecal processes bifurcate and are more strongly developed in the former, a tendency that continued in later pseudorthograptids.

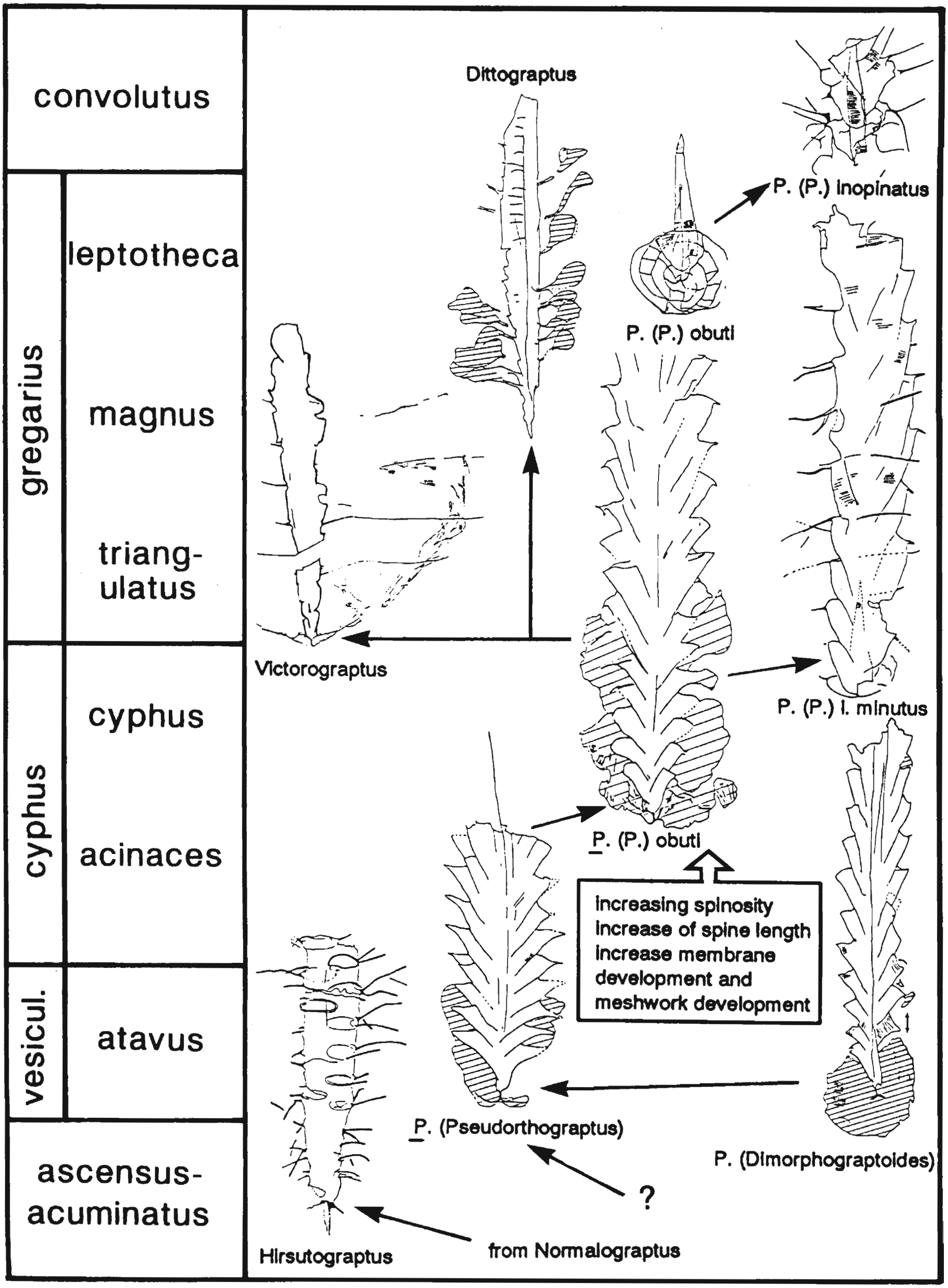
In the *triangulatus* Biozone (base of the *gregarius* Biozone) *P.* (*P.*) *obuti* continues, but gives rise here to the following forms: *P.* (*P.*?) sp. C, by excessive growth of the pseudancora which tightly envelops the rhabdosome; *Dittograptus*, by increased thecal or rhabdosomal spinosity and development of sac-like membranes along the length of the rhabdosome; and *Victorograptus*, by increased thecal geniculation, and the development of yet longer and more extensive spinose structures and membranes, and genicular (as opposed to thecal ventral) spines.

Above the *triangulatus* level, the main line of *P.* (*Pseudorthograptus*) evolution continues (Text-fig. 3) resulting in such forms as *P.* (*P.*) *insectiformis* and *P.* (*P.*) *inopinatus*. These changes also result in increased rhabdosomal spinosity.

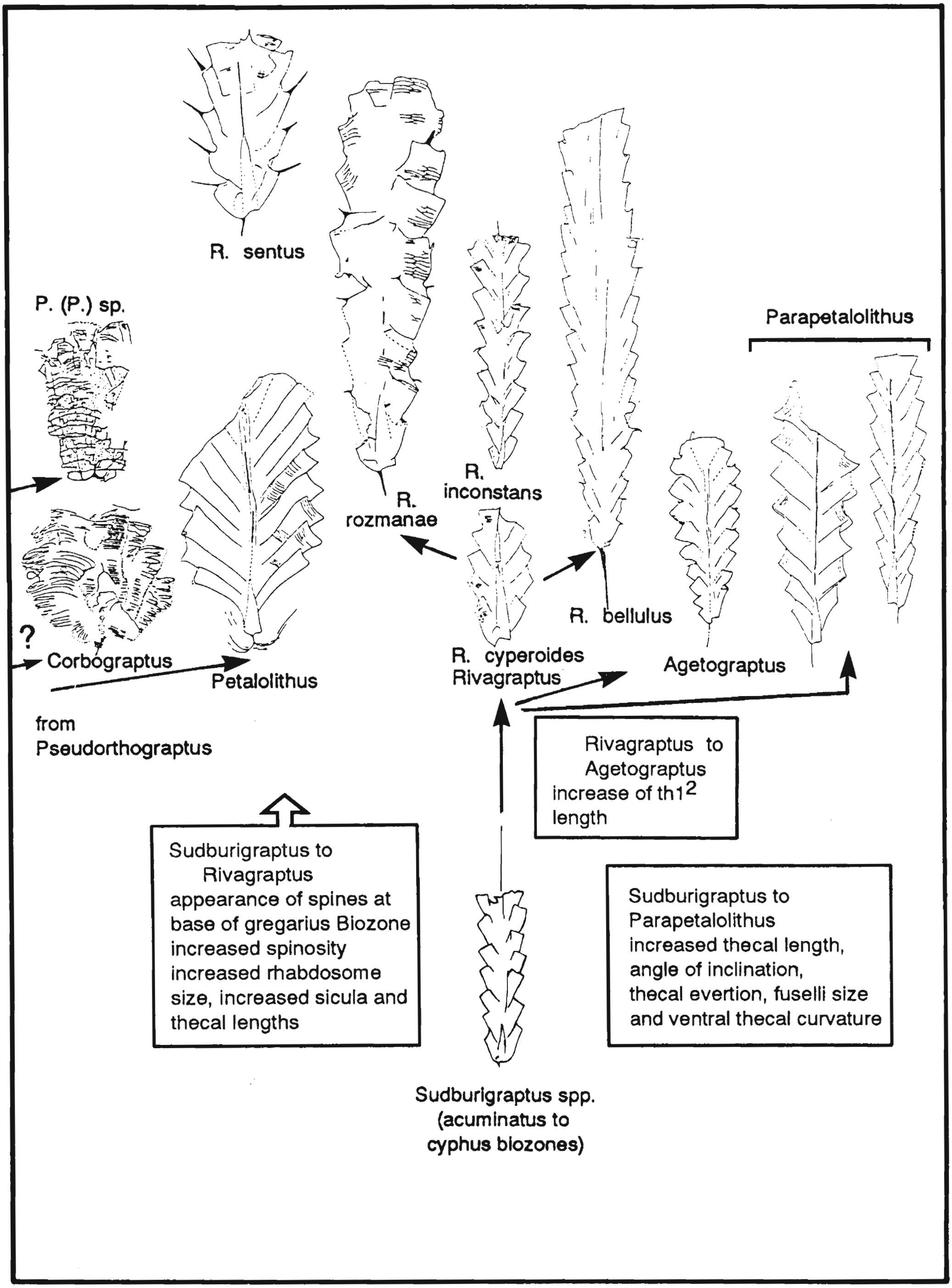
It should be noted that *Rivagraptus* and *Agetograptus* are also part of the lower *gregarius* evolutionary explosion: they have not, so far, been found below this level but range upwards into the *sedgwickii* Biozone. They also exhibit reasonable diversity. In contrast to the *Pseudorthograptus* lineages their spinosity is more subdued and they have an undivided virgella and no other sicular spines, and totally lack membranes. The long-ranging *R. cyperoides*, a species which may lack spines or have small ventral apertural spines, seems to be central to the evolution of the genus: it is the earliest and outlasts the others. *Agetograptus primus* Obut and Sobolevskaya was probably derived directly from *R. cyperoides* (Törnquist) in the *triangulatus* Biozone by elongation of $th1^2$ so that its aperture is above that of $th2^1$, and by having small lateral apertural spines and thecae inclined to the rhabdosomal axis at a higher angles.

Succeeding species of *Rivagraptus* do not exhibit the unusual proximal end of *Agetograptus*, but *R. rozmanae* sp. nov. (*gregarius* Biozone) and *R. sentus* sp. nov. (*convolutus* Biozone) are closely similar to the earlier *Agetograptus* but show progressive increase in thecal spinosity, lateral apertural spines being present in *R. rozmanae* and possibly ventral spines also in *R. sentus*, in which the thecal spines are also longer. *R. inconstans* sp. nov. (*gregarius* Biozone) and *R. bellulus* (Törnquist) (*convolutus* Biozone) are rather more robust forms with very similar rhabdosomes to *R. cyperoides* but with more constant spinosity. In general, there is a stratigraphical increase in rhabdosomal size in *Rivagraptus*, and an increase in the length of spines.

The origins of *Rivagraptus* itself must lie in the rare lineages previously referred to late amplexicaulid orthograptids ('*Rectograptus*') but which we prefer to place in a new genus *Sudburigraptus*. These have either *normalis* or *tamariscus* patterns of development, lack any form of thecal or sicular spines (save the virgella) and are remarkably inconspicuous and conservative. The genus includes: *Orthograptus eberleini* Churkin and Carter, 1970; *Orthograptus* sp. (?ex gr.



TEXT-FIG. 3. For legend see opposite.



TEXT-FIG. 3. Suggested evolution of the Llandovery spinose biserial graptoloids.

amplexicaulis Hall) (Rickards 1988); *Orthograptus truncatus abbreviatus* Elles and Wood, 1907 (*sensu* Toghill 1968 and Hutt 1974), '*Orthograptus*'? *cabanensis* Zalasiewicz and Tunnicliff, 1994 and *Orthograptus*? sp. Melchin (1989), and may derive from late Ordovician forms of *Rectograptus amplexicaulis* by loss of all proximal thecal and sicular spines. The rivagraptid derivatives, of course, have thecal spines with a quite different origin and which occur throughout the rhabdosome (but not on the free ventral wall of th1[1] as is the case in *Rectograptus*). *Sudburigraptus* is relatively rare in the Llandovery but forms may persist into the lower *gregarius* Biozone. Text-figure 3 illustrates such a species, but whether it should be referred to *Sudburigraptus* or is a diminutive parapetalolithid is perhaps open to question.

The origin of some parapetalolithids may rest here too. For example, *Parapetalolithus dignus* gen. et sp. nov., a very slim parapetalolithid, certainly has features recalling those of *Sudburigraptus* and perhaps it is borderline between the two genera. It seems to us, with Loydell (1992), that there are two basic groups of '*Petalolithus*', both having their origins in the *gregarius* Biozone. They originate independently and perhaps should be referred to different genera: *Parapetalolithus* gen. nov. and *Petalolithus*.

Group 1 are those relatively slender species, including *Pa. dignus*, with a simple virgella, slim rhabdosome and lacking strong ventral curvature of the thecal tubes: they probably originated from *Sudburigraptus* spp. Species in our material from Kazakhstan are *Pa. dignus* gen. et sp. nov., *Pa. kurcki* (Rickards)? and *Pa.* ex gr. *palmeus* (Barrande).

Group 2 are those forms with a strongly divided virgella (i.e. they are pseudancorate), in which the thecae tend to be ventrally curved and strongly everted in the apertural regions, and in which the rhabdosomes are relatively robust. Species in our material are *Pe. minor* (Elles), *Pe. ovatoelongatus* (Kurck), *Pe. folium* (Hisinger) and *Pe. wuxiensis* (Ye)?. *Cephalograptus cometa* (Geinitz) is certainly related to these forms in that there seems to be an evolutionary lineage from *Pe. folium* through *C. c. cometa* to *C. c. extrema*.

The metaclimacograptids from the Urals show an unexpected diversity with no less than five species, including the well known *Me. hughesi* (Nicholson) and *Me. undulatus* (Kurck), and, in addition, *Me. khabakovi* sp. nov., *Me. khvorovi* sp. nov. and *Me. orcus* sp. nov. The origin of metaclimacograptids may be as suggested by Rickards *et al.* (1977), through late Ordovician representatives of the genus *Pseudoclimacograptus*; or they may have been an independent line of evolution from diminutive normalograptids. Considering this last point further, it is clear that *Me. khabakovi* (Text-fig. 23B) differs from *Normalograptus* only in having a slightly smaller but more compact rhabdosome (with the higher thecal spacing and undulating median septum reflecting this compactness). The developmental style may be *normalis* Pattern in both *Me. khabakovi* and *Normalograptus*, but later metaclimacograptids *may* have a *tamariscus* Pattern.

Glyptograptus tamariscus (Nicholson) is the type species of the genus and the species group is largely Llandovery in age, but appears first in the *persculptus* Biozone (Koren' *et al.* 1979). Mitchell (1987) suggested his Pattern H (*normalis* Pattern herein) for development, but subsequently (Melchin and Mitchell 1991) changed this to Pattern I (*tamariscus* Pattern herein). Packham (1962), in his extensive study of the group, drew attention to the arbitrary differences between *G.* ex gr. *tamariscus* and some derived climacograptids, such as *Cl. tamariscoides* Packham. The use of *Climacograptus* in his sense, in which the infragenicular wall was inclined at 45° or more, was largely followed by other workers (e.g. Rickards *et al.* 1977) as a convenience. However, as pointed out by Mitchell (1987) such forms cannot be regarded as *Climacograptus sensu stricto* and they really should be encompassed in the definition of *Glyptograptus s. s.* or placed in new genera. In the systematic section we have redefined *Glyptograptus* and, as part of the definition, have embraced such 'climacograptids'.

Rickards *et al.* (1977) distinguished evolution of the *persculptus* group (fig. 8) from that of the *tamariscus* group (fig. 6), but the small, undescribed pre-late *acinaces* Biozone forms (except for *G. avitus* Davies) may, of course, derive from the *persculptus* group in the latest Ordovician: we have no good information to substantiate or refute this. *Glyptograptus* sp. (Rickards 1988) is an excellent example of a small, undescribed *tamariscus* group form, in this case from the *acuminatus* Biozone, which may have evolved from the *persculptus* group. '*G.*' *persculptus* itself possibly has a *normalis* Pattern of development but later forms in the lineages almost certainly have *tamariscus* Pattern developments (e.g. *Pseudoglyptograptus*) and others an *ascensus* Pattern (e.g. *Rhaphidograptus*), but this is in accord with similar changes taking place in parallel in other biserials (see above).

The genus *Glyptograptus* is well represented in the Uralian fauna with at least 11 different forms, but despite their often exquisite preservation they do not modify materially the evolutionary scenarios advanced by Packham (1962) and Rickards *et al.* (1977).

The Kos-Istek collections which form the basis of this work are housed in the museum of the A. P. Karpinsky All-Union Geological Research Institute (VSEGEI), St Petersburg (specimen numbers prefixed CNIGR Museum). Other abbreviations used are SM and X., both referring to specimens in the Sedgwick Museum, Cambridge.

SYSTEMATIC PALAEONTOLOGY

Suborder VIRGELLINA Fortey and Cooper, 1986
Superfamily DIPLOGRAPTACEA Lapworth, 1873 (emend. Fortey and Cooper, 1986)
Family GLYPTOGRAPTIDAE Mitchell, 1987

Diagnosis. Biserial or uni-biserial graptoloids with *normalis* (H) or *tamariscus* (I) development patterns; septate, aseptate or partially septate; stratigraphically younger taxa with proximal ends becoming increasingly protracted or with increasing upward growth of $th1^1$ and $th1^2$; virgellate or pseudancorate; thecae simple 'orthograptid' to doubly sigmoidal; thecae spinose or non-spinose, lacking free ventral wall spines on $th1^1$.

Remarks. There is a strong contrast with most Ordovician biserials, which commonly have rather broader, robust proximal ends relative to the dorso-ventral width of the mature rhabdosome, and very commonly have anti-virgellar sicular spines and spines on the free ventral walls of $th1^1$. Moreover, the development patterns (*sensu* Mitchell 1987) are more complex than *normalis* (H), which is the most complex seen in the Glyptograptidae.

Genus GLYPTOGRAPTUS Lapworth, 1873; emend herein

Type species. *Diplograpsus tamariscus* Nicholson, 1868; original designation, according to Bulman (1970); from the Llandovery of the English Lake District.

Diagnosis. Proximal development of *tamariscus* (I) Pattern: thecae with sigmoidal curvature varying from gentle to sharp ('climacograptid'); supragenicular wall vertical in some, to, more commonly, sloping outwards; apertures generally everted but may be horizontal; may be septate, aseptate or partially septate; thecal and sicular spinosity uncommon; nemal vanes not uncommon; sicula usually less than 2 mm long.

Glyptograptus auritus Bjerreskov, 1975

Text-figure 4A–B

1975 *Glyptograptus auritus* n. sp., Bjerreskov, p. 31, pl. 4G; text-fig. 11E.
1992 *Glyptograptus auritus* Bjerreskov, 1975; Loydell, p. 27; pl. 1, figs 1–2; text-fig. 11, fig. 20.

Material. Three flattened specimens, from localities 671-1-7, 671-14 and 671-8/74-59 in the Zhaksy-Kargala Valley.

Horizon. Telychian, *turriculatus* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome 5–6 mm long, septate; tapering gradually from 0·6–0·7 mm wide at $th1^1$ aperture to 1·2 mm at $th6^1$; thecal spacing 12–14 in 10 mm; thecal overlap about one-half; $th1^2$

rather long, resulting in marked alternation of thecal apertures; thecal apertures at right angles to thecal tubes; thecal tubes approximately 1·0–1·2 mm long; downward-growing part of $th1^1$ 0·4 mm long; sicular aperture 0·25 mm wide; virgella short, stumpy; nema a fine thread.

Remarks. G. auritus resembles *G. enodis enodis* Packham but differs in having a closer thecal spacing (compare Text-fig. 4A with 4E): the thecal spacing of *G. e. enodis* is 8·5–11 in 10 mm, and *G. e. latus* 9–11 in 10 mm.

Glyptograptus bulbus sp. nov.

Plate 1, figures 1–2; Text-figure 6D

Holotype. CNIGR Museum 3/12879, Plate 1, figure 1: *vesiculosus* Biozone, Rhuddanian, Sakmara Formation, southern Urals.

Derivation of name. From *bulbus* (Latin) = bulb.

Material. Eight specimens, flattened or in low relief, from localities 671-2/73-201, 671-2/73 206 and 200, 671-8/74-116 and B671-8/74-108? in the Kos-Istek region.

Horizon. Rhuddanian, *vesiculosus* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Robust glyptograptid, septate, more than 10 mm long and 1·8 mm wide with massive virgella, 4·5–5 mm long, with bulb-like structure at the distal end; thecae strongly geniculate with supragenicular walls slightly inclined to the rhabdosomal axis.

Description. The rhabdosome widens slowly from 0·8 mm at $th1^1$ to 1·3 mm at $th5^1$; a maximum of 1·8 mm is attained 10 mm from the sicular aperture.

The thecae have a sharp geniculation; supragenicular walls are inclined at 7–8° to the rhabdosomal axis. Thecal overlap is less than one-half. Thecae number 10–11 in the first 10 mm. The proximal end tapers and is provided with a stout virgella (0·15–0·2 mm thick), up to 5 mm long. The virgella terminates with a bulb, 0·5 mm long and 0·25 mm wide.

Remarks. Specimens preserved in ventro-lateral view predominate in our collection which presents some difficulties in understanding the thecal shape. The most conspicuous feature is the presence of a long virgella, possessing a distal bulb. *G.* cf. *enodis enodis* has a similar thecal spacing, but has a gently tapered proximal end and a short, fine virgella. *G.* cf. *serratus* also has a short, fine virgella and no sign of a sharp geniculum.

EXPLANATION OF PLATE 1

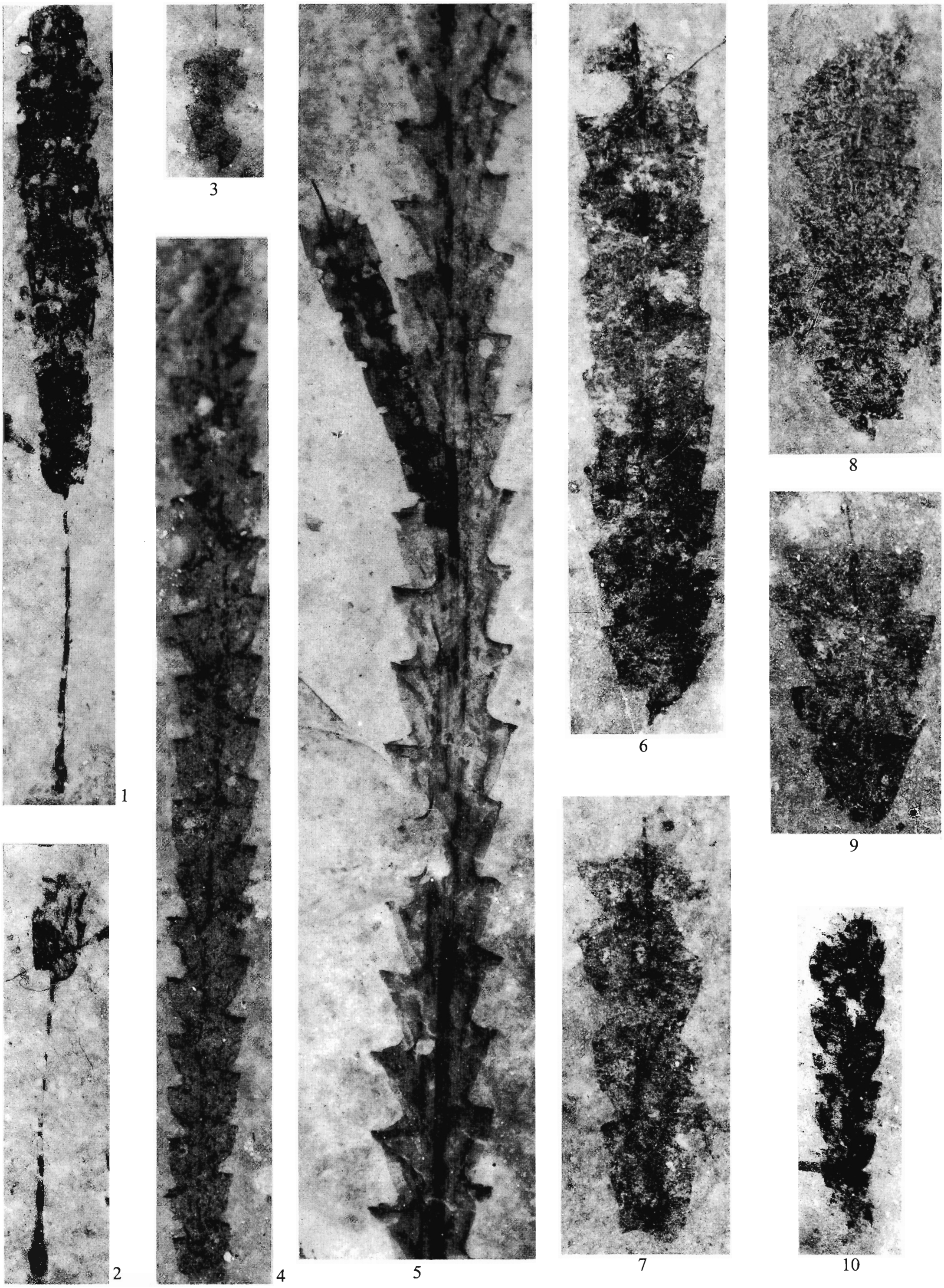
Figs 1–2. *Glyptograptus bulbus* sp. nov.; *vesiculosus* Biozone; Kos-Istek region. 1, holotype, CNIGR Museum 3/12879; rhabdosome possessing long virgella with bulb-like structure at the end; 2, CNIGR Museum 4/12879; both ×10.

Figs 3–5. *Glyptograptus* aff. *elegans* Packham; *cyphus* Biozone; Zhaksy-Kargala Valley. 3, CNIGR Museum 5/12879; juvenile rhabdosome with rounded proximal end; 4, CNIGR Museum 6/12879; incomplete adult rhabdosome; thecae showing flowing genicula; 5, CNIGR Museum 7/12879; distal fragment, fusellar structure and thickened horizontal apertures well developed; the small rhabdosome at top left is *Metaclimacograptus hughesi* (Nicholson); all ×10.

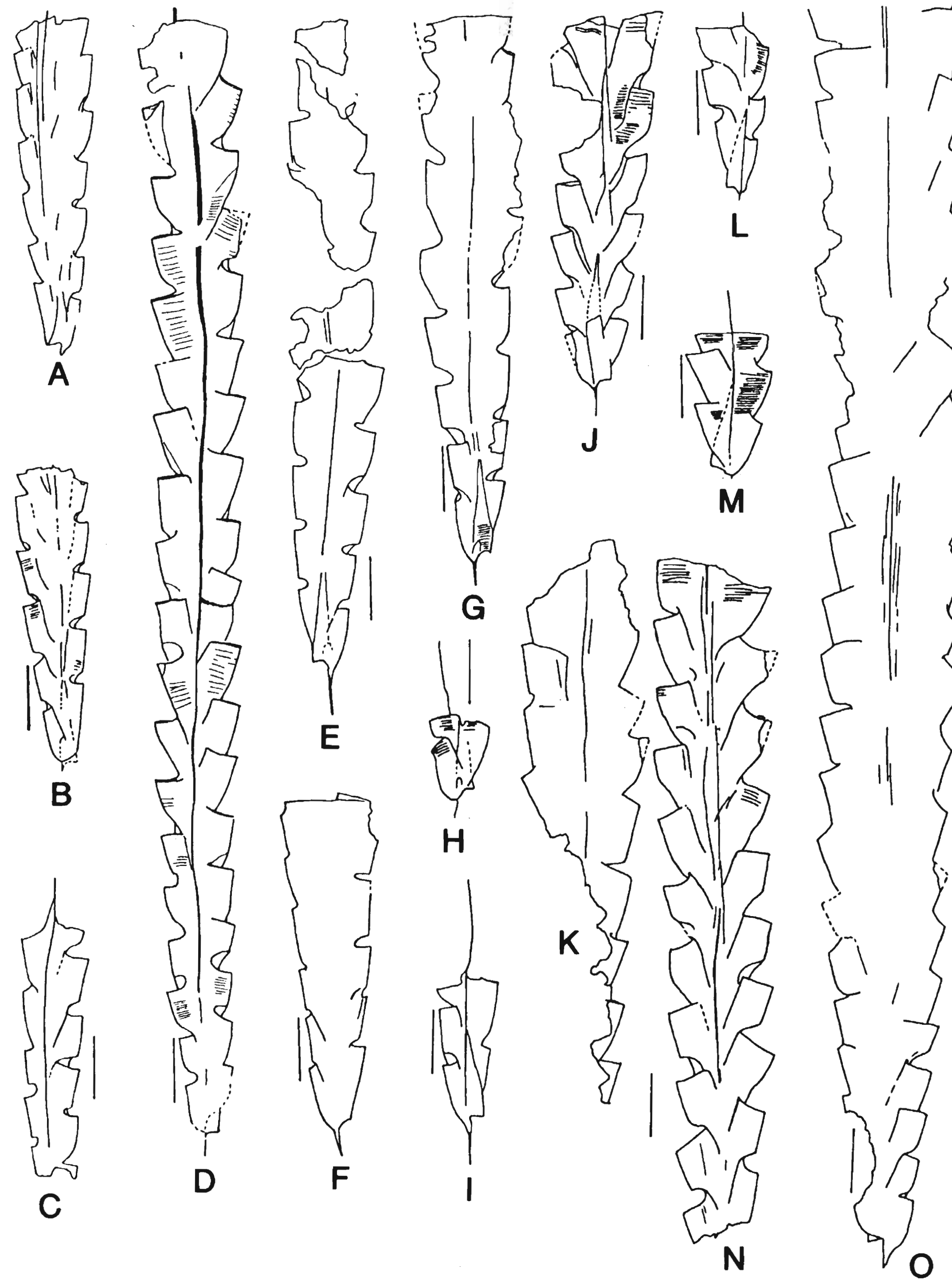
Figs 6–9. *Glyptograptus incertus* Elles and Wood; *gregarius* to *convolutus* biozones; Kos-Istek region. 6, 8, CNIGR Museum 13/12879 and 15/12879; incomplete, slightly tilted rhabdosomes, widening quickly proximally. 7, 9, CNIGR Museum 14/12879 and 16/12879; young rhabdosomes; reverse views; all ×20.

Fig. 10. *Glyptograptus* cf. *serratus* Elles and Wood; CNIGR Museum 28/12879; proximal fragment; *gregarius* Biozone, Kos-Istek region; ×10.

PLATE 1



KOREN' and RICKARDS, *Glyptograptus*



TEXT-FIG. 4. For legend see opposite.

Glyptograptus aff. *elegans* Packham, 1962

Plate 1, figures 3–5; Text-figure 4C–D

aff. 1962 *Glyptograptus elegans* sp. nov., Packham, p. 519, pl. 72, figs 4, 10–12; text-fig. 5*a–i*.

Material. Five flattened specimens, from localities B481, B671-1-7, B671-2-B and B671-2-41 in the Kos-Istek region.

Horizon. Rhuddanian, *cyphus* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome more than 10 mm long; slender, gradually increasing from 0·75 mm wide at the level of $th1^1$ aperture to 1·5 mm or a little more, distally, possibly to as much as 1·9 mm; thecal spacing 12 in 10 mm proximally, 8·5–10 in 10 mm distally; thecal overlap ?one-third throughout; supragenicular walls inclined at 10° in proximal thecae to 20° at the distal end of the rhabdosome; presence of septum uncertain; nema a robust rod; virgella a slim, short spine; sicula unclear; sicular aperture approximately 0·25 mm wide; distal thecal excavations may be 0·3–0·35 mm deep; thecal apertures at right angles to thecal axes; thecae more or less alternating; distal thecae have a more open, 'isolated' appearance than proximal thecae.

Remarks. The proximal end is perhaps slightly less drawn out than Packham's originals. Otherwise the two forms are very close, especially in overall rhabdosomal shape, form of thecal excavations and thecal spacing.

Glyptograptus cf. *enodis enodis* Packham, 1962

Text-figure 4E–I

cf. 1962 *Glyptograptus enodis enodis* subsp. nov.; Packham, p. 517, p. 71, figs 18–19, 21; pl. 72, fig. 1; text-figs 4*g–j*.

Material. Seven flattened specimens, from localities 587-8-2, 587-8-6, B671-1-2, B671-1-6, B671-1-9, 791 and 1643 in the Kos-Istek region.

Horizon. Aeronian, *gregarius* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosomes less than 10 mm long; dorso-ventral width at the level of $th1^1$ aperture 0·7–0·8 mm, distally 1·5 mm; thecal spacing *c*. 10 in 10 mm; sicula about 1·5 mm long; thecal overlap uncertain, possibly one-third; virgella 0·75 mm long; down-growing portion of $th1^1$ 0·3 mm long, proximal extremity below sicular aperture; possible median septum in obverse view: nema thread-like.

Remarks. Our material agrees in all measurements with Packham's originals but is perhaps less well preserved and has a proximal end less elongated than in the type material.

TEXT-FIG. 4. A–B, *Glyptograptus auritus* Bjerreskov; CNIGR Museum 1/12879, and 2/12879; *turriculatus* Biozone; Zhaksy-Kargala Valley. C–D, *Glyptograptus* aff. *elegans* Packham; CNIGR Museum 8/12879 and 6/12879; *cyphus* Biozone; Zhaksy-Kargala Valley. C, fragment of a young rhabdosome; D, complete adult rhabdosome, obverse view. E–G, I, *Glyptograptus* cf. *enodis enodis* Packham; *gregarius* Biozone, Kos-Istek region. E–G, CNIGR Museum 9/12879, 10/12879, and 11/12879; incomplete adult specimens; I, CNIGR Museum 12/12879; juvenile rhabdosome with thread-like nema, obverse view. H–O, *Glyptograptus incertus* (Elles and Wood); *gregarius* to *convolutus* biozones, Kos-Istek region. H, L–M, CNIGR Museum 17/12879, 20/12879 and 16/12879; juvenile specimens showing well preserved fusellar structure, one of them (L) slightly tilted, J, CNIGR Museum 18/12879; fragment showing rounded proximal end with almost complete median septum, obverse view; K, N, CNIGR Museum 19/12879 and 21/12879; distal fragments; O, CNIGR Museum 22/12879; adult rhabdosome, incomplete, reverse view with completely covered sicula. Scale bars represent 1 mm.

Glyptograptus incertus (Elles and Wood, 1907)

Plate 1, figures 6–9; Text-figure 4H–O

1907 *Diplograptus* (*Glyptograptus*) *tamariscus* var. *incertus* var. nov., Elles and Wood, p. 249, pl. 30, fig. 9*a–d*; text-fig. 168*a*.
1922 *Diplograptus tamariscus incertus* Elles and Wood; Gortani, p. 104, pl. 17, fig. 24.
1962 *Glyptograptus incertus* Elles and Wood; Packham, p. 518, pl. 72, figs 6–7; text-fig. 4*a–d*.
?1974 *Glyptograptus* (*G.*) *incertus* (Elles and Wood, 1907); Hutt, p. 25, pl. 3, fig. 3; pl. 4, figs 12–13; text-fig. 8.11.

[For further synonymy details see Loydell 1992].

Material. Eleven specimens, flattened or in low relief, from localities 399-4, B411-1, B611-6/72-106, B671-2-42, B671-8/74-57, B671-8/74-76, B671-8/74-77 and 1508 in the Kos-Istek region.

Horizon. Aeronian, *gregarius* and *convolutus* biozones of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosomes up to 30 mm long, robust; dorso-ventral width at $th1^1$ aperture 0·75–0·85 mm; distal dorso-ventral width a maximum of 2·5 mm; considerable variation in dorso-ventral width mesially, from 1–2 mm; proximal thecal spacing 12 in 10 mm, distally 7·5–8·5 in 10 mm; sicula less than 1·5 mm long; thecal overlap about one-half proximally, possibly also distally; rhabdosome at least partially septate, interthecal interval $th1^1$ to $th2^1$, 0·6–0·75 mm; angle of thecal inclination of thecal mid-line 15–20° in true profile; virgella short, 0·5–0·6 mm long; nema increasingly robust distally, almost vane-like; thecal excavation deep and long 0·4 mm × 0·5 mm mesially, 0·3 mm × 0·2 mm proximally; proximal end rounded; distal thecae less alternating than proximal thecae.

Remarks. Our specimens seem more robust distally than the types, but they are considerably longer. At comparable lengths they are the same width. The distal thecae are more widely spaced than the figures given by Packham (1962). It is possible that these are early forms of *G. incertus*, which seems more typically to be recorded from the *convolutus* Biozone and above. They are not that close to other species and differ from such robust forms as *G. serratus* in having a more rounded proximal end and quite different distal thecae, the thecal excavations taking up a greater proportion of the width of the rhabdosome.

Glyptograptus cf. *serratus* (Elles and Wood, 1907)

Plate 1, figure 10; Plate 2, figures 1–10

cf. 1907 *Diplograptus* (*Glyptograptus*) *serratus* sp. nov., Elles and Wood, p. 249 (*pars*), pl. 30, fig. 10*a–c*; text-fig. 169.

Material. Twenty-two specimens, flattened or in low relief, from localities 399-4, 474-2, B587-11-16, B671-8-59, B671-8-77, B671-8-136, B671-8-12, B671-8-427, 1508-11 and 1643/50-4 in the Kos-Istek region.

Horizon. Upper Rhuddanian–lower Aeronian, ?*cyphus* and *gregarius* biozones, Sakmara Formation.

Diagnosis. Long (> 30 mm), probably septate rhabdosome, robust (2·5 mm dorso-ventral width distally); thecal spacing 10 in 10 mm proximally to 8 in 10 mm distally; thecal overlap about one-half; angle of metathecal inclination 10–20°, the higher figure distally; proximal dorso-ventral width, at $th1^1$, 0·85 mm; virgella may be > 10 mm long.

Remarks. Elles and Wood (1907) gave a proximal thecal spacing of 14 in 10 mm. This agrees with the form we describe below as *G.* aff. *serratus* Elles and Wood, but does *not* agree with any of their figures, including the 'typical specimen' (pl. 30, fig. 10*a*): all these have a thecal spacing of 10 in 10 mm as does our present material from the Urals. Furthermore, the dorso-ventral width at $th1^1$ of the Elles and Wood figures agrees with our Uralian specimen, *not* with their text (i.e. 0·8 mm, not 1·0 mm). *G.* aff. *serratus* (see below) does have a more robust proximal end, and it seems likely to us that Elles and Wood confused two not dissimilar forms, one with closely spaced thecae and the other with widely spaced thecae. Further work on this group is clearly needed.

Glyptograptus aff. *serratus* (Elles and Wood, 1907)

Text-figure 5A–E

aff. 1907 *Diplograptus* (*Glyptograptus*) *serratus*, sp. nov., Elles and Wood, p. 249 (*pars*), *non* pl. 30, fig. 10*a–c*; text-fig. 169.

Material. Ten flattened specimens with well-preserved fusellar structure, from localities B258-8-4, B607-3-1, B671-14, B671-8/74-77, B671-8/74-59, B671-8/74-139 and B671-9-701 in the Kos-Istek region.

Horizon. Aeronian, the *gregarius* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Robust rhabdosome, initially 0·8–1 mm in dorso-ventral width, rapidly reaching 2 mm; proximal thecal spacing 14 in 10 mm; 11–12 in 10 mm when the rhabdosome is 2 mm wide; thecae inclined outwards strongly, supragenicular wall inclined at 20–30°; thecal overlap greater than one-third; nema thread-like; metathecal growth bands wide, about 7–8 on the supragenicular wall; virgella short (0·5 mm long) and spike-like.

Remarks. In dorso-ventral width and thecal spacing our limited material of this form resembles the original description of Elles and Wood (1907). However, some of their specimens seem closer in thecal spacing on their plates to what we have described above as *G.* cf. *serratus* Elles and Wood. It may be that there are two distinct forms in the original material, one with a high proximal thecal spacing and the other with longer, larger proximal thecae, with more overlap and a thecal spacing of only 10 in 10 mm.

Glyptograptus tamariscus tamariscus (Nicholson, 1868)

Plate 2, figures 11–12; Text-figure 5F–I

1868 *Diplograpsus tamariscus* sp. nov., Nicholson, p. 526, pl. 19, figs 10–11, 13 (*non* 12). [See Packham (1962) and Loydell (1992) for thorough synonymies of this species.]

Material. Ten specimens, flattened or in low relief, some of them with well preserved fusellar structure, from localities B329, B399-4, B571-8-168, B607-3-601, B671-8/74-149, B671-8/74-168, B671-8/74-310, B671-8-600, B671-8-700 and 1508-603 in the Kos-Istek region and the Zhaksy-Kargala Valley.

Horizon. Aeronian, the *gregarius* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome, more than 4–5 mm long, widening from 0·55 mm–0·7 mm at $th1^1$ to 0·8 mm–1 mm at $th5^1$. Thecae are with flowing genicula and are strongly alternating, with slightly everted apertures. Ventral thecal walls are inclined at 17–20° to the rhabdosomal axis; thecal overlap is less than one-half. One of the specimens has a virgella, *c.* 3 mm long.

Remarks. We have several specimens which fit well into Packham's redefinition of the type subspecies, but do not have enough material to recognize his forms A–C with certainty. Our specimens have characteristically slim rhabdosomes, with strongly alternating thecae and slightly everted apertural margins. We note them here only for completeness sake and because they are probably central to the main line of glyptograptid evolution, as Packham (1962) indicated.

Glyptograptus tamariscus distans Packham, 1962

Plate 2, figure 13; Text-figure 5J–L

1962 *Glyptograptus tamariscus distans* subsp. nov., Packham, p. 507, pl. 71, figs 9–10, text-fig. 1*k–l*.

Material. Four specimens, flattened or in low relief, from localities 611-6/72, 116, B671/8-277*a*, B671/8-170 and B671/8-138 in the Zhaksy-Kargala Valley.

Horizon. Upper Rhuddanian–lower Aeronian, *cyphus* and *gregarius* biozones of the southern Urals, Sakmara Formation. In Britain it is described from the *cyphus* and *gregarius* biozones at Dob's Linn and the Rheidol Gorge (Packham 1962).

Description. A small rhabdosome, 7–8 mm long with a maximum dorso-ventral width of 0·6–0·8 mm reached at the third pair of thecae. Initial width at $th1^1$ is 0·5–0·55 mm and at $th2^1$ is 0·6–0·7 mm; more distally the rhabdosome is parallel-sided. Thecae are strongly alternating with almost horizontal apertures. Excavations are 0·15 mm deep and 0·2 mm long. Supragenicular walls, 0·9 mm long, are almost parallel to the rhabdosomal axis. Thecal overlap is no more than one-fifth; number of thecae is 5·5 in 5 mm proximally (11 in 10 mm). The nema is quite stout; a median septum is not visible.

$Th1^1$ extends below the sicular aperture for 0·15–0·2 mm. Its downward growing portion is 0·25–0·3 mm long. The length of the upgrowing portion of $th1^1$ is 0·65–0·8 mm. The sicular apex reaches the level of the middle part of $th2^1$. Dimensions of sicula: length no more than 1·3 mm; width at aperture 0·16–0·2 mm. The virgella is up to 0·7 mm long.

Remarks. The specimens agree well with the original description given by Packham (1962). The most characteristic features of the subspecies are the small size of the rhabdosome, straight supragenicular walls, slightly rounded geniculum and deep, strongly alternating excavations.

Glyptograptus tamariscus linearis (Perner, 1897)

Plate 3, figure 1; Text-figure 5M–N

1897 *Diplograptus tamariscus linearis* n. subsp., Perner, p. 4, text-fig. 2 (? pl. 9, fig. 23).
1907 *Diplograptus* (*Glyptograptus*) *tamariscus* Nicholson; Elles and Wood (*pars*), p. 247, pl. 30, fig. 8*c* (*non* text-fig. 167*a–d*, pl. 30, fig. 8*a–b*, *d*).
1962 *Glyptograptus tamariscus linearis* Perner; Packham, p. 506, pl. 72, fig. 8; text-fig. 1*v* [see for synonymy].

Material. Two specimens flattened, from localities B671/8-74, sp. 175 and 791 in the Zhaksy-Kargala Valley.

Horizon. Aeronian, *gregarius* and *convolutus* biozones of the southern Urals, Sakmara Formation. It is known from the *convolutus* Biozone of Bohemia (Perner 1897) and *cyphus* Biozone of southern Scotland (Packham 1962).

Description. The rhabdosome is more than 15 mm long, with a slightly tapering extreme proximal end. Its dorso-ventral width at $th1^1$ is 0·7–0·8 mm; at $th2^1$ 1 mm; at $th3^1$ 1·2 mm; at $th4^1$ 1·3 mm and at $th5^1$ 1·2–1·4 mm. It reaches a maximum width, 1·5–1·7 mm, at the level of th7–8. The rhabdosome is at least partially septate and the nema is quite stout.

Thecae show a sharp geniculum in the first three pairs; further on the geniculum is smoother, and excavations are not deep, although this may be due to torsion of the stipe. Thecal apertures are slightly

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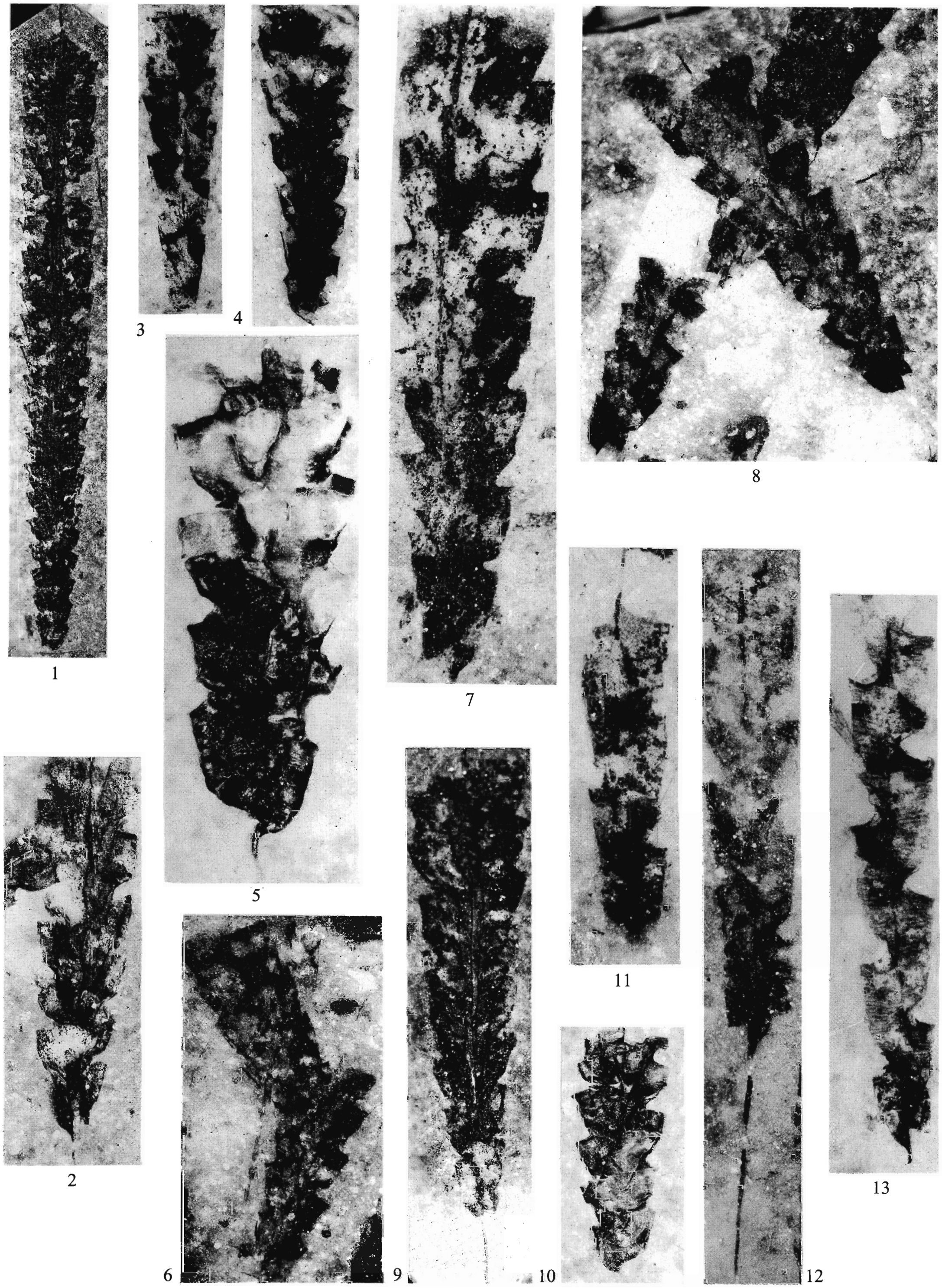
EXPLANATION OF PLATE 2

Figs 1–10. *Glyptograptus* cf. *serratus* Elles and Wood; *gregarius* Biozone; Kos-Istek region. 1, CNIGR Museum 28*a*/12879; adult rhabdosome, septate, slowly widening; ×5. 2–6, 10, CNIGR Museum 29/12879, 30/12879, 31/12879, 32/12897, 33/12879 and 37/12879; proximal fragments; 5, ×20, others, ×10; 7–9, CNIGR Museum 34/12879, 35/12879 and 36/12879, young rhabdosomes, one with complete median septum (9); 7, ×20, 8–9, ×10.

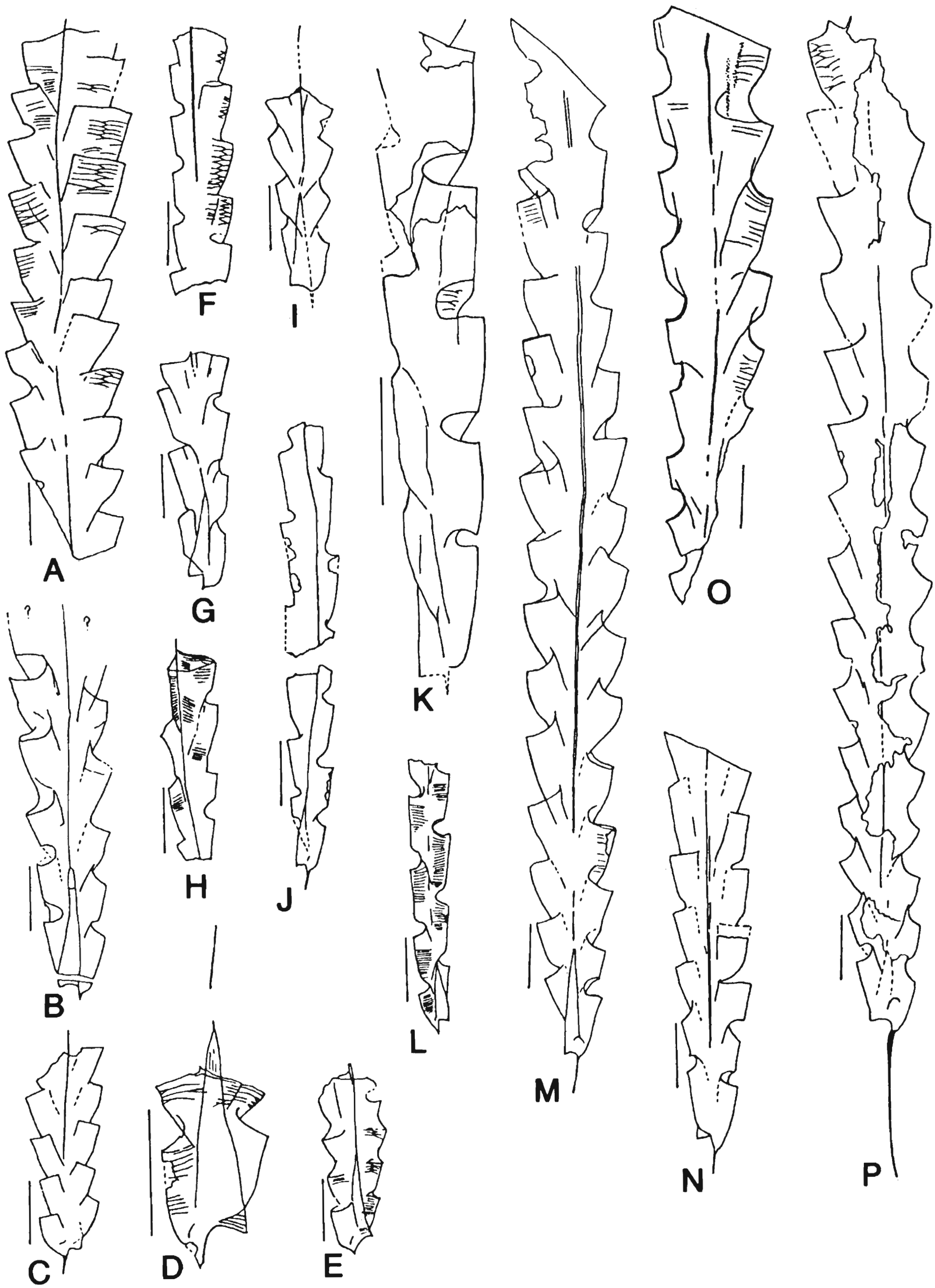
Figs 11–12. *Glyptograptus tamariscus tamariscus* (Nicholson); *gregarius* Biozone; Kos-Istek region. 11, CNIGR Museum 38/12879; young rhabdosome; reverse view; 12, CNIGR Museum 39/12879; proximal fragment possessing long virgella; reverse view; both ×20.

Fig. 13. *Glyptograptus tamariscus distans* Packham; CNIGR Museum 44/12879; incomplete tiny rhabdosome with strongly alternating thecae, fuselli are well preserved; *cyphus*/*gregarius* biozones; Zhaksy-Kargala Valley; ×20.

PLATE 2



KOREN' and RICKARDS, *Glyptograptus*



TEXT-FIG. 5. For legend see opposite.

asymmetrical and everted, more or less alternating. Thecal number is 5·5 in 5 mm and 10·5 in 10 mm proximally, 4·5 in 5 mm distally.

$Th1^1$ extends below the sicular aperture for 0·12 mm, its upward-growing portion being 0·9–1·1 mm long. The sicular apex reaches the aperture of $th2^1$. The sicula is 1·5 mm long, and 0·3 mm wide at the aperture. The virgella is 0·3 mm long. From the reverse side the ventral margin of the sicula is free for a distance of up to 0·4 mm.

Remarks. The distinguishing features of this subspecies include: slightly tapering proximal end, parallel-sides to the rhabdosome beginning at the 7th pair of thecae, and the low number of thecae both proximally and distally.

G. t. linearis shows some similarity to *G. elegans* Packham and *G. incertus* Elles and Wood. From the former it differs in having a much wider rhabdosome both proximally and distally, less deep excavations, generally less everted thecal apertures and in its less densely packed thecae. From the latter it can be distinguished by the less sigmoidally curved thecae, the tapering proximal end (longer th^1, 1·0 mm cf. 0·5 mm) and by the smaller number of thecae in 10 mm. The less tapering and broader extreme proximal end, almost horizontal thecal apertures and more pronounced geniculum are characters distinguishing it from *G. enodis* Packham.

Glyptograptus tamariscus nikolayevi Obut, 1965

Plate 3, figure 2; Text-figure 5O–P

1965 *Glyptograptus nikolayevi* n. sp., Obut, p. 36, pl. 1, fig. 5.
1966 *Glyptograptus tamariscus nikolayevi* Obut; Obut and Sobolevskaya, p. 14, pl. 3, figs 8–9; text-fig. 6.
1967 *Glyptograptus tamariscus nikolayevi* Obut; Obut *et al.*, p. 56, pl. 2, figs 10–11.
1968 *Glyptograptus tamariscus nikolayevi* Obut; Obut *et al.*, p. 67, pl. 5, figs 4–10.
1989 *Glyptograptus nikolayevi* Obut; Melchin, p. 1738, fig. 9C.

Material. Five specimens, preserved in low relief or flattened, from localities B378/72-1, B399-4-8, B671-8/74-139, B371-8/74-625 and 1508 in the Kos-Istek region.

Horizon. Aeronian, *gregarius* Biozone, of the southern Urals, Sakmara Formation. Previously, the subspecies was described from the Middle Llandovery (the *triangulatus* Biozone) of the Norilsk and Kolyma regions. Recently it was found in the *cyphus* Biozone in the Canadian Arctic Islands (Melchin 1989).

Description. The rhabdosome is 15–20 mm long, steadily increasing in dorso-ventral width which is, at $th1^1$, 0·9 mm; $th2^1$, 1·1 mm; $th3^1$, 1·25 mm; $th4^1$, 1·3 mm; $th5^1$, 1·35 mm; and up to 1·8 mm distally. The characteristic, stout virgella is about 2·5 mm long. The rhabdosome is septate. The thecae have gently flowing genicula of typical glyptograptid appearance, and broad excavations. The thecae are 1·5 mm long and 0·4 mm wide at the apertures. Interthecal septae are inclined at 15–20° to the rhabdosome axis and thecal overlap is not more than one-third. Thecal apertures are moderately asymmetrical and everted. Thecae number 5·5 in 5 mm and 10–11 in 10 mm proximally; and 9 in 10 mm towards the distal end.

TEXT-FIG. 5. A–E, *Glyptograptus* aff. *serratus* (Elles and Wood); *gregarius* Biozone, Kos-Istek region. A–B, CNIGR Museum 23/12879 and 24/12879; incomplete fragments of adult rhabdosomes; one showing zig-zag fusellar structure (A); C–E, CNIGR Museum 25/12879, 26/12879 and 27/12879; juvenile rhabdosomes with rounded proximal end and well preserved, coarse fusellar structure, obverse views; F–I, *Glyptograptus tamariscus tamariscus* (Nicholson); CNIGR Museum 40/12879, 41/12879, 42/12879, and 43/12879; mostly incomplete tiny rhabdosomes at different astogenetic stages; *gregarius* Biozone, Kos-Istek region. J–L, *Glyptograptus tamariscus distans* Packham; CNIGR Museum 45/12879, 46/12879 and 44/12879; tiny rhabdosomes with strongly undulating and distant thecae; fusellar structure is well shown, almost completely free sicula in obverse view (L); *cyphus* to *gregarius* biozones; Zhaksy-Kargala Valley. M–N, *Glyptograptus tamariscus linearis* (Perner); *gregarius* Biozone; Zhaksy-Kargala Valley; M, CNIGR Museum 45/12879; adult rhabdosome with complete median septum, obverse view; N, CNIGR 46/12879; proximal fragment, reverse view, proximal end tapering, sicula is completely covered. O–P, *Glyptograptus tamariscus nikolayevi* Obut; *cyphus* Biozone; Kos-Istek region. O, CNIGR Museum 48/12879; distal fragment; P, CNIGR Museum 47/12879; adult rhabdosome with prominent virgella. Scale bars represent 1 mm.

The extreme proximal end is slightly tapering. The first theca grows down slightly below the sicular aperture, bends sharply and its upward-growing portion is 0·7–0·8 mm long. The sicular aperture is 0·35 mm wide; its ventral margin is free for a distance of 0·2–0·35 mm in reverse view.

Remarks. G. t. nikolayevi differs from *G. t. tamariscus* in having a broader rhabdosome, a less tapering extreme proximal end and less strongly expressed sigmoidal curvature of the thecae. From *G. t. linearis* the subspecies can be distinguished by the longer and stouter virgella; and by the slightly larger rhabdosome, both proximally and distally. It differs from *G. incertus* Elles and Wood in having a smaller maximum dorso-ventral width (1·8 mm compared with 2 mm).

The material studied agrees well with the description of *G. tamariscus nikolayevi* from the Norilsk and Kolyma regions given by Obut (1965).

Genus PSEUDOGLYPTOGRAPTUS Bulman and Rickards, 1968

Type species: *Ps. vas* Bulman and Rickards, 1968; original designation; Llandovery of Cross Fell, northern England.

Pseudoglyptograptus sp.

Plate 3, figure 3; Text-figure 6E

1972 *Glyptograptus* (*Pseudoglyptograptus*) sp. 1, Rickards, p. 277, fig. 1.1, 1.4.

Material. One specimen and its counterpart, from locality B671-8/74-12 in the Zhaksy-Kargala Valley.

Horizon. Aeronian, *gregarius* Biozone of the southern Urals, Sakmara Formation.

Description. Pseudoglyptograptid with mesial apertural elevations of proximal thecae; rhabdosome's lateral width (flattened, scalariform) at $th1^1$ aperture, 0·7 mm; at $th3^1$, 1·1 mm; proximal thecal spacing 11 in 10 mm; sicular length uncertain (but > 1 mm); virgella robust, straight 3·75 mm long.

Remarks. This form is clearly very close to *Pseudoglyptograptus* sp. 1 (Rickards 1972) (= *Climacograptus scalaris sensu* Törnquist, 1890) and *Ps. barriei* Zalasiewicz and Tunnicliff, 1994, but as the number of thecae with ventral apertural processes is unknown in our material it cannot yet be ascribed to either form: other dimensions agree with both *Ps.* spp.

Genus COMOGRAPTUS Obut and Sobolevskaya (*in* Obut *et al.*, 1968)

Type species. Comograptus comatus Obut and Sobolevskaya (*in* Obut *et al.*, 1968) (Text-fig. 6G herein) original designation; Llandovery of Norilsk, Siberia.

Diagnosis. Long, robust biserials; thecae vary from paraclimacograptid-like (in the type species) to glyptograptid-like in *Co. barbatus* (Elles and Wood, 1907); first 4–6 pairs of thecae heavily spinose,

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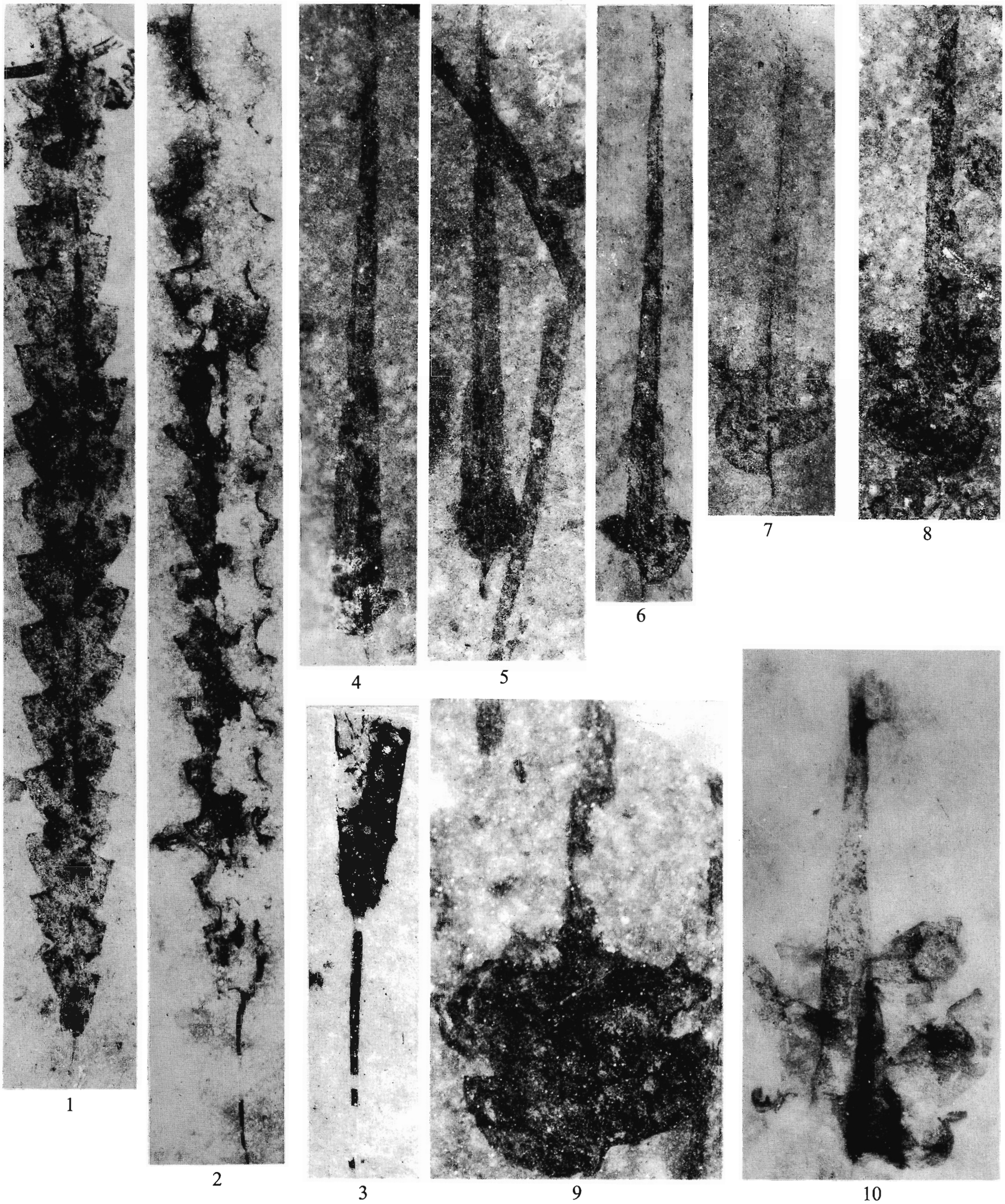
EXPLANATION OF PLATE 3

Fig. 1. *Glyptograptus tamariscus linearis* (Perner); CNIGR Museum 45/12879; well-preserved adult rhabdosome with somewhat tapering proximal end; reverse view; *gregarius* Biozone; Zhaksy-Kargala Valley; × 10.

Fig. 2. *Glyptograptus tamariscus nikolayevi* Obut and Sobolevskaya; CNIGR Museum 47/12879; *cyphus* Biozone; Kos-Istek region; × 10.

Fig. 3. *Pseudoglyptograptus* sp.; CNIGR Museum 51/12879; *gregarius* Biozone; Zhaksy-Kargala Valley; × 10.

Figs 4–10. *Cystograptus vesiculosus* (Nicholson); CNIGR Museum 52/12879, 53/12879, and 58/12879; *vesiculosus* Biozone; Zhaksy-Kargala Valley; early astogenetic stages from sicula and $th1^1$ (4–5) to sicula and three incomplete pairs of thecae; 4–8, × 10; 9–10, × 20.



KOREN' and RICKARDS, graptoloids from the southern Urals

with genicular, apertural, and sub-apertural, long, dependent spines; most spines are curved and directed ventro-proximally; sicula virgellate, but sicular apertural rim adorned with many slim, bifurcating spines; proximal thecal spines are developed at a late growth stage, the sicular spines somewhat earlier; *tamariscus* (I) Pattern of development.

Remarks. Obut and Sobolevskaya (*in* Obut *et al.* 1968) drew attention to the similarity of *Co. comatus* to *Glyptograptus serratus barbatus* suggesting that, despite thecal differences, they might be placed in the same genus, namely *Comograptus*. We support this suggestion and broaden the definition accordingly to embrace both thecal types: the differences are not all that great, in fact, and may partially reflect differences of preservation, the Parys Mountain (Anglesey) originals of *G. s. barbatus* being slightly deformed as well as flattened. *G. s. serratus* is very close indeed to *G. s. barbatus*: further work may show it to be an earlier growth stage than the spinose form. Proximal sicular spinosity of this kind has also been recorded by Rickards and Koren' (1974) in some species of *Pseudoglyptograptus*. *Pseudoglyptograptus* differs from *Comograptus* in having doubly sigmoidal thecal tubes and everted apertures, and none of the species has thecal spines. *Comograptus* is best regarded as a derivative of *Glyptograptus*, via *G. serratus* leading to *Co. barbatus*; and, via the tendency to produce climacograptid-like thecae, resulting in *Co. comatus*. It is possible, therefore, that two separate lineages are involved in the origin of *Comograptus* as currently understood, so that generic redefinition may be needed at a future date to reflect more fully the phylogeny. On the other hand, as Packham (1962) has shown, climacograptid-like thecae seem to have been easily developed in the *tamariscus* lineages.

Genus PERSCULPTOGRAPTUS gen. nov.

Type species. *Diplograpsus persculptus* Salter, 1873; from the upper Ordovician of Pumpsaint, Wales.

Diagnosis. Robust biserials, septate to aseptate, up to 40 mm long and with a distal dorso-ventral width sometimes in excess of 2·5 mm (relief); proximal development *normalis* Pattern (H); thecae doubly sigmoidal with slight geniculum in proximal thecae of some species; thecal overlap considerable; median septum commonly undulating in proximal region, less so distally; sicula of moderate length, often well exposed in reverse view; virgellate, virgella usually short, spike-like; nema may be expanded slightly distally.

Remarks. The thecal curvature is greater than in *Glyptograptus* to the extent that there is often a rounded geniculum on the proximal thecae. On flattening, this feature can be exaggerated and distinction may then be difficult from *Neodiplograptus*, *Rhaphidograptus* (except proximal extremity) and even *Normalograptus*. *Per. persculptus* itself may well derive from *G. ojsuensis* Koren' and Mikhaylova, which possibly should be included in *Persculptograptus*. The *Per. persculptus* species group is being studied by the authors and more information about the composition and relationships of the genus will be given at a later stage.

Genus CYSTOGRAPTUS Hundt, 1942 emend. Rickards, 1970

Type species. *Diplograptus vesiculosus* Nicholson, 1868; subsequently designated Jones and Rickards 1967; from Llandovery of the English Lake District.

Cystograptus vesiculosus (Nicholson, 1868)

Plate 3, figures 4–10

1868 *Diplograptus vesiculosus* Nicholson, pl. 3, fig. 11.

1907 *Diplograptus* (*Orthograptus*) *vesiculosus* Nicholson; Elles and Wood, p. 229, pl. 28, fig. 8*a–f*, text-fig. 151*a–f*.

1970 *Cystograptus vesiculosus* (Nicholson); Rickards, p. 44, pl. 1, fig. 11; pl. 2, figs 12, 14.
1974 *Cystograptus vesiculosus* (Nicholson); Hutt, p. 45, pl. 4, fig. 15; text-fig. 9, figs 4–5 [see for synonymy].
1975 *Cystograptus vesiculosus* (Nicholson); Bjerreskov, p. 29, fig. 10E.
1979 *Cystograptus vesiculosus* (Nicholson), Koren' *et al.*, pl. 32, figs 8–11.
1982 *Cystograptus vesiculosus* (Nicholson); Urbanek *et al.*, p. 207, figs 19, 21–22.
1985 *Cystograptus vesiculosus* (Nicholson); Štorch, p. 96, pl. 2, figs 1, 5, 7; ?pl. 4, figs 2, 7–8; text-fig. 3E–H.

Material. About 30 flattened specimens, early astogenetic stages, such as siculae with the first pairs of thecae, dominating the collection; from localities B671-2-7, 671-2-8, B671-1, B671-8, B671-8a-18, B671/9, 607-3/74, 67/1, 67/25, P267/3, 1643/50-33 in the Kos-Istek Region south of Aktjubinsk.

Horizon. Rhuddanian, *vesiculosus* Biozone of the southern Urals, Sakmara Formation.

Description. Large rhabdosome, about 20 mm long, with nematularium projecting distally for 30–40 mm. The rhabdosome widens from 1·7–2 mm at $th1^1$ and 2–2·7 mm at $th2^1$ to a maximum of 3·0–3·5 mm at $th3^1$. It is almost parallel-sided for most of its length, narrowing slightly at the distal end. The thecae are doubly sigmoidal with thecal apertures facing ventrally. They number 5 in the first 5 mm and 4·5 in 5 mm distally.

The extreme proximal end is rounded with a well-expressed keel on the ventral sides of $th1^1$ and $th1^2$. The sicula and $th1^1$ are extremely long. The nematularium starts about 3 mm above the sicular aperture (0·45–0·5 mm wide). Sicular length varies from 8·5 to 9·5 mm. The downward-growing portion of $th1^1$ is 3–3·5 mm long. It turns upwards 0·4 mm below the sicular aperture. The sicula is almost completely covered in reverse view.

Remarks. The most prominent feature of *Cy. vesiculosus* is its long sicula and the presence of the nematularium which started its development early in the astogeny and overlaps the apical portion of the prosicula. Siculae with a thread-like nemal appendage have not been observed in the present material despite the fact that it includes numerous sicular stages. This supports an idea (Urbanek *et al.* 1982) that the nematularium is rather a virgula replacement than a derivative. Among the juvenile specimens measured there are several which are narrower at the proximal end with two pairs of thecae. They could belong to *Cy. penna* (Hopkinson), but the present material is not sufficient to be certain.

Genus NEODIPLOGRAPTUS Legrand, 1987

Type species. *Diplograptus magnus* H. Lapworth, 1900; designated Legrand 1987; from the Llandovery of central Wales.

Diagnosis. Robust biserials, occasionally exceeding a length of 40 mm and a dorso-ventral width of 4 mm; usually septate; thecae weakly to strongly biform, those proximally having a geniculum, which then declines distally so that in some species distal thecae may be almost orthograptid; in one species proximal thecae exhibit apertural hook-like outgrowths; proximal development probably of either *normalis* (H) Pattern or *tamariscus* (I) Pattern; virgellate; virgella usually short and spike-like; nema often expanded distally, and a vane is present in some species; there are no proximal or other thecal spines.

Remarks. *Neodiplograptus* has a simpler mode of proximal development than the Ordovician genus *Diplograptus* and the thecal apertures are also simpler; whilst the rhabdosome is non-spinose. *Neodiplograptus* may at times be difficult to distinguish from flattened *Persculptograptus*, from which genus it probably derived by increased thecal geniculation proximally and hence development of a biform rhabdosome.

Neodiplograptus korinevskii sp. nov.

Plate 4, figures 1–5, 8–9; Text-figure 6H

Holotype. CNIGR Museum 59/12879, Plate 4, figure 1, Text-figure 6H, *cyphus* Biozone, Rhuddanian, Sakmara Formation, southern Urals.

Derivation of name. After Dr V. G. Korinevski.

Material. Fourteen specimens, in full or low relief or flattened, from localities B258-8-14, B399-4, B587-11-4, B614-1-1, B671-2-46, B671-2-64, B671-8/74-4, 1508-12, 1643/50-32 and 1643/50-54 in the Kos-Istek region to the south of Aktjubinsk City.

Horizon. Rhuddanian–Aeronian, the *cyphus* to *gregarius* biozones of the southern Urals, Sakmara Formation.

Diagnosis. Neodiplograptid, more than 20 mm long and about 2·5 mm wide in profile distally. Median septum is complete in obverse view and partial in reverse view; nema robust. Thecae are 'climacograptid' proximally to glyptograptid distally, numbering 11–9 in 10 mm. Some specimens have peculiar apertural outgrowths on several proximal thecae, which may be subgenicular in origin.

Description. The rhabdosome widens gradually from 0·9–1·1 mm dorso-ventral width at $th1^1$, to 1·7–1·8 mm at $th5^1$. The width 5 mm from the sicular aperture is 2 mm, and most distally is up to 2·5 mm.

The proximal thecae have excavations 0·2 mm deep and 0·25 mm long with thickened genicular rims. Distally the interthecal septae and supragenicular walls (0·9 mm long) are sigmoidally curved and inclined away from the rhabdosome axis. The proximal thecae possess apertural outgrowths, 0·3–0·35 mm long, extending below the thecal aperture. The outgrowths resemble thecal hooks but have little periderm attached to them, being preserved as siliceous (opaline) internal moulds. Above the processes a short ridge is apparent on the geniculum, suggesting that these are not strictly genicular processes but are of independent origin, subgenicular in position: because they are preserved as internal moulds this statement cannot be proved. Thecae number 11 in 10 mm proximally and 10 in 10 mm distally. The sicula is free for 1·25 mm in obverse view; its aperture is 0·25 mm wide. The virgella, 0·5 mm long, is not prominent.

Remarks. From *Ne. modestus sensu lato* the new species differs in having a climacograptid appearance of both proximal and distal thecae. The new species is also characterized by the presence of outgrowths at the thecal apertures. Their origin can be seen clearly in our present material. It seems most likely that they are not of genicular origin, but are a continuation of the preceding dorsal thecal wall, because a sharp ridge of the geniculum is clearly visible above the outgrowth. No fuselli have been detected on the outgrowths, but the overall impression is of a thecal hook. These are probably late astogenetic growth stages because the majority of our specimens show no signs of the feature.

EXPLANATION OF PLATE 4

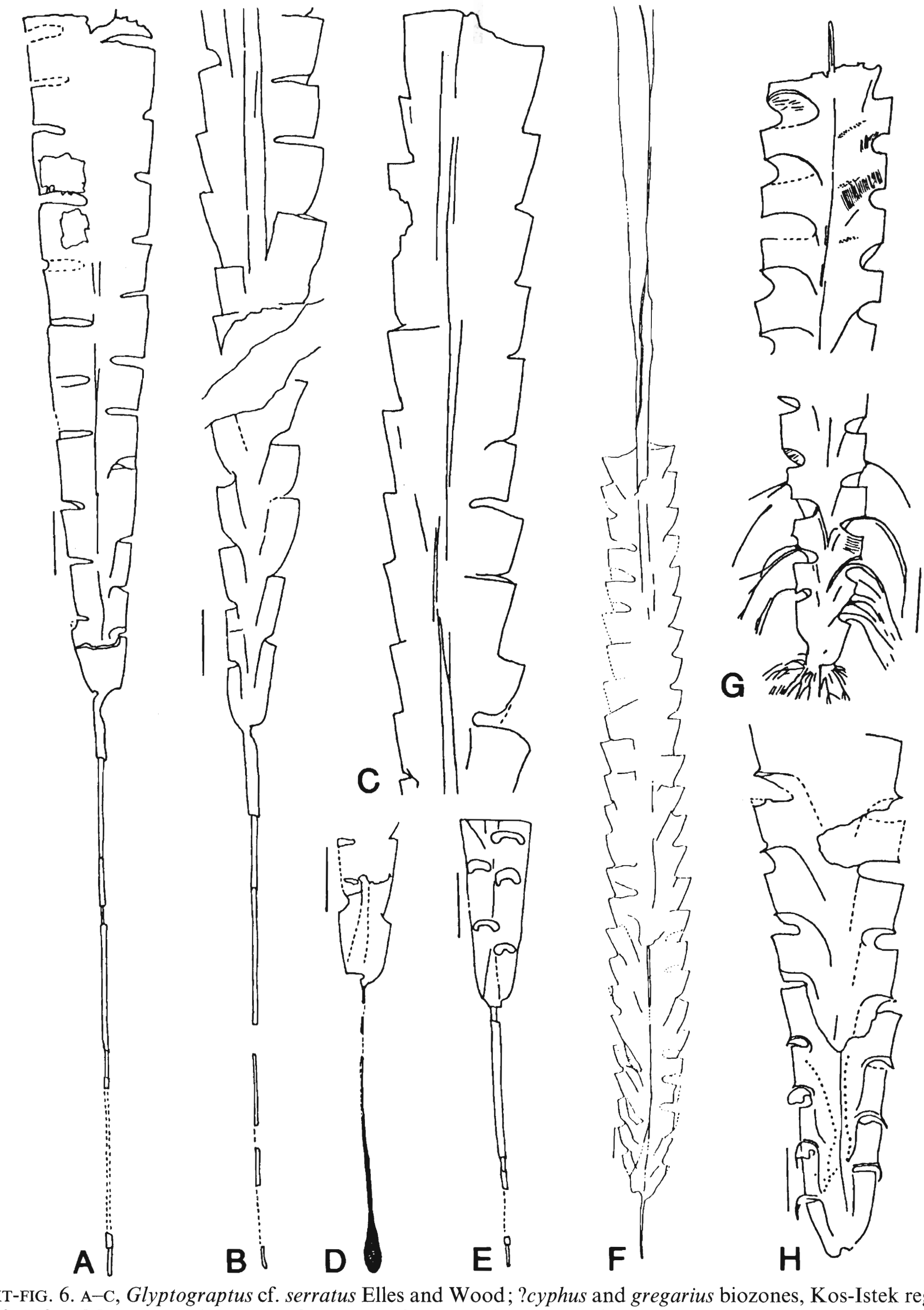
Figs 1–5, 8–9. *Neodiplograptus korinevskii* sp. nov.; *cyphus* Biozone, Zhaksy-Kargala Valley. 1, holotype, CNIGR Museum 59/12879; rhabdosome in full relief proximally and in low relief distally, preserved as an opaline silica infill; 2–3, 8–9, CNIGR Museum 60/12879, 61/12879, 64/12879, and 65/12879; young rhabdosomes, flattened or in low relief; 4–5, CNIGR Museum 62/12879 and 63/12879; fragments of adult rhabdosomes in low relief; 4, ×7·5; 5, ×5; others ×10.

Figs 6–7. *Normalograptus medius* (Törnquist); CNIGR Museum 68/12879 and 69/12879; fragments of adult rhabdosomes showing rounded proximal ends; *gregarius* Biozone; Zhaksy-Kargala Valley; ×10.

Fig. 10. *Normalograptus* cf. *balticus* (Pedersen); CNIGR Museum 67/12879; proximal fragment with long, stout virgella; *ascensus-acuminatus* Biozone; Zhaksy-Kargala Valley; ×20.

Figs 11–12. *Normalograptus miserabilis* (Elles and Wood); CNIGR Museum 70/12879 and 71/12879; narrow, parallel-sided rhabdosomes; *gregarius* Biozone; Zhaksy-Kargala Valley; ×10.

KOREN' and RICKARDS, *Neodiplograptus*, *Normalograptus*



TEXT-FIG. 6. A–C, *Glyptograptus* cf. *serratus* Elles and Wood; ?*cyphus* and *gregarius* biozones, Kos-Istek region. A, CNIGR Museum 49/12879; a fragment of proximal part of adult rhabdosome, possessing long stout virgella, reverse view; B–C, CNIGR Museum 50/12879; proximal and distal parts of the same rhabdosome. D,

Neodiplograptus sp.

Text-figure 6F

Material. Two specimens in low relief, in places with preserved fusellar structure, from localities B408 and G7/25 in the Kos-Istek region.

Horizon. Rhuddanian, *ascensus-acuminatus* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome > 20 mm (excluding vane and virgella); robust (dorso-ventral width at $th1^1/1^2$ pair 1·45 mm; 2·5 mm at distal end); sicula 2·25 mm long, apex reaching third thecal pair; thecal overlap greater than one-half; base of interthecal septum just below previous aperture; virgella robust and *c.* 2 mm long; nema within rhabdosome is increasingly robust distally and extends distally as a vane fully 15 mm long, possibly tripartite with the nema *sensu stricto* running along its centre.

Description. The proximal thecae are doubly sigmoidal and although the geniculum is typically glyptograptid it is sharper proximally than distally, and upon flattening would approach neodiplograptid profiles. The proximal end development is unclear, it could be of *normalis* (H) or *tamariscus* (I) type. Thecal overlap remains about the same throughout the colony. Metathecal growth bands number around ten.

Remarks. Future work may show a relationship to *Persculptograptus persculptus*.

Genus NORMALOGRAPTUS Legrand, 1987

Type species. Climacograptus scalaris var. *normalis* Lapworth, 1877; designated Legrand 1987; from the Llandovery of County Down, Ireland.

Normalograptus cf. *baltícus* (Pedersen, 1922)

Plate 4, figure 10

cf. 1975 *Climacograptus balticus* Pedersen; Bjerreskov, p. 24, pl. 4B.

Material. One specimen in low relief and its counterpart, from locality 474-2-11 and 12 in the Kos-Istek region.

Horizon. Lower Rhuddanian, *ascensus-acuminatus* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome more than 6 mm long with stout virgella over 25 mm long. Rhabdosome widens from 0·7–0·8 mm at $th1^1$ to 1·05 mm at $th5^1$. Thecae number 5·5 in the first 5 mm. Sicula is exposed for 1 mm in obverse view; its aperture is 0·25–0·3 mm wide. $Th1^1$ bends at the sicular aperture and grows upwards for 1·2 mm.

Remarks. The single specimen in our collection is assigned to *N. balticus* (Pedersen) with some reservation. The rhabdosome is slightly tilted and covered with thick periderm, which makes it

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Glyptograptus bulbus sp. nov.; CNIGR Museum 4/12879; *vesiculosus* Biozone; Kos-Istek region. E, *Pseudorthograptus* sp.; CNIGR Museum 51/12879; a proximal part of adult rhabdosome in hemiscalariform view, showing the mesial apertural elevation and stout, long virgella; *gregarius* Biozone; Zhaksy-Kargala Valley. F, *Neodiplograptus* sp.; CNIGR 66/12879; an adult septate rhabdosome with well developed nemal vane; *ascensus-acuminatus* Biozone; Zhaksy-Kargala Valley. G, *Comograptus comatus* Obut and Sobolevskaya, 1968; holotype, CNIGR Museum 27/9765; specimen showing proximal sicular and thecal spinosity and geniculate thecae throughout the rhabdosome; lower *triangulatus* Biozone; Norilsk region. H, *Neodiplograptus korinevskii* sp. nov.; holotype, CNIGR Museum 59/12879; shows the proximal thecal outgrowths, preserved as siliceous internal moulds; *cyphus* Biozone; Zhaksy-Kargala Valley. Scale bars represent 1 mm.

difficult to observe the thecal shape. Their glyptograptid appearance, however, may be real (compare with *G.* cf. *serratus* above). In the dimensions of the rhabdosome, possession of a long virgella, and in stratigraphical occurrence it agrees well with the Bornholm material.

Normalograptus trifilis trifilis Manck, 1923

Plate 5, figures 9–12; Text-figure 23G

1906 *Climacograptus medius* Törnquist; Elles and Wood, pl. 26, fig. 4*f*.
1923 *Climacograptus trifilis* spec. nov., Manck, p. 228, fig. 32.
1975 *Climacograptus trifilis trifilis* Manck; Bjerreskov, p. 23, fig. 9B.

Material. Four flattened rhabdosomes, incomplete or preserved in ventro-lateral view, from localities 671-2/73-203, 671-8/74-108 and 671-8/74-56*a* in the Zhaksy-Kargala Valley.

Horizon. Lower Rhuddanian, *ascensus-acuminatus* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome septate, less than 10 mm long, widening from 0·7–0·8 mm at $th1^1$ to a maximum of 1·2–1·4 mm *c.* 5 mm from sicula, then parallel-sided. Thecae are of normalograptid type numbering 5·5–6·5 in the first 5 mm. Proximal end rounded and thickened by cortical(?) peridermal layers; virgella stout, more than 1 mm long. There are two additional proximal spines directed ventro-proximally. One of them could be an anti-virgellar spine; the other could be formed at the ventral side of $th1^1$ close to its flexing point. Sicula not seen except for its aperture, 0·2–0·25 mm wide.

Remarks. A few poorly preserved rhabdosomes reveal the important diagnostic feature of *N. trifilis* (Manck) namely the prominent virgella and two other proximal spines. The origin of the spines is not seen on our specimen. The character itself is unique for the Silurian normalograptids.

Genus HIRSUTOGRAPTUS gen. nov.

Type species. Hirsutograptus longispinosus gen. et sp. nov., from the *ascensus-acuminatus* Biozone of the Kos-Istek region.

Diagnosis. Small multispinose biserial, probably with *normalis* Pattern (H) development; thecae broadly normalograptid with deep excavations, relatively short, vertical supragenicular walls and genicular thickening; rhabdosomes probably septate; thecae alternating, overlapping about one-half; sicula of moderate length; virgella conspicuous, thread-like; five or six other sicular, apertural spines; thecal apertures with up to four genicular spines (essentially lateral in position), except on proximal two to four thecae where there may be more; spines occur subaperturally less regularly.

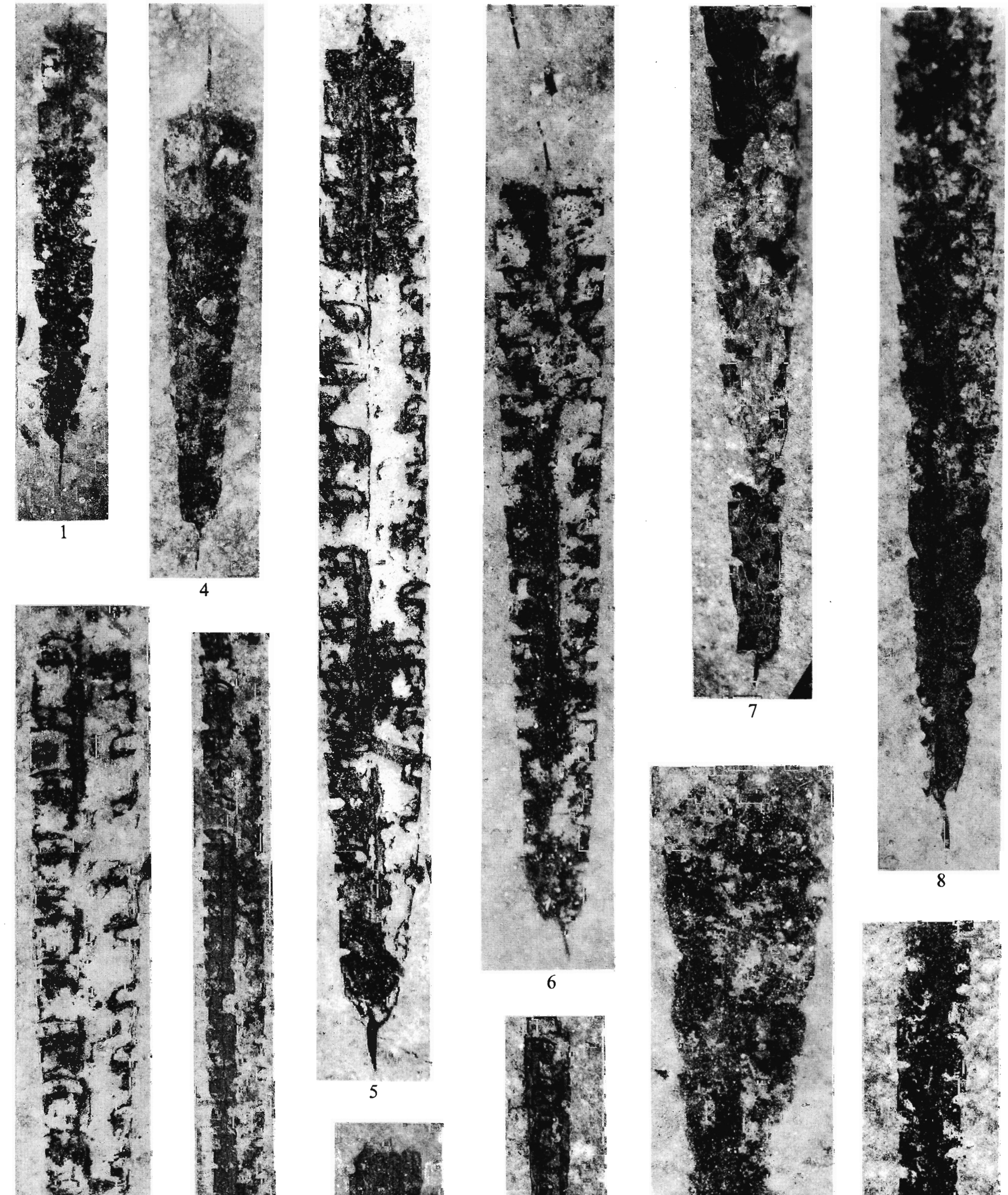
EXPLANATION OF PLATE 5

Fig. 1. *Normalograptus* cf. *mirnyensis* (Obut and Sobolevskaya); CNIGR Museum 72/12879; narrow rhabdosome with closely spaced thecae and long virgella; *ascensus-acuminatus* Biozone, Kos-Istek region; × 10.

Figs 2–3, 6. *Normalograptus normalis* (Lapworth); CNIGR Museum 73/12879, 74/12879 and 75/12879; *vesiculosus* to *gregarius* biozones; Kos-Istek region; 2, 6, × 10; 3, × 5.

Figs 4–5, 7–8. *Normalograptus rectangularis* (McCoy); CNIGR Museum 76/12879, 77/12879, 78/12879 and 79/12879; *cyphus* to *gregarius* biozones; Kos-Istek region; all × 10.

Figs 9–12. *Normalograptus trifilis* (Manck); CNIGR Museum 80/12879, 81/12879, 82/12879 and 83/12879; two proximal spines in addition to the virgella are preserved in all specimens; 9, 11–12, *ascensus-acuminatus* Biozone, Zhaksy-Kargala Valley; 10, *vesiculosus* Biozone; Zhaksy-Kargala Valley; 9–10, 12, × 10; 11, × 20.



KOREN' and RICKARDS, *Normalograptus*

Remarks. Such spinosity has not previously been recorded in Llandovery graptolites and the two species of *Hirsutograptus* are quite unlike any other described species. They differ from *Victorograptus* gen. nov. in lacking a pseudancora and membrane structure, and also in the extent of genicular spinosity. *Hirsutograptus* is probably closely related to non-spinose normalograptids such as *N. mirnyensis* Obut and Sobolevskaya (see Evolution section). It occurs in association with non-spinose normalograptids such as *N. normalis* (Lapworth).

Both *Paraclimacograptus sinitzini* Chaletskaya, 1960, from the northern slope of the Alai Range, Southern Tien Shan, and *Orthograptus sinitzini* (Chaletskaya, 1960), from the Kolyma region, should be included in *Hirsutograptus*. These forms have sicular and thecal spinosity and may have the same thecal profile: nevertheless, more needs to be known about the thecal structure before direct comparisons can be made with *H. longispinosus* gen. et sp. nov. and *H. villosus* gen. et sp. nov.

Hirsutograptus longispinosus gen. et sp. nov.

Plate 7, figure 4; Text-figure 8A, F–G

Holotype. CNIGR Museum 103/12879, Plate 7, figure 4; Text-figure 8A; *ascensus-acuminatus* Biozone, Rhuddanian, Sakmara Formation, southern Urals.

Derivation of name. Reflecting the long thecal spines.

Material. Five specimens, flattened or in low relief, from localities 474-2-11, 671-8-286, 671-8-66 and 1643-105 in the Kos-Istek region of the southern Urals, and from localities 745/6, 745/7 and V-22-13 in the Kurama Range, Uzbekistan, Central Asia.

Horizon. The same as for holotype in the southern Urals; the *ascensus-acuminatus* Biozone of Central Asia, Mashrab Formation.

Diagnosis. Rhabdosome, septate, large, more than 15 mm long and 1·7 mm wide, with proximal spinosity, including virgella, antivirgellar and thecal spines. Thecae are geniculate, with slightly inclined supragenicular walls, possessing long thick spines on each.

Description. The rhabdosome widens gradually from about 0·65 mm to a maximum (sub-lateral) width of 1·7 mm, that is, in subapertural view; distally it is parallel-sided.

Thecae have semicircular excavations and supragenicular walls 0·7–0·8 mm long distally, slightly inclined to the rhabdosomal axis. The geniculum is provided with one mesial spine, more than 1·4 mm long and 0·1–0·12 mm thick at the base. These genicular spines are straight or broadly curved, ventrally directed and hanging down proximally at their ends. Occasionally, a single apertural spine is present or a bifurcation of a genicular spine has taken place. There are some outgrowths from the thecal apertures attached to the proximal parts of the genicular spines and these reveal the fusellar structure (Text-fig. 8A). Thecal number 10·5–11 in 10 mm. The proximal end is rounded, possessing, besides a virgella (0·4 mm long) another two pairs of spines: one of antivirgellar, sicular spines, the other most probably thecal, originating at the bending point of the ventral wall of $th1^1$. Proximal spines are 0·5–0·7 mm long. Sicula not seen.

EXPLANATION OF PLATE 6

Figs 1–6. *Hirsutograptus villosus* gen. et sp. nov.; *ascensus-acuminatus* Biozone; Kos-Istek region. 1, 4, CNIGR Museum 84/12879 and 87/12879; adult rhabdosomes with numerous thecal spines and well developed proximal spinosity (1); ×20; 2, CNIGR Museum 85/12879; proximal fragment in hemiscalariform view, possessing virgella, two antivirgellar and two ?thecal spines; ×10; 3, CNIGR Museum 86/12879; fragment of adult rhabdosome in scalariform view; thecal apertures possessing four long dorso-lateral spines; ×10; 5, CNIGR Museum 88/12879; adult rhabdosome possessing numerous thecal spines; ×10; 6, CNIGR Museum 89/12879; young rhabdosome with well developed thecal spinosity; ×20.

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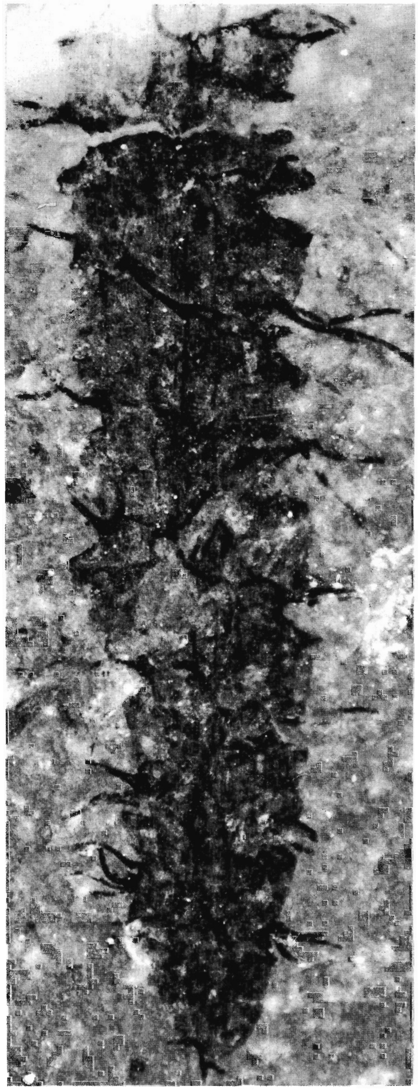

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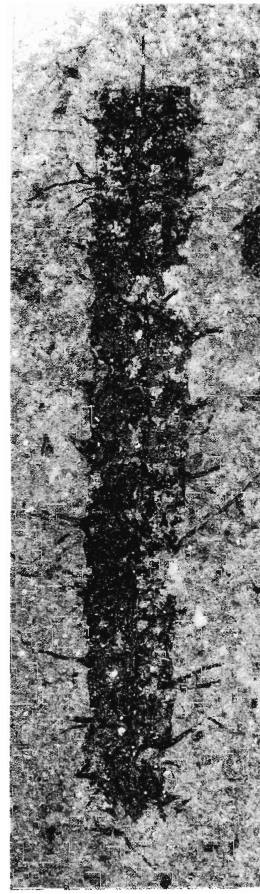

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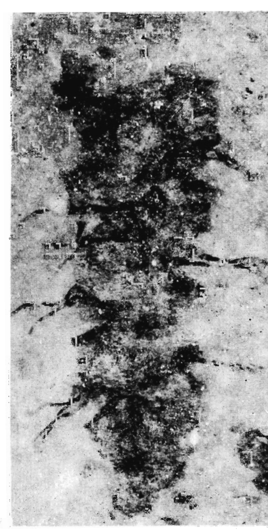

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KOREN' and RICKARDS, *Hirsutograptus*

Remarks. *H. longispinosus* gen. et sp. nov. can be distinguished easily from *H. villosus* gen. et sp. nov. in having single thecal spines, which are generally longer and stouter; and in its larger rhabdosome size. The thecal shape is not clear, as most of the adult specimens are preserved in ventro-lateral view with no extreme proximal ends. A comparison of the new species with *Orthograptus sinitzini* (Chaletzkaya, 1960), described from the same horizon in Central Asia and north-east Russia (Obut *et al.* 1967), presents some difficulties. The latter species possesses long thecal spines, not unlike those of *H. longispinosus*, but their number and position are not clear because of poor preservation in black shales; it is possible that they are closely related. *O. sinitzini* apparently has more closely spaced thecae, although this is not too clear from the original photographs; plate 3, figures 9–10 may have a lower thecal spacing than stated in the text.

Hirsutograptus villosus gen. et sp. nov.

Plate 6, figures 1–6; Plate 7, figures 1–3; Text-figures 7, 8B–D

Holotype. CNIGR Museum 90/12879, Plate 7, figure 1; Text-figure 8C; the *ascensus-acuminatus* Biozone, Rhuddanian, Sakmara Formation, southern Urals.

Derivation of name. From the Latin *villosus*, refers to spines.

Material. More than 40 specimens at different astogenetic stages, preserved flattened or in low relief, from localities 474/2/61-3, 474-2/61-12, B671-8/74-64, 1643/50-25, 1643/50-26 and 1643/50-85 in the Kos-Istek region.

Horizon. Rhuddanian, *ascensus-acuminatus* Biozone of the southern Urals, Sakmara Formation and of the Kurama Range, Central Asia, Mashrab Formation.

Diagnosis. Medium-sized rhabdosome, 10 to 14 mm long, up to 1·6 mm wide, parallel sided and with a rounded proximal end. Thecae have short supragenicular walls and semicircular excavations. Up to four closely spaced spines are formed along each geniculum; occasionally some additional spines can be seen on the supragenicular walls. Prominent virgella, paired antivirgellar and other spines on the apertural margin of sicula form characteristic spinose bundles. The number and size of spines on both the sicular and thecal apertures increase during astogeny.

Description. Rhabdosome 10–14 mm long, widening quickly proximally: width at $th1^1$ 0·85–0·95 mm; at $th2^1$, 0·9–1 mm; at $th3^1$, 1·2 mm; at $th4^1$, 1·2 mm, and at $th5^1$, 1·4 mm; a maximum dorso-ventral width of 1·5 mm is reached 5 mm from the sicular aperture. The rhabdosome is fully septate.

The thecae have a distinctive geniculum and semicircular excavations 0·2 mm deep. Suprapertural walls, 0·4–0·6 mm long, are slightly inclined outwards proximally and almost parallel to the rhabdosomal axis distally. Numerous spines (four or more), usually 0·7–0·9 mm long, occasionally reaching 1·2–1·4 mm, are formed at the geniculum, and sometimes on the ventral walls. They are thickened at the base and originate mostly from both lateral sides of the geniculum. Their size and number increase during astogeny. Thecae number 6·5 in 5 mm and about 12 in 10 mm.

EXPLANATION OF PLATE 7

Figs 1–3. *Hirsutograptus villosus* gen. et sp. nov.; *ascensus-acuminatus* Biozone; Zhaksy-Kargala Valley. 1, holotype, CNIGR Museum 90/12879; adult rhabdosome showing complete median septum; supragenicular thecal walls, slightly outward sloping; well developed thecal and sicular spinosity; reverse view; ×20; 2, CNIGR Museum 91/12879; adult rhabdosome in hemiscalariform view; ×10; 3, CNIGR Museum 92/12879; young rhabdosomes; ×20.

Fig. 4. *Hirsutograptus longispinosus* gen. et sp. nov.; holotype, CNIGR Museum 103/12879; adult rhabdosome with long genicular spines; *ascensus-acuminatus* Biozone; Zhaksy-Kargala Valley; ×10.

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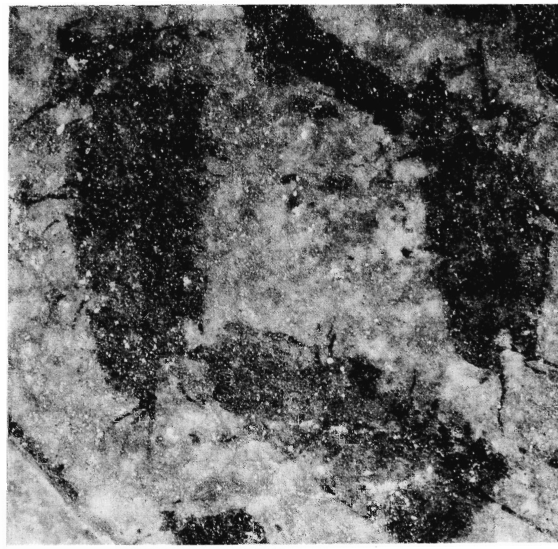

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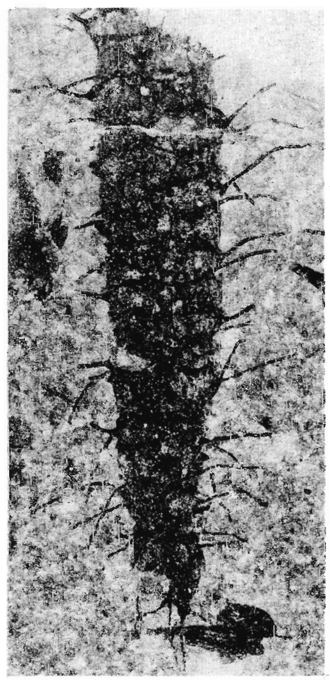

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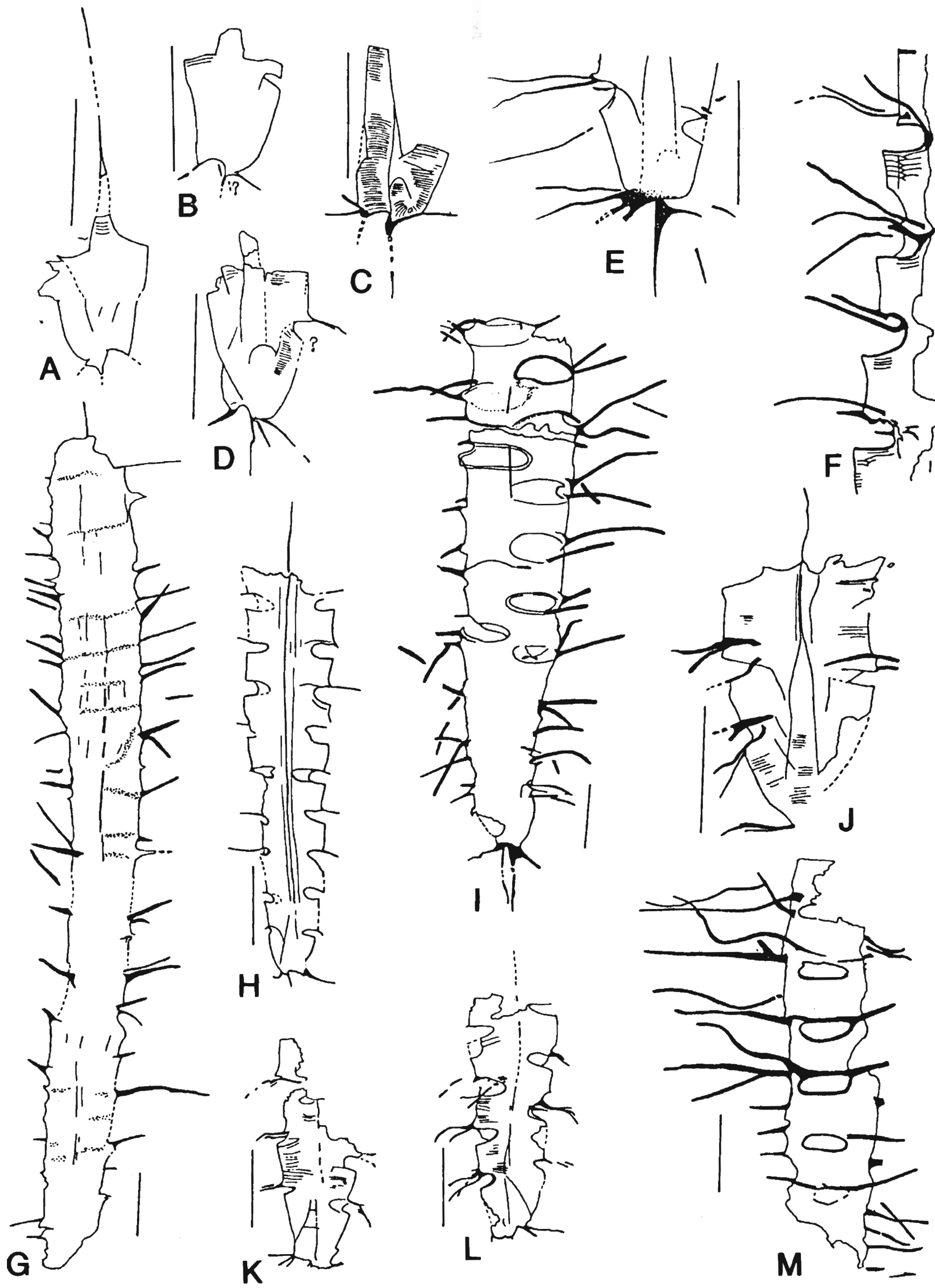
KOREN' and RICKARDS, *Hirsutograptus*



TEXT-FIG. 7. For legend see opposite.

The proximal end is rounded, and th1[1] extends below the sicular aperture, for a distance of 0·3–0·32 mm. Its upgrowing portion is 0·7–0·8 mm long. The sicula is almost completely covered in reverse view. It is up to 1·6 mm long and 0·2–0·25 mm wide at the aperture, with an apex reaching the geniculum of th2[1]. Apertural sicular spines, including paired antivirgellar ones, are 0·6–0·8 mm long. All proximal spines were formed at an early astogenetic stage before the first pair of thecae was completed. The virgella is the longest spine and can be distinguished easily. The other spines spread at different angles in a plane approximately at right angles to the virgella or the rhabdosomal axis. In the adult specimens, the periderm is so heavily carbonized that the point of origin of individual spines, within the thick bundle, is difficult to distinguish. The same is true for thecal genicular spines.

Remarks. The main diagnostic features of the species are: well developed thecal and sicular spinosity, as well as the positions of all the spines at approximately right angles to the medium septum. The species has some affinity with *Paraclimacograptus sinitzini* Chalteskaya in the size of the rhabdosome, thecal shape and nature of spines, but the poor preservation of the Alai Range forms precludes direct comparison at present. *H. villosus* sp. nov. differs from *O. sinitzini* Obut and Sobolevskaya (*in* Obut *et al.* 1967) in having more distant thecae (about 12 in 10 mm cf. 18–14 in 10 mm) and by its shorter and more numerous thecal spines (no more than 2 mm long, cf. 4 mm long). The Kolyma specimens of Obut and Sobolevskaya (and also of Koren' *et al.* 1979) are preserved in subscalariform view and hence the basic nature of the thecal spines is difficult to determine exactly. On the number and lengths of spines the Kolyma specimens are closer to *H. longispinosus* than to *H. villosus*.

Genus VICTOROGRAPTUS gen. nov.

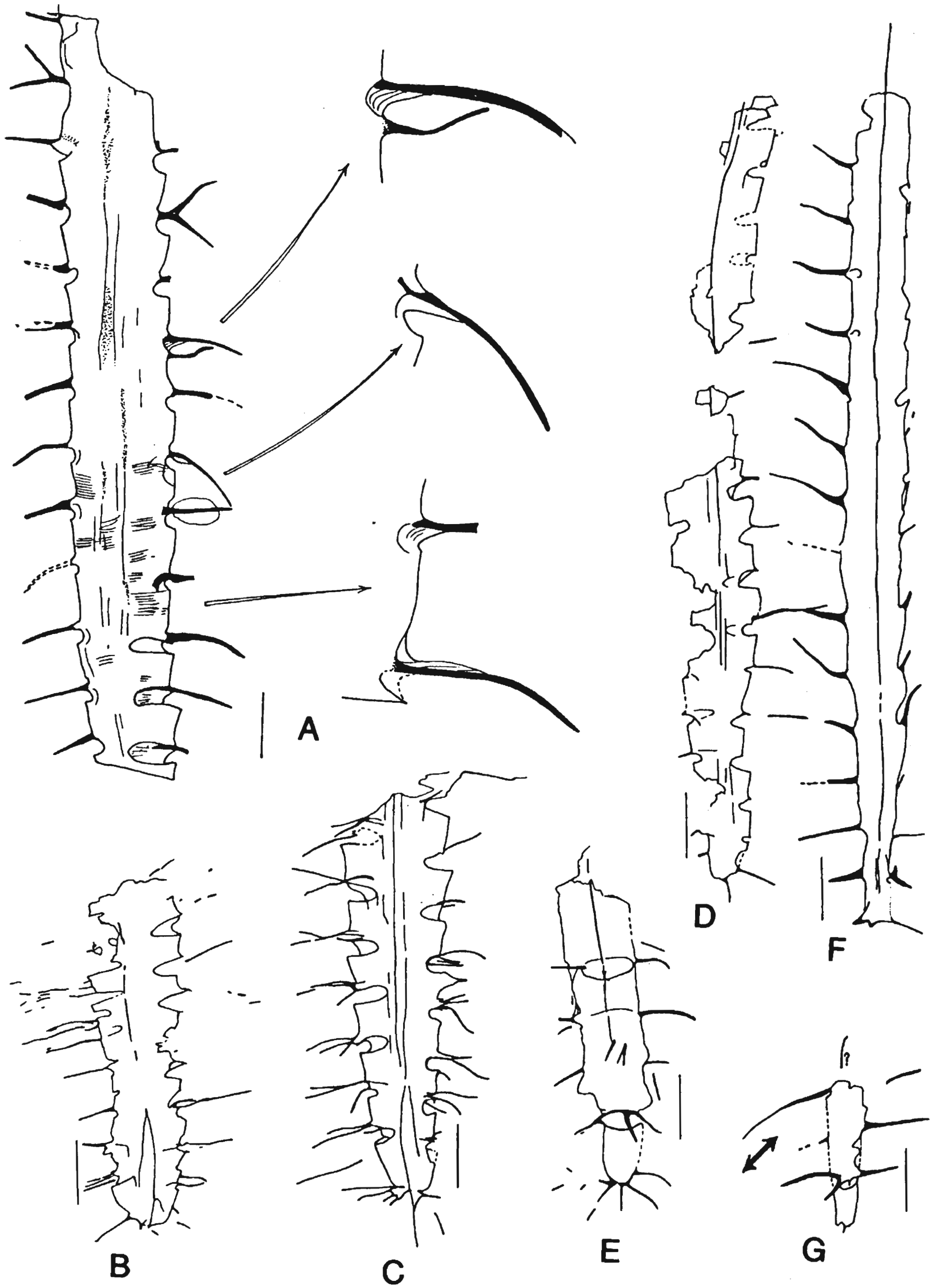
Derivation of name. After Dr I. Victor.

Type species. Victorograptus morosus gen. et sp. nov., *gregarius* Biozone, Sakmara Formation, southern Urals.

Diagnosis. Spinose and 'laciniate' biserial, probably with *tamariscus* Pattern (I) development; spinose meshworks and membranes extend to ten times the rhabdosome width, and the main ?supporting spines of these networks are genicular in origin, possibly mesial (rather than paired); a conspicuous pseudancora is developed which grows outwards and upwards possibly connecting with the meshworks developed from the genicular processes; thecae probably glyptograptid *sensu lato*; pseudancora well developed before th1[1] completed.

Remarks. Victorograptus resembles pseudorthograptids in having a pseudancora and membrane, but differs in the nature of the thecal spinosity, in the large extent of the meshwork developed therefrom, and in the nature of the thecal geniculum which is absent in pseudorthograptids. The 'lacinia' recalls similar developments in some Ordovician genera such as *Lasiograptus* and *Neurograptus* but the resemblance is superficial, and the developmental pattern is of a much later kind.

TEXT-FIG. 7. *Hirsutograptus villosus* gen. et sp. nov.; *ascensus-acuminatus* Biozone. A–E, J, CNIGR Museum 93/12879, 85/12879, 93A/12879, 94/12879, 95/12879 and 87/12879; juvenile rhabdosomes showing an early development of proximal sicular and thecal spinosity; F, CNIGR Museum 96/12879; incomplete rhabdosome showing the number and position of thecal spines and fusellar zig-zag structure; Kos-Istek region. G, I, M, CNIGR Museum 97/12879, 91/12879 and 86/12879; adult rhabdosomes in hemiscalariform (G, I) or scalariform (M) view showing dorso-lateral position of bifurcating spines; Kos-Istek region. H, K–L, CNIGR Museum 98/12879, 99/12879 and 89/12879; adult rhabdosomes and their fragments showing strongly geniculate climacograptid thecae and more (K–L) or less (H) developed sicular and thecal spinosity, Central Asia, Kurama Range, Mashrad saj. Scale bars represent 1 mm.



TEXT-FIG. 8. For legend see opposite.

Victorograptus morosus gen. et sp. nov.

Plate 8, figure 1; Text-figure 9A–B

Holotype. CNIGR Museum 106/12879, Plate 8, figure 1; Text-figure 9A; *gregarius* Biozone, Aeronian, Sakmara Formation, southern Urals.

Derivation of name. From the Latin, *morosus* = capricious.

Material. Two specimens flattened, one an adult rhabdosome, the other a proximal end, from localities B671-8/74-3049 and 1643/50-10 in the Kos-Istek region.

Horizon. Aeronian *gregarius* and *convolutus* biozones of the southern Urals, Sakmara Formation.

Description. Robust, tapering rhabdosome, with sub-lateral width at $th1^1$ of *c*. 0·5 mm, and at the 7th thecal pair of 1·7 mm (excluding processes); overall dorso-ventral width, including processes, at least 12 mm; proximal thecal spacing 10 in 10 mm, distally 8+ in 10 mm; prominent robust genicular spines (? a pair) at least 5 mm long, possibly dividing into numerous more slender spines; thecae glyptograptid though with strong geniculum, apertures everted; supragenicular walls long and inclined gently outwards; virgella divides into at least four pseudancorate rods after 0·2 mm, and thereafter into many smaller rods supporting a membranous structure. The main rods have fine cross-bars in places. The pseudancora structure grows ventro-distally at about 45°, and by the level of the fifth thecal pair is *c*. 4 mm away from the thecae and lying across the elongate genicular processes. The pseudancora is developed extensively when $th1^1$ is only partially grown (Text-fig. 9B), and a membrane may be present at this stage. The sicula has a length of 1·3 mm (prosicula 0·4 mm); and $th1^1$ has a downgrowing portion of 0·5 mm. Some fusellar material may grow out from the geniculum along the base of the genicular spines, effectively thickening them. Thecal overlap is not seen; and the presence of a median septum cannot be established.

Remarks. *Victorograptus morosus* is a spectacular and unique graptolite, the peridermal part of the rhabdosome (the thecae) being totally enclosed by an extensive meshwork and probable membrane, perhaps connected to very elongate genicular spines. In these characters it differs from *O. sinitzini* (Chaletskaya) *sensu* Obut and Sobolevskaya (*in* Obut *et al.* 1968), which has similar thecae and genicular spines; and the scale of these processes distinguishes it from *Pseudorthograptus* spp. (see below) which have a pseudancora, meshwork and membrane. *Pseudorthograptus* is the nearest genus and a *Pseudorthograptus* species may be ancestral to *V. morosus*.

Genus SUDBURIGRAPTUS gen. nov.

Type species. *Orthograptus eberleini* Churkin and Carter, 1970, from the *vesiculosus* and *cyphus* biozones; from the Llandovery of south-east Alaska.

Diagnosis. Small, non-spinose biserials with either *normalis* (H) Pattern or *tamariscus* (I) Pattern development; rhabdosomes usually less than 20 mm long; and 1–2 mm wide; thecae simple tubes with low overlap (one-third to one-half) and apertures at right angles to thecal tube axis or slightly everted; thecal or proximal rhabdosomal spines absent.

TEXT-FIG. 8. A, F–G. *Hirsutograptus longispinosus* gen. et sp. nov. A, holotype, CNIGR Museum 103/12879; shows geniculate thecae possessing long and stout dorsal spines with membrane-like outgrowths attached to them; F, CNIGR Museum 104/12879; complete adult rhabdosome preserved in scalariform view, proximal end is unclear; G, CNIGR Museum 105/12879; proximal end in a hemiscalariform view, showing a bifurcating spine on ?$th1^1$ aperture, arrows show direction of tectonic elongation; *ascensus-acuminatus* Biozone; Zhaksy-Kargala Valley. B–D, *Hirsutograptus villosus*, gen. et sp. nov.; CNIGR Museum 100/12879, 90/12879 and 101/12879; incomplete adult rhabdosomes (B, D) fully septate rhabdosome with 'climacograptid'-like thecae and well developed proximal and thecal spinosity (C). E, *Hirsutograptus* cf. *villosus* gen. et sp. nov.; CNIGR Museum 102/12879; a proximal fragment in scalariform view; *ascensus-acuminatus* Biozone; Kos-Istek region. Scale bars represent 1 mm.

TEXT-FIG. 9. For legend see opposite.

Remarks. These rare and inconspicuous forms occur from the *acuminatus* to *cyphus* biozones and possibly higher. They differ from *Orthograptus* in having a simpler proximal development and in the absence of thecal and proximal rhabdosomal spines. Their derivation is problematical, but was possibly from the *amplexicaulis* group by simplification of development and loss of spines. They differ from *Pseudorthograptus* in being only virgellate rather than pseudancorate, but also lack spines, membranes and meshworks. *Sudburigraptus* species are very similar to some *Parapetalolithus* species and undoubtedly gave rise to that genus by development of the petalolithid style of upward-growing, outward-growing, and overlapping thecae. We include the following in *Subdurigraptus*: the type species; *Orthograptus* sp. (Rickards 1988); *Orthograptus attenuatus* Rickards, 1970?; *Orthograptus abbreviatus* Elles and Wood (*sensu* Hutt 1974, *pars*); *Orthograptus abbreviatus* Elles and Wood, 1907 (*pars*); '*Orthograptus*' *cabanensis* Zalasiewicz and Tunnicliff, 1994?.

Genus PARACLIMACOGRAPTUS Přibyl, 1947

Type species. *Climacograptus innotatus* Nicholson, 1869; original designation; from the Llandovery of Dob's Linn, Scotland.

Paraclimacograptus innotatus (Nicholson, 1869)

Plate 8, figures 2–3

1869 *Climacograptus innotatus* Nicholson, p. 238, pl. 11, figs 16–17.
1974 *Climacograptus innotatus innotatus* Nicholson; Hutt, p. 21, pl. 1, figs 6–7, 12; text-fig. 8, fig. 7 [see for synonymy].
1977 *Paraclimacograptus innotatus* (Nicholson); Crowther and Rickards, p. 19, pl. 4, fig. 3.
1981 *Paraclimacograptus innotatus innotatus* (Nicholson), Crowther, p. 88, pl. 13, figs 4–7.

Material. Ten specimens flattened and at different astogenetic stages, from localities B671-1-14, B671-2, B671-3/73, B671-8/74-300, B671-8*a*, B671-9 (several specimens) of the Zhaksy-Kargala Valley.

Horizon. Rhuddanian, *vesiculosus* and *cyphus* biozones of the southern Urals, Sakmara Formation.

Description. The rhabdosome is small, 10 mm long, up to 1·4–1·5 mm wide, and aseptate. It widens rapidly: width is 0·7–0·85 at $th1^1$, 0·9–1·1 mm at $th2^1$, 1·3 mm at $th3^1$ and reaches a maximum at about $th4^1$. It is parallel-sided further on and narrows slightly at the distal end.

The thecae are strongly geniculate with ventral supragenicular walls inclined away from the rhabdosomal axis at 15° proximally and 10° or less distally. Each theca has a single genicular flange, 0·2–0·4 mm long. The thecae number 7–7·5 in the first 5 mm.

The extreme proximal end ($th1^1$ and $th1^2$) is slightly tapering. $Th1^1$ extends below the sicular aperture, then bends sharply, and its upward-growing portion is 0·7–0·8 mm long. The sicula is 1·5–1·65 mm long, and 0·15 mm wide at the aperture. The virgella is thorn like, up to 0·4 mm long.

Remarks. Geniculate thecae, inclined supragenicular walls and specific processes of a genicular origin make this species easily distinguishable. The details of morphological structure of the thecae and processes will be the subject of a future study by us based on isolated material from the Ural River Basin, southern Urals.

TEXT-FIG. 9. *Victorograptus morosus* gen. et sp. nov.; *gregarius* Biozone; Zhaksy-Kargala Valley. A, holotype, CNIGR Museum 106/12879; adult rhabdosome with well developed pseudancora and meshwork structure, fragments of membranous tissue are partly preserved; B, CNIGR Museum 107/12879; a juvenile rhabdosome with sicula and incomplete $th1^1$ possessing a meshwork and probably a membrane (to the left). Scale bars represent 1 mm.

Genus PETALOLITHUS Suess, 1851

Type species. Prionotus folium Hisinger, 1837; subsequently designated Lapworth (1873); from the Llandovery of Sweden.

Diagnosis. Robust or ovate rhabdosome with tabular cross section; protracted proximal end caused by marked upward growth of th1^1 and 1^2, both of which have concave ventral walls, curved to varying degrees; development of *tamariscus* (I) Pattern; virgella divides quickly to a pseudancora which may grow upwards to varying distances and envelop the proximal end of the rhabdosome with a fine meshwork; thecae long, overlapping up to nine-tenths, often with everted thecal apertures; fuselli conspicuous, wide, and possibly thickened at their junctions; thecal angles, mesially, up to 45° in some species.

Remarks. Differs from *Parapetalolithus* in having usually more robust rhabdosomes with a pseudancora. The evolutionary origin of this genus, which appears in the *triangulatus* Biozone, is difficult to deduce, but it is likely that it relates to the pseudorthograptids in the immediately underlying biozones.

Petalolithus folium (Hisinger, 1837)

Plate 8, figures 4–5; Text-figure 10A–B

1837 *Prioniotus folium* n. sp., Hisinger, p. 114, pl. 35, fig. 8.
1908 *Petalograptus folium* (Hisinger); Elles and Wood, p. 282, pl. 32, fig. 8*a–b*, *e* (*non c–d*); text-fig. 195.
1941 *Petalolithus folium* (Hisinger); Bouček and Přibyl, 1941, p. 7, pl. 1, figs 6–7, text-fig. 2*a–c*.
1975 *Petalograptus folium* (Hisinger); Bjerreskov, p. 35, fig. 12C, table 2 [see for synonymy].

Material. Specimens flattened and in low relief, from localities 671-2-66, 80, 671-8-81, 74; 1643/50-205, 5050/70-6, 6*a* in the Kos-Istek region, River Medes near the Kensajran Village and in the Zhaksy-Kargala Valley.

Horizon. Aeronian, *convolutus* Biozone, Sakmara Formation.

Description. Broad rhabdosome, *c.* 10 mm long with extremely elongated first thecae and tapering proximal end. Rhabdosome is 2·4–2·5 mm wide at th1^1/th1^2 and reaches a maximum dorso-ventral width of 4·7 mm at th2^1, in the present collection, then narrows quickly distally. Thecae are up to 5 mm long and no more than 0·4 mm wide, inclined at 30–20° (distally) to the rhabdosomal axis. They overlap each other for most of their length. Straight thecal apertures are normal to the thecal axis and number 7·5 in 5 mm.

Th1^1 extends below the sicular aperture for 0·12 mm and its upward-growing portion is *c.* 2·65 mm long. The sicula is free in obverse view for 1·5 mm and in reverse view for 0·35 mm. The virgella divides about 0·2 mm below the sicular aperture and two primary rods are directed ventrally. Close to the divergence point they bifurcate and four secondary rods are sharply bent upwards parallel to the ventral thecal walls and enveloping

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EXPLANATION OF PLATE 8

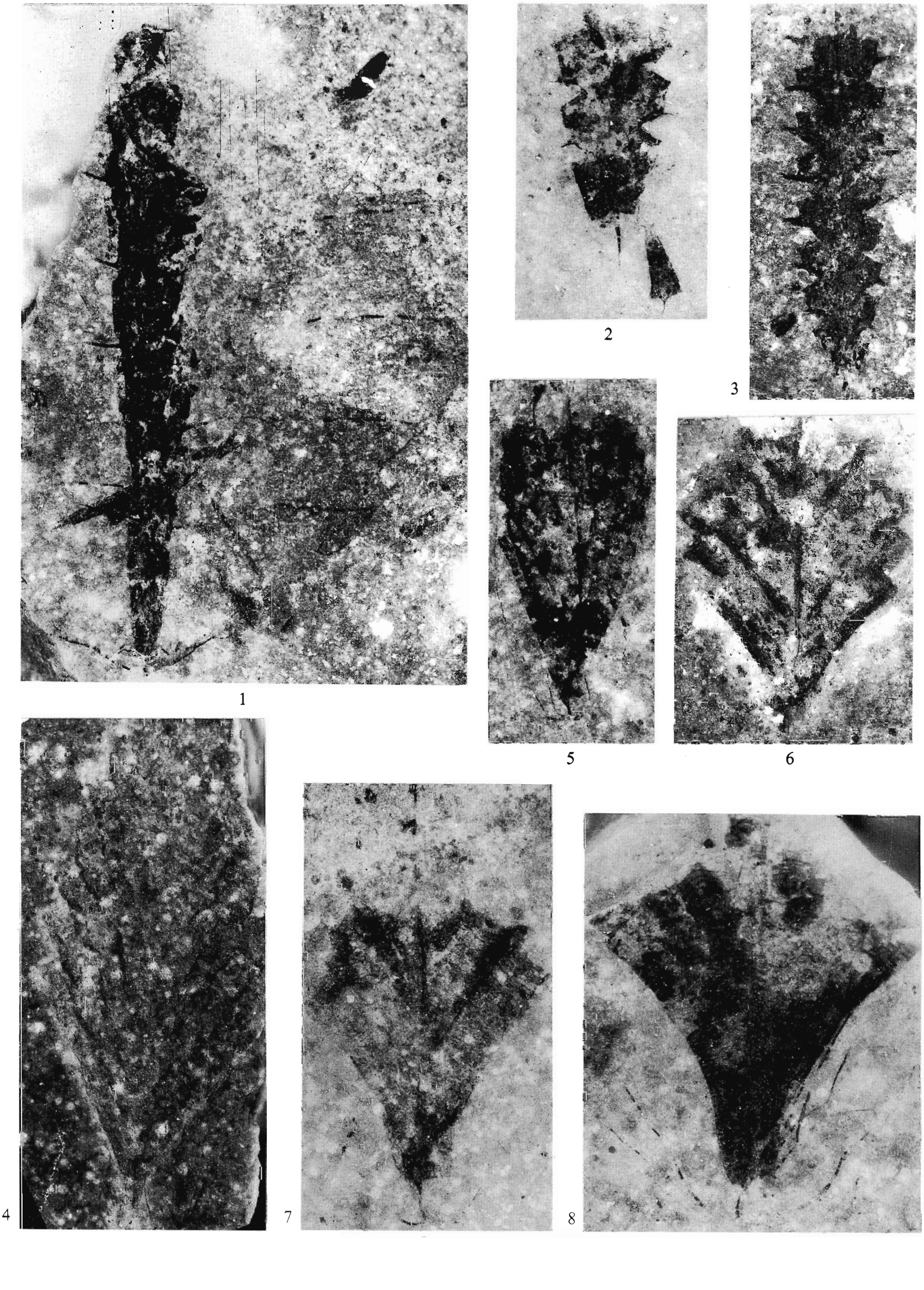
Fig. 1. *Victorograptus morosus* gen. et sp. nov.; holotype CNIGR Museum 106/12879; adult rhabdosome possessing long thecal spines, pseudancora and meshwork; *gregarius* Biozone; Zhaksy-Kargala Valley; ×10.

Figs 2–3. *Paraclimacograptus innotatus* (Nicholson); *vesiculosus* Biozone; Zhaksy-Kargala Valley. 2, CNIGR Museum 108/12879; proximal part of rhabdosome; obverse view; ×20; 3, CNIGR Museum 109/12879; adult rhabdosome possessing well-developed genicular flanges; reverse view; ×10.

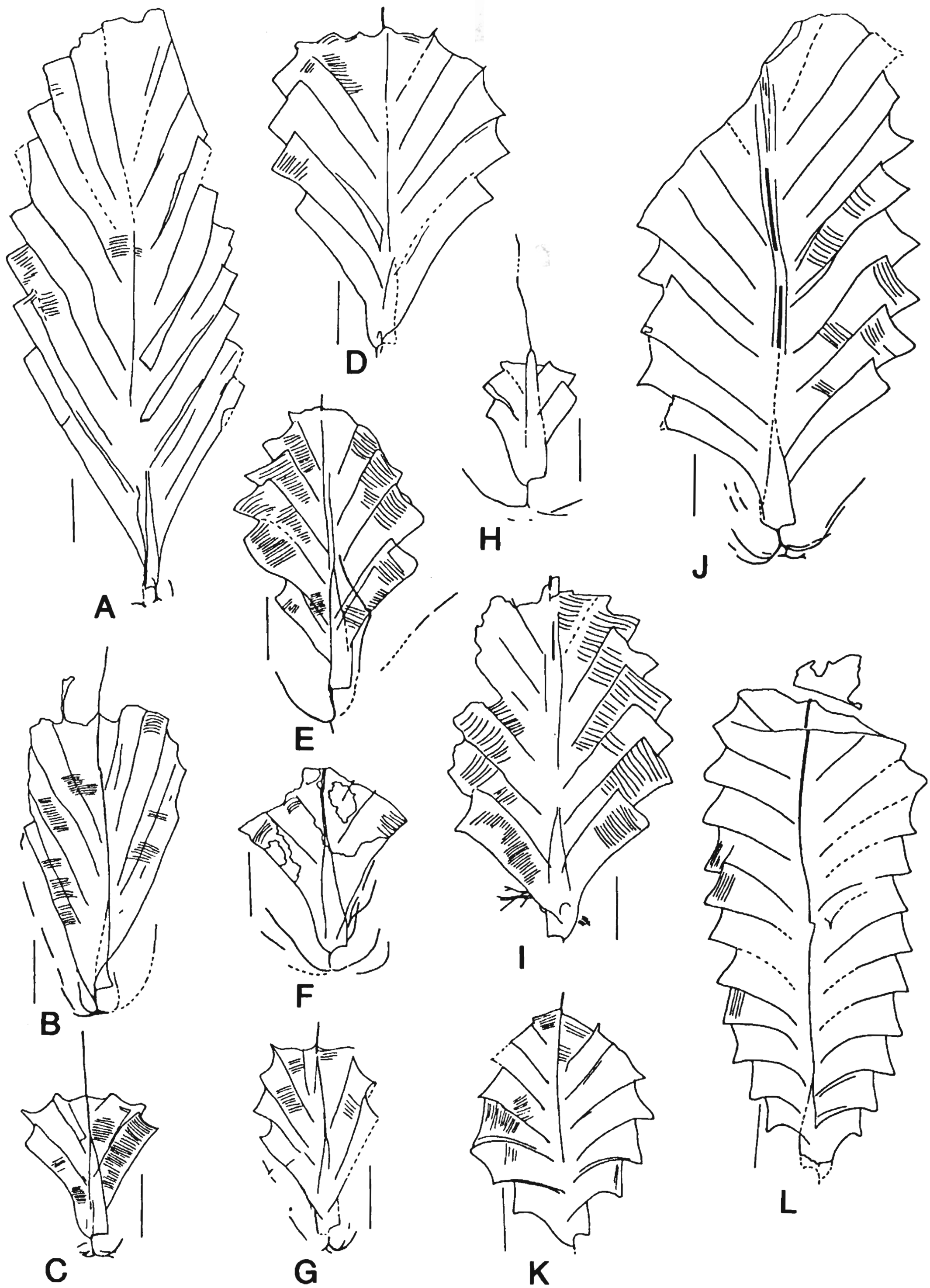
Figs 4–5. *Petalolithus folium* (Hisinger); CNIGR Museum 110/12879 and 111/12879; *convolutus* Biozone; Zhaksy-Kargala Valley; ×10.

Figs 6–8. *Petalolithus minor* (Elles); CNIGR Museum 112/12879, 113/12879 and 114/12879; *gregarius* to *convolutus* biozones; Kos-Istek region. 6, adult rhabdosome; ×10; 7–8, young rhabdosomes with well developed pseudancorae; ×20.

PLATE 8



KOREN' and RICKARDS, graptoloids from the southern Urals



TEXT-FIG. 10. For legend see opposite.

them. These rods, 3·5–3·6 mm long, reach to the apertures of $th1^1$ at least. A pseudancora is developed at an early astogenetic stage.

Remarks. The present material compares well with previously described collections from the Barrandium.

Petalolithus minor (Elles, 1897)

Plate 8, figures 6–8; Text-figure 10C–G

1893 *Diplograptus palmeus* Barrande; Törnquist, pl. 1, figs 29–31.
1897 *Petalograptus minor* sp. nov., Elles, p. 201, pl. 14, figs 17–21.
1908 *Petalograptus minor* Elles; Elles and Wood, p. 279, pl. 32, fig. *5a–e*; text-fig. 193*f–g*.
1967 *Petalograptus minor* Elles; Koren', p. 194, pl. 1, figs 10–11.
1974 *Petalograptus minor* Elles; Hutt, p. 39, pl. 10, figs 2, 7–10.
1975 *Petalograptus minor* Elles; Bjerreskov, p. 33, pl. 4J.
1992 *Petalograptus minor* Elles; Bates and Kirk, p. 30, figs 29–43, 252*b*.

Material. Thirteen specimens, flattened or in low relief, with early growth stages predominating, from localities L1643/50-58, B671/2-72, B671/8-136*a*, 141, 256; B411, 1508 in the Kos-Istek region, Medes River near the Kensajran Village and the Zhaksy-Kargala Valley.

Horizon. Aeronian, *gregarius* to *convolutus* biozones of the southern Urals, the Sakmara Formation.

Description. Rhabdosome short, up to 6 mm long, rounded distally and with an elongated proximal end. It widens from 2–3·2 mm at $th1^1$ to 2–3·75 mm at $th2^1$ and it reaches maximum dorso-ventral width of 3·8 mm at $th3^1$. Distally the rhabdosomal width diminishes resulting in an overall ovate shape. The median septum is partially developed in obverse view.

Thecae show slight widening of the apertures, which are straight or slightly concave and symmetrical. Thecal length increases from > 2–2·8 mm at $th1^1$ to 2–3·75 mm at $th2^1$ and a maximum length of 3·75 mm is reached at $th3^1$. Distally the width diminishes resulting in an ovate shape to the rhabdosome. Thecae number 4 in the first 2·5 mm, overlapping three-quarters at th2, and more than this distally; angle of inclination diminishes from 35–40° at the first pair, to 30° distally.

The sicula is exposed for 1·4–1·9 mm in obverse view, and is seen for 0·35 mm in reverse view. The full sicular length is not known. The aperture is 0·25 mm wide. $Th1^1$ grows upwards for *c*. 1·75–2·2 mm, and it extends below the sicular aperture for 0·08 mm. The virgella divides *c*. 0·25–0·4 mm below the sicular aperture, then bifurcates almost immediately giving rise to long threads up to 2·5–4 mm long. These are bent broadly and directed ventro-distally thinning out to their ends. The pseudancora structure is already developed at the earliest astogenetic stages.

TEXT-FIG. 10. A–B, *Petalolithus folium* (Hisinger); *convolutus* Biozone; Zhaksy-Kargala Valley. A, CNIGR Museum 110/12879; adult rhabdosome, showing fully grown long thecae; pseudancora is not completely preserved; B, CNIGR Museum 111/12879; an immature rhabdosome with pseudancora based on dividing virgella; long secondary ribs reach the aperture of $th1^1$. C–G, *Petalolithus minor* (Elles); *gregarius* to *convolutus* biozones; Kos-Istek region, River Medes. C, F–G, CNIGR Museum 113/12879, 114/12879 and 115/12879; young rhabdosomes, showing early astogenetic development of the pseudancora structures; D, CNIGR Museum 112/12879; an almost complete rhabdosome, pseudancora not preserved. E, CNIGR Museum 116/12879; a rhabdosome with well preserved fusellar structure and pseudancora with long secondary ribs; H, *Petalolithus* sp. A; CNIGR Museum 119*a*/12879; young rhabdosome with well developed pseudancora, partly preserved; ?*gregarius* Biozone; Zhaksy-Kargala Valley. I–J, *Petalolithus ovatoelongatus* (Kurck); *guerichi* (= *minor*) Biozone; Kos-Istek region. I, CNIGR Museum 115/12879; adult rhabdosome with well preserved pseudancora; J, CNIGR Museum 116/12879; incomplete rhabdosome with partly preserved pseudancora and well preserved fusellar structure, reverse view. K–L, *Petalolithus wuxiensis* Ye; CNIGR Museum 118/12879 and 117/12879; both rhabdosomes, young (K) and adult (L) show strongly curved thecae with apertures parallel to the rhabdosomal axis; proximal ends incomplete, reverse views; ?*cyphus* to *gregarius* biozones; Zhaksy-Kargala Valley. Scale bars represent 1 mm.

Remarks. The present material fits well with the earlier descriptions (see synonymy). However, we agree with Hutt's (1974, p. 39) remarks, about the considerable difficulty in distinguishing *Pe. minor* from early growth stages of *Pe. ovatoelongatus* (Kurck, 1882).

Petalolithus ovatoelongatus (Kurck, 1882)

Plate 9, figures 2, 4; Text-figures 10I–J, 11D

1850 *Graptolithus palmeus* Barrande, pp. 59–63 (*pars*), pl. 3, fig. 7 (*non* figs 1–6).
1882 *Cephalograptus ovato-elongatus* n. sp., Kurck, p. 303, pl. 14, fig. 10.
1908 *Petalograptus palmeus* var. *ovato-elongatus* (Kurck); Elles and Wood, p. 277, pl. 32, fig. 4*a* (*non b–d*), ?text-fig. 191*a–c*.
1967 *Petalograptus ovatoelongatus* (Kurck); Koren', pl. 1, fig. 12.
1974 *Petalograptus ovatoelongatus* (Kurck); Hutt, pl. 9, figs 3–5, pl. 10, fig. 6 [see for synonymy].
1975 *Petalograptus ovatoelongatus* (Kurck); Bjerreskov, p. 32, pl. 4H.

Material. Seven specimens, flattened or in low relief, with well-preserved fusellar structure and pseudancora development, from localities 258-8/74-8, 671/8-117, 5044/70-5 and 8*a*, H-1251*a* and B505/69-5, 6 and 8*a* in the Kos-Istek Region, Zhaksy-Kargala Valley.

Horizon. Telychian, *guerichi* (= *minor*) Biozone of the southern Urals, the Sakmara Formation. Note that this is somewhat higher than most previous records of the species.

Description. Rhabdosome broad, more than 10 mm long, oval proximally, almost parallel-sided in the middle part and slightly narrowing distally. The dorso-ventral width increases from 3·2–3·7 mm at $th1^1$ to 4·2–4·4 mm at $th3^1$ or $th4^1$, being no more than 4·5 mm distally.

The thecae are inclined at 50° to the rhabdosome axis at the extreme proximal end, at 40–35° more distally. They are 2·5–3 mm long, 0·4–0·5 mm wide, widening slightly aperturally, and are at right angles to the thecal axis. Proximal thecae overlap for most of their length; overlap is diminished slightly distally. Fuselli are widely spaced and well developed. Thecae number *c.* 6·5 in the first 5 mm.

The ventral walls of $th1^1$ and $th1^2$ are strongly concave. The upward-growing portion of $th1^1$ is 2·3–2·4 mm long. The sicular aperture is 0·25 mm wide. The pseudancora structure is well developed and the virgella divides 0·2–0·25 mm below the sicular aperture, then bifurcates into four thinner and broadly curved rods growing

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EXPLANATION OF PLATE 9

Fig. 1. *Petalolithus minor* (Elles); CNIGR Museum 114/12879; rhabdosome with partly preserved pseudancora; *gregarius* Biozone; Zhaksy-Kargala Valley; ×10.

Figs 2–4. *Petalolithus ovatoelongatus* (Kurck); *guerichi* (= *minor*) Biozone, Kos-Istek region. 2, CNIGR Museum 115/1289; adult rhabdosome showing well preserved fuselli; 4, CNIGR Museum 116/12879; adult rhabdosome with forking virgella and secondary rods; both ×10.

Fig. 3. *Petalolithus wuxiensis* Ye; CNIGR Museum 118/12879; adult rhabdosome; reverse view; ?*cyphus* to *gregarius* biozones; Zhaksy-Kargala Valley; ×10.

Fig. 5. *Petalolithus* sp. A; CNIGR Museum 119/12879; young rhabdosome with pseudancora; obverse view; *gregarius* Biozone; Zhaksy-Kargala Valley; ×10.

Fig. 6. *P.* (*Pseudorthograptus*) sp. G; CNIGR Museum 188/12879; juvenile rhabdosome showing long sicula, tapering extreme proximal end and well-developed pseudancora; *convolutus* Biozone; Zhaksy-Kargala Valley; ×20.

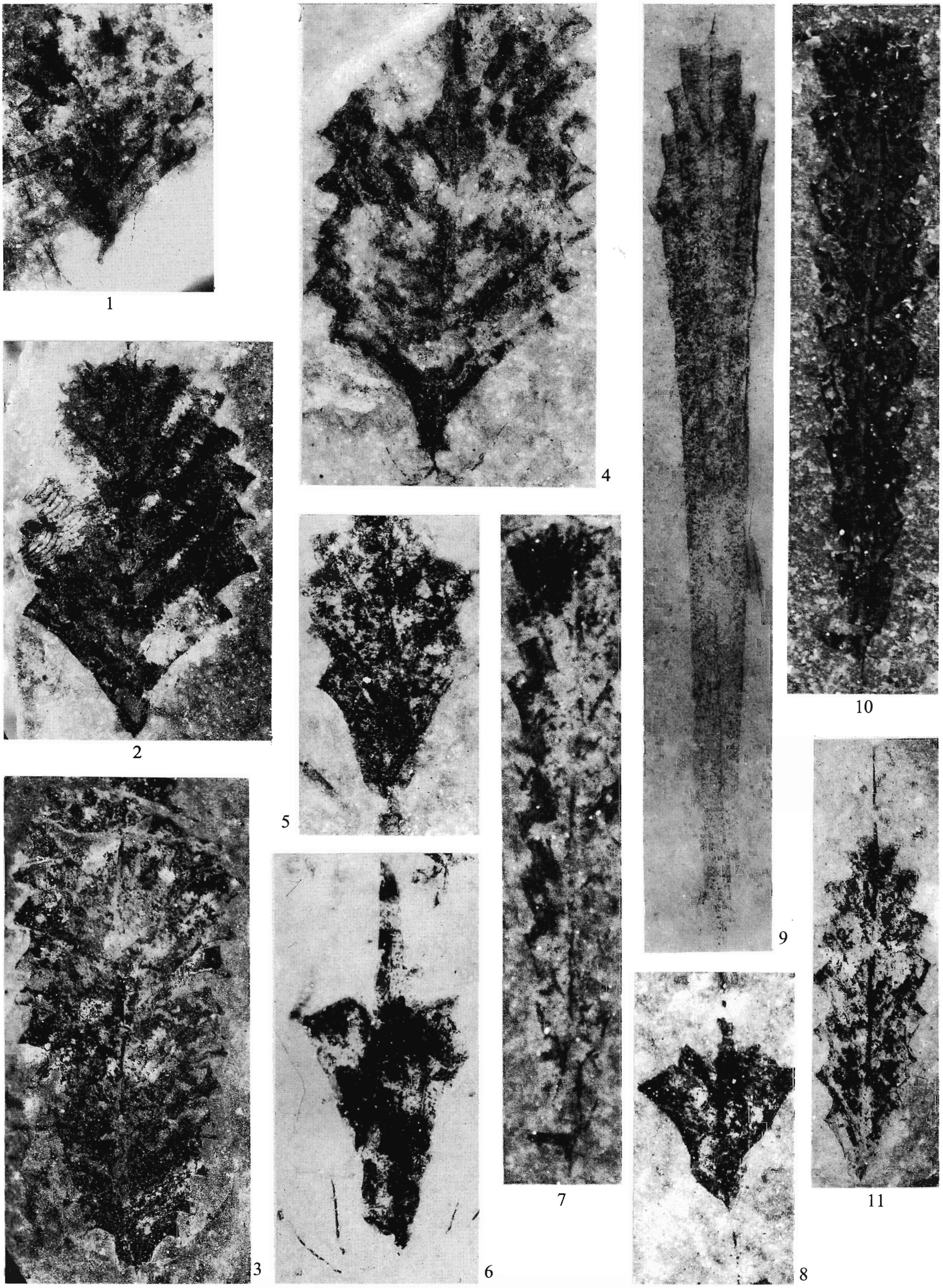
Figs 7, 10. *Parapetalolithus dignus* gen. et sp. nov.; *turriculatus* Biozone; Kos-Istek region. 7, CNIGR Museum 123/12879; adult, slightly tilted rhabdosome; 10, holotype, CNIGR Museum 124/12879; rhabdosome with simple, slightly everted thecae, and thorn like virgella; both ×10.

Fig. 8. *Parapetalolithus* sp. A; CNIGR Museum 130/12879; juvenile rhabdosome with long thread-like virgella; *gregarius* Biozone; Zhaksy-Kargala Valley; ×20.

Fig. 9. *Cephalograptus cometa extrema* Bouček and Přibyl; CNIGR Museum 122/12879; proximally incomplete adult rhabdosome with well preserved fuselli; upper *convolutus* Biozone; Kos-Istek region; ×10.

Fig. 11. *Parapetalolithus* ex. gr. *palmeus* (Barrande); CNIGR Museum 128/12897; young rhabdosome; virgella not preserved; *convolutus* to *guerichi* (= *minor*) biozones; Kos-Istek region; ×10.

PLATE 9



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upwards almost parallel to the ventral walls of th1[1] and th1[2]. One beautifully preserved proximal end (Text-fig. 11D) shows the pseudancora developed as a ladder-like meshwork of radial and transverse rods, and that this grows, even at such an early growth stage, up to the level of the second thecal pair.

Remarks. Our material agrees in all measurements with British and Czech descriptions. However, it sheds new light on the pseudancora which, with its meshwork, is developed more extensively than in any previously-described petalolithid, recalling the developments seen in some pseudorthograptids (see below).

Petalolithus wuxiensis Ye, 1978

Plate 9, figure 3; Text-figure 10K–L

1978 *Petalolithus wuxiensis* Ye, p. 469, pl. 176, figs 15–16.
1989 *Petalolithus ovatus wuxiensis*, Ye; Melchin, p. 1740, text-fig. 11F.

Material. Two flattened specimens, from locality B671-8/74 in the Zhaksy-Kargala Valley.

Horizon. ?Upper Aeronian to lowermost Telychian, Sakmara Formation.

Description. The rhabdosome is broad, 75 mm long, widening slowly until it reaches a maximum width of 3·5 mm at about th5[1] or th6[1]. The proximal width is 1·5–1·8 mm at th1[1], 2·1–2·5 mm at th2[1], 2·5–2·7 mm at th3[1], 2·8 mm at th4[1] and 3·0–3·2 mm at th5[1]. The thecae, 1·7–1·8 mm long distally and 0·6 mm wide, are very characteristic, being strongly curved proximally with slightly flaring apertures parallel to the rhabdosomal axis. The curvature lessens distally, but thecal apertures remain strongly everted. The angle of thecal inclination diminishes distally from 65° to 55°. The thecae overlap for most of their length, and number 7–8 in 5 mm. Sicular details are not clear; it is free for 0·4–0·45 mm in reverse view. The upward-growing portion of th1[1] is *c.* 0·8 mm long.

Remarks. The present material seems identical with the species found in the Cape Phillips Formation of the Canadian Arctic Islands and very close to the type material, even though the preservation of the latter does not make for easy detailed comparison. It is very characteristic in having strongly curved or highly inclined thecae and everted thecal apertures almost parallel to the rhabdosomal axis.

Petalolithus sp. A

Plate 9, figure 5; Text-figure 10H

Material. Two pseudancorate proximal ends, from locality B671-2, Zhaksy-Kargala Valley.

Horizon. Aeronian, *gregarius* Biozone, southern Urals, Sakmara Formation.

Remarks. There is some resemblance to pseudorthograptids and the placement in *Petalolithus* is arbitrary, but suggested by the curvature of th1[1]. The sicula, at 2·1 mm long, is also possibly a little long for such a small petalolithid, which may have a dorso-ventral width of only 1·5 mm. However, it is at this horizon that *Petalolithus* probably evolved from *Pseudorthograptus*.

Petalolithus sp. B

Text-figure 11B

Material. One specimen 199*a*/12879, from locality 671-8/14; *convolutus* Biozone.

Remarks. The relatively short sicula and slightly concave ventral wall of th1[1] suggests attribution to *Petalolithus* rather than *Pseudorthograptus*. This form is smaller than *Pe. folium*, *Pe. minor* or *Pe. ovatoelongatus* and lacks the very robust pseudancora of *Pe.* sp. A.

Genus CEPHALOGRAPTUS Hopkinson, 1869

Type species. Diplograptus cometa Geinitz, 1852; original designation, according to Bulman (1970); from the Llandovery of Germany.

Diagnosis. Like *Petalolithus*, with *tamariscus* (I) Pattern development, but with proximal end drawn out and thorn-like to an even greater extent than in *Pe. folium*; relatively few thecae in the rhabdosome.

Remarks. There is an undoubted evolutionary succession from *Petalolithus*, through *Pe. folium* to *Cephalograptus c. cometa* to *C. c. extrema* (Bouček and Přibyl 1942; Rickards *et al.* 1977), which is supported by the stratigraphical record, in which proximal end protraction and reduction of thecal number, as well as elongation of the thecae, are the main changes.

Cephalograptus cometa extrema Bouček and Přibyl, 1942

Plate 9, figure 9; Text-figure 11B–C

1908 *Cephalograptus cometa* (Geinitz); Elles and Wood, p. 285 (*pars*), pl. 32, fig. 10*a–c* (*non* 10*d*).
1942 *Cephalograptus cometa extrema* n. subspec., Bouček and Přibyl, p. 14, pl. 1, fig. 10, text-fig. 2*l–m*.
1974 *Cephalograptus cometa extrema* Bouček and Přibyl; Hutt, p. 43, pl. 6, fig. 1; pl. 10, figs 3, 5; text-fig. 11, figs 1–5 [see for synonymy].
1975 *Cephalograptus cometa extrema* Bouček and Přibyl; Bjerreskov, p. 37, pl. 5C, table 2.

Material. Three flattened specimens, with proximal ends missing, from localities 288-8/74-9 and B671-2-51, 6 in the Kos-Istek region.

Horizon. Upper Aeronian, *convolutus* Biozone, Sakmara Formation.

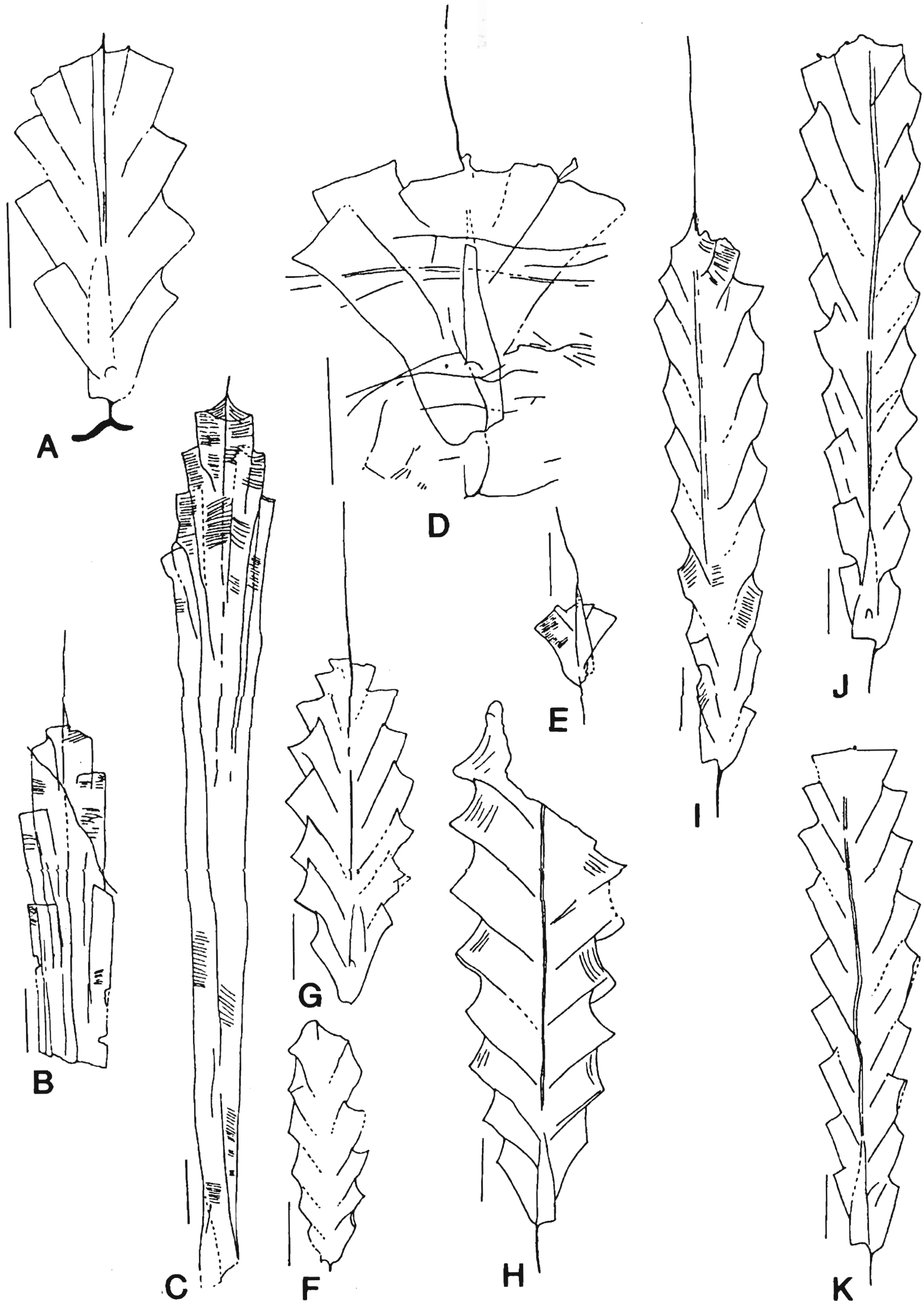
Diagnosis. Acicular rhabdosome more than 15 mm long with four pairs of thecae. It widens from 0·4 mm close to the level of the sicula to 1·6 mm opposite the aperture of $th1^1$. Thecae are straight tubes inclined at 3–5°. The visible length of $th1^1$ is at least 12 mm. Succeeding thecae are shorter and they overlap for most of their length. Thecal apertures are straight and almost horizontal. The sicula is not visible in our material.

Remarks. By its extremely elongated thecae resulting in a peculiar acicular rhabdosomal shape our specimens belong without doubt to *C. c. extrema*, a subspecies with a wide geographical distribution, and a restricted stratigraphical range in the uppermost *convolutus* and *sedgwickii* biozones.

Genus PARAPETALOLITHUS gen. nov.

Type species. Parapetalolithus dignus sp. nov., from the *guerichi* (= *minor*) Biozone of the southern Urals.

Diagnosis. Like *Sudburigraptus* but with proximal end more protracted, $th1^1$ and 1^2, especially, growing upwards and outwards, exposing the sicular apertural region more fully; rhabdosomes may



TEXT-FIG. 11. For legend see opposite.

be more robust than *Sudburigraptus* and longer; development probably of *tamariscus* (I) Pattern, short down-growing portion of th1^1, reaching below but close to sicular aperture; thecae simple tubes overlapping at least one-half, usually at a high angle (20–30°) to the rhabdosomal axis; thecal apertures at right angles to thecal axis or, more usually, everted.

Remarks. *Parapetalolithus* differs from *Petalolithus* in lacking a pseudancora; and in having a narrower rhabdosome with shorter thecae, not usually at so high an angle and usually with less apertural evertion. For the most part they are stratigraphically later than *Petalolithus* species. The species in the genus include: the type species, *Pa. tenuis* (Barrande) and three species left in open nomenclature. However, it should be stated that the pseudancora/virgella of some petalolithids is unknown and in time we can expect further apportionment of described species either to *Parapetalolithus* or to *Petalolithus*.

Parapetalolithus dignus gen. et sp. nov.

Plate 9, figures 7, 10; Text-figure 11I–K

Holotype. CNIGR Museum 124/12879; Plate 9, figure 10; Text-figure 11J; *guerichi* Biozone, lower Telychian, southern Urals; Sakmara Formation, Zhaksy-Kargala Valley.

Derivation of name. From *dignus* (Latin) = dignified.

Material. Six flattened specimens, from localities B671-1-1, B671-1-13, B671-1-25, B296-2/72-1 and 1543-1 in the Kos-Istek Region and the Zhaksy-Kargala Valley.

Horizon. Lower Telychian, *guerichi* (= *minor*) Biozone, Sakmara Formation.

Diagnosis. Gracile rhabdosome, 10 mm long, 0·9–1 mm wide at th1^1, attaining a maximum width of 1·9 mm distally. Rhabdosome is completely or partially septate. Thecae are strongly inclined, with everted apertures; they overlap no more than half of their length. Virgella thorn-like with no division.

Description. The rhabdosome is small with a slightly tapering extreme proximal end. The median septum seems to be complete in obverse view, and its base reaches the fourth pair of thecae on the reverse side. The rhabdosome widens from 0·9–1 mm at th1^1, to 1·6–1·7 mm at th5^1 attaining a maximum dorso-ventral width of 1·8–1·9 mm distally. The thecae are 0·4–0·5 mm wide, up to 2 mm long, and with an inclination to the axis

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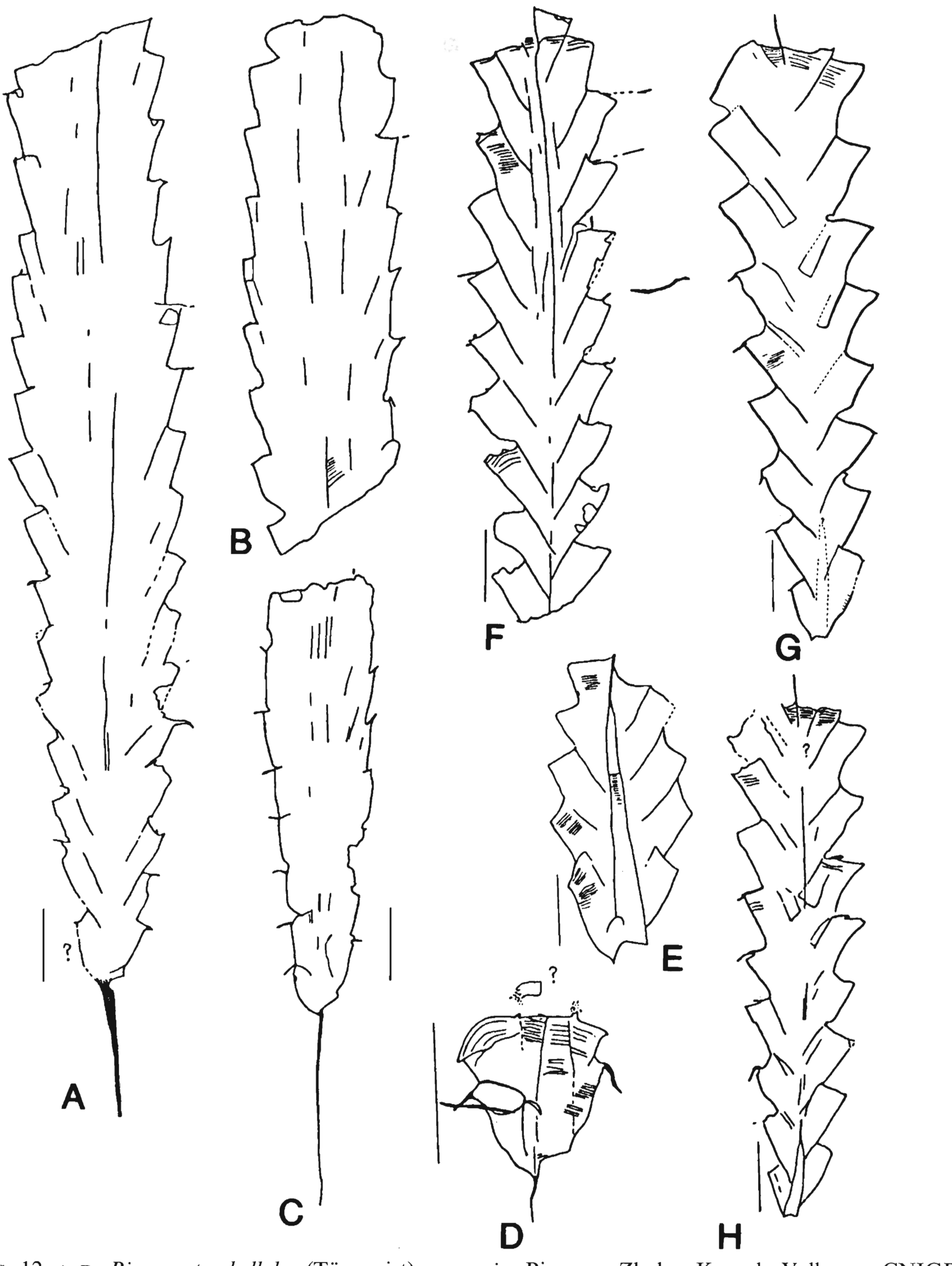
TEXT-FIG. 11. A, *Petalolithus* sp. B; CNIGR Museum 120/12879; young rhabdosome with a forking virgella, reverse view; *gregarius* Biozone; Zhaksy-Kargala Valley. B–C, *Cephalograptus cometa extrema* Bouček and Přibyl; CNIGR Museum 121/12879 and 122/12789; distal fragment and almost complete rhabdosome showing extremely elongated thecae with well preserved fusellar structure; *convolutus* Biozone; Kos-Istek region. D, *Petalolithus ovatoelongatus* (Kurck); CNIGR 121/12879; young rhabdosome with well developed, but only partly preserved, pseudancora and meshwork with transverse rods; reverse view; *guerichi* (= *minor*) Biozone; Kos-Istek region. E, *Petalolithus* sp. A; CNIGR Museum 130/12879; juvenile rhabdosome possessing long thread-like virgella and nema; obverse view; *gregarius* Biozone; Zhaksy-Kargala Valley. F, *Parapetalolithus* cf. *kurcki* (Rickards); CNIGR Museum 127/12879; tiny rhabdosome; reverse view; *gregarius* Biozone; Kos-Istek Region. G–H, *Parapetalolithus* ex gr. *palmeus* (Barrande); CNIGR Museum 128/12879 and 129/12879; incomplete rhabdosomes; obverse views. Aeronian to lower Telychian; Kos-Istek region. I–K, *Parapetalolithus dignus* gen. et sp. nov. I, CNIGR Museum 125/12879; adult rhabdosome, slightly tilted; reverse view; J, holotype, CNIGR Museum 124/12879; obverse view; K, CNIGR Museum 123/12879; adult rhabdosome; *turriculatus* Biozone; Kos-Istek region. Scale bars represent 1 mm.



TEXT-FIG. 12. A–D, *Rivagraptus bellulus* (Törnquist); *gregarius* Biozone; Zhaksy-Kargala Valley. A, CNIGR Museum 133/12879; almost complete rhabdosome possessing long stout virgella and ventral apertural spines; B–C, CNIGR Museum 134/12879 and 132/12879; distal and proximal fragments of adult rhabdosomes with complete median septa; D, CNIGR Museum 135/12879; extreme proximal part of rhabdosome with well preserved fusellar structure; obverse view. E, *Rivagraptus cyperoides* (Törnquist); CNIGR Museum 136/12879; *gregarius* Biozone; Kos-Istek region; incomplete rhabdosome possessing long sicula, completely free in of about 20°. They overlap for half of their length. The alternating thecal apertures are slightly concave and distinctly everted. Thecae number 10 in 10 mm.

The sicula is 1·7–1·75 mm long, and 0·2–0·3 mm wide at the aperture. It is free in obverse view and exposed for 0·5–0·7 mm in reverse view. Its apex reaches the aperture of $th2^1$. The thorn-like virgella is 0·5–0·7 mm long.

Remarks. The new species is characterized by a slowly widening rhabdosome until it reaches a maximum width distally. In thecal proportions and outlines it resembles *Pa. tenuis*, but differs in its gradually widening, smaller rhabdosome and more distant thecae. From all other Telychian parapetalolithids the new species can be distinguished by its smaller size.

Parapetalolithus cf. *kurcki* (Rickards, 1970)

Text-figure 11F

cf. 1970 *Petalograptus kurcki* sp. nov., Rickards, p. 48, text-fig. 14, figs 22–24.

Material. One incomplete specimen, from locality 587-8, sp. 13, in the Kos-Istek region.

Horizon. Aeronian, *gregarius* Biozone of southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome 7 mm long, widening from 0·75 mm at $th1^1$ to 1·2 mm at $th3^1$, more distally becoming parallel-sided. Thecae inclined at 25–30° to the rhabdosomal axis, overlapping one-half and numbering 4 in 2·5 mm. They have everted, slightly concave apertures. No septum is present. The sicula is almost completely covered in reverse view. The virgella is 0·15 long, and shows no bifurcation.

Remarks. The measurements resemble those of *Pa. kurcki* (Rickards) from the *sedgwickii* Biozone of the Howgill Fells.

Parapetalolithus ex gr. *palmeus* (Barrande, 1850)

Plate 9, figure 11; Text-figure 11G–H

Material. Four flattened specimens, from localities 296-2/72-10 and 671/8*a*-16 in the Kos-Istek region and the Zhaksy-Kargala Valley.

Horizon. Aeronian–lower Telychian, Sakmara Formation.

Description. Rhabdosome narrow, 10 mm long, widening from 1·3–1·4 mm at $th1^1$ to a maximum of *c.* 2·4–2·5 mm reached at $th4^1$ or $th5^1$. The thecae are 1·6 mm long and 0·7 mm wide, have strongly everted apertures and overlap for one-half to two-thirds their length. They are inclined at 30–40° to the rhabdosomal axis and number 6·5 in 5 mm proximally and 5·5 in 5 mm distally. The sicula is exposed for 1·1 mm in obverse view. The upwards-growing portion of $th1^1$ is 1·25 mm long and the virgella is 1·3–1·4 mm long and shows no divisions.

Remarks. Pa. ex gr. *palmeus* differs in dimension from both *Pa. palmeus* and *Pa. tenuis*, but has the overall thecal style of *Pa. palmeus*, in other words slightly outgrowing thecae rather than the slightly

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obverse view. F–H, *Rivagraptus inconstans* gen. et sp. nov.; *cyphus* and *gregarius* biozones; Zhaksy-Kargala Valley. F, CNIGR Museum 137/12879 adult rhabdosome lacking extreme proximal end; some thecae have long apertural spines; G, CNIGR Museum 139/12879; adult rhabdosome with occasional aperture spines; H, holotype, CNIGR Museum 138/12879; adult rhabdosome with fully exposed sicula in obverse view; a few apertural spines are preserved. Scale bars represent 1 mm.

axially elongate thecae of *Pa. tenuis*. We provisionally refer all these forms to *Parapetalolithus* because they seem to be virgellate rather than pseudancorate and their rhabdosomes are slim and parallel-sided rather than tending towards ovate or fusiform.

Parapetalolithus sp. A

Plate 9, figure 8; Text-figure 11E

Material. One specimen from locality B671-2 in the Zhaksy-Kargala Valley.

Horizon. Aeronian, *gregarius* Biozone of southern Urals, Sakmara Formation.

Remarks. This form is distinctly virgellate with no trace of a pseudancora. It may be one of the earliest representatives of the genus which is typically later than *Petalolithus* and characteristic of the late Middle and Upper Llandovery. The sicula is small and $th1^1$ has slight ventral curvature. The overall size of the rhabdosome cannot be deduced but it may be small, as the dorso-ventral width at the level of the aperture of $th3^1$ is only 1·25 mm.

Genus RIVAGRAPTUS gen. nov.

Type species. Diplograptus bellulus Törnquist, 1890; from the Llandovery of Sweden.

Diagnosis. Spinose biserials with *tamariscus* Pattern (I) development; virgellate; thecae 'orthograptid', relatively simple tubes, lacking a geniculum; but with thecal apertural spines, usually short, paired and directed ventrally or ventro-laterally; proximal end narrow, slightly attenuated, $th1^1$ and $th1^2$ growing upwards and outwards strongly; rarely $th1^2$ unusually long, resulting in spurious uniserial position.

Remarks. Rivagraptus differs from *Pseudorthograptus*, *Dittograptus* and *Victorograptus* in the complete absence of a pseudancora and membrane (rather it has a conspicuous and often robust, simple, straight virgella). Both Štorch (1985) and Loydell (1991) recorded an ancora on *O. cyperoides* (see description below), but we are uncertain whether their material should strictly be referred to Törnquist's species. *Rivagraptus* also has shorter apertural spines than many pseudorthograptids, especially those at the same horizons of *gregarius–convolutus* biozones. We recognize two closely similar genera, namely *Rivagraptus* gen. nov. and *Agetograptus* (see below) which differ in that the latter has an unusually long $th1^2$, the aperture of which opens above that of $th2^1$, resulting in a spurious uniserial position (see also Loydell 1991, p. 675). Included species are those described below.

Rivagraptus bellulus (Törnquist, 1890)

Plate 10, figures 1, 3; Text-figure 12A–D

1890 *Diplograptus bellulus* n. sp., Törnquist, p. 28, pl. 1, figs 25–29.
1967 *Rectograptus*(?) *bellulus* (Törnquist): Obut *et al.*, p. 62, pl. 3, fig. 6.
1970 *Orthograptus bellulus* (Törnquist): Rickards, p. 46, pl. 3, fig. 5 [see for synonymy].
1974 *Orthograptus bellulus* (Törnquist): Hutt, p. 37, pl. 3, figs 1–2; pl. 6, fig. 13; text-fig. 8, figs 2–4.
1975 *Orthograptus bellulus* (Törnquist): Bjerreskov, p. 28, pl. 4, fig. F.
1985 *Orthograptus bellulus* (Törnquist): Štorch, p. 92, pl. 11, fig. 6 (?4).

Material. Twenty specimens preserved flattened, and also several distal fragments which belong most probably to the species, from localities B614-1/72-1, B671-2-40, B671-8/74-126*a*, B671-8/74-127 and B671-8/74-17 in the Zhaksy-Kargala Valley.

Horizon. Aeronian, *gregarius* Biozone of the southern Urals, Sakmara Formation.

Description. The rhabdosome is more than 50 mm long with a prominent virgella up to 3 mm long. The rhabdosome widens quickly within the first five to seven pairs of thecae. Successive measurements of dorso-ventral width are: at $th1^1$, 0·8–1 mm; $th2^1$, 0·95–1·2 mm; $th3^1$, 1·1–1·4 mm; $th4^1$, 1·25–1·5 mm and at $th5^1$, 1·35–1·8 mm. More distally, the rhabdosome is more or less parallel-sided but some reach a width of 2·2 mm. The rhabdosome seems to be fully septate distally and only partially septate proximally.

The thecae are simple tubes, 0·3 mm wide in the subapertural part, overlapping each other for half of their length. The free ventral walls are 0·75–0·8 mm long distally; they are inclined at *c.* 20° to the rhabdosomal axis. Thecae number 6–7 in 5 mm and 12–13 in 10 mm proximally, 6 in 5 mm distally. They bear paired apertural spines of ventro-lateral origin which are 0·25 mm long. The spines are slightly curved with their ends hanging down.

The sicula is visible in obverse view for at least 1 mm. The sicular aperture is 0·40–0·42 mm wide. $Th1^1$ bends close to the sicular aperture; its upward-growing portion is 0·8–0·9 mm long.

Remarks. From other rivagraptids with apertural spines *R.* (*R.*) *bellulus* differs in having a stout, long virgella and a large septate rhabdosome.

Rivagraptus cyperoides (Törnquist, 1897)

Text-figure 12E

1897	*Diplograptus cyperoides* n. sp., Törnquist, p. 16, pl. 2, figs 30–32.
1907	*Diplograptus* (*Orthograptus*) *cyperoides* Törnquist; Elles and Wood, p. 238, pl. 29, fig. 8*a–c*; text-fig. 158*a–b*.
1970	*Orthograptus cyperoides* (Törnquist, 1897); Rickards, p. 45, text-fig. 14; figs 12, 17.
1974	*Orthograptus cyperoides* (Törnquist, 1897); Hutt, p. 35, pl. 6, figs 2–5; text-fig. 9, figs 6–7.

Material. One flattened specimen, from locality 474-2/61 in the Kos-Istek region to the south of Aktjubinsk City.

Horizon. Aeronian, *gregarius* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Tiny 'orthograptid' with relatively simple thecal tubes, lacking any geniculum, but with occasional short, fine, apertural spines and prominent virgella; sicula conspicuous in reverse view, fully 3·5 mm long in some specimens, apex reaching level of apertures of fourth thecal pair; sicular aperture 0·15–0·22 mm wide; virgella short, generally fine; downgrowing part of $th1^1$ 0·6 mm long, of which 0·25 mm grows below the level of the sicular aperture; thecal tubes *c.* 1 mm long, overlapping one-third to one-half; ventral apertural spines (?ventro-lateral) are not always present, but when they are they are fine, usually short, and inconspicuous; rhabdosome up to 7 mm long; maximum dorso-ventral width 1·1–1·2 mm; thecal spacing 11–12 in 10 mm.

Remarks. R. cyperoides occasionally seems to lack apertural spines, but it is almost always difficult to say whether this is preservational or not. Without the spines it is very close indeed to *Sudburigraptus* gen. nov., its suggested ancestor (Text-fig. 2) but differs in the protracted proximal end, exposed and long sicula, and the strongly upward growth direction of the early thecae. We are uncertain as to the true specific identity of Štorch's (1985) and Loydell's (1991) material in which an ancora was identified, and have not included this in the synonymy above. Such forms may form a side branch from *Sudburigraptus* and an alternative way of deriving petalolithids.

Rivagraptus inconstans gen. et sp. nov.

Plate 10, figures 2, 5; Text-figure 12F–H

Holotype. CNIGR Museum 138/12879, Plate 10, figure 5; Text-figure 12H; the *gregarius* Biozone, Aeronian, southern Urals, Sakmara Formation.

Derivation of name. From *inconstans* (Latin) = unstable.

Material. Three specimens in low relief, from localities B603-9/72-97 and 1643-11 in the Kos-Istek region.

Horizon. Upper Rhuddanian and ?lower Aeronian, *cyphus* and *gregarius* biozones of the southern Urals, Sakmara Formation.

Diagnosis. Rivagraptid, less than 10 mm long, 0·8–0·9 mm wide at $th1^1/1^2$ attaining the maximum dorso-ventral width of 2·1 mm within the first 5–7 mm. Paired apertural spines are occasionally developed on the lateral margins of the thecal apertures. Rhabdosome is at least partially septate.

Description. The rhabdosome is tiny, with slightly tapering extreme proximal end. The successive measurements of dorso-ventral width are as follows: at $th1^1$, 0·8–0·9 mm; $th2^1$, 1·2 mm; $th3^1$, 1·5 mm, $th4^1$, 1·6 mm; and $th5^1$, 1·7 mm. A maximum dorso-ventral width of 2·1 mm is reached in 5–7 mm from the proximal end. The rhabdosome is up to 1·5 mm long. The thecae are simple tubes 0·35–0·4 mm wide, overlapping for one-half of their length. The free ventral walls are 0·85 mm long distally, and they are inclined to the rhabdosomal axis at *c.* 25–30°. Apertures are at right angles to the thecal axis. Some thecae are provided with spines, 0·4 mm long, thickened at the base. They are most probably paired apertural spines of lateral position, but in flattened material the second spine is rarely seen. The thecae number 6–6·5 in 5 mm proximally, 5–6 in 5 mm distally.

The extreme proximal end is slightly tapering. From the obverse side the sicula is exposed for 0·85–0·9 mm. The sicular apex is not clear, but it reaches above the aperture of $th2^1$. The upward-growing portion of $th1^1$ is 0·65 mm long, and bends close to the sicular aperture.

Remarks. *R. inconstans* gen. et sp. nov. has some affinities with *R. cyperoides* (Törnquist) in general rhabdosomal aspect and thecal structure and dimensions. It differs, however, in having a less exposed sicula in obverse view and in paired lateral (and not single ventral) apertural spines. From *R.* (*R.*) *rozmanae* gen. et sp. nov. it can be distinguished by its tapering and narrower extreme proximal end, and by the presence of only occasionally developed spines on the thecal apertures.

EXPLANATION OF PLATE 10

Figs 1, 3. *P.* (*Pseudorthograptus*) *bellulus* (Törnquist); CNIGR Museum 131/12879 and 132/12879; fragments of adult rhabdosomes possessing apertural spines and long virgella; *gregarius* Biozone; Zhaksy-Kargala Valley; both ×10.

Figs 2, 5. *P.* (*Pseudorthograptus*) *inconstans* sp. nov.; *cyphus* and ?*gregarius* biozones, Zhaksy-Kargala Valley. 2, CNIGR Museum 137/12879; proximally incomplete adult rhabdosome; 5, holotype, CNIGR Museum 138/12879; both ×10.

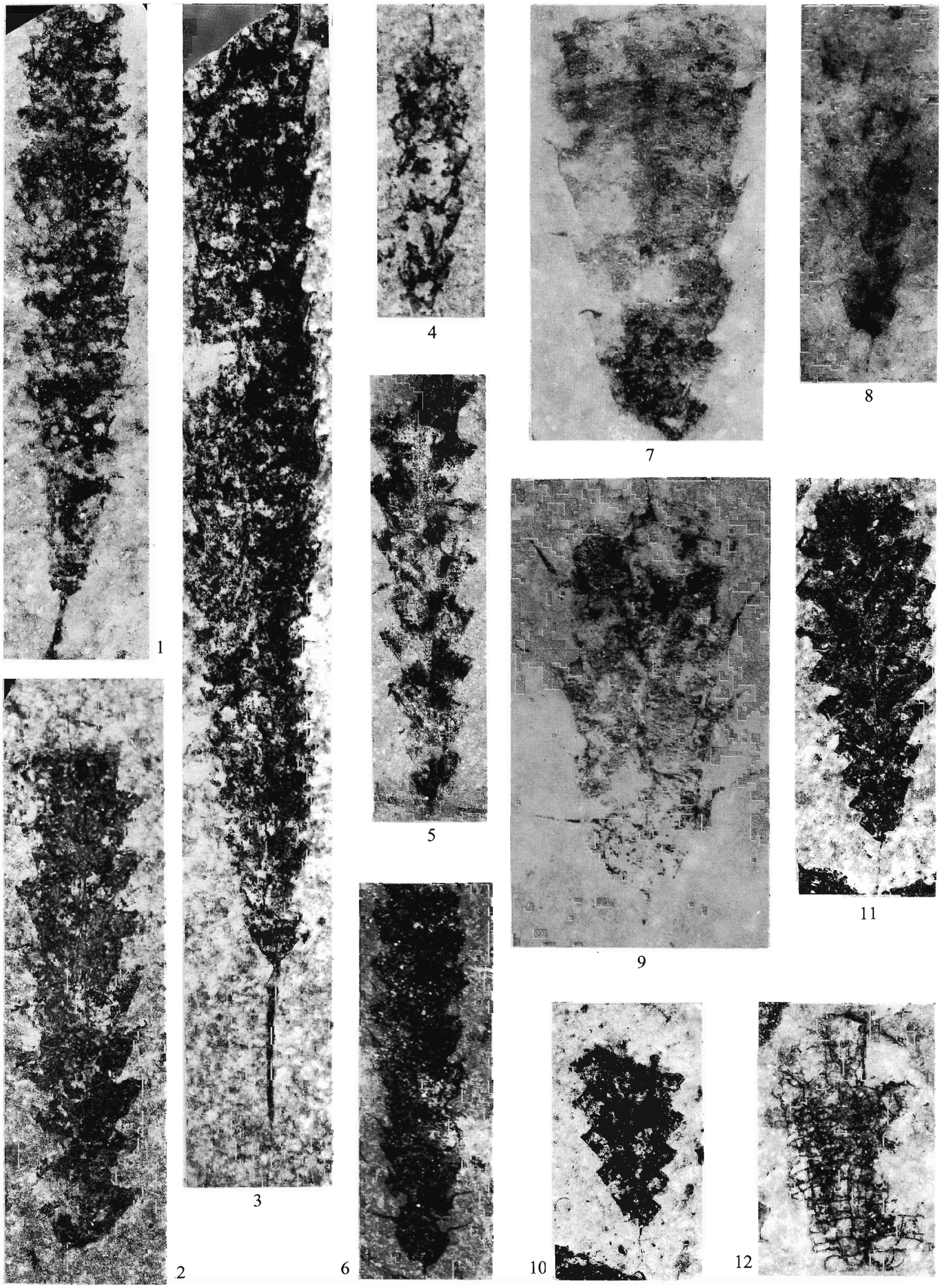
Fig. 4. *Parapetalolithus dignus* sp. nov.; CNIGR Museum 126/12879; *guerichi* Biozone, Zhaksy-Kargala Valley; ×10.

Figs 6–8. *Rivagraptus rozmanae* gen. et sp. nov.; *gregarius* Biozone; Kos-Istek region. 6, CNIGR Museum 140/12879; adult rhabdosome, reverse view with well-preserved thecal spines; 7, CNIGR Museum 141/12879; proximal part with thecae showing well-developed spines and fuselli; 8, holotype, CNIGR Museum 142/12879. 6, 8, ×10; 7, ×20.

Fig. 9. *Rivagraptus sentus* gen. et sp. nov.; holotype, CNIGR Museum 152/12879; *gregarius* Biozone; Zhaksy-Kargala Valley; ×20.

Figs 10–11. *Agetograptus primus* Obut and Sobolevskaya; CNIGR Museum 156/12879 and 157/12879; specimens showing short $th1^1$ and 2^1 in comparison with $th1^2$ in both reverse (10) and obverse (11) view; *gregarius* Biozone; Zhaksy-Kargala Valley; both ×10.

Fig. 12. *P.* (*Pseudorthograptus*) sp. C; CNIGR Museum 183/12879; young rhabdosome with well-developed basket-like meshwork based on dividing virgella; *gregarius* Biozone; Zhaksy-Kargala Valley; ×20.



KOREN' and RICKARDS, graptoloids from the southern Urals

Rivagraptus rozmanae gen. et sp. nov.

Plate 10, figures 6–8; Text-figures 13, 14A

Holotype. CNIGR Museum 142/12879, Plate 10, figure 8; Text-figure 13D; *gregarius* Biozone, Aeronian, southern Urals, Sakmara Formation, Kos-Istek region.

Derivation of name. In honour of the Russian palaeontologist, Khana S. Rozman, who collected graptolites in the southern Urals.

Material. Fifteen specimens, flattened or in low relief, from localities 2588-13, B587-8/74, B611-6-118, B671-2/74-13*a*, B671-2/74-15, B671-2/74-70, B671-8/74-40, B671-8/74-251, B671-8/74-405 and 1643/50-205 in the Kos-Istek region and Zhaksy-Kargala Valley.

Horizon. Aeronian, *gregarius* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome slightly tapering at the proximal end and slowly attaining maximum width; thecae with short, paired spines originating at the lateral sides of apertural margins. Virgella is prominent, but undivided.

Description. Rhabdosome 8–10 mm long, attaining maximum dorso-ventral width of 1·6 mm mesially. Rhabdosome width within the proximal part is as follows: at th1^1, 0·9–1 mm; th2^1, 1·1–1·2 mm; th3^1, 1·2–1·3 mm; th4^1, 1·4 mm and th5^1, 1·5–1·6 mm. The rhabdosome is probably partially septate. The thecae are simple tubes, 1–1·15 mm long and 0·3 mm wide, overlapping half of their length. Their number is 6–7 in 5 mm proximally and distally. They are inclined at 20° to the rhabdosomal axis; thecal apertures are everted at right angles to the thecal axis. Both lateral thecal margins bear short spines (0·25–0·4 mm long) which are curved slightly and directed latero-proximally. Usually in flattened material only one spine of each theca is seen.

Th1^1 extends slightly below the sicular aperture and then bends sharply upwards for 0·6–0·7 mm. In reverse view the sicula is completely covered, but is seen pressed through. Its dimensions are: length, 1·35–1·7 mm; and width at aperture, 0·25 mm. The sicular apex, seen when pressed through, reaches the aperture of th2^1. The virgella is stout at the base and up to 1 mm long.

Remarks. From *R. sentus* gen. et sp. nov., this species differs in having a smaller rhabdosome, tapering proximally, and in having short, paired spines of lateral origin. The same characters and the absence of virgellar structures are important for distinguishing this form from *Pseudorthograptus* (*Pseudorthograptus*) *insectiformis* (Nicholson). From *R. cyperoides* the new species can be distinguished by having regularly developed lateral apertural thecal spines, and in having a smaller sicula.

Rivagraptus sentus gen. et sp. nov.

Plate 10, figure 9; Text-figure 14B–E

Holotype. CNIGR Museum 152/12879, Plate 10, figure 9; Text-figure 14C; *gregarius* Biozone, southern Urals, Sakmara Formation, Kos-Istek region.

Derivation of name. From *sentus* (Latin) = thorny.

Material. Three flattened specimens, from localities B614-1/72-1 and B671-8/74-304*a* in the Zhaksy-Kargala Valley.

Horizon. Aeronian, *gregarius* Biozone, most probably the upper part, southern Urals; equivalent to the *leptotheca* Biozone in Britain.

Diagnosis. Robust rivagraptid with rounded proximal end, short virgella and thecae provided with single (long) spines, formed on the ventral extremities of the apertural margins.

Description. The rhabdosome is about 3–4 mm long, and its dorso-ventral width at the successive proximal thecae is: at $th1^1$, 1–1·1 mm; $th2^1$, 1·15–1·3 mm; $th3^1$, 1·4–1·6 mm. Observed maximum dorso-ventral width is 1·6 mm at the level of the aperture of $th5^1$.

The thecae are simple tubes overlapping for half of their length. They are 0·2 mm wide, with apertures horizontal or slightly everted. Single, thorn-like spines, 0·5–0·8 mm long, are formed on the ventral sides of the thecal apertures. The spines are straight, thickened at the base, and directed latero-distally.

$Th1^1$ is conspicuously short: its downgrowing portion is 0·2 mm long and the upward-growing position is 0·6 mm long. It extends below the sicular aperture for 0·15–0·2 mm. The sicula is 1·25–1·8 mm long with its apex reaching the middle part or the aperture of $th3^1$. The virgella is 0·3 mm long. In some specimens a single anti-virgellar spine, 0·4 mm long, is seen (Text-fig. 14B).

Remarks. From the other spiny rivagraptids the new species differs in having a broad proximal end and a very characteristic, thorn-like, single ventral apertural spines.

Genus AGETOGRAPTUS Obut and Sobolevskaya (*in* Obut *et al*., 1968)

Type species. *Agetograptus secundus* Obut and Sobolevskaya (*in* Obut *et al*., 1968); original designation; from the Llandovery of Norilsk, Siberia.

Diagnosis. As for *Rivagraptus* except that *Agetograptus* species have an unusually long $th1^2$ the aperture of which opens above the aperture of $th2^1$. This results in the appearance of a uniserial position, but no thecae are missing.

Remarks. *Agetograptus* has a close similarity, in terms of its proximal end, to *Rhaphidograptus*, but in *Agetograptus* $th1^2$ derives low down in the colony, from $th1^1$: in *Rhaphidograptus* a theca is supposedly missing and the first theca in the second series is $th2^2$, deriving from $th2^1$ (see *Remarks*, under *Rhapidograptus*). The thecae are also more 'climacograptid' than 'orthograptid'. The form described by Obut and Sobolevskaya (*in* Obut *et al*. 1968) as *Agetograptus zintchenkoae* may, in fact, be a rhaphidograptid. Otherwise we include their species in the genus *Agetograptus*.

Agetograptus primus Obut and Sobolevskaya (*in* Obut *et al*., 1968)

Plate 10, figures 10–11; Plate 11, figures 1–2; Text-figure 14F–H

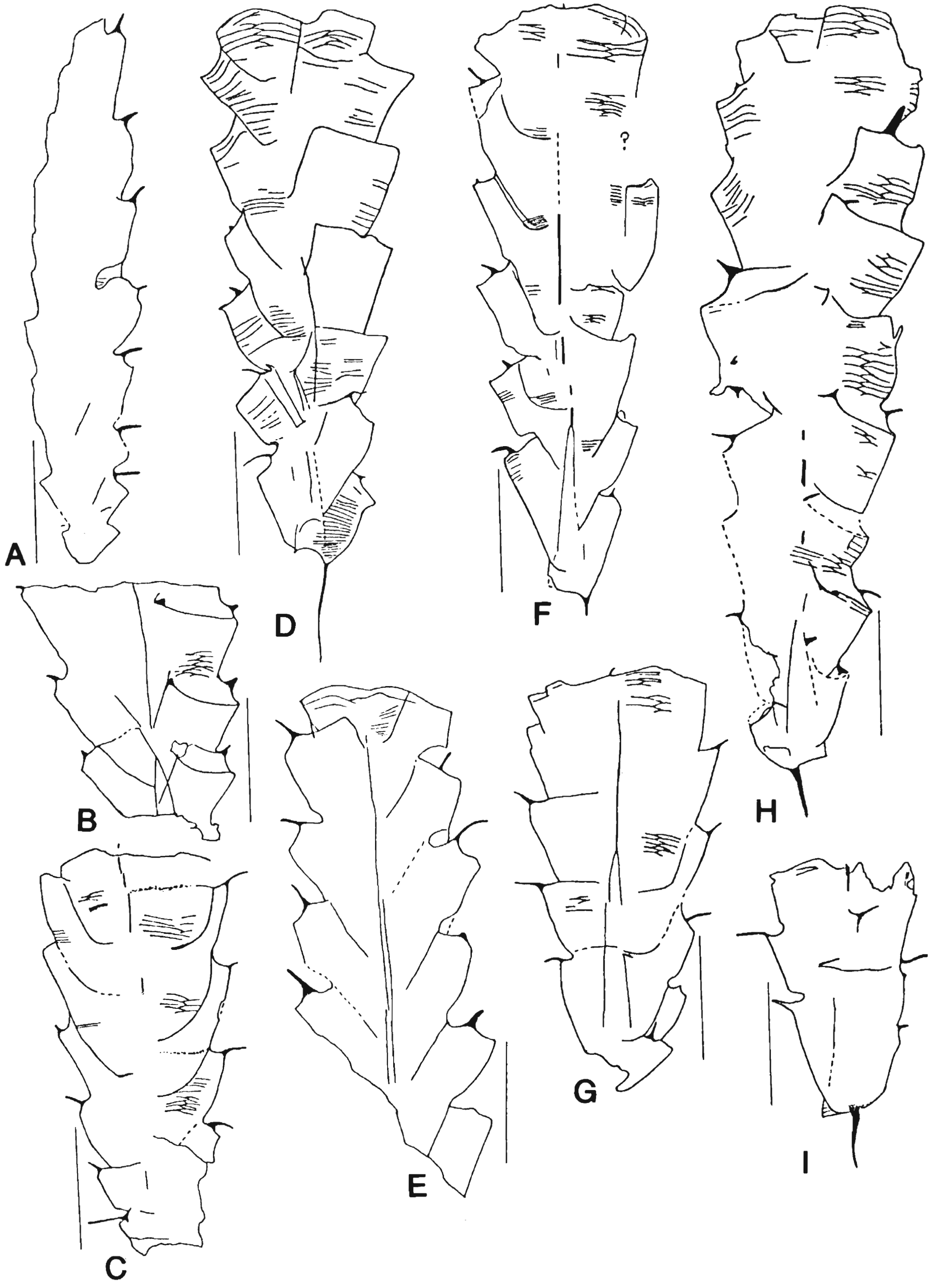
1968 *Agetograptus primus* n. sp. Obut and Sobolevskaya *in* Obut *et al*., p. 80, pl. 10, figs 6–12.
1989 *Agetograptus primus* Obut and Sobolevskaya; Melchin, p. 1738, fig. 9N.
1991 *Agetograptus primus* Obut and Sobolevskaya; Loydell, p. 676, pl. 1, figs 11, 16, 18–19; pl. 2, fig. 2 [see for synonymy].

Material. More than 30 specimens at different astogenetic stages, flattened but well preserved, from localities B671-2-57 and B671-8/74-90 in the Zhaksy-Kargala Valley.

Horizon. Aeronian, *gregarius* Biozone of the southern Urals, Sakmara Formation.

Description. The rhabdosome is 5–6 mm long, widening from 0·7 mm at $th1^1$ to the maximum dorso-ventral width of 2·4 mm at $th7^1$–8^1. Dorso-ventral width measurements at the successive thecae proximally are: at $th1^1$, 0·7 mm; $th2^1$, 1–1·1 mm; $th3^1$, 1·3–1·5 mm; and $th5^1$, 2 mm.

The thecae are simple tubes inclined at *c*. 30–35° to the rhabdosomal axis. Thecal apertures are strongly everted; thecal overlap is about one-half. Thecae are up to 0·4 mm wide and 1·6–1·7 mm long. Apertural margins bear paired spines, which originate at the middle of lateral margins. They are directed ventro-distally being 0·2 mm long and 0·05 mm thick at the base. In flattened rhabdosomes, preserved in subapertural view, spines appear to be ventral (Text-fig. 14F, upper rhabdosome). Traces of a partial medium septum are seen in some specimens, in reverse view.



TEXT-FIG. 13. For legend see opposite.

The proximal end structure, characteristic for *Agetograptus*, is well seen in this species. $Th1^2$ is much longer (0·9–1 mm) than $th1^1$ (0·4 mm) and its aperture lies above the aperture of $th2^1$. The sicula is visible on the obverse side for a distance of 0·8 mm. Its whole length is 1·25 mm with the aperture being 0·35–0·4 mm wide. The virgella is 0·4 mm long.

Remarks. The species agrees well with the description of Swedish material given by Loydell (1991), who was the first to distinguish the paired apertural spines. From both Norilsk (Obut *et al.* 1968) and Swedish material our specimens differ only in having a shorter virgella.

Genus PSEUDORTHOGRAPTUS Legrand, 1987

Type species. *Diplograpsus insectiformis* Nicholson, 1869; originally designated Legrand 1987; from the Llandovery of the Lake District, England.

Diagnosis (emend. herein). Proximal development of *tamariscus* Pattern (I); pseudancorate, often with complex meshwork of radiating and concentric rods; usually membranous; thecae simple 'orthograptid' tubes, lacking a geniculum, but spinose, usually with paired ventral, sometimes bifurcating spines, occasionally quite long, sometimes short and blunt; 'uniserial' portion in one subgenus; rare spines on lateral rhabdosomal walls.

Remarks. For differences with other spinose genera see discussions of *Hirsutograptus* and *Rivagraptus*. Two subgenera are recognized: *P*. (*Pseudorthograptus*) subgen. nov. and *P*. (*Dimorphograptoides*) subgen. nov., the latter having a short 'uniserial' portion caused by an elongate $th1^2$.

Subgenus PSEUDORTHOGRAPTUS (PSEUDORTHOGRAPTUS) Legrand, 1987

Type species. *Diplograpsus insectiformis* Nicholson, 1869.

Diagnosis. As for genus, except that *P*. (*Dimorphograptoides*) subgen. nov. is excluded, that is those species with a short uniserial portion.

Pseudorthograptus (*Pseudorthograptus*) *inopinatus* (Bouček, 1944)

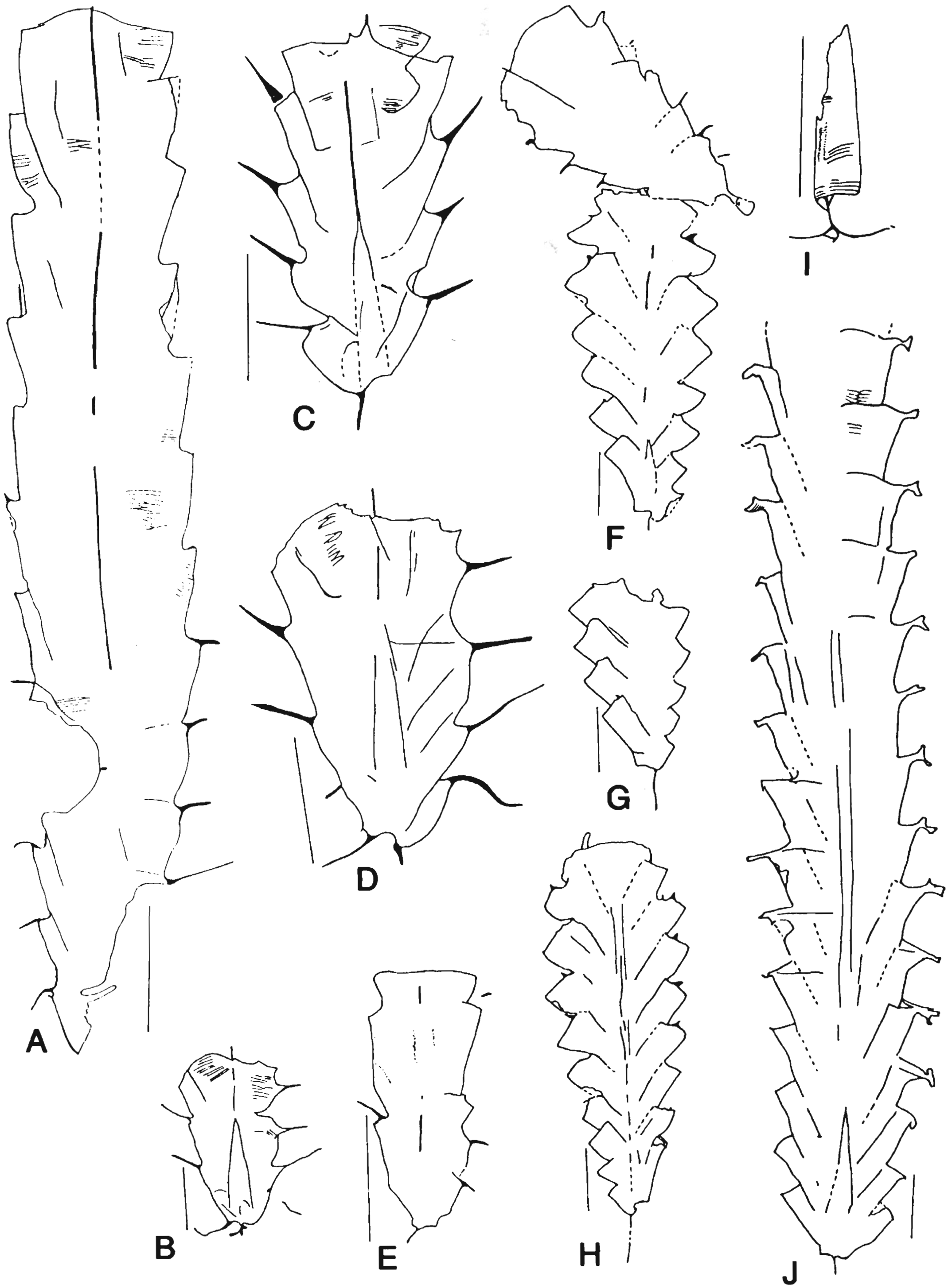
Plate 11, figure 10; Text-figures 16B–F, 17

1944 *Orthograptus* (?) *inopinatus* n. sp., Bouček, p. 2, pl. 1, fig. 8; text-fig. 1*b–c*.
1971 *Orthograptus* (?) *inopinatus* Bouček: Schauer, p. 37, pl. 7, fig. 14.
1985 *Orthograptus inopinatus* Bouček: Štorch, p. 91, pl. 1, figs 6–9; pl. 2, fig. 3; text-fig. 2A–E, K.

Material. Four specimens, flattened or in low relief, from localities B611-2-54, B611-6/74-6 and 427, Kos-Istek region; one specimen etched, see Thorsteinsson 1958, p. 91.

Horizon. Rhuddanian–Aeronian, *cyphus* to *gregarius* biozones, southern Urals, Sakmara Formation; *cyphus* Biozone for the Canadian Arctic, Cape Phillips Formation specimen.

TEXT-FIG. 13. *Rivagraptus rozmanae* gen. et sp. nov.; *gregarius* Biozone; Kos-Istek region. A–C, E, CNIGR Museum 143/12879, 144/12879, 145/12879 and 146/12879; fragments of adult rhabdosomes exhibiting paired apertural spines of lateral position; D, holotype, CNIGR Museum 142/12879; rhabdosome with apertural spines and well preserved fusellar zig-zag structure, sicula is covered in reverse view; F–H, CNIGR Museum 147/12879, 148/12879 and 149/12879; adult rhabdosomes with symmetrical apertural spines of lateral position; sicula is free in obverse view (F, H); I, CNIGR Museum 150/12879; fragment of proximal part of rhabdosome in reverse view; sicula is covered. Scale bars represent 1 mm.



TEXT-FIG. 14. For legend see opposite.

Description. The rhabdosome is no more than 5 mm long, being incomplete in the material studied. It widens from 0·8–1·1 mm at th1^1 aperture to 1·1–1·5 mm at th3^1; maximum dorso-ventral width is difficult to evaluate because of incompleteness. The isolated specimen (Text-fig. 17) is rather wider: 1·15–1·2 mm at th1^1; 1·4 mm at th2^1; 1·4 mm at th3^1 and 1·5 mm at th4.

The thecae are straight tubes about 0·2 mm wide, but widening aperturally to 0·3 mm, overlapping one-half. The thecal spacing is 7–8·5 in the first 5 mm (4·5 in 2·5 mm). Slightly everted and thickened apertures bear paired bifurcating spines of latero-ventral position. The bifurcations are at 40–60°, close to the origin of the primary spine. The spines may be more than 0·7 mm long, straight and directed proximo-laterally or proximo-ventrally. Near the bifurcation point additional thickening of cortical tissue is characteristic.

Th1^1 extends 0·15 mm below the sicular aperture; its upward-growing portion is 0·85 mm long. The sicula is visible for about 1 mm in reverse view. Its whole length is about 2 mm, and the aperture is 0·2 mm wide. The apex reaches the level of the aperture of th3^2. The extreme proximal end shows a pseudancora based on virgellar division (Text-fig. 16F). It cannot be fully understood because of its incompleteness in the flattened material available. Some small fragments of membranae attached to the peripheral lists are present. Proximally, within the first two thecal pairs, apertural spinosity (Text-fig. 16E) resembles in part lasiograptid lacinia.

Remarks. The last feature has been mentioned for the distal part of Bohemian specimens (Štorch 1985). Loydell (1991) noted that spines also originate from the nema in *P.* (*P.*) *inopinatus*, a feature not detected on our material. The species has close affinities with *P.* (*P.*) *insectiformis* but differs from it in having distinctly bifurcating, stout spines on the thecal apertures. The concave ventral margins of th1^1 and th1^2 are similar to those in *Petalolithus*, although whether an evolutionary relationship could be claimed is uncertain.

Pseudorthograptus (*Pseudorthograptus*) *insectiformis minutus* (Churkin and Carter, 1970)

Plate 11, figure 11; Text-figure 16A

1970 *Orthograptus insectiformis minutus* n. subsp., Churkin and Carter, p. 30, text-fig. 12C, H–J.

Material. One complete specimen, preserved flattened, from locality B671-8/74-258 in the Zhaksy-Kargala Valley.

Horizon. Aeronian, upper part of the *gregarius* Biozone. In south-eastern Alaska the subspecies occurs in the *gregarius* and *convolutus* biozones (Churkin and Carter 1970).

Description. Incomplete rhabdosome, 6 mm long, with maximum dorso-ventral width about 1 mm. Successive measurements of dorso-ventral width in the proximal part are: at th1^1, 0·85 mm; th2^1 0·9 mm; th3^1, 0·95 mm; th4^1, 1 mm.

The thecae are simple tubes, 0·3 mm wide with subhorizontal or slightly everted apertures, overlapping less than one-half of their length. Thecal apertures bear paired apertural spines 0·02–0·025 mm wide at the base and up to 0·7 mm long. They are directed ventro-proximally. Their position on the thecal apertures is unclear, though most probably they are paired lateral spines. Thecal number is 8 in 5 mm proximally. In obverse view, the sicula is seen for 0·75 mm; its full length is 1·3 mm. The sicular apex reaches the level of the middle part

TEXT-FIG. 14. A, *Rivagraptus rozmanae* gen. et sp. nov.; CNIGR Museum 151/12879; incomplete distal fragment; *gregarius* Biozone; Kos-Istek region. B–E, *Rivagraptus sentus* gen. et sp. nov.; *gregarius* Biozone; Zhaksy-Kargala Valley. B, CNIGR Museum 153/12879; young rhabdosome; C, holotype, CNIGR Museum 152/12879; rhabdosome with well preserved thorn-like apertural thecal spines directed ventro-distally and presumably of ventral position; sicula is free in obverse view; D–E, CNIGR Museum 154/12879 and 155/12879; incomplete fragments. F–H, *Agetograptus primus* Obut and Sobolevskaya; CNIGR Museum 159/12879, 156/12879 and 157/12879; short rhabdosomes with small apertural spines, of lateral position, and extremely long th1^2; *gregarius* Biozone; Zhaksy-Kargala Valley. I–J, *Pseudorthograptus* (*Pseudorthograptus*) *obuti* (Rickards and Koren'); *cyphus* Biozone; Kos-Istek region. I, CNIGR Museum 167/12879; juvenile specimen at metasicular stage showing a forking virgella; J, CNIGR Museum 165/12879; adult rhabdosome, fully septate with blunt and slightly bifurcating aperture processes; reverse view. Scale bars represent 1 mm.

of th3^1. Th1^1 extends 0·12 mm below the sicular aperture; its upward growing portion is 0·65 mm long. Dimensions of sicula: length, 1·3 mm, width at aperture, 0·2 mm.

The extreme proximal end possesses a simple pseudancora structure based on a dividing virgella. For preservational reasons the structure is not complete. The virgella divides close to the base of the ventral wall of th1^1; further bifurcation of the primary rods is unclear. Apart from concentric rods, fragments of peripheral threads are preserved.

Remarks. From *P.* (*P.*) *i. insectiformis* this subspecies can be distinguished by its smaller rhabdosome size, more densely packed thecae having paired apertural spines, and by its smaller sicula.

Pseudorthograptus (*Pseudorthograptus*) *mutabilis* (Elles and Wood, 1907)

Text-figure 18C–D

1907 *Orthograptus mutabilis* n. sp., Elles and Wood, p. 232, pl. 29, fig. 1*a–d*, text-fig. 153*a–c*.

Material. The original Elles and Wood (1907) specimens.

Diagnosis (revised). Robust, septate rhabdosome with dorso-ventral width of up to 4 mm and a length of several tens of mm; thecal spacing 13+ in 10 mm proximally, to 10 in 10 mm distally; apertures drawn out into a short, blunt spine or mucro, the tip of which may be turned backwards slightly; thecal overlap about one-half; thecal inclination 40–45°; sicula 2+ mm long, the apex reaching above the apertures of the second thecal pair; sicular aperture 0·3 mm wide; virgella pseudancorate, dividing almost immediately; membrane extensive, reaching 5th thecal pair in some specimens; with faint traces of striations; ?supporting meshwork.

Remarks. P. (*P.*) *mutabilis* differs from *P.* (*Dimorphograptus*) *physophora* in its lack of a long th1^2 (and pseudo-uniserial portion) and in its more robust rhabdosome. From *P.* (*P.*) *obuti* it differs in having a wider proximal end with strongly diverging thecae, and in the lack of the apertural division of the mucros.

Pseudorthograptus (*Pseudorthograptus*) *obuti* (Rickards and Koren', 1974)

Plate 11, figures 3–9; Text-figure 15

1974 *Orthograptus obuti* sp. nov., Rickards and Koren', p. 199, pl. 1, figs *a–c*; text-figs 6–9, *non* 10–12.

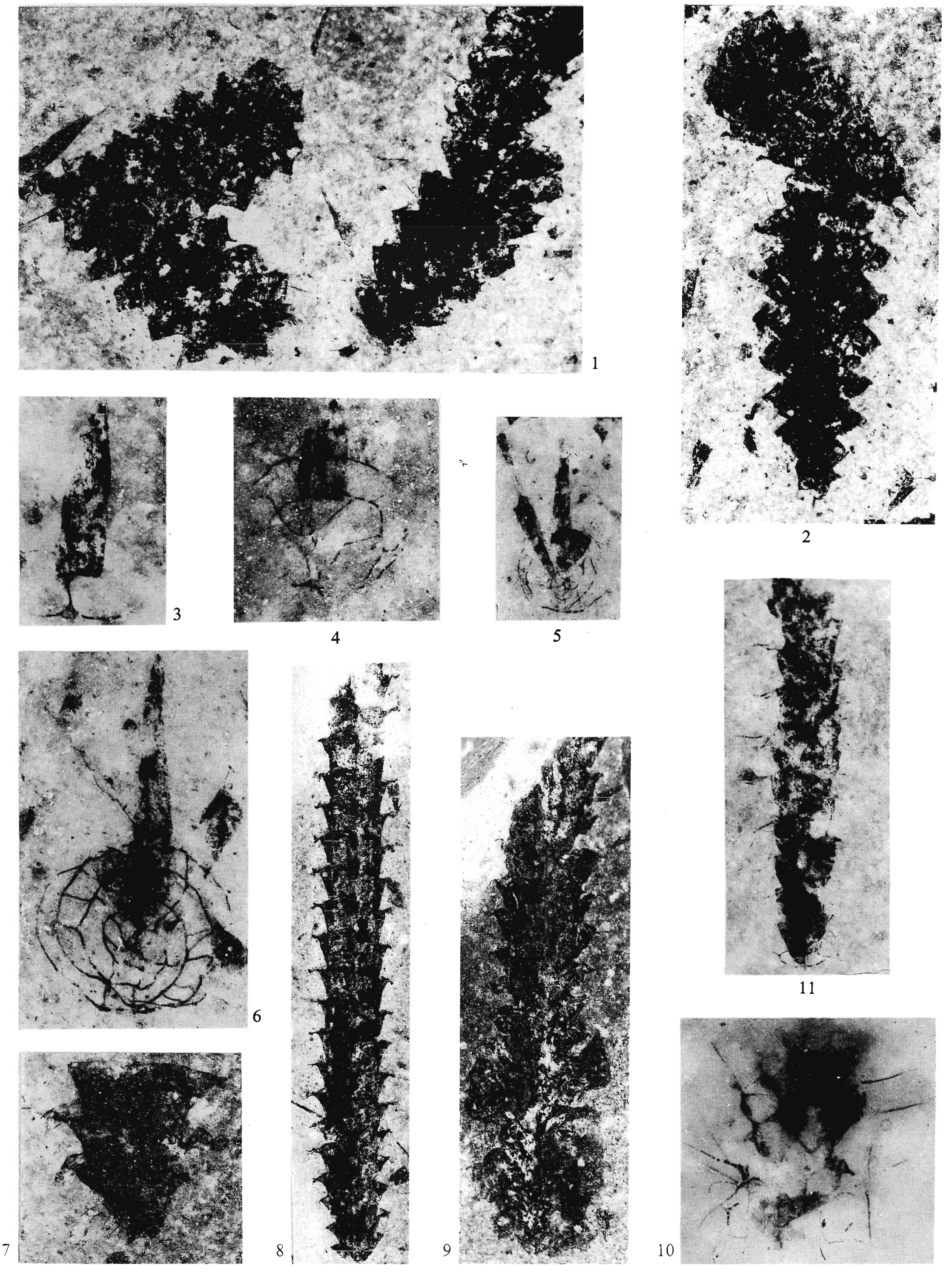
EXPLANATION OF PLATE 11

Figs 1–2. *Agetograptus primus* (Obut and Sobolevskaya); CNIGR Museum 158/12879 and 159/12879; slabs showing several rhabdosomes, preserved in low relief; ×10.

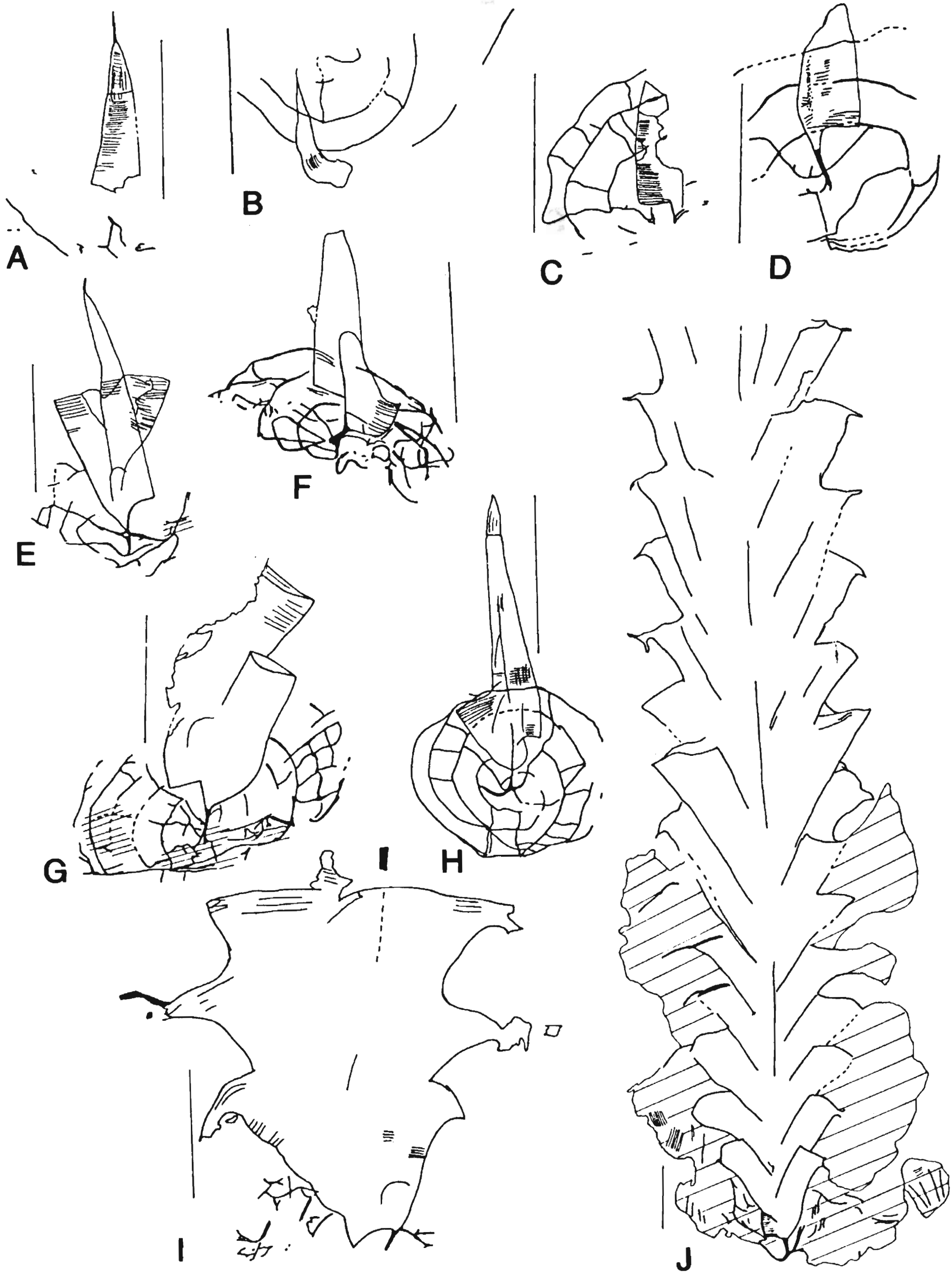
Figs 3–9. *Pseudorthograptus* (*Pseudorthograptus*) *obuti* (Rickards and Koren'); *gregarius* Biozone; Kos-Istek region. 3–6, CNIGR Museum 160/12879, 161/12879, 162/12879 and 163/12879; successive stages of early astogenetic development, with umbrella-like ancorae; 7, CNIGR Museum 164/12879; young rhabdosome with partly preserved meshwork and blunt, bifurcating, apertural processes; 8, CNIGR Museum 165/12879; adult specimen with incomplete proximal part; 9, CNIGR Museum 166/12879; adult rhabdosome showing extreme development of membranous structures; 3–7, ×20; 8–9, ×5.

Fig. 10. *P.* (*Pseudorthograptus*) *inopinatus* (Bouček); CNIGR Museum 174/12879; proximal part of rhabdosome showing numerous bifurcating rods and apertural spines; *gregarius* Biozone; Kos-Istek region; ×20.

Fig. 11. *P.* (*Pseudorthograptus*) *insectiformis minutus* (Churkin and Carter); CNIGR Museum 174/12879; rhabdosome showing pseudancora and paired apertural spines; upper part of *gregarius* Biozone; Zhaksy-Kargala Valley; ×10.



KOREN' and RICKARDS, *Agetograptus*, *Pseudorthograptus*



TEXT-FIG. 15. For legend see opposite.

1982 *Orthograptus obuti* Rickards and Koren'; Howe, pl. 1, figs *d–e*.
1985 *Orthograptus obuti* Rickards and Koren'; Štorch, p. 92, figs 1–2, 4–5; pl. 4, fig. 6; text-fig. 2H–J.
1987 *Orthograptus obuti*(?) Rickards and Koren'; Bates and Kirk, p. 92, fig. 6*c*.
1992 '*Orthograptus*' cf. *obuti* Rickards and Koren'; Bates and Kirk, p. 45, pls 3–4, figs 44–53, 252C.

Material. Five adult specimens and about 25 proximal fragments or juvenile rhabdosomes, flattened or in low relief, from localities 67/30, K-126-3, 379B/72-1, 587-11, 671-2-68, 607-3-8 and 671-8/74 in the Kos-Istek region.

Horizon. Uppermost Rhuddanian–lower Aeronian, *cyphus* and *gregarius* biozones of the southern Urals, Sakmara Formation.

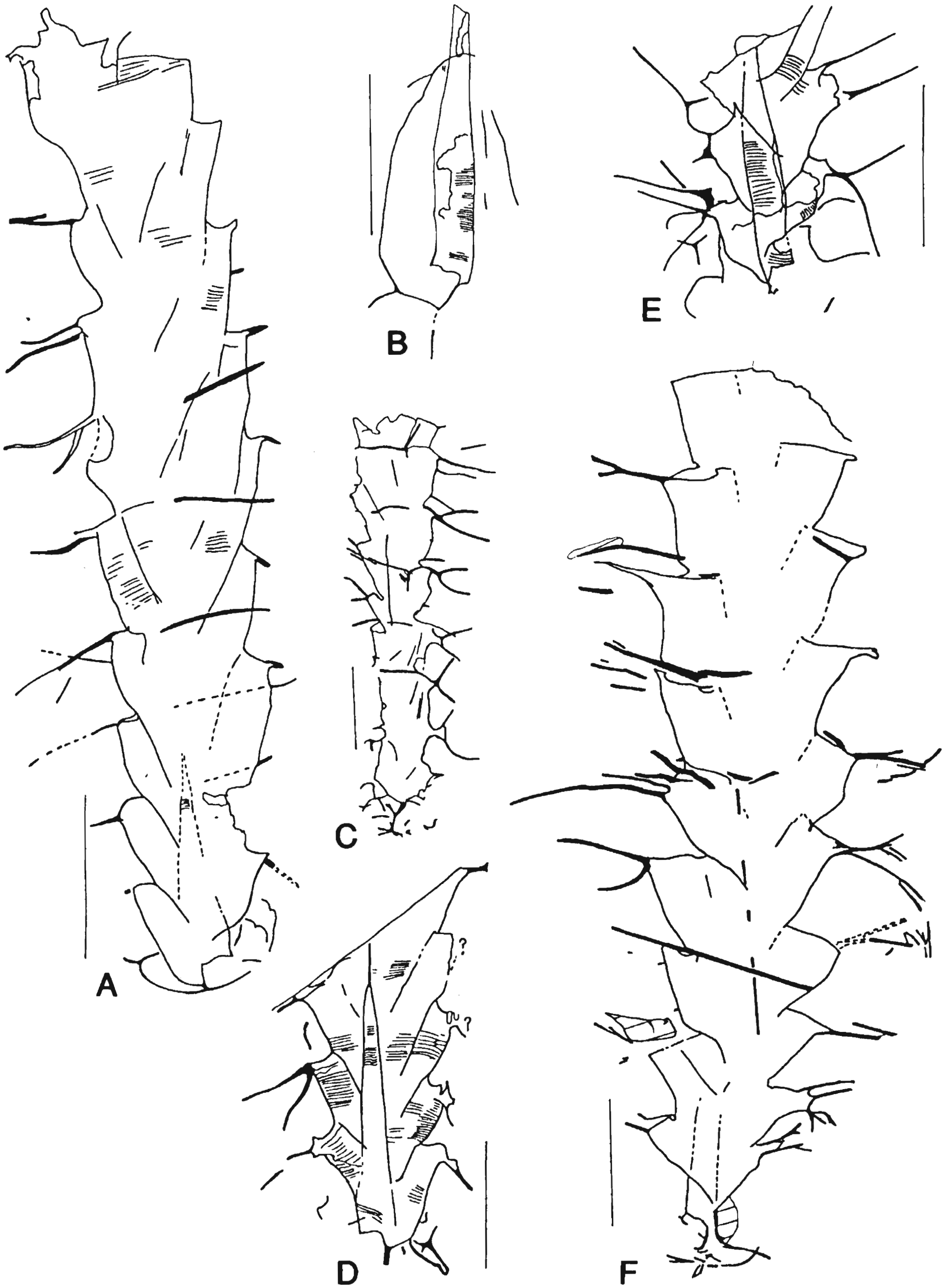
Description. The large rhabdosome, 25–30 mm long, and over 3 mm wide in profile, has well developed proximal structures including pseudancora, meshwork and membranes. Its dorso-ventral width increases as follows: at $th1^1$, 1·4–1·6 mm; $th2^1$, 2–2·1 mm; $th3^1$, 2·4 mm; $th4^1$, 2·5 mm; and at $th5^1$, 2·5 mm. The maximum dorso-ventral width of 3–3·4 mm (excluding blunt apertural processes) is reached at a distance of 5–7 mm from the sicular aperture; thereafter the rhabdosome is parallel-sided.

The thecae are straight tubes, 1·7–2 mm long and 0·3–0·5 mm wide, inclined outwards at 20° to the rhabdosomal axis and overlapping for about one-half of their length. The thecal apertures are rounded and slightly everted, possessing blunt ventral processes, 0·3 mm long, directed ventrally. These show transverse bifurcation into short processes.

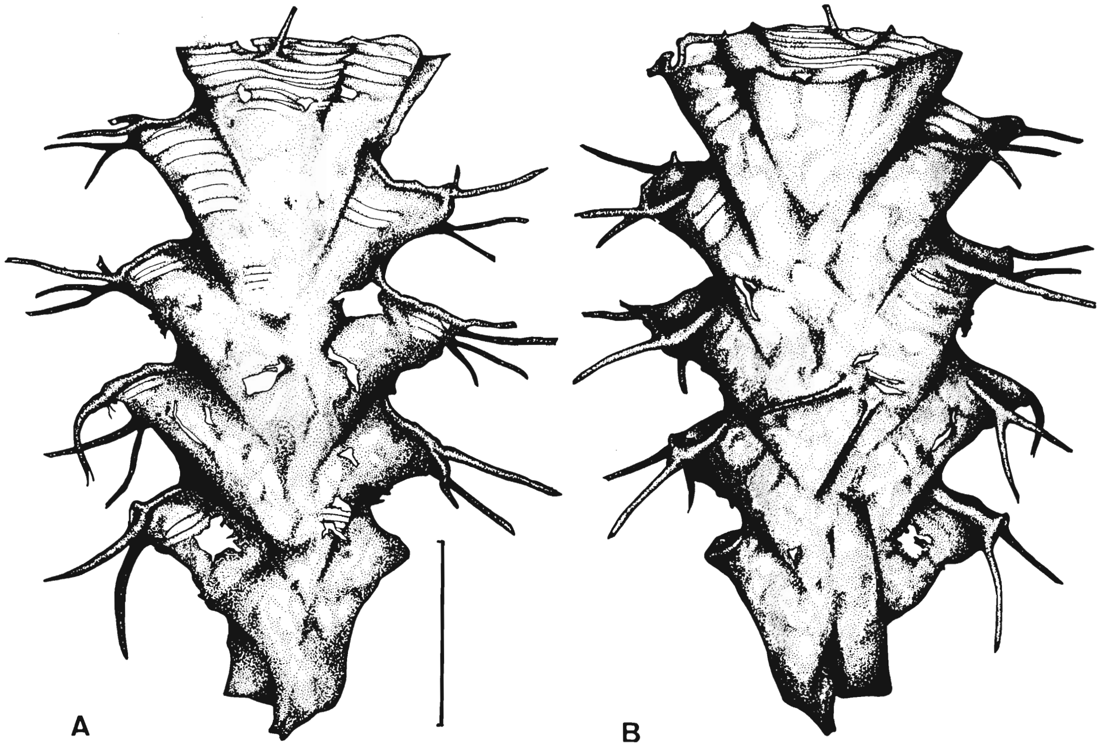
The sicula is up to 2 mm long and 0·25 mm wide at the aperture. It is completely covered in reverse view. $Th1^1$ originates 0·4–0·5 mm above the sicular aperture, and grows down slightly below it; the upward-growing portion is 1·1 mm long. The pseudancora is formed at the earliest astogenetic stage when the sicula is not yet complete (no more than 1 mm long). A stout virgella extends for 0·15–0·35 mm below the metasicular aperture before it forks. At the same metasicular stage secondary rods 0·8 mm long are formed. They are curved broadly and directed upwards. At this growth stage, the sicula and $th1^1$ are still down-growing, and the umbrella-like structure is almost circular, 1·3–1·5 mm in diameter. The central part of the umbrella is probably concave, the rest of it broadly convex, opening upwards and enveloping the sicula and the first thecae. In the proximal parts of adult rhabdosomes, there are present large membranes of semicircular, oval or irregular shape. They are most probably attached to the virgella meshwork enveloping the umbrella, and then grow in a distal direction. They envelop the proximal end of the rhabdosome at least up to $th4^1$ or even $th8^1$. They seem to be structureless, showing in places indistinct concentric thickening.

Remarks. *P*. (*P*.) *obuti* is unique in having thecae possessing bifurcating, blunt processes, and a large rhabdosome with a well developed membranous meshwork at the proximal end. This structure resembles that of *P*. (*Dimorphograptoides*) *physophora*, which differs in being less regular as far as the umbrella is concerned, as well as in having a 'uniserial' part. It is still unclear in the present material whether membranes always originate proximally or whether they can grow from thecal apertures as suggested perhaps by the figured specimen. The original description was based mostly on adult rhabdosomes (Rickards and Koren' 1974). The present material contains numerous juvenile specimens which show successive stages of early astogenetic development of the proximal meshwork. The new material shows that the formation of the pseudancora and basic meshwork is synchronous with the developing metasicula, and growth of the first thecal pair.

TEXT-FIG. 15. *Pseudorthograptus* (*Pseudorthograptus*) *obuti* (Rickards and Koren'); *gregarius* Biozone; Kos-Istek region. A–H, CNIGR Museum 168/12879, 169/12879, 170/12879, 161/12879, 171/12879, 172/12879, 173/12879, 162/12879; successive astogenetic stages showing early development of pseudancora and umbrella structure; fragments of membranous tissue are probably preserved in only one specimen (G); I, CNIGR Museum 164/12879; young rhabdosome showing blunt apertural processes; umbrella structure partly preserved; J, CNIGR Museum 166/12879; adult rhabdosome with well developed meshwork and membranous tissue, the latter distally as far as the seventh or eighth thecal pairs. Scale bars represent 1 mm.



TEXT-FIG. 16. A, *Pseudorthograptus* (*Pseudorthograptus*) *insectiformis minutus* (Churkin and Carter); CNIGR Museum 174/12879; adult rhabdosome with pseudancora and paired apertural spines; upper part of *gregarius* Biozone, Zhaksy-Kargala Valley. B–F, *P.* (*Pseudorthograptus*) *inopinatus* Bouček; *gregarius* biozone; Kos-Istek



TEXT-FIG. 17. A, *Pseudorthograptus* (*Pseudorthograptus*) *inopinatus* (Bouček); SM X.25935; isolated specimen from the O. M. B. Bulman collection, 1960; Cape Phillips Formation; *cyphus* Biozone (Thorsteinsson 1958, p. 91); rhabdosome aseptate, showing two pairs of bifurcating apertural spines of ventral-lateral position on each theca except th1^1; reverse view. B, the same specimen in obverse view, showing sicula free for about two-thirds of its length and a pair of spines growing from the lateral side of the protheca of th3^2. Scale bar represents 1 mm.

Pseudorthograptus (*Pseudorthograptus*) sp. A

Plate 12, figures 2–3; Text-figure 18A–B

Material. Two specimens, from localities 671-2 and 671-8/74-177 in the Zhaksy-Kargala region.

Horizon. Aeronian, *gregarius* Biozone, southern Urals, Sakmara Formation.

Diagnosis. Characterized by very long sicula (4·75 mm long), with a tiny prosicula, 0·32 mm long; thecae strongly upward-growing; rhabdosome rapidly achieving a dorso-ventral width at the level of th1^1 of 1·5 mm; sicular aperture 0·3 mm; robust virgella pseudancorate, latter well developed before th1^1 completed; origin of th1^1 low on sicula, 0·35 mm above its aperture, and th1^1 turns upwards after growing downwards for only 0·25 mm.

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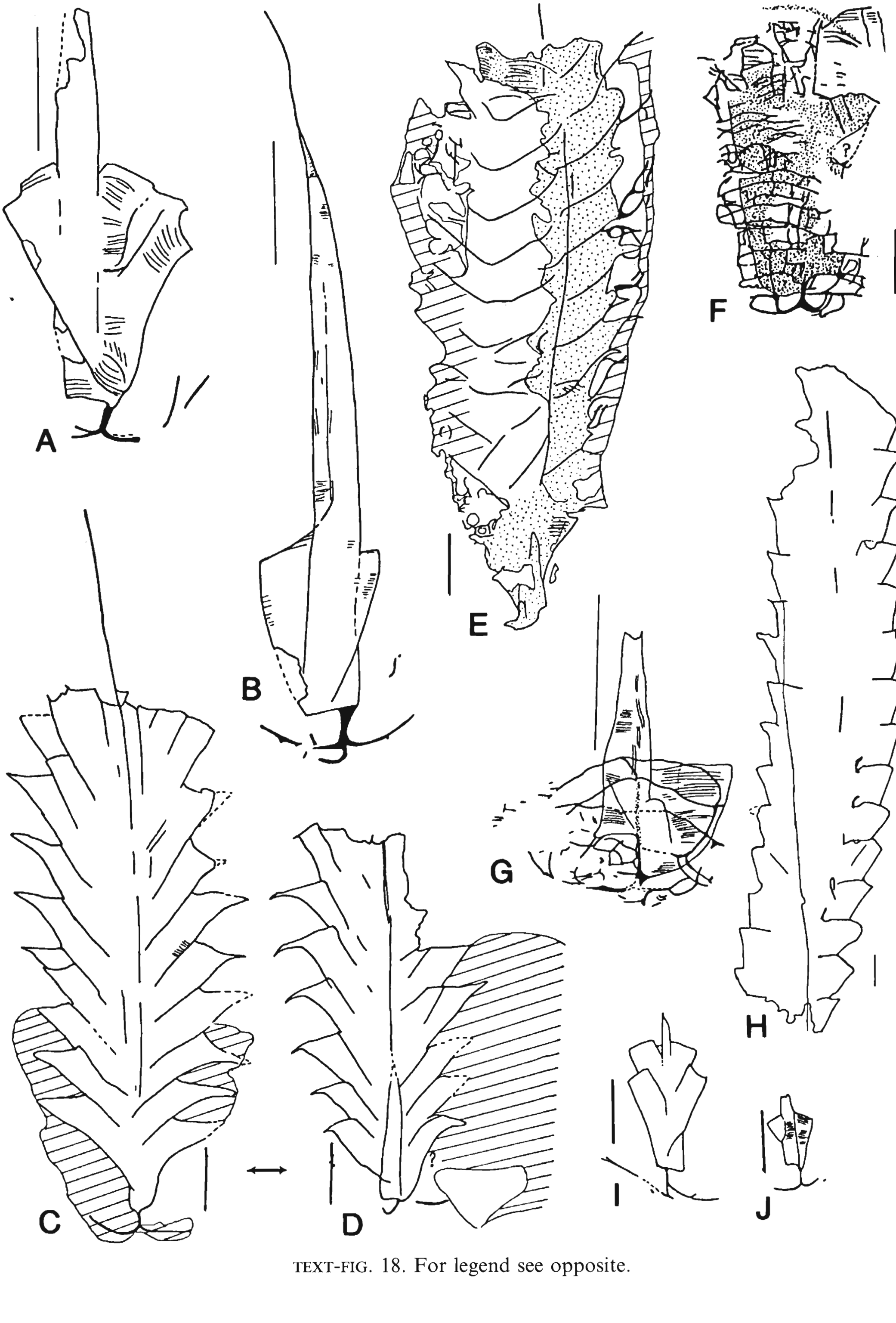
region. B, CNIGR Museum 177/12879; early growth stage, sicula possessing forking virgella and bifurcating secondary ribs; D–E, CNIGR Museum 178/12879 and 175/12879; proximal fragments of adult rhabdosomes in obverse view, thecae having long paired spines, pseudancora partly preserved; fusellar structure is well developed; C, F, CNIGR Museum 176/12879 and 179/12879; adult rhabdosomes showing additional spines, both apertural and lateral, well developed pseudancora partly preserved; reverse view. Scale bars represent 1 mm.



TEXT-FIG. 18. For legend see opposite.

Remarks. The specimens are very distinctive, and yet we are unable to assign them to any described species, and lack the necessary material to describe them as a new form.

Pseudorthograptus (*Pseudorthograptus*?) sp. B

Text-figure 18E

Material. A single well preserved, flattened specimen from borehole H-1, Norilsk region; on the same slab as *Comograptus comatus* Obut and Sobolevskaya, 1968, CNIGR Museum 27/9765.

Description. The rhabdosome reaches a length of 10 mm and a maximum width, seen in sub-scalariform view, of 4·3 mm: it is, therefore, a robust biserial even allowing for flattening. A nema projects distally, but is not seen within the rhabdosome. There is no obvious virgella but the base of the sicula may well have a thickened pseudancora, the virgella having subdivided very close to the sicular aperture. The sicula itself is far from clear but seems to be *c*. 1·5 mm long. The down-growing part of $th1^1$ is 0·45 mm long. The first two thecae grow upwards in the manner typical of pseudorthograptids; and the rhabdosome widens very quickly. Thecae are difficult to discern, but a series of possible ventral apertural processes, leading to a membranous lacinia, is seen on the right side of the specimen, giving a possible thecal spacing of 13–15 in 10 mm. There are two unusual and spectacular features of the colony: one is membranous lacinia (shown with diagonal shading on Text-fig. 18E) in which are spinose threads; the second is a lateral meshwork of fine threads (clathria-like) which envelop the whole colony from proximal end to distal end. There seems to be one major diagonal thread for each theca, and the threads may be connected to the apertural region of each theca, or to the lacinia. As preserved, the meshwork is pressed down upon the fusellar periderm of the colony (seen with fuselli in several places) and there is clearly another such set on the opposite side of the colony for threads can be seen pressed through. On Text-figure 18E the preserved periderm is shown stippled.

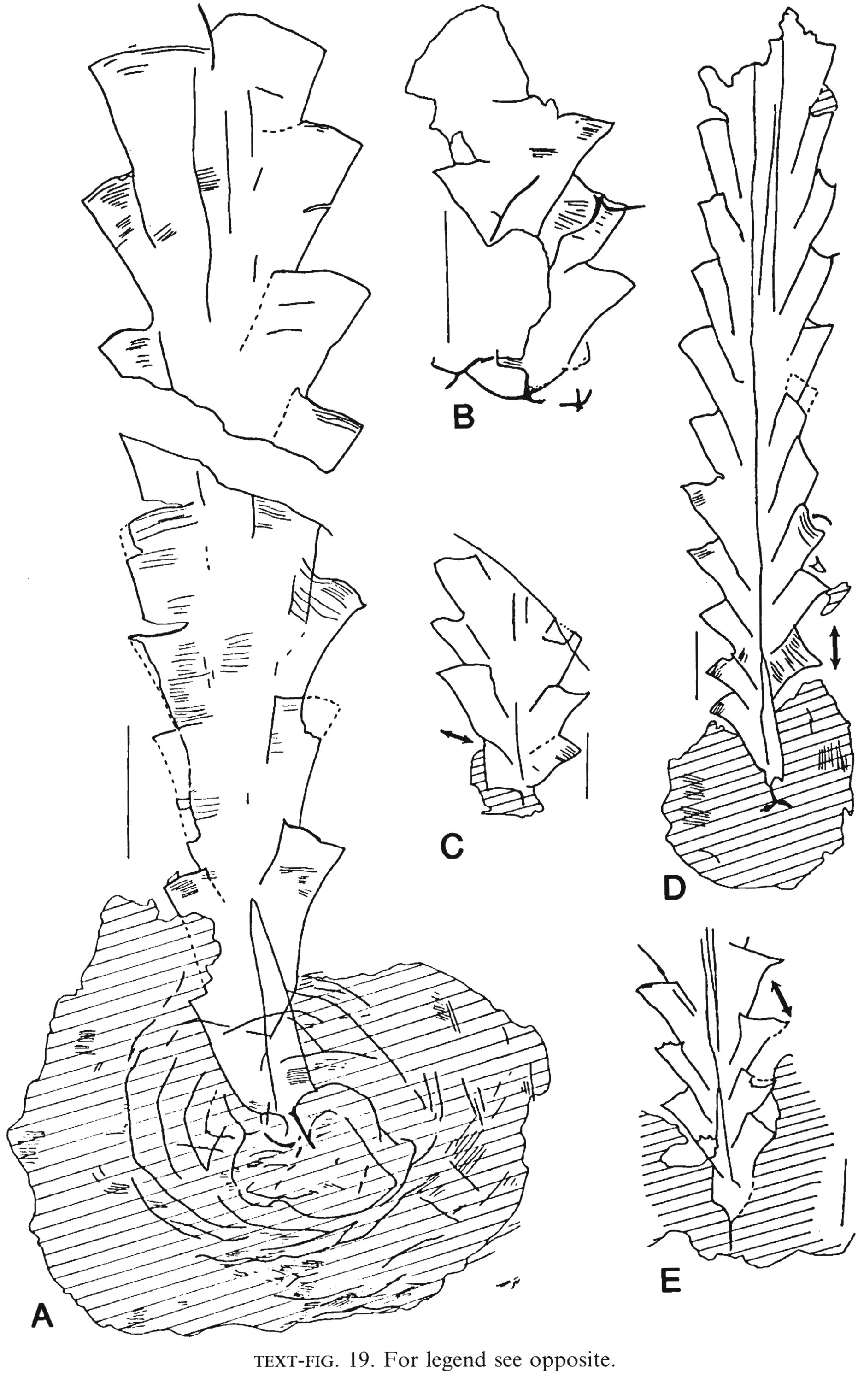
Remarks. This is a unique graptolite and a full interpretation of its structure is impossible. However, it is clear that a lacinial network and a lateral meshwork completely envelop a biserial colony which seems close to *Pseudorthograptus*. We see no similarity here to *Retiolites perlatus*, a retiolitid with fusellar periderm at least on the interthecal septa. Other pseudorthograptids have the pseudancora leading to membranous processes or envelopes, but none resembles this form in either the extent or the nature of this feature.

Pseudorthograptus (*Pseudorthograptus*?) sp. C

Text-figure 18F

Material. Three flattened specimens, early growth stages, from localities B671-2-23 and 379 6/72-1 in the Kos-Istek region.

TEXT-FIG. 18. A–B, *P.* (*Pseudorthograptus*) sp. A; CNIGR Museum 182/12879 and 180/12879; juvenile rhabdosome with extremely long sicula and pseudancora; *gregarius* Biozone; Kos-Istek region. C–D, *P.* (*Pseudorthograptus*) *mutabilis* Elles and Wood; SM A20365; *cyphus* Biozone; Dob's Linn. C, specimen figured Elles and Wood 1907, text-fig. 153*b*; D, specimen on the same slab as SM A20365; both rhabdosomes show pseudancora and well developed membranes. E, *P.* (*Pseudorthograptus*?) sp. B; CNIGR Museum 27/9765; specimen on the same slab as the holotype of *Comograptus comatus* Obut and Sobolevskaya, 1968; *triangulatus* Biozone; Norilsk region; preserved periderm stippled; membranous tissue oblique shading; faint trace of sicula; black rods of 'lacinial' meshwork are outside fusellar periderm but preserved flattened on to it. F, *P.* (*Pseudorthograptus*?) sp. C; CNIGR Museum 183/12879, a proximal end, consisting of two pairs of thecae, enveloped in basket-like meshwork based on dividing virgella; thecae are unclear but, as in *P.* (*P.*) sp. B, are within and separate from the meshwork; $th1^2$ may be unusually long, opening above $th2^1$; *cyphus* to *gregarius* biozones; Zhaksy-Kargala Valley. G, *P.* (*Pseudorthograptus*?) sp. E; CNIGR Museum 187/12879; juvenile rhabdosome with broadly curved $th1^1$; *cyphus* to *gregarius* biozones. H, *P.* (*Pseudorthograptus*) sp. F; CNIGR Museum 186/12879; *cyphus* or *gregarius* Biozone; Kos-Istek region. I–J, *P.* (*Pseudorthograptus*) sp. D; CNIGR Museum 184/12879 and 185/12879; juvenile specimens with slightly tapering proximal end possessing forked virgella and bifurcating primary rods (I); *cyphus* to *gregarius* biozones; Zhaksy-Kargala Valley.



TEXT-FIG. 19. For legend see opposite.

Horizon. Aeronian, *gregarius* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Pseudancorate proximal end, possibly with elongate th1^2; dorso-ventral width at level of th1^1 aperture is 0·6 mm and at the first thecal pair 1·2 mm (excluding meshwork); virgella divides 0·1 mm below the sicular aperture, each branch dividing again after a further 0·1 mm; thereafter all meshwork divisions are directed distally, very close to the peridermal layers of the thecae, resulting in a retiolitid-like fibrosity; arrangement of meshwork fibres seems crudely to mirror the thecal form.

Remarks. This form differs from *Corbograptus enigmatica* in having a pseudorthograptid proximal end with strongly upward-growing th1^1 and th1^2, rather than a rounded neodiplograptid proximal end. It is not certain that th1^2 is unusually elongate for the apertures of th1^2 and th2^1 are not seen. A further difference from *Corbograptus* is that the meshwork fibres seem not to reflect growth fuselli, but are more typically pseudorthograptid with radial and concentric arrangements, albeit tightly embracing the rhabdosome. None of the other pseudorthograptid species show the meshwork so closely fitted to the colony. The umbrella structure is 2·1 mm high and 0·62 mm wide near its base. It consists of *c*. 10–12 spiral rods, connected by radial ribs, which number 5–6 along one lateral side. The distance between both spiral and radial ribs is about 0·12 mm.

Pseudorthograptus (*Pseudorthograptus*) sp. D

Plate 12, figure 5; Text-figure 18I–J

Material. Two proximal ends, from locality B671-2, Zhaksy-Kargala Valley.

Horizon. Rhuddanian–Aeronian, *cyphus* to *gregarius* biozones, Sakmara Formation.

Remarks. The small pseudancorate proximal ends show both obverse and reverse views and the sicula, fully 2·5 mm long. The dimensions do not fit easily into the above-described species and we prefer at present to leave it in open nomenclature. The overall aspect is of a typical but small pseudorthograptid. Such forms are not dissimilar to some forms of *Petalolithus* (see Text-fig. 10H) and an evolutionary connection between the two genera is likely, requiring only the development of petalolithid thecae from pseudorthograptid ones, the upward and outward mode of growth already having been established in the earlier genus.

Pseudorthograptus (*Pseudorthograptus*?) sp. E

Text-figure 18G

Material. One flattened specimen, at an early growth stage, from locality B671-1-5 in the Zhaksy-Kargala Valley.

Horizon. Rhuddanian, *cyphus* Biozone of the southern Urals, Sakmara Formation.

TEXT-FIG. 19. *Pseudorthograptus* (*Dimorphograptoides*) *physophora* (Nicholson). A, CNIGR Museum 189/12876; rhabdosome with well developed pseudancora, umbrella-like meshwork and membrane; obverse view; B, CNIGR Museum 190/12876; a fragment of proximal part of the rhabdosome possessing pseudancora; reverse view; *cyphus* Biozone; Kos-Istek region; C–E, SM A207638, A210464*a*, figured Elles and Wood 1908, p. 354, text-fig. 231*a*, and A207626, *cyphus* Biozone; Dob's Linn; proximal fragments (C, E) and adult rhabdosome (D) with partly preserved membrane and forking virgella. Arrows show the direction of tectonic elongation. Scale bars represent 1 mm.

Diagnosis. The specimen consists of a sicula, almost complete th1^1, and well developed convex umbrella structure. Prosicula not present, metasicular aperture 0·25 mm wide. Down-growing portion of th1^1, 0·4 mm long; it bends at 0·25 mm below the sicular aperture and grows up for 0·7 mm. Virgella forking point is about 0·1 mm below the base of th1^1, and 0·35 mm below the sicular aperture. The umbrella is convex, opening upwards. It consists of four spiral rods with partly preserved cross-bars. The umbrella, 1·25 mm wide and 0·9 mm high, envelops part of the metasicula and the first half of th1^1.

Remarks. The broadly curved th1^1 results in a rounded appearance of the extreme proximal end. It is the only peculiar feature but sufficient to distinguish it from other pseudorthograptids, including *P*. (*P*.) *obuti*.

Pseudorthograptus (*Pseudorthograptus*) sp. F

Plate 12, figure 4; Text-figure 18H

Material. A single flattened specimen, showing mesial and distal thecae only, locality 671-1-5, Zhaksy-Kargala Valley.

Horizon. Uncertain, possibly *cyphus* Biozone (Rhuddanian), southern Urals, Sakmara Formation.

Diagnosis. Very robust rhabdosome, with a dorso-ventral width of almost 5 mm; thecal spacing 7·5 in 10 mm in the most proximal part seen, and 7 in 10 mm in the most distal part; thecal overlap and inclination uncertain; thecal processes present, short, and possibly lateral in position; nema present; presence of median septum doubtful.

Remarks. The specimen is distinguished by its robust size and low thecal spacing. The thecae seem to be of typical pseudorthograptid type, possibly not strongly spinose.

Pseudorthograptus (*Pseudorthograptus*) sp. G

Plate 9, figure 6

Material. A single specimen, from locality 671-8, specimen number 81, Zhaksy-Kargala Valley.

Horizon. Aeronian, uppermost *convolutus* Biozone, southern Urals, Sakmara Formation.

EXPLANATION OF PLATE 12

Fig. 1. *P*. (*Pseudorthograptus*) *inopinatus* (Bouček); CNIGR Museum 176/12879; *gregarius* Biozone; Kos-Istek region; ×20.

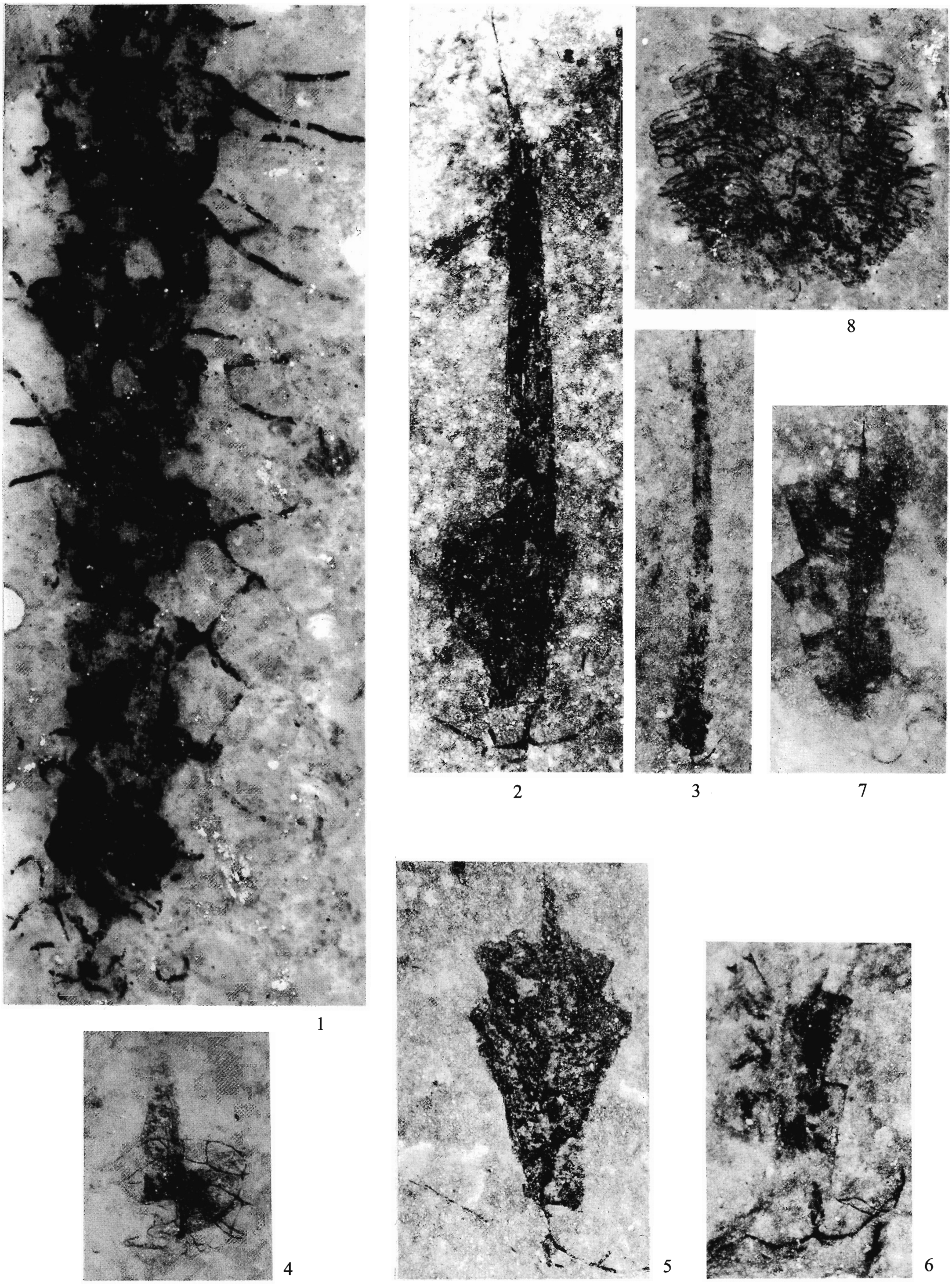
Figs 2–3. *P*. (*Pseudorthograptus*) sp. A; CNIGR Museum 180/12879 and 181/12879; juvenile rhabdosomes; sicula is more than 4·5 mm long, and possesses pseudancora; *gregarius* Biozone; Kos-Istek region; 2, ×20; 3, ×10.

Fig. 4. *P*. (*Pseudorthograptus*) sp. F; CNIGR Museum 187/12879; juvenile rhabdosome with broadly curved th1^1, umbrella-like meshwork of spiral rods and cross bars; *cyphus* to *gregarius* biozones; Zhaksy-Kargala Valley; ×20.

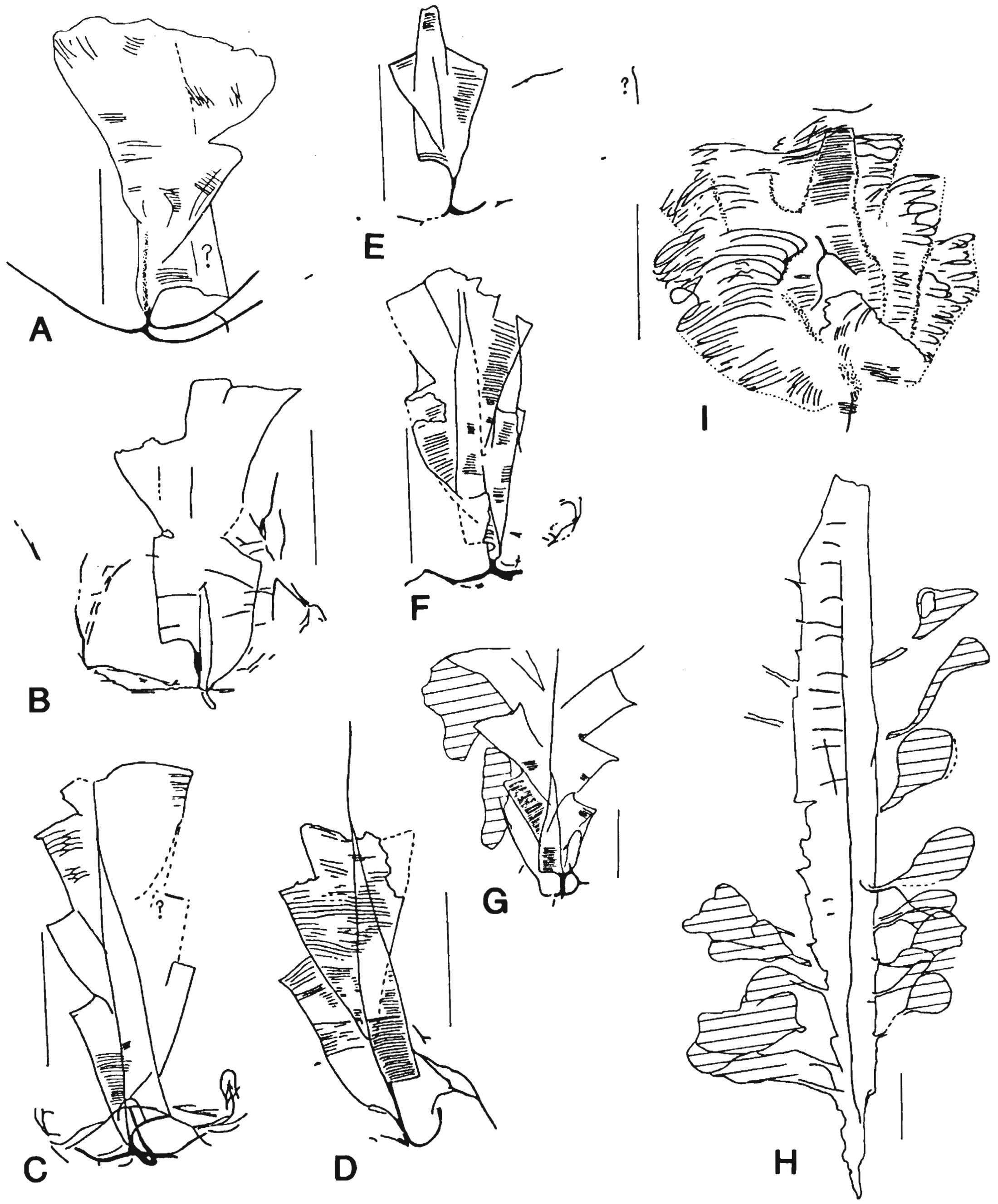
Fig. 5. *P*. (*Pseudorthograptus*) sp. D; CNIGR Museum 184/12879; young rhabdosome with sicula possessing pseudancora and two pairs of thecae; obverse view; *cyphus* to *gregarius* biozones, Zhaksy-Kargala Valley; ×20.

Figs 6–7. *Pseudorthograptus* (*Dimorphograptoides*) *physophora* (Nicholson); CNIGR Museum 191/12879 and 192/12879; juvenile rhabdosomes with th1^2 elongated; pseudancora present; *cyphus* Biozone; Kos-Istek region; ×20.

Fig. 8. *Corbograptus enigmatica* gen. et sp. nov.; CNIGR Museum 197/12879; juvenile rhabdosome; *cyphus* Biozone; Zhaksy-Kargala Valley; ×20.



KOREN' and RICKARDS, *Pseudorthograptus*, *Corbograptus*



TEXT-FIG. 20. A–F, *Pseudorthograptus* (*Dimorphograptoides*) cf. *physophora* (Nicholson); CNIGR Museum 193/12879, 194/12879, 195/12879, 192/12879, 196/12879 and 191/12879; juvenile rhabdosomes possessing pseudancorae and partly formed or preserved meshwork; ?*cyphus* Biozone; Kos-Istek region. G–H, *Dittograptus fortuitus* Obut and Sobolevskaya, 1968; lower part of *triangulatus* Biozone; Norilsk region. G, holotype, CNIGR Museum 61/9765; figured Obut *et al.* 1968, pl. 6, fig. 1; proximal part, showing pseudancora and partly preserved membranous proximal structures; H, CNIGR Museum 64/9765, specimen figured Obut *et al.* 1968, pl. 6, fig. 4; adult rhabdosome preserved in scalariform view with bulb-like membranous structures, *Diagnosis*. Extreme proximal end with th1^1 and th1^2 diverging upwards at 22–25°; sicula 3 mm long, but incomplete; apex of prosicula missing; sicular aperture 0·3 mm wide; pseudancora forks and then bifurcates again quickly, the rods growing upwards markedly.

Remarks. This form is similar to *P.* (*P.*) sp. A, but has a smaller sicula. Some slight resemblance to *Petalolithus*, such as the curvature is th1^1 and 1^2, is present, but the sicula is much longer than is usual in petalolithids.

Subgenus PSEUDORTHOGRAPTUS (DIMORPHOGRAPTOIDES) subgen. nov.

Type species. *Diplograpsus physophora* Nicholson, 1868; from the Llandovery of the Lake District, England.

Diagnosis. As for genus, except that the subgenus embraces only those forms with a short uniserial portion, with a long th1^2, which accentuates both the drawn-out appearance of the proximal end and the upward-growing aspect of the early thecae.

Pseudorthograptus (*Dimorphograptoides*) *physophora* (Nicholson, 1868)

Plate 12, figures 6–7; Text-figure 19A–E

1868 *Diplograpsus physophora* n. sp., Nicholson, pp. 56, 61, pl. 3, fig. 7.
1880 *Diplograpsus physophora* Nicholson; Lapworth, pl. 5, fig. 20.
1908 *Dimorphograptus physophora* (Nicholson); Elles and Wood, p. 353, pl. 35, fig. 7*a–d*; text-fig. 231*a–b*.
1974 *Dimorphograptus*? *physophora* (Nicholson, 1868); Hutt, p. 52, pl. 8, fig. 5.

Material. Elles and Wood (1908) and Hutt (1974) specimens; two flattened specimens with well preserved fuselli, from localities 587-11-1, B671-470, Kos-Istek region.

Horizon. Rhuddanian, ?*atavus–cyphus* biozones, Sakmara Formation, southern Urals.

Diagnosis. Robust, septate biserial, 10–22 mm long; distal dorso-ventral width *c*. 2 mm achieved by th5^1–th7^1; dorso-ventral width at th1^1 aperture 0·75–0·85 mm; proximal thecal spacing 10–12 in 10 mm; distal thecal spacing 10 in 10 mm; Urals specimens 10–11 throughout; sicula *c*. 1·8–2 mm long, completely free in obverse view; sicular apex almost reaches to the top of the aperture of th2^1; thecae simple straight tubes, 2 mm long, 0·5 mm wide, but with undulating margin; tubes inclined at 20–25° to the rhabdosomal axis; ?mucronate, or with ?ventral spines/processes; conspicuous pseudancora, with associated meshwork and membrane, both growing upwards to embrace the proximal two to four thecal pairs of the colony, at least; virgella divides 1·7 mm from its base and gives rise to spiral rods as well as oblique cross bars; in some specimens the meshwork is 4 mm wide and 3 mm long; the membrane itself has faint striations. First theca of second series is derived from

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based on bifurcating spines, possibly originating on the lateral side of rhabdosome; I, *Corbograptus enigmatica* gen. et sp. nov.; holotype, CNIGR Museum 197/12879; incomplete rhabdosome in obverse view showing rods broadly reflecting fuselli and zig-zags, thecal outlines and thecal overlaps; sicula visible centrally, with narrow growth fuselli, but no peridermal layers; fine virgella at base; *cyphus* Biozone; Zhaksy-Kargala Valley. Scale bars represent 1 mm.

$th1^1$, its aperture opening above that of $th2^1$; $th1^1$ is down-growing for 0·5 mm, turning upwards slightly above the sicular aperture, then growing upwards for 1·1 mm.

Remarks. P. (*Dimorphograptoides*) is the morphological equivalent of *Agetograptus* in that both have an unusually elongate $th1^2$. However the latter is a virgellate subgenus, totally lacking a pseudancora, meshwork or membrane. *P.* (*Dimorphograptoides*) may have evolved directly from *P.* (*P.*) *mutabilis* in the *atavus* Biozone; or both may have been derived from a species such as *Parakidograptus praematurus* (Davies, 1929) (see Evolution section).

Pseudorthograptus (*Dimorphograptoides*) cf. *physophora* (Nicholson, 1868)

Text-figure 20A–F

cf. 1868 *Diplograpsus physophora* n. sp., Nicholson, pp. 56, 61, pl. 3, fig. 7.

Material. Six specimens, predominantly at early growth stages, from localities B671-2-21, B671-2-67, B671-2-73, B671-8/74-22, B671-8/74-250 and B671-8/74-254*a* in the Zhaksy-Kargala Valley.

Horizon. Approximately *cyphus* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Some specimens may lack the elongate $th1^2$ so that the rhabdosome appears to lack a 'uniserial' portion; pseudancora and meshwork well-developed and established before $th1^1$ and $th1^2$ completed; ?membrane; sicula *c.* 1·5–2 mm long, apex *below* third thecal pair; thecal spacing proximally 14 in 10 mm (no distal thecae known); short $th1^2$ (Text-fig. 20C, F) is *c.* 1 mm long; long $th1^2$ (Text-fig. 20B, D) is *c.* 2 mm long.

Remarks. This form may be referable to *P.* (*D.*) *physophora*, but the material is not well enough preserved to be sure. They differ only in the proximal thecal spacing and in the presence of a short or long $th1^2$.

Genus DITTOGRAPTUS Obut and Sobolevskaya (*in* Obut *et al.*, 1968)

Type species. Dittograptus fortuitus Obut and Sobolevskaya (*in* Obut *et al.*, 1968) (Text-figs 20G–H herein); original designation; from the Llandovery of Norilsk, Siberia.

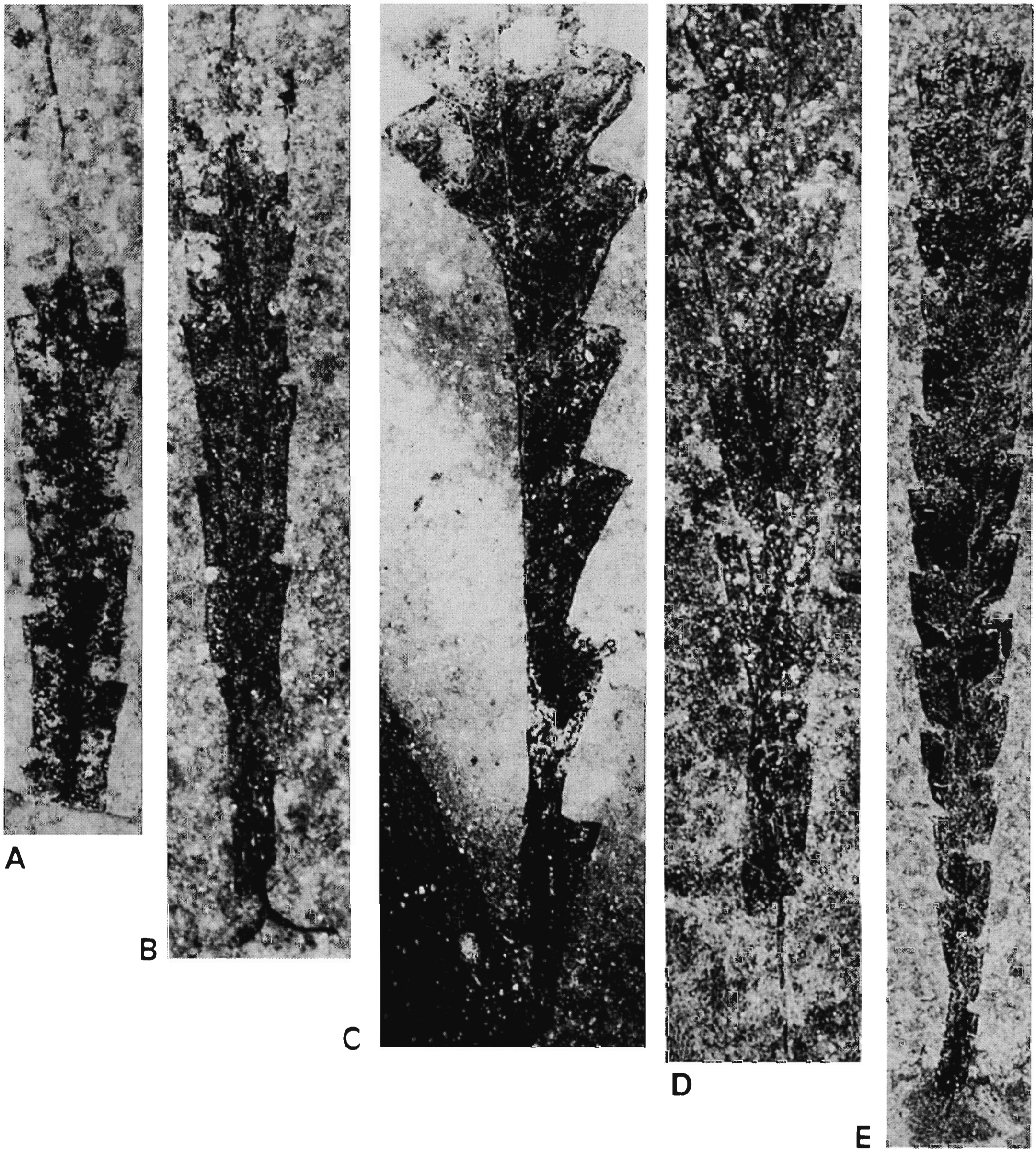
Diagnosis. Multispinose biserial with pronounced pseudancora, meshwork and extensive membranes, reaching distally to at least the 29th thecal pair; development pattern of *tamariscus* (I) type; thecae simple, straight tubes but with multiplicity of, mostly, ventral apertural spines, some long, a few genicular spines, and others irregularly positioned on lateral walls of the rhabdosome; sicula long, robust, but not well seen except for short length in obverse aspect. Thecal membranes of unknown origin are quite common (Text-fig. 2).

Remarks. Dittograptus is similar to *Pseudorthograptus* but differs in having much greater rhabdosomal spinosity. It might possibly be regarded as a subgenus of *Pseudorthograptus* derived, in the *triangulatus* Biozone, from a form like *P.* (*P.*) *obuti*. *D. fortuitus* may have given rise to *Victorograptus morosus* gen. et sp. nov. (see Evolution section). The genus includes the type and *Orthograptus monstrosus* (Štorch), which widens more gradually and has its sac-like growth concentrated at the proximal end.

Genus CORBOGRAPTUS gen. nov.

Type species. Corbograptus enigmatica gen. et sp. nov.; from the Llandovery of the Kos-Istek region, Kazakhstan.

Derivation of name. From *corbis* (Latin) = basket.



TEXT-FIG. 21. A–B, *Akidograptus ascensus* Davies; A, CNIGR Museum 198/12879; distal fragment showing median septum and thecae with sharp genicula; B, CNIGR Museum 199/12879; complete rhabdosome with forked virgella; *ascensus-acuminatus* Biozone; Kos-Istek region; both ×20. C, *Dimorphograptus confertus swanstoni* Lapworth; CNIGR Museum 210/12879; rhabdosome showing uniserial portion of five thecae; *cyphus* Biozone; Zhaksy-Kargala Valley; ×20. D–E, *Rhaphidograptus toernquisti* (Elles and Wood); CNIGR Museum 211/12879 and 212/12879; in both specimens the origin of th1^2 remains unclear in spite of good preservation in low relief; reverse views, *cyphus* Biozone; Kos-Istek region; both ×10.

Diagnosis. Virgellate, ?septate, robust biserial with rounded proximal end; proximal development probably *normalis* (H) Pattern or *tamariscus* (I) Pattern; thecae neodiplograptid (?); periderm much reduced and represented largely by thickenings outlining the fuselli, including zig-zag contacts thereof; sicula present; downward growth of th1^1 *c.* 0·75 mm; thecal overlap *c.* one-half; thecal length 1·5+ mm.

Remarks. The peridermal thickening recalls that sometimes seem (to a lesser extent) in *Petalolithus* where the periderm may be very thin but the fusellar outlines are thickened. However, the proximal thecae of *Corbograptus* resemble those of neodiplograptids rather than those of petalolithids. The meshwork is not a development from an ancora or pseudancora, hence *Corbograptus* cannot be closely related to either retiolitids or pseudorthograptids. At present it is a unique form, superficially 'retiolitid' but, in all probability, related to *Neodiplograptus*.

Corbograptus enigmatica gen. et sp. nov.

Plate 12, figure 8; Text-figure 20I

Holotype. CNIGR Museum 197/12876, Plate 12, figure 8; Text-figure 20I, Rhuddanian, *cyphus* Biozone, Kos-Istek region, southern Urals, Sakmara Formation.

Derivation of name. Reflecting its enigmatic nature.

Material. A single well-preserved specimen, 1643-16.

Diagnosis. As for genus.

Remarks. It is just possible that the strands we refer to as fusellar thickenings are actually meshwork threads in a membrane of the kind seen in *Pseudorthograptus*, but the presence of a probably undivided virgella argues against this interpretation.

Family AKIDOGRAPTIDAE Li and Ge, 1981

Diagnosis. Biserials with *ascensus* (J) proximal development resulting in narrow and pointed proximal ends with sicula well-exposed and conspicuous; thecae 'climacograptid' to 'glyptograptid' but often with a unique, but little understood undulation of the apertural margin.

Remarks. *Akidograptus* Davies, 1929 and *Parakidograptus* Li and Ge, 1981 are included.

EXPLANATION OF PLATE 13

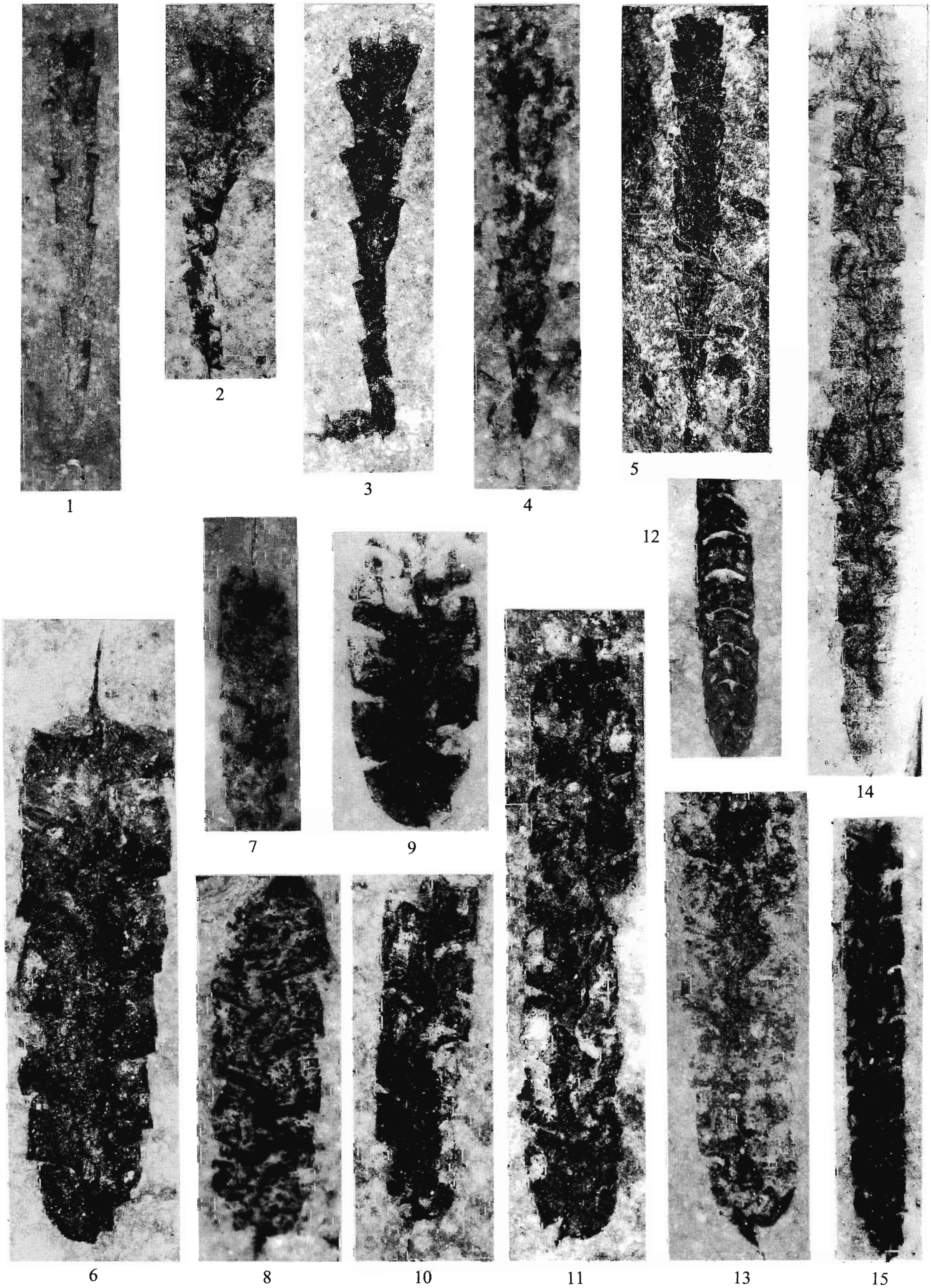
Fig. 1. *Akidograptus ascensus* Davies; CNIGR Museum 206/12876; incomplete specimen with geniculated thecae having slightly outward-sloping ventral walls; *acuminatus-ascensus* Biozone, Zhaksy-Kargala Valley; ×10.

Figs 2–3. *Dimorphograptus erectus* Elles and Wood; CNIGR Museum 208/12876 and 209/12876; *vesiculosus* Biozone; Zhaksy-Kargala Valley; both ×10.

Figs 4–5. *Rhaphidograptus toernquisti* (Elles and Wood); CNIGR Museum 213/12876 and 214/12876; *cyphus* Biozone; Kos-Istek region; 4, ×10; 5, ×5.

Figs 6–8. *Metaclimacograptus khabakovi* sp. nov.; *gregarius* Biozone; Kos-Istek region. 6, holotype, CNIGR Museum 225/12879; 7–8, CNIGR Museum 226/12879 and 227/12879. All specimens show supragenicular walls slightly convex and sloping inwards; 6, 8, ×20; 7, ×10.

Figs 9–14. *Metaclimacograptus hughesi* (Nicholson); *gregarius* Biozone; Kos-Istek region. 9–10, CNIGR Museum 218/12876 and 219/12876; young rhabdosomes showing rounded proximal end; 11, 13–15, CNIGR Museum 220/12879, 222/12879, 224/12879 and 223/12879; 12, CNIGR Museum 221/12879; scalariform view. 9, 11, 13, ×20; 10, 12, 14–15, ×10.



KOREN' and RICKARDS, graptoloids from the southern Urals

Genus AKIDOGRAPTUS Davies, 1929

Type species. Akidograptus ascensus Davies, 1929; original designation; from the Llandovery of Dob's Linn, Scotland.

Remarks. In some collections, distinguishing between *A. ascensus* and *Parakidograptus acuminatus* (see below) is not easy. For example, in material seen by one of us (RBR) from Thailand, the very earliest forms in the *ascensus-acuminatus* Biozone seem intermediate between the two species. It is possible that they originated from the same source and diverged early in the *ascensus-acuminatus* Biozone. Both genera have the *acuminatus* (J) Pattern of development.

Akidograptus ascensus Davies, 1929

Plate 13, figure 1; Text-figures 21A–B, 22A–H

1929 *Diplograptus* (*Akidograptus*) *ascensus* sp. nov., Davies, p. 9, figs 22–27.
1974 *Akidograptus ascensus* Davies; Hutt, p. 55, text-fig. 9, figs 9–10 [see for synonymy].
1975 *Akidograptus ascensus* Davies; Bjerreskov, p. 42, fig. 13D–E.
1979 *Akidograptus ascensus* Davies; Koren' *et al.*, pl. 32, fig. 3.
1983 *Akidograptus ascensus* Davies; Štorch, p. 297, pl. 11, figs 5–9, text-fig. 1B–C, F, H.
1986 *Akidograptus ascensus* Davies; Štorch, pl. 5, fig. 1.

Material. Ten flattened specimens, many of them with a well-preserved pseudancora, from localities 671/8-74, 671/8-134*a*, 671/8-147, 671/8-108, 671-1-28, 671/2-65, 587/11-20, 587/11-28, 587/11-29, 1643/50-49, 1643/50-111, 11 53-5, 53-9 and 53-11 in the Kos-Istek Region, Rivers Medes and Alimbek, Zhaksy-Kargala Valley.

Horizon. Lower Rhuddanian, *ascensus-acuminatus* Biozone, Sakmara Formation.

Description. Rhabdosome small, thorn-like, less than 10 mm long, widens from 0·4 mm at $th1^1$ to 0·9–1·2 mm distally. The thecae are strongly geniculate with supragenicular walls inclined to the rhabdosomal axis at 5–7°. Their apertures, 0·17–0·18 mm wide, are almost horizontal, and the excavations 0·1 mm long and high. Thecae number 4·5–5 in 5 mm. The proximal end is extremely protracted resulting from a long portion of free sicula. $Th1^1$ may have, in some specimens, an extremely short downward-growing part; it bends 0·4 mm above the sicular aperture and the upward-growing portion is about 1·3 mm long. In reverse view the sicula is free for 1·3 mm. Its whole length is no more than 2 mm and its aperture is 0·17–0·2 mm wide. A pseudancora, based on virgella division, is formed at the sicular stage. The virgella forks 0·15–0·16 mm below the sicular aperture and it bifurcates again into four rods which grow horizontally in ventral and lateral directions. Further irregular divisions and anastomosis of rods take place and these are usually directed downwards. Pseudancora rods are thickened, often at the sicular stage.

Remarks. In the present collection juvenile specimens dominate and they show an early astogenetic construction of a peculiar pseudancora which forms a downward-growing bundle. *A. ascensus* is the earliest species among Silurian diplograptaceans to develop this structure.

Genus PARAKIDOGRAPTUS Li and Ge, 1981

Type species. Diplograptus acuminatus Nicholson, 1867; original designation; from the Llandovery of Scotland.

Parakidograptus cf. *acuminatus* (Nicholson, 1867)

Text-figure 22I

cf. 1867 *Diplograptus acuminatus* n. sp., Nicholson, p. 109, pl. 7, figs 17–19.

Material. Two incomplete flattened specimens, from locality B408 in the Kos-Istek region.

Horizon. Lower Rhuddanian, the *ascensus-acuminatus* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome 9 mm long, with strongly elongated tapering proximal end. It widens from 0·5–0·6 mm at th1^2 to 1·4–1·6 mm at th5^2. Thecae are of simple 'orthograptid' type, with straight ventral walls inclined at *c*. 20° to the rhabdosomal axis. They overlap distally slightly more than one-half of their length. The thecal apertures are everted proximally and almost horizontal distally. The extreme proximal end with sicula is not preserved, but we have in our collections from other regions, specimens showing a divided virgella.

Family DIMORPHOGRAPTIDAE Elles and Wood, 1908

Diagnosis. Uni-biserials with proximal region with *ascensus* (J) development and uniserial involving a variable number of the thecae. Distal part biserial. Thecae more or less simple tubes but with apertures of some little known; geniculate in some species.

Remarks. *Dimorphograptus* Lapworth, 1876 and *Rhaphidograptus* Bulman, 1936 are included. *Agetograptus* Obut and Sobolevskaya, 1968 (*in* Obut *et al.* 1968) is not included because of its known evolutionary relationship with *Rivagraptus* gen. nov.: both are placed in Glyptograptidae in the present work.

Genus DIMORPHOGRAPTUS Lapworth, 1876

Type species. *Dimorphograptus elongatus* Lapworth, 1876; subsequently designated by Bassler (1915); from the Llandovery of Scotland.

Dimorphograptus confertus swanstoni (Lapworth, 1876)

Text-figure 21C

1876 *Dimorphograptus swanstoni*, Lapworth, p. 548, pl. 20, fig. 13*a–c*.
1908 *Dimorphograptus confertus* var. *swanstoni* (Lapworth); Elles and Wood, p. 350, pl. 35, figs 4*a–f*.
1979 *Dimorphograptus swanstoni* Lapworth; Koren' *et al.*, pl. 32, figs 12–16.

Material. One specimen and its counterpart, in low relief, from locality B671/8-10, Zhaksy-Kargala Valley.

Horizon. Rhuddanian, *vesiculosus* Biozone of the southern Urals, Sakmara Formation.

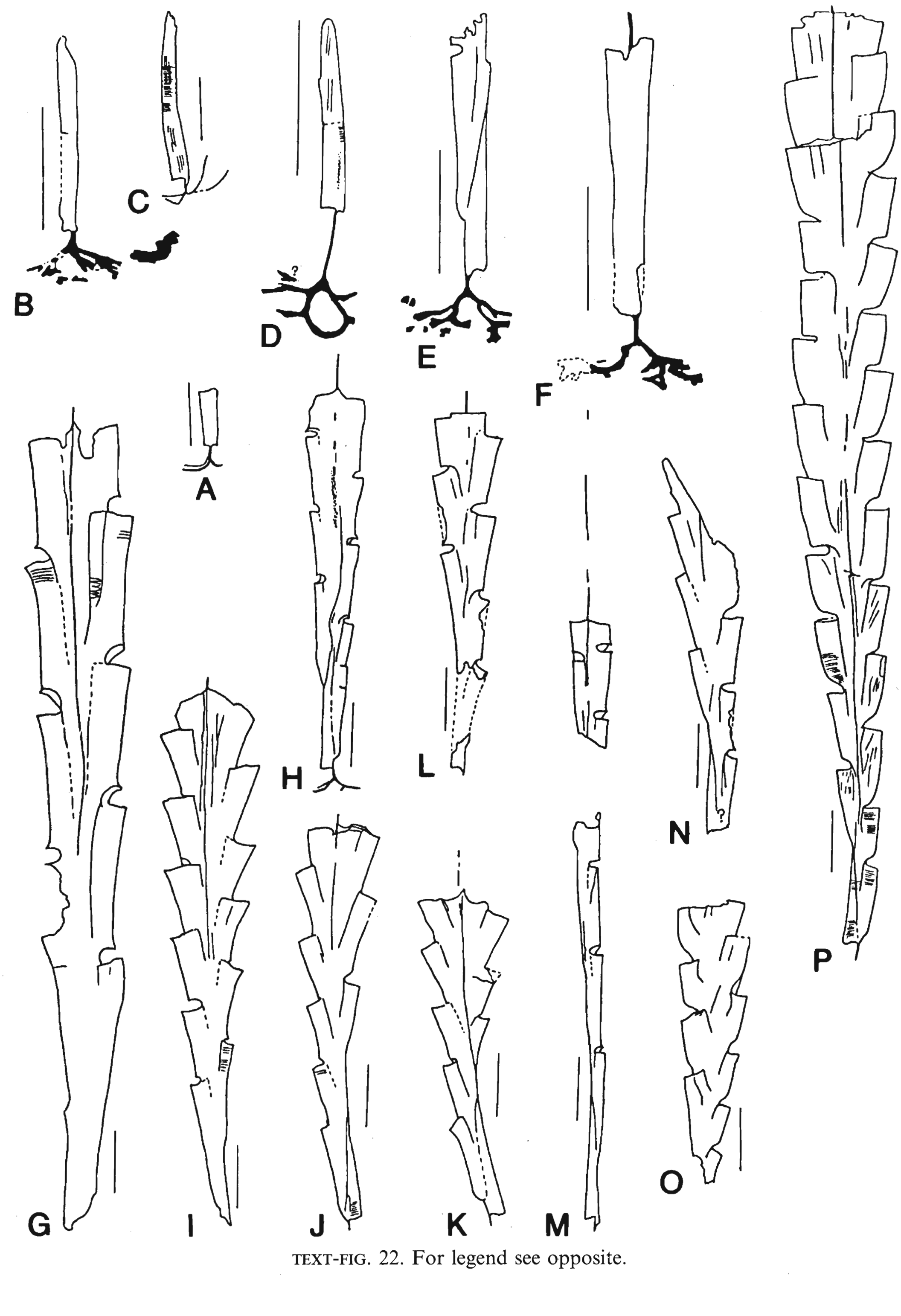
Diagnosis. Rhabdosome, 7·5 mm long, with uniserial part 5 mm long, consisting of 5 thecae. It widens from 0·55 mm at th1 to 0·8 mm at th3 and then to 1·9–2·1 mm at the beginning of the biserial part. Th1^2 originates most probably from th5^1. The apertures of succeeding thecae are strongly alternating. Th1^1 originates near the sicular aperture. The sicula is 1·7 mm long, its apex slightly above the aperture of th1^1.

Remarks. The dimensions of the Urals specimen agree well with those for *D. c. swanstoni* given by Elles and Wood (1908).

Dimorphograptus erectus Elles and Wood, 1908

Plate 13, figures 2–3; Text-figure 22J–K

1908 *Dimorphograptus erectus* sp. nov., Elles and Wood, p. 355, pl. 35, fig. 9*a–d*, text-fig. 233*a–b*.
1975 *Dimorphograptus erectus* s.l.; Elles and Wood; Bjerreskov, p. 41, fig. 13A.



TEXT-FIG. 22. For legend see opposite.

Material. Four specimens, flattened or in low relief, from localities 671-2-69, 671-8-4, 1643/50-44, and 1643/50-50 in the Zhaksy-Kargala Valley.

Horizon. Rhuddanian, *vesiculosus* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome 8·5 mm long, with short and straight uniserial part comprising two or three thecae. It widens from 0·45–0·6 mm at th1 and 0·7–0·8 mm at the beginning of biserial portion to a maximum of 1·3–1·4 mm at $th5^1$. $Th1^2$ arises from $th3^1$. The proximal thecae have a flowing geniculum. The ventral thecal walls are inclined at 18–20° to the rhabdosomal axis; thecal apertures are slightly everted. The sicula is about 2 mm long and 0·25 mm wide at its aperture. Its apex reaches a level between the apertures of $th1^1$ and $th2^1$. The virgella is most probably not fully preserved.

Remarks. The species can be distinguished easily by its slightly geniculate thecae and by a gradual increase of rhabdosomal width at the transition from the short uniserial part to the biserial part. Our specimens differ from the types only in having a shorter rhabdosome and in the absence of a long virgella.

Genus RHAPHIDOGRAPTUS Bulman, 1936

Type species. *Climacograptus toernquisti* (Elles and Wood, 1906); original designation; from the Llandovery of Dob's Linn, Scotland.

Diagnosis. Moderate sized biserial with *ascensus* (J) Pattern of development, septate or partially so, and with an attenuated, thorn-like proximal end caused by either the loss of $th1^2$ or by elongation of $th1^2$ (it is uncertain which); thecae broadly 'climacograptid', or with glyptograptid tendencies; virgella long, robust, thickened; nema long, unthickened.

Remarks. Having reviewed the evidence that $th1^2$ is missing we have concluded that it remains uncertain: $th1^2$ may be elongated as in *Agetograptus*.

Rhaphidograptus toernquisti (Elles and Wood, 1906)

Plate 13, figures 4–5; Text-figures 21D–E, 22L, N–P

1906 *Climacograptus toernquisti* sp. nov., Elles and Wood, p. 190, pl. 26, fig. 6*a–f*; text-fig. 123*a–b*.
1965 *Rhaphidograptus toernquisti* (Elles and Wood); Obut and Sobolevskaya, 1966, p. 23, pl. 4, fig. 10; text-fig. 14.
1967 *Rhaphidograptus toernquisti* (Elles and Wood); Obut *et al*., p. 77, pl. 6, fig. 18; pl. 7, fig. 1.

TEXT-FIG. 22. A–H, *Akidograptus ascensus* Davies; *ascensus-acuminatus* Biozone; Kos-Istek region. A–F, CNIGR Museum 200/12879, 201/12879, 202/12879, 203/12879, 204/128799 and 205/12879; successive stages of early astogeny of juvenile rhabdosomes, possessing well developed meshwork based on forking virgella; G, CNIGR Museum .../12879; incomplete rhabdosome; H, CNIGR Museum 199/12879 young rhabdosome showing forked virgella and partly preserved secondary ribs. I, *Parakidograptus* cf. *acuminatus* (Nicholson); CNIGR Museum 207/12879; adult rhabdosome with incomplete proximal end; *ascensus-acuminatus* Biozone; Kos-Istek region. J–K, *Dimorphograptus erectus* Elles and Wood; CNIGR Museum 209/12879 and 208/12879; rhabdosomes showing short uniserial part; obverse views, *vesiculosus* Biozone; Zhaksy-Kargala Valley. L, N–P, *Rhaphidograptus toernquisti* (Elles and Wood). L, N, CNIGR Museum 215/12879 and 216/12879; incomplete proximal fragments; origin of $th2^2$ is unclear; reverse view; O, CNIGR Museum, 217/12879; proximal fragment with no median septum; P, CNIGR Museum 212/12879; adult rhabdosome with 'climacograptid' to glyptograptid thecae showing fusellar structure; reverse view; *cyphus* Biozone; Kos-Istek region. M, *Rhaphidograptus extenuatus* Elles and Wood; CNIGR Museum 217*a*/12879; adult rhabdosome showing the long uniserial portion; *vesiculosus* Biozone; Zhaksy-Kargala Valley. Scale bars represent 1 mm.

1968 *Rhaphidograptus toernquisti* (Elles and Wood); Obut *et al.*, p. 76, pl. 7, figs 10–11.
1970 *Rhaphidograptus toernquisti* (Elles and Wood); Hutt *et al.*, p. 7, pl. 1, figs 21–22.
1970 *Rhaphidograptus toernquisti* (Elles and Wood); Rickards, p. 54, text-fig. 13, figs 1–3.
1974 *Rhaphidograptus toernquisti* (Elles and Wood); Hutt, p. 53, pl. 9, figs 1–2; text-fig. 13, figs 7–9.

Material. Ten specimens, mostly adult rhabdosomes, preserved in low relief, from localities 488*a*-57, B611-6-6, B611-6-7, B671/8-139, 1643/5-44, 1643/5-111, and 53 in the Kos-Istek region and Zhaksy-Kargala Valley.

Diagnosis. Rhabdosome up to 17 mm long, with attenuated proximal end and robust virgella. Rhabdosome widens slowly from 0·45 mm at $th1^1$ to 1·2–1·3 mm at $th5^1$, and reaches a maximum of 1·5–1·6 mm at about $th6^1$ or $th7^1$. Thecae are of climacograptid shape, strongly geniculated but with supragenicular walls inclined at *c.* 10° to the rhabdosomal axis. They number 4·5 in 5 mm and 9 in 10 mm proximally. $Th1^1$ grows downwards to the level of the sicular aperture and then grows upwards for 1·15 mm. The sicula is 1·7 mm long and 0·25 mm wide at the aperture, its apex reaching a level at the middle part of $th2^1$ supragenicular wall.

Remarks. In the present material, preserved in low relief, both fusellar and bandage-like structure is clearly seen on some specimens. However, we cannot be sure about the origin of the first theca in the second row; it could well derive from $th1^1$ rather than from $th1^2$.

Rhaphidograptus extenuatus (Elles and Wood, 1908)

Text-figure 22M

1908 *Dimorphograptus extenuatus* sp. nov., Elles and Wood, 1908, p. 358, pl. 35, fig. 10*a–e*, text-fig. 235.

Material. One flattened specimen, from locality B671-1-1 in the Zhaksy-Kargala Valley.

Horizon. Rhuddanian, *vesiculosus* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Gracile rhabdosome, 9·5 mm long, with 5 thecae in the uniserial part, 7·5 mm long. Rhabdosome dorso-ventral width is 0·22 mm at $th1^1$, 0·3 mm at $th2^1$, 0·35 mm at $th3^1$, 0·5 mm at $th5^1$ and 0·7 mm at the very beginning of the biserial part. Sharply geniculate thecae, having semicircular excavations, and small genicular flanges; supragenicular walls almost parallel to the rhabdosomal axis; thecal apertures horizontal, 0·15–0·2 mm wide. The point of origin of $th1^1$ is not seen. Sicula, 1·7–1·8 mm long, its aperture less than 0·2 mm wide. Apex is well below $th1^1$ aperture. Thread-like virgella is not prominent.

Family METACLIMACOGRAPTIDAE fam. nov.

Diagnosis. Small or tiny biserials with *normalis* (H) or ?*tamariscus* (I) proximal development; median septum undulating to zig-zag, especially proximally; thecae strongly alternating, apertures even or introverted, with supragenicular wall vertical to inwardly inclined; supragenicular wall usually thickened, often with a flange or hood.

Remarks. Only *Metaclimacograptus* Bulman and Rickards (1968) is included at present. The superficially similar genus *Clinoclimacograptus* Bulman and Rickards (1968) is placed in the Glyptograptidae.

Genus METACLIMACOGRAPTUS Bulman and Rickards, 1968

Type species. Diplograpsus hughesi Nicholson, 1869; original designation; from the Llandovery of the Lake District, England.

Diagnosis (revised). Tiny rhabdosomes, usually less than 10 mm long, and less than 1·2 mm wide; proximal development of *normalis* (H) Pattern; thecae tightly packed, usually strongly alternating about an undulating or rounded zig-zag median septum; excavations deep, sometimes introverted, sometimes overhung with a genicular hood; supragenicular wall may be straight, but more commonly is rounded or inward-sloping; sicula small; nema and virgella short, fine; proximal end rounded; conspicuous down-growing part to $th1^1$.

Remarks. *Metaclimacograptus* differs from *Pseudoclimacograptus* in having *normalis* (H) Pattern development rather than a more complicated, primitive type, and in having a simpler median septum lacking the bar-like ingress or fold into the protheca, and the sharp zig-zag of the Ordovician genus.

Metaclimacograptus hughesi (Nicholson, 1869)

Plate 13, figures 9–14; Text-figure 23A

1869 *Diplograpsus hughesi* Nicholson, p. 235, pl. 11, figs 9–10.
1906 *Climacograptus hughesi* (Nicholson); Elles and Wood, p. 208, pl. 27, fig. 11*a–e*, text-fig. 140*a–d*.
1968 *Pseudoclimacograptus hughesi* (Nicholson 1869); Obut *et al.*, p. 62, pl. 4, figs 2–11 [see for synonymy].
1968 *Pseudoclimacograptus* (*Metaclimacograptus*) *hughesi* (Nicholson); Bulman and Rickards, p. 3, text-fig. 1*a–c* [see for synonymy].
1974 *Pseudoclimacograptus* (*Metaclimacograptus*) *hughesi* (Nicholson); Hutt, p. 22, pl. 2, figs 6–7, 13–14 [see for synonymy].
1991 *Metaclimacograptus hughesi* (Nicholson, 1869); Loydell, p. 675, pl. 1, figs 3–4, 6, 9, 12.

Material. Forty specimens, in full or low relief, some flattened, from localities 67/81, B339-4-3, B411-1, 488*a*/73, 544/70, 587-8-6, B587-11-12, B603-9/72-26, B607-1-2, B671-2-74, B671-8-4, B671-8-129, B671-8-135, B671-8-36, H1251*a*, 15085044/70, and 5049/70-5 in the Kos-Istek region south of Aktjubinsk.

Horizon. Rhuddanian–Aeronian, *vesiculosus* to *gregarius* biozones of the southern Urals, Sakmara Formation.

Description. The rhabdosome is small, parallel-sided, usually less than 10 mm long, with a strongly undulating median septum. It is 0·7–0·75 mm wide in specimens in full relief, and 0·8–1 mm wide when in low relief. Thecal excavations are 0·2–0·3 mm deep and no more than 0·1 mm high. The supragenicular walls are straight and 0·5–0·65 mm long. Thecae number 7·5–8 in 5 mm proximally. Their apertures are strongly everted. The proximal end is rounded, with $th1^1$ originating 0·25 mm above the sicular aperture. The visible part of $th1^1$ grows downwards for 0·2 mm before turning upwards for a distance of 0·6–0·7 mm. The sicula is completely covered in reverse view and it is exposed for 0·4 mm in obverse view. The sicular aperture is 0·15–0·18 mm wide; virgella threadlike, 0·4 mm long.

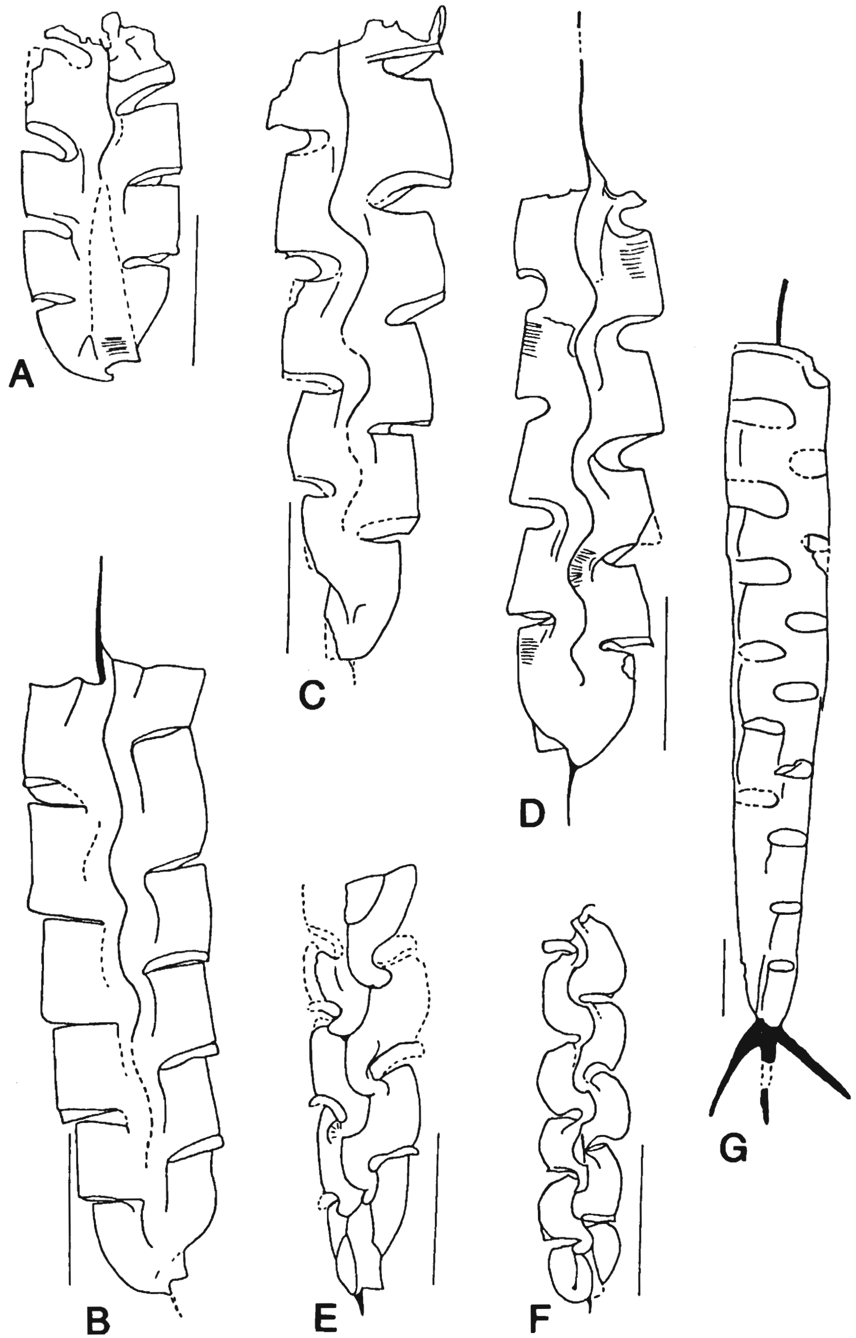
Remarks. In the present material specimens are often preserved as three-dimensional moulds, filled with siliceous material. When the periderm is preserved the fusellar structure is very distinctive. In all dimensions our material agrees well with that described in detail by Bulman and Rickards (1968). However, genicular hoods have not been seen; and the dorso-ventral width is a little higher. Isolated material was described by Loydell (1991).

Metaclimagograptus khabakovi sp. nov.

Plate 13, figures 6–8; Text-figure 23B

Holotype. CNIGR Museum 225/12879, Plate 13, figure 6; Text-figure 23B; *cyphus* Biozone, Zhaksy-Kargala Valley.

Derivation of name. In honour of Prof. A. V. Khabakov who was one of the first to study the geology of the southern Urals.



TEXT-FIG. 23. A, *Metaclimacograptus hughesi* (Nicholson); CNIGR Museum 218/12879; *vesiculosus* Biozone; Kos-Istek region. B, *Metaclimacograptus khabakovi* sp. nov.; holotype, CNIGR Museum 225/12879; rhabdosome shows small genicular hoods; *cyphus* Biozone; Zhaksy-Kargala Valley. C–D, *Metaclimacograptus khvorovi* sp. nov.; *gregarius* Biozone; Zhaksy-Kargala Valley. C, CNIGR Museum 228/12879; shows strongly undulating median septum, and supragenicular walls sloping inwards; reverse view; D, holotype, CNIGR Museum 231/12879. E, *Metaclimacograptus undulatus* (Kurck); CNIGR Museum 237/12876; specimen in three dimensions filled with opaline silica, showing angular median septum. F, *Metaclimacograptus orcus* sp.

Material. Six specimens, in low relief or flattened, from localities 448*a*/73, B671-2, B671-2-28, B671-8-131, B671-8-140 and B671-8/74-254 in the Kos-Istek region to the south of Aktjubinsk.

Horizon. Rhuddanian, *vesiculosus* and *cyphus* biozones of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome 6–8 mm long and 1·1–1·2 mm wide, with a smoothly undulating median septum. Thecae with everted apertures and sloping supragenicular walls; they number 3–4 in the first 2·5 mm.

Description. The rhabdosome widens from 0·8 mm at $th1^1$ and 0·9 mm at $th2^1$ to a maximum of 1·1–1·2 mm at $th3^1$–4^1. A massive nema is characteristic. The thecae have straight, everted apertures, inclined at 60–80° to the rhabdosomal axis, and slit-like excavations. Their slightly convex supragenicular walls slope outwards. The genicula are protracted ventrally and provided with small hoods filling the excavations and overhanging the ventral margin of the apertures of preceding thecae. The dorso-ventral width measured at the aperture of $th1^1$ (0·8 mm) is less than that at the geniculum of $th2^1$ (1 mm). The sicula is almost completely covered in reverse view and is probably free for 0·85–0·9 mm in obverse view. The sicular aperture is 0·2 mm wide. $Th1^1$ grows down slightly below the sicular aperture before it turns upwards for a distance of 0·6–0·65 mm. The virgella is short and thorn-like.

Remarks. Me. khabakovi sp. nov. differs from *Me. hughesi* in having distinctly sloping supragenicular walls, straight and more strongly everted apertures, only a moderately undulating median septum, and a wider rhabdosome.

Metaclimacograptus khvorovi sp. nov.

Plate 14, figures 1–7; Text-figure 23C–D

Holotype. CNIGR Museum 231/12879, Plate 14, figure 4; Text-figure 23D; *gregarius* Biozone, Zhaksy-Kargala Valley.

Derivation of name. In honour of B. A. Khvorov, the geologist who, for many years, led the geological mapping of the Kos-Istek region.

Material. Twenty specimens flattened or in low relief from localities B671-2-26, B671-8-129, B671-8-140 (several specimens), B671-8-188, B671-8-284 (several specimens), 1508-10*a*, 1643/50-54 and 1643/50-80, Kos-Istek region and Zhaksy-Kargala Valley.

Horizon. Aeronian, *gregarius* Biozone of the southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome 12–14 mm long, 1·1–1·3 mm wide, parallel-sided for most of its length, with strongly undulating median septum. Supragenicular thecal walls slightly to strongly inwards sloping; excavations semicircular. Thecae number from 6·5 in 5 mm proximally to 10·5–11 in 10 mm distally.

Description. The rhabdosome is long and comparatively narrow, slowly widening from 0·75 mm at $th1^1$ to 1·1 mm at $th5^1$, further on being 1·2–1·3 mm wide. Thecal apertures tend to be almost horizontal. The slightly convex supragenicular walls slope inwards. Thecal excavations are 0·2 mm long and 0·25–0·35 mm deep, outlined by genicular and apertural, thickened rims. The sicula is *c.* 1·2–1·3 mm long with an aperture 0·2 mm wide. It is visible for half of its length in obverse view, and almost completely covered in reverse view. $Th1^1$ grows down for 0·1 mm below the sicular aperture before turning upwards for 0·6–0·7 mm.

Remarks. Me. khvarovi sp. nov. can be distinguished from the other metaclimacograptids in having more widely spaced thecae with strongly inward-sloping supragenicular walls. From *Me. hughesi*

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nov.; holotype, CNIGR Museum 236/12876; shows double-sigmoidally curved thecae with barrel-like supragenicular walls; obverse view; *gregarius* Biozone; Kos-Istek region. G, *Normalograptus trifilis* Manck; CNIGR Museum 81/12876; adult rhabdosome in hemiscalariform view showing thickened virgella and a pair of proximal spines; *vesiculosus* Biozone; Zhaksy-Kargala Valley. Scale bars represent 1 mm.

and *Me. khabakovi* sp. nov. it differs in its larger size, and from the latter also by the almost horizontal thecal apertures and longer semicircular excavations.

Metaclimacograptus orcus sp. nov.

Plate 14, figures 8–9; Text-figure 23F

Holotype. CNIGR Museum 235/12879, Plate 14, figure 8, Text-figure 23F; Aeronian, *gregarius* Biozone, the Kos-Istek region, south of Aktjubinsk city, Sakmara Formation.

Derivation of name. From *orca* (Latin) = a jar with a big belly.

Material. Eight specimens in full relief, from locality 5044/70.

Horizon. The same as for the holotype.

Diagnosis. Dwarf-like metaclimacograptid up to 3·5 mm long and 0·55–0·6 mm wide. Thecae strongly doubly sigmoidally curved with barrel-like supragenicular walls. They number 5–5·5 in 2·5 mm. Median septum complete and angulate.

Description. The rhabdosome is 0·325–0·4 mm wide at $th1^1$; farther on it is parallel-sided with a maximum dorso-ventral width of 0·55–0·6 mm for specimens preserved in three dimensions and 0·8 mm for those which are flattened. Thecae show double sigmoidal curvature; their supragenicular ventral walls are broadly convex. The thecal apertures are slightly everted or tend to be horizontal, with the exception of $th1^1$ which has more strongly everted subapertural part. Excavations are deep and short showing a slit-like appearance. Genicular hoods are difficult to distinguish. Thecae are closely spaced, up to 5·5 in 2·5 mm proximally. The proximal end is rounded. $Th1^1$ grows down for 0·3 mm until it bends below the sicular aperture and grows upwards for 0·35–0·4 mm. In obverse view the sicula is partly free, for 0·3 mm. On the reverse side, most of it is covered by the strongly curved prothecal portion of $th2^1$. The virgella is thread-like, 0·1 mm long.

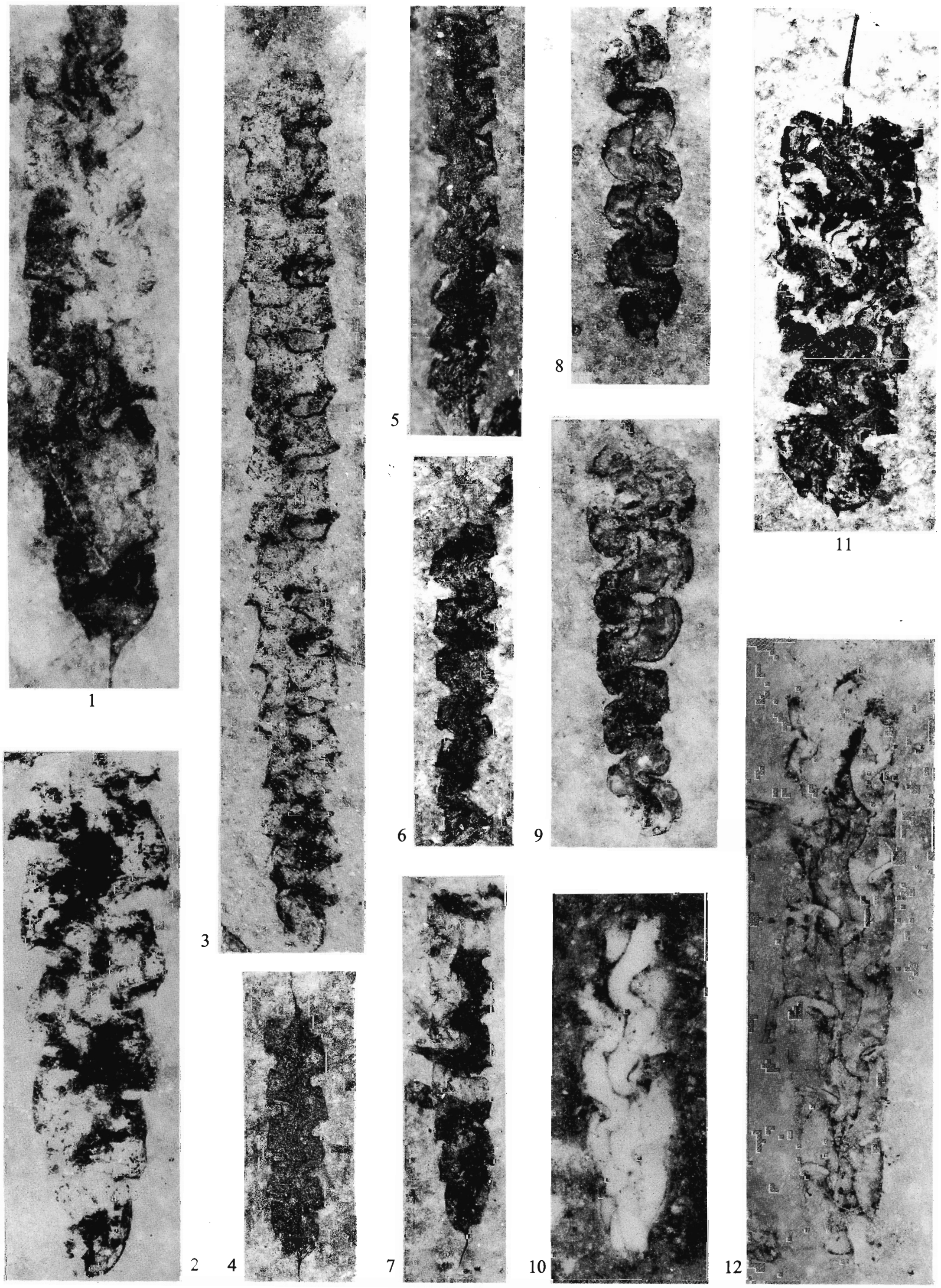
Remarks. *Me. orcus* is the smallest known metaclimacograptid. In rhabdosomal size it resembles most closely *Me. undulatus* (Kurck). It differs, however, in having an even smaller rhabdosome, and a slightly more angular median septum, more prounounced double sigmoidal curvature of the thecae and, especially, in the barrel-like supragenicular walls and more closely spaced thecae.

EXPLANATION OF PLATE 14

Figs 1–7. *Metaclimacograptus khvorovi* sp. nov.; *gregarius* Biozone; Kos-Istek region. 1–2, CNIGR Museum 228/12879; rhabdosomes in low relief, showing strongly undulating median septa and supragenicular walls sloping inwards; reverse views; 3, CNIGR Museum 230/12879; adult rhabdosome in hemiscalariform view; flattened; geniculum overhanging the aperture of preceding theca; 4, holotype, CNIGR Museum 231/12789; 5–6, CNIGR Museum 232/12879 and 233/12879; incomplete rhabdosomes with supragenicular walls sloping inwards; 7, CNIGR Museum 234/12879. 1–2, ×20; 3–7, ×10.

Figs 8–9. *Metaclimacograptus orcus* sp. nov.; *gregarius* Biozone; Kos-Istek region. 8, holotype, CNIGR Museum 235/12879; rhabdosome in full relief filled with opaline silica; obverse view; 9, CNIGR Museum 236/12879; preservation as for holotype, but rhabdosome is slightly flattened distally; reverse view; both ×20.

Figs 10–12. *Metaclimacograptus undulatus* (Kurck); *vesiculosus* Biozone; Zhaksy-Kargala Valley. 10, 12, CNIGR Museum 237/12879 and 239/12879; rhabdosomes preserved in full relief filled with opaline silica; both are parallel-sided, showing angular median septum; obverse views; 11, CNIGR Museum 238/12879; rhabdosome in low relief, showing rounded proximal end; sicula covered; reverse view; all ×20.



KOREN' and RICKARDS, *Metaclimacograptus*

Metaclimacograptus undulatus (Kurck, 1882)

Plate 14, figures 10–12; Text-figure 23E

1882 *Climacograptus undulatus*, Kurck, p. 303, pl. 14, fig. 11.
1906 *Climacograptus extremus* H. Lapworth; Elles and Wood, p. 210, pl. 27, fig. 13*a–b*, text-fig. 141*a–c*.
1968 *Pseudoclimacograptus* (*Metaclimacograptus*) *undulatus* (Kurck); Bulman and Rickards, p. 6, text-figs 1*d–j*, 3*e*.
1975 *Pseudoclimacograptus undulatus* (Kurck); Bjerreskov, p. 26, fig. 4E [see for synonymy].
1989 *Metaclimacograptus undulatus* (Kurck); Melchin, p. 1739, fig. 10B.

Material. Two specimens, one in full and the other in low relief, from localities B408 and 5044/70 in the Kos-Istek region.

Horizon. Upper Rhuddanian to lower Aeronian, southern Urals, Sakmara Formation.

Diagnosis. Rhabdosome small, parallel-sided, no more than 6 mm long and 0·5–0·7 mm wide. Medium septum complete and angular with characteristic profile. Thecae doubly sigmoidally curved, their supragenicular walls slightly concave. Delicate genicular hoods overhanging everted thecal apertures almost completely filling deep and short excavations. Thecae number 4·5 in 2·5 mm. $Th1^1$ extends for 0·35 mm downwards, to the level of the sicular aperture; its upward-directed portion is 0·5 mm long. Virgella short, incomplete.

Remarks. *Me. undulatus* is remarkable in its angulate medium septa and small size of rhabdosome. Dimensions of the Urals specimens agree with those of specimens described previously. The mode of preservation, as a three-dimensional mould filled by light blue opaline silica, shows clearly that the small hoods have a genicular origin.

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REFERENCES

BARRANDE, J. 1950. *Graptolites de Bohême*. Published by the author, Prague, vi + 74 pp., 4 pls.
BASSLER, R. 1915. Bibliographic index of American Ordovician and Silurian fossils. *Bulletin of the U.S. National Museum*, **92,** 1–718.
BATES, D. E. B. and KIRK, N. H. 1987. The role of extrathecal tissue in the construction and functioning of some Ordovician and Silurian retiolitid graptolites. *Bulletin of the Geological Society of Denmark*, **35,** 85–102.
—— 1992. The ultrastructure, mode of construction, and functioning of a number of Llandovery ancorate diplograptid and retiolitid graptolites. *Modern Geology*, **17,** 1–270.
BJERRESKOV, M. 1975. Llandoverian and Wenlockian graptolites from Bornholm. *Fossils and Strata*, **8,** 1–94.
BOUČEK, B. 1944. O nekterych ostnitych diplograptidech ceskeho a saského Siluru. *Rozpravy Česke Akademie Věd. Uměni. Tř. II*, **53,** no. 25, 1–6.
—— and PŘIBYL, A. 1941. Über die Gattung *Petalolithus* Suess aus dem böhemischen Silur. *Mitteilungen der Tschechischen Akademie der Wissenschaften*, 1–17.
—— —— 1942. Über Petalolithen aus der Gruppe *P. folium* (His.) und über *Cephalograptus* Hopk. *Rozpravy II. Třídy České Akademie*, **52,** 31, 1–22.
BULMAN, O. M. B. 1936. *Rhaphidograptus*, a new graptolite genus. *Geological Magazine*, **73,** 19–26.

—— 1970. *In* TEICHERT, C. (ed.). *Treatise on invertebrate paleontology. Part V. Graptolithina, with sections on Enteropneusta and Pterobranchia.* (2nd edition). Geological Society of America and University of Kansas Press, Boulder, Colorado and Lawrence, Kansas, xxxii + 163 pp.

—— and RICKARDS, R. B. 1968. Some new diplograptids from the Llandovery of Britain and Scandinavia. *Palaeontology*, **11,** 1–15.

CHALETZKAYA, O. N. 1960. [New species of the Llandovery graptolites of Central Asia.] *In Novye vidy drevnikh rastenii i bespozvonochnykh SSSR, chast' II.* Moskva, gosudarstvennoe nauchno-teknicheskoje izdatel'stovo, 73–75. [In Russian].

CHEN XU and LIN YAO-KUN. 1978. Lower Silurian graptolite from Tongzi, northern Guizhou. *Memoirs of the Nanjing Institute of Geology and Palaeontology, Academia Sinica*, **12,** 1–76.

CHURKIN, M. and CARTER, C. 1970. Early Silurian graptolites from southeastern Alaska and their correlation with graptolite sequences in North America and the Arctic. *Professional Papers of the U.S. Geological Survey*, **653,** 1–51.

CROWTHER, P. R. 1981. The fine structure of graptolite periderm. *Special Papers in Palaeontology*, **26,** 1–119.

—— and RICKARDS, R. B. 1977. Cortical bandages and the graptolite zooid. *Geologica et Palaeontologica*, **11,** 9–46.

DAVIES, K. A. 1929. Notes on the graptolite faunas of the Upper Ordovician and Lower Silurian. *Geological Magazine*, **66,** 1–27.

ELLES, G. L. 1897. The subgenera *Petalograptus* and *Cephalograptus*. *Quarterly Journal of the Geological Society, London*, **53,** 186–212, pls 13–14.

—— and WOOD, E. M. R. 1901–18. A monograph of British graptolites. *Palaeontolographical Society Monograph*, i–clxxi, 1–539, 52 pls.

FORTEY, R. A. and COOPER, R. A. 1986. A phylogenetic classification of the graptoloids. *Palaeontology*, **29,** 631–654.

GEINITZ, H. B. 1852. *Die Versteinerungen der Grauwacken-Formation* (*Die Graptolithen*). Verlag Wilhelm Engelmann, Leipzig, 58 pp., 6 pls.

GORTANI, M. 1922. Faune paleozoiche della Sardegna. Pt. 1. Le graptoliti di Goni. Pt. 2. Graptoliti della Sardegna Orientale. *Palaeontographica italica*, **28,** 41–68, 85–112.

HISINGER, W. 1837. *Lethaea Suecica, seu Petrificata Sueciae. Supplementum I.* Stockholm, 124 pp., 2 pls.

HOPKINSON, J. 1869. On British Graptolites. *Journal of the Quekett Microscopical Club*, **1,** 151–166, pl. 8.

HOWE, M. P. A. 1982. The Lower Silurian graptolites of the Oslo Region. *Palaeontological Contributions from the University of Oslo*, **278,** 21–32.

—— 1983. Measurement of thecal spacing in graptolites. *Geological Magazine*, **120,** 635–638.

HUNDT, R. 1942. Beiträge zur Kenntnis des Mitteldeutschen graptolithenmeeres. *Beitrage zur Geologie von Thüringen*, **6,** 205–231, pls 1–7.

HUTT, J. E. 1974. The Llandovery graptolites of the English Lake District. Part 1. *Palaeontographical Society Monograph*, **128** (540), 1–56, pls 1–10.

—— RICKARDS, R. B. and SKEVINGTON, D. 1970. Isolated Silurian graptolites from the Bollerup and Klubbudden Stages of Dalarna, Sweden. *Geologica et Palaeontologica*, **4,** 1–23.

JONES, W. D. V. and RICKARDS, R. B. 1967. *Diplograptus penna* Hopkinson 1869, and its bearing on vesicular structures. *Paläontologische Zeitschrift*, **41,** 173–185.

KOREN', T. N. 1967. [Some Llandovery graptolites in the Urals.] *Trudy VSEGEJ, Novaya Seria*, **129,** 189–197. [In Russian].

—— ORADOVSKAYA, M. M., SOBOLEVSKAYA, R. F. and CHUGAEVA, M. N. 1979. [*Atlas of the paleontological plates. Supplement to a guidebook of the field excursion to the Omulev Mountains* (*Tour VIII*)]. Pacific Science Association. XIV Pacific Science Congress. Magadanskoje knizhnoje isdatel'stvo. 15 pp., 32 pls. [In Russian].

—— —— PYLMA, L. J. and SOBOLEVSKAYA, R. F. 1983. [The Ordovician and Silurian boundary in the north-east of the USSR]. *Trudy Mezhvedomstvennogo Stratigraficheskogo Komiteta SSSR*, 11. Nauka, Leningrad, 205 pp. [In Russian].

KURCK, C. 1882. Nagra nya Graptolitarter från Skåne. *Geologiska Föreningens i Stockholm Förhandlingar*, **6,** 294–304.

LAPWORTH, C. 1873. On an improved classification of the Rhabdophora. *Geological Magazine*, (1), **10,** 500–504, 555–560.

—— 1876. On Scottish Monograptidae. *Geological Magazine*, (2), **3,** 308–321, 350–360, 499–507, 541–552, pls 10–13, 20.

LAPWORTH, C. 1877. On the graptolites of County Down. Appendix (107–123). *In* SWANSTON, W. On the Silurian rocks of the County Down. *Proceedings of the Belfast Naturalists' Field Club*, **1876–77**, 107–147.

—— 1880. On new British graptolites. *Annals and Magazine of Natural History*, (5), **5**, 149–177.

LAPWORTH, H. 1900. The Silurian sequence of Rhayader. *Quarterly Journal of the Geological Society, London*, **56,** 67–137.

LEGRAND, P. 1987. [Mode of development of the Suborder Diplograptina in the Upper Ordovician and Silurian. Taxonomic implications.] *Revista Española de Paleontologia*, **2,** 59–64. [In Spanish].

LEONENOK, N. I. 1955. Silurian deposits of the Kos-Istek Region (Northern Mugodzhary). *Trudy Laboratorii Geologii Uglia AN SSR*, **3,** 116–125. [In Russian].

LI JI-JIN and GE MEI-YU. 1981. Development and systematic position of akidograptids. *Acta Palaeontologica Sinica*, **20,** 225–234.

LOYDELL, D. K. 1991. Isolated graptolites from the Llandovery of Kallholen, Sweden. *Palaeontology*, **34,** 671–693.

—— 1992. Upper Aeronian and Lower Telychian (Llandovery) graptolites from Western mid-Wales. Part 1. *Palaeontographical Society Monograph*, **146** (589), 1–55, pl. 1.

McCOY, F. 1850. On some new genera and species of Silurian Radiata in the collection of the University of Cambridge. *Annals and Magazine of Natural History*, (2), **6,** 270–290.

MANCK, E. 1923. Untersilurische graptolithenarten der Zone 10 des Obersilurs ferner *Diversograptus* gen. nov. sowie einige neue Arten anderer Gattungen. *Natur*, **14,** 282–289.

MELCHIN, M. J. 1989. Llandovery graptolite biostratigraphy and paleobiogeography, Cape Phillips Formation, Canadian Arctic Islands. *Canadian Journal of Earth Sciences*, **26,** 1726–1746.

—— and MITCHELL, C. E. 1991. Late Ordovician extinction in the Graptoloidea. *In* BARNES, C. R. and WILLIAMS, S. H. (eds). Advances in Ordovician geology. *Geological Survey of Canada, Paper*, 90–99, 143–156.

MITCHELL, C. E. 1987. Evolution and phylogenetic classification of the Diplograptacea. *Palaeontology*, **30,** 353–405.

NICHOLSON, H. A. 1967. On some fossils of the lower Silurian rocks of the South of Scotland. *Geological Magazine*, **4,** 107–113.

—— 1868. On the graptolites of the Coniston Flags; with notes on the British species of the genus *Graptolites. Quarterly Journal of the Geological Society, London*, **24,** 521–545.

—— 1869. On some new species of graptolites. *Annals and Magazine of Natural History*, (4), **4,** 231–242, pl. 11.

OBUT, A. M. 1965. [Silurian graptolites in the Omulev Mountains (River Kolyma basin)]. *In Stratigrafia i Paleontologia Asiatskoy chasti SSSR*. Tsdatlestvo 'Nauka' Moskva, 33–46. [In Russian].

—— and SOBOLEVSKAYA, R. F. 1966. [Lower Silurian graptolites in Kazakhstan.] *Akademia Nauk SSSR, Sibirskoje otdelenije, Institut Geologii i Geofiziki. Minsterstvo Geologii SSSR, Nauchno-Issledovatel'sky Institut Geologii Arktiki*. Moskva. 1–56, pls 1–8. [In Russian].

—— —— and BONDAREV, V. I. 1965. Graptoliti silura Taymira. *Akademia Nauk SSSR, Sibirskoje otdelenije, Institut Geologii i Geofiziki. Minsterstvo Geologii SSSR, Nauchno-Issledovatel'sky Institut Geologii Arktiki*, 1–120. [In Russian].

—— —— and MERKUREVA, A. P. 1968. Graptoliti Llandoveri v kernach burovitch skvazhin Norilskogo raiona. *Akedemia Nauk SSSR, Sibirskoje otdelenije, Institut Geologii i Geofiziki. Minsterstvo Geologii SSSR, Nauchno-Issledovatel'sky Institut Geologii Arktiki*, 1–137, pls 1–35.

—— —— and NIKOLAEV, A. A. 1967. Graptoliti i stratigrafiya nizhnego silura okrainnykh podnyatii kolymskogo massiva. *Akademia Nauk SSSR, Sibirskoje otdelenije, Institut Geologii i Geofiziki. Minsterstvo Geologii SSSR, Nauchno-Issledovatel'sky Institut Geologii Arktiki*, 1–162. [In Russian].

PACKHAM, G. H. 1962. Some diplograptids from the British Lower Silurian. *Palaeontology*, **5,** 498–526.

PAVLINOV, V. N. Stratigraphy and tectonics of the southern part of the South Urals. *Trudy Geologie Bezyedogbnogo Instituta*, **9,** 1–164. [In Russian].

PEDERSEN, T. B. 1922. Rastritesskiferen på Bornholm. *Meddelelser fra Dansk Geologisk Forening*, **6**(11), 29 pp.

PERNER, J. 1897. *Études sur les Graptolites de Bohême. IIième Partie. Monographie des Graptolites de l'Étage E. Section a.* Gerhard, Prague, 25 pp., pls 9–13.

PŘIBYL, A. 1947. Classification of the genus *Climacograptus* Hall, 1865. *Bulletin international de l'Académie Tchèque des Sciences*, **48,** 1–12.

RICKARDS, R. B. 1970. The Llandovery (Silurian) graptolites of the Howgill Fells, Northern England. *Palaeontographical Society Monograph*, **123** (524), 108 pp., 8 pls.

—— 1972. *Climacograptus scalaris* (Hisinger) and the subgenus *Glyptograptus* (*Pseudoglyptograptus*). *Geologiska Föreningens i Stockholm Förhandlingar*, **94,** 271–280.

—— 1976. The sequence of Silurian graptolite zones in the British Isles. *Geological Journal*, **11**, 153–188.
—— 1988. Anachronistic, heraldic, and echoic evolution: new patterns revealed by extinct planktonic hemichordates. 211–230. *In* LARWOOD, G. P. (ed.). *Extinction and survival in the fossil record.* Systematics Association Special Volume, 34.
—— 1995. Utility and precision of Silurian graptolite zones. *Lethaia*, **28**, 129–137.
—— and HUTT, J. E. 1970. The earliest monograptid. *Proceedings of the Geological Society, London*, **1663,** 115–119.
—— —— and BERRY, W. B. N. 1977. Evolution of the Silurian and Devonian graptoloids. *Bulletin of the British Museum (Natural History), Geology Series*, **28**, 1–120.
—— and KOREN', T. N. 1974. Virgellar meshworks and sicular spinosity in Llandovery graptoloids. *Geological Magazine*, **111,** 193–272.
SALTER, J. W. 1873. *A catalogue of the collection of Cambrian and Silurian fossils contained in the Geological Museum of the University of Cambridge.* i–xlviii + 1–204.
SCHAUER, M. 1971. Biostratigraphie und Taxonomie der Graptolithen des Tieferen Silurs unter besonderer Berücksichtigung der tektonischen deformation. *Freiberger Forschungshefte*, **C373** Palaeontologie, 1–185.
ŠTORCH, P. 1983. Subfamily Akidograptinae (Graptolithina) from the lowermost Silurian of Bohemia. *Věstnik Ústředního ústavu geologického*, **58,** 295–299.
—— 1985. *Orthograptus* s.l. and *Cystograptus* (Graptolithina) from the Bohemian lower Silurian. *Věstnik Ústředního ústavu geologického*, **60,** 87–100.
—— 1986. Ordovician-Silurian boundary in the Prague Basin (Barrandian area, Bohemia). *Sbornik geologických Věd, Geologie*, **41,** 69–103.
—— and SERPAGLI, E. 1993. Lower Silurian graptolites from southwestern Sardinia. *Bolletino della Società Paleontologica Italiana*, **32,** 3–57.
SUESS, E. 1851. Über böhmische Graptolithen. *Naturwissenschaftliche Abhandlungen*, **4,** 87–134.
THORSTEINSSON, R. 1958. Cornwallis and Little Cornwallis Islands, District of Franklin, Northwest Territories. *Memoir of the Geological Survey of Canada*, **294**, i–v, 1–134.
TOGHILL, P. 1968. The graptolite assemblages and zones of the Birkhill Shales (Lower Silurian) at Dobb's Linn. *Palaeontology*, **13,** 511–521.
TÖRNQUIST, S. L. 1890. Undersokningar öfver Siljansområdets graptoliter. Part 1. *Acta Universitet Lund*, **26,** 1–33.
—— 1893. Observations on the structure of some Diprionidae. *Acta Universitet Lund*, **29,** 1–14.
—— 1897. On the Diplograptidae and Heteroprionidae of the Scanian Rastrites Beds. *Acta Universitet Lund*, **33,** 1–24.
URBANEK, A., KOREN', T. N. and MIERZEJEWSKI, P. 1982. The fine structure of the virgular apparatus in *Cystograptus vesiculosus*. *Lethaia*, **15,** 207–228.
YE SHAO-HUA. 1978. Class Graptolithina. 431–686. *In* CHENGDU INSTITUTE OF GEOLOGY AND MINERAL RESOURCES (eds). *Atlas of fossils of southwest China. Sichuan volume. Part 1: Sinian to Devonian.* Geological Publishing House, Beijing.
ZALASIEWICZ, J. and TUNNICLIFF, S. 1994. Graptolite biostratigraphy of the latest Ordovician to early Silurian sequence in the Wye Valley, Central Wales. *Palaeontology*, **37,** 695–720.

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