

# AN UNUSUALLY DIVERSE LLANDOVERY (SILURIAN) DIPLOGRAPTID FAUNA FROM THE SOUTHERN URALS OF RUSSIA AND ITS EVOLUTIONARY SIGNIFICANCE

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**ABSTRACT.** This *vesiculosus* Biozone assemblage of chemically-isolated graptolites from the Orenburg District of Russia was obtained from limestones associated with pillow lavas of the Sakmara Formation of Silurian–Early Devonian age. It comprises 30 species, of which 24 are described. Nine are new, one is a new subspecies, and eight are left under open nomenclature. The assemblage is unique in its diversity of minute biserial graptolites referable to the genera '*Glyptograptus*', *Normalograptus*, *Sudburigraptus*, and *Metaclimacograptus*; and is unusual in that well-preserved graptolite faunas are rare at this stratigraphical level, which is fixed by the occurrence of *Cystograptus vesiculosus* (Nicholson) *s.l.* and *Paraclimacograptus innotatus* (Nicholson). The following new forms are described: '*Glyptograptus*' *tamariscus praecursor* subsp. nov., *G. mazovoensis* sp. nov., *G. nikitini* sp. nov., *G. pavlinovi* sp. nov., *G. telarius* sp. nov., *G. zimai* sp. nov., *Normalograptus legrandi* sp. nov., *N. melchini* sp. nov., *N. sobolevskayae* sp. nov., and *Metaclimacograptus bjerreskovae* sp. nov. Five evolutionary lineages are defined within the '*Glyptograptus*' *tamariscus* (Nicholson) plexus, modifying and extending the pioneer work of Packham (1962). The diverse '*Glyptograptus*' faunas are considered to be a replacement for the *Normalograptus* fauna which peaked in the late Ordovician and early Silurian. *Metaclimacograptus*, although reasonably diverse in its speciation, exhibits a conservative style of evolution with little fundamental change throughout the Llandovery. It is suggested that cortical bandages have species-specific dimensions and micro-features. Some problematical micro- and ultrastructural features are described, notably fibrillar textures, parallel to the fusellar margins, in several species.

**KEY WORDS:** Llandovery, Silurian, graptolites, diplograptids, Russia, evolution.

GRAPTOLITE-BEARING deposits of Silurian age in the southern Urals belong to the Sakmara Formation which ranges in age from the *ascensus-acuminatus* Biozone of the lower Llandovery to the *hercynicus* Biozone of the lower Devonian (Koren' 1986). They are widely distributed in the eastern and western reaches of the Ural River in the Orenburg District of Russia, and in the At'yubinsk District of western Kazakhstan (Text-fig. 1). The dominant lithology is black carbonaceous shales, intercalated with cherty shales and siltstones, sometimes forming packages within volcanogenic assemblages. The Llandovery graptolites and biostratigraphy of the Sakmara Formation have been studied by Koren' (1964, 1967). Early to mid Llandovery diplograptids collected in the Mugodzhyr Range of the Kos-Istek region of western Kazakhstan (Text-fig. 1) were described by Koren' and Rickards (1996).

## LOCALITY AND AGE OF FAUNA

The graptolite-bearing locality is situated on the low, flat hills on the eastern bank of the Dergaish River (a tributary of the Guberl'ja River, which in turn flows into the Ural River), 800 m east of Mazovo village about 50 km north-west of Orsk (Text-fig. 1). It was discovered by members of the South Urals Geological Survey (Nikitin and Maegov 1972). Graptolites were found in grey sandy limestones which form thin-bedded intercalations (0.05–0.1 m thick) and lenses within amygdaloidal spilites and spilitic porphyries exhibiting pillow lava structure. The limestones are most probably of turbiditic origin. The limestone layers are intercalated with thin-bedded cherts, which locally also yield some graptolites. The volcanogenic deposits containing pockets of sedimentary rocks are about 500 m thick in the exposure near



TEXT-FIG. 1. Location of the Mazovo locality (cross hatched) in the Orenburg district of the southern Urals. Russia/Kazakhstan boundary is indicated by double dot-dashed lines.

Mazovo. However, their stratigraphical relationships with the underlying carbonaceous shales and basalts are difficult to establish.

Graptolites are preserved in relief in the coarse-grained limestones, but they are infilled with calcite and the periderm is often damaged. The first graptolite collection, identified by TNK in the early 1970s included '*Glyptograptus*' sp. indet., *Diplograptus* sp. indet., *Dimorphograptus* sp. indet., *Pseudoclimacograptus* sp. indet., *Orthograptus* sp., *Normalograptus miserabilis* (Elles and Wood) and *Rhaphidograptus* sp. indet. This assemblage was considered to be of late early Llandovery age, presumably about the *cyphus* Biozone (Nikitin and Maegov 1972). They were the first finds of the early Llandovery graptolites in the Urals and the only biostratigraphical markers used to date the pillow lavas. During the 1980s further collections were made from the Mazovo locality, which was visited by TNK together with V. Korinevsky, V. T. Tischenko and V. Khvorov, from local geological institutions. During this period some other localities with volcanogenic rocks of similar lithology were discovered within the Sakmara structural zone (Orenburg District). However, only in a few of them did the limestone intercalations contain graptolites, which are much less numerous than in the Mazovo locality. The present work establishes the presence of 30 graptolite species, and the age indicated is *vesiculosus* Biozone, possibly about the *atavus/acinaces* biozonal boundary.

#### MATERIAL AND PREVIOUS INVESTIGATIONS

The first attempt at chemical treatment of some limestone samples from the Mazovo locality revealed small graptolite fragments, most of them being early astogenetic stages. In many cases the graptolite periderm is strongly carbonized and is easily destroyed during chemical treatment, even when dealing with low concentrations of HCl. Nevertheless after several years a reasonable collection of isolated graptolites, mostly from the first locality near the Mazovo Village, was accumulated.

Graptolites rhabdosomes isolated chemically are represented mostly by young rhabdosomes and numerous siculae, or the sicula with the first pair of thecae beginning to form. Both are often unidentifiable specifically. Large rhabdosomes or their fragments are usually destroyed because of the type of coarse-grained recrystallized carbonates from which specimens are etched. The present paper is based on specimens of early astogenetic stages, mostly those which have 3–6 pairs of thecae. They exhibit the full range of relative relief from fully three-dimensional to flattened and preserved in lateral view or have been compressed obliquely. Some specimens are extremely brittle and fragile and easily destroyed by

bleaching. However, almost all specimens in the collection bear well-preserved cortical bandages and fibril lineation, and some of them show granular sheet fabric structure. A study of the main elements of the micro- and ultrastructure was one of the purposes of the present paper because there have been few SEM (scanning electron microscope) studies of early Silurian species.

Part of the collection which includes numerous specimens of *Cystograptus vesiculosus* (Nicholson) *s.l.*, is represented mostly by early astogenetic stages such as the sicula and the first or second pair of thecae, as well as a few fragments of nematularia, and was investigated using the TEM (transmission electron microscope) and light microscopes at Warsaw University (Urbanek *et al.* 1982). It was shown that the extra-rhabdosomal portion of the nematularium is a three-vented, single-walled structure consisting of fusellar material without a cortex or cortical bandages.

Some isolated specimens of diplograptids from the southern Urals collection were given to RBR in the late 1970s for the first SEM photography. Several well-preserved specimens of *Paraclimacograptus innotatus* (Nicholson), displaying numerous cortical bandages, were described and illustrated (Crowther and Rickards 1977; Crowther 1981). All this material together with the main collection of the biserial graptolites from the Orenburg District is included in present work. A part of the collection, which includes several species of monograptids, is now being examined by TNK with M. Melchin at the St. Francis University of Antigonish, Canada.

The technique used for mounting graptolites for SEM work, SEM examination procedure and electron-photomicrography is that described by Crowther and Rickards (1977) and Rickards and Dumican (1984). All microscopy was carried out by us on a JEOL JSM-820 SEM.

Graptolite dimensions given in the systematic descriptions were measured both directly from the SEM photographs and directly from the specimens on the stubs or in glycerine. In addition, some graptolites have been drawn from isolated specimens. The collection is deposited in the Sedgwick Museum, Cambridge, numbers SM X25756–25910, X25934–25935, X26243–4, SM A108555–556, A108576–593, A108625–637.

#### THE OVERALL NATURE OF THE FAUNA

The fauna is quite diverse taxonomically and includes 30 species belonging to 11 genera. Among the most diverse genera are '*Glyptograptus*' (five new species, one new subspecies and two in open nomenclature), *Normalograptus* (three new species), *Metaclimacograptus* (five species, among them one new, two in open nomenclature) and *Sudburigraptus* (five species in open nomenclature). The high specific diversity of these genera is unusual for the *vesiculosus* Biozone; this is especially true for *Glyptograptus* and *Metaclimacograptus*. The other genera, such as *Cystograptus* and *Paraclimacograptus*, are monospecific, which is quite typical for this particular interval. The occurrences of *Pseudoglyptograptus?* sp. and *Clinoclimacograptus* sp. are the earliest known for these genera.

Larger rhabdosomes of *Normalograptus*, *Glyptograptus*, *Rhaphidograptus* and *Dimorphograptus* have been identified in the limestone samples. They are usually preserved in full or low relief with a calcite infilling, their periderm being extremely brittle and fragile. This explains why they are so easily destroyed during chemical treatment of the samples. As a result only short and unidentifiable distal fragments have been isolated.

Some minute monograptids, having broadly dorsally curved rhabdosomes, a short sicula and simple geniculate thecae with well-developed hoods, form quite a distinctive part of the graptolite assemblage. They belong to a new species and will be described elsewhere, together with other monograptids of a *vesiculosus* Biozone fauna discovered in Bornholm (Koren' and Bjerreskov 1997).

As for numerical abundance of the isolated graptolites, *Paraclimacograptus innotatus* (Nicholson) dominates the assemblage, being represented by abundant specimens at all successive astogenetic stages from the sicula to rhabdosomes of six or seven pairs of thecae. *Normalograptids*, such as *N. melchini* sp. nov. and *N. sobolevskayae* sp. nov., occur quite frequently and at different astogenetic stages. A majority of glyptograptid species shows only a limited number of specimens which are mostly early astogenetic growth stages. However, *G. telarius* sp. nov., *G. nikitini* sp. nov. and *G. pavlinovi* sp. nov. are more common than the others. Metaclimacograptids are comparatively diverse for this stratigraphical level, but

individual species are represented by a few specimens with only *M. orcus* Koren' and Rickards being more common. Sudburigraaptid species can be distinguished comparatively easily by their thecal morphology, in spite of the fact that a majority of them are represented by scarce and fragmentary material, which does not allow a safe specific identification.

The diplograaptid fauna of the *vesiculosus* Biozone is not widely known nor studied in detail elsewhere. Some graptolite assemblages from the lower Llandovery sequences in Arctic Canada (Melchin 1998), Bornholm (Bjerreskov 1975; Koren' and Bjerreskov 1997) and the Prague Basin (Störch 1985) are exceptions.

Biserial graptolites from this stratigraphical interval were described by us from the Sakmara Formation in the Kos-Istek Region (Koren' and Rickards 1996). Their diversity, however, is not as high as in the present locality. Of the species described in this paper the following also occur in Kos-Istek: *Cystograptus vesiculosus* (Nicholson), *Paraclimacograptus innotatus* (Nicholson), *Metaclimacograptus orcus* (Koren' and Rickards) and *M. undulatus* (Kurck). Some dimorphograaptids are probably common to both regions. The important difference between the faunas is that no minute glyptograaptids and normalograaptids with closely spaced thecae have been discovered at Kos-Istek. The only glyptograaptid species known there is *G. bulbosus* Koren' and Rickards, represented by robust rhabdosomes with a long stout virgella. Glyptograaptids are not common there even in the overlying *cyphus* Biozone.

From the evolutionary point of view the diplograaptid fauna of the *vesiculosus* Biozone is important as it precedes the main and last evolutionary explosion of the Silurian diplograaptids at the beginning of the *gregarius* Biozone (see also Packham 1962).

At first examination the large number of very minute graptolites might suggest a dwarfed or stunted fauna, but the co-occurrence of several well-known species with normal dimensions precludes this possibility. However, no other locations have yielded such a proportion of very small rhabdosomes, and it may well be that special palaeobiogeographical or palaeoecologic conditions exerted some control on the fauna. Only future work will confirm this. It must be pointed out that such minute glyptograaptids and normalograaptids might easily be overlooked in normal black shale environments, or be dismissed as bad preservational views of well-known species such as *N. normalis* or *N. angustus*.

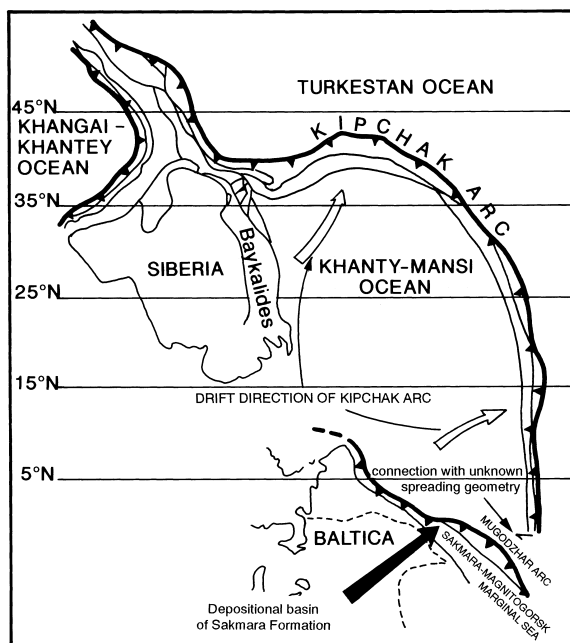
#### PALAEOGEOGRAPHICAL SETTING

Continuous sequences within the Sakmara Formation are rarely preserved because of the very complicated geological structure. The rocks are strongly deformed, frequently overthrust and usually exposed within different nappes or in chaotically arranged tectonic slabs. In general they form a linear belt aligned from north to south, which is called the Sakmara Structural Zone, and which is interpreted as a marginal Sakmara allochthon, differentiated in the southern part of the Uralian collisional fold belt (Ruzhentsev and Samygin 1979).

A relatively detailed plate-tectonic pattern of the southern Urals development was introduced by Zonenshein *et al.* (1984) and was later summarized by Zonenshein *et al.* (1990). This interpretation was adopted and further developed within a broad Eurasian plate-tectonic scenario by Sengor *et al.* (1993). This latest model shows that the early Silurian terrigenous-volcanogenic rocks of the Sakmara Formation could have been formed in palaeoequatorial latitudes within the Sakmara-Magnitogorsk marginal sea, to the east of East European Plate (Text-fig. 2). Here, from the late Ordovician, submarine eruption of basaltic lava took place in the centre of the trough, resulting in the formation of an inner volcanic ridge (the Guberlinskaya Arc; Korinevsky 1975), which was responsible for the accumulation of basalt-liparite complexes (Ruzhentsev and Samygin 1979). The Sakmara trough continued to expand in early Silurian time and this prevented the supply of terrigenous material to the central parts of the trough. Sedimentation mainly involved the accumulation of the cherty shales and siltstones of the Sakmara Formation. To the east the calc-alkaline volcanics with insignificant packages of sedimentary deposits were formed in the Early Silurian. Usually they are overlain by deep-water sediments such as cherts and shales with late Llandovery graptolites. These are compared most often with the bathyal sediments of marginal basins and island arc complexes.



TEXT-FIG. 2. Suggested tectonic and palaeogeographical location of the Sakmara Formation from where the collection of graptolites was made (after Sengor *et al.* 1993).



#### EVOLUTION

Biserial graptolites from the Orenburg District shed considerable light especially on the evolution of Llandovery species of the genera *Glyptograptus*, *Normalograptus* and *Metaclimacograptus*. The genera *Glyptograptus* and *Metaclimacograptus* do have their origins early in the Llandovery, or in the late Ordovician *persculptus* Biozone. But here their representatives are rare; for example, *M. orientalis* (Obut and Sobolevskaya) and *G. avitus* Davies (see Rickards *et al.* 1977). Indeed, Packham (1962) took the latter as possible root stock for his *cyphus* Biozone diversification of the *G. tamariscus* group of species. The problem with this was that it was a no-choice-scenario because faunas of the *vesiculosus* Biozone (approximately *atavus* and *acinaces* biozones of some schemes) were relatively little known: so we had the *persculptus* and *acuminatus* levels with a few rare species, little in the *vesiculosus* level, and then a spectacular diversification in the *cyphus* level and above. The Orenburg (Mazovo) fauna bridges that gap in part at least.

In recent years it has become apparent that the latest Ordovician and earliest Llandovery (*acuminatus* Biozone) is dominated by *Normalograptus* biserials, such species as *N. normalis* (Lapworth), *N. angustus* (Pernier), *N. medius* (Törnquist) and *N. mirnyensis* (Koren' and Mikhaylova) being common and often cosmopolitan. Representatives of the genus continue through the mid-Llandovery, but as a smaller proportion of the diversifying fauna; and, as biserials, they were replaced by species of *Glyptograptus* and *Metaclimacograptus*. As both these latter genera may have derived directly from *Normalograptus* lines of evolution, they can be regarded as replacement faunas.

Packham (1962) drew attention to the considerable difficulty, at times, in referring species to *Normalograptus* or *Glyptograptus*, and this is echoed here. Packham (*op. cit.*) took the main distinguishing feature between *Normalograptus* and *Glyptograptus* as the angle to slope of the infragenicular wall. Thus, an angle greater than 45 degrees resulted in a sharp geniculum of climacograptid type (now *Normalograptus*) and an angle of less than 45 degrees resulted in *Glyptograptus* with its more flowing geniculum. To this we would add, and have done so in the formal generic diagnoses below, that the supragenicular walls in *Glyptograptus* do, for the most part, incline outwards (in *Normalograptus* they are more or less vertical) and the thecal apertures are often everted, all these features resulting in longer, more open thecal excavations.

Melchin (1998) recognized the mode of astogenetic development as the main feature for distinguishing *Glyptograptus* (Pattern I) and *Normalograptus* (Pattern H). He has stressed the importance of astogeny and internal structure in deducing phylogenetic relationships. The present study is based on the assumption that all 'glyptograptids' are Pattern I taxa in spite of the fact that they possess a full medium septum, a character taken by Melchin as a feature indicating Pattern H. The evolutionary scenario outlined below results primarily from examination of external morphology. Therefore, the phylogeny presented may be the subject for further revision.

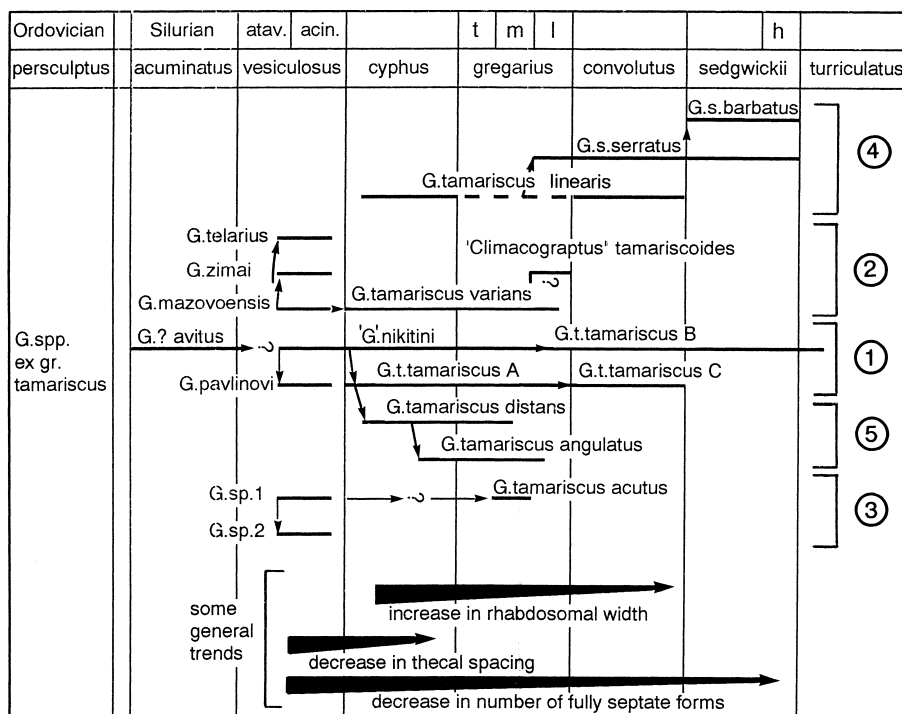
Of the lineages defined by Packham (1962) for the *cyphus* Biozone and above, one gives *G. tamariscus varians* Packham deriving from *G. t. tamariscus* in the *cyphus* Zone. However, *G. mazovoensis* sp. nov. (Text-fig. 6A–D) is remarkably like *G. varians*, differing only in having a higher thecal spacing (14–16 cf. 10–14) and, related to this, in having shorter thecal tubes. *G. t. varians* might well have evolved directly in the earlier, *vesiculosus* Biozone species *G. mazovoensis*, thus bypassing the main *G. t. tamariscus* line above the *vesiculosus* level (Text-fig. 3).

*G. nikitini* sp. nov. (Text-fig. 6E) is very close to *G. t. tamariscus* form B Packham, from the *gregarius* Biozone. However, one of the specimens figured by Packham (1962, text-fig. 1n) is almost identical to *G. nikitini*, especially in the presence of strongly geniculate thecae proximally, and more typical glyptograptid thecae distally. It seems possible that the full stratigraphical range of *G. nikitini* might be *vesiculosus* to *gregarius* biozones inclusive, and that *G. t. tamariscus* form B was derived from it. This suggestion appeals more than does Packham's lineage because it takes the root of *G. tamariscus* back to the *vesiculosus* Biozone, and with forms characterized by some normalograptid-like thecae. One can thus envisage the *G. tamariscus* line evolving from *Normalograptus* by distal introduction and spread of glyptograptid thecae. On this model *G. t. tamariscus* forms A and C of Packham were derived from *G. tamariscus* form B (or *G. nikitini*) and not the other way round. *G. pavlinovi* sp. nov. (Pl. 1, figs 3–5), a species quite close to *G. nikitini*, is probably a sideline from the latter which developed increased thecal spacing. *G. zimai* sp. nov. (Text-figs 10A–B, 11C) also resembles *G. t. varians* but differs from this species, and from *G. mazovoensis*, in its high thecal spacing. It may have been derived from the last form and thus bears the same relationship to *G. mazovoensis* as *G. pavlinovi* does to *G. nikitini*.

It is clear from the above considerations that we are able to take the roots of the *tamariscus* group evolution much earlier, and several distinct lines of evolution can be identified (Text-fig. 3). Lineages numbered 4 and 5 on Text-figure 3 may have derived, as suggested by Packham, from the *G. tamariscus tamariscus* line (numbered 1), and we have no evidence from Orenburg to take those particular evolutionary lines earlier than the *cyphus* Biozone. Packham (1962) seemed to take the view that there is no strong evidence for a systematic change from septate to aseptate forms as reported in *Normalograptus* by Davies (1929). However, all the Mazovo specimens are septate or partially septate, whereas from the *cyphus* Biozone upwards there is an increased proportion of partially septate and aseptate species. As a general feature, therefore, there is an increased tendency to median septum loss higher up the sequence (Text-fig. 3).

*Pseudoglyptograptus* species have been recorded from the *triangulatus* and *magnus* biozones (*gregarius* Biozone) but not from as low down as the Orenburg specimen of *Pseudoglyptograptus?* sp. (Text-fig. 11E). Whilst not adding greatly to the evolutionary story, it does raise the possibility that the origin of *Pseudoglyptograptus* from *Glyptograptus* may be earlier than previously supposed. Double curvature of the supragenicular wall also occurs in *Clinoclimacograptus* and this is already established in the *cyphus* Biozone. In the Orenburg collection we have a single specimen referable to *Clinoclimacograptus* (Pl. 5, fig. 8), but differing from *C. retroversus* Bulman and Rickards in having a slightly higher thecal spacing (14–16 cf. 10–13) and possibly in having the apertural region, beneath the geniculum, slightly less everted. As in the case of *Pseudoglyptograptus* the stratigraphical appearance of *Clinoclimacograptus* may be earlier than previously supposed.

Understanding the evolution of *Metaclimacograptus* has been fraught with the same difficulties as *Glyptograptus* in the sense that strata between the *acuminatus* and *cyphus* biozones are poorly represented (see, for example, Rickards *et al.* 1977). Since then more metaclimacograptids have been identified, as for example by Koren' and Mikhaylova (Koren' *et al.* 1980) and by Koren' and Rickards (1995). A further problem when considering metaclimacograptid lineages is that most of the generic characters seem to be



TEXT-FIG. 3. Suggested evolution of *Glyptograptus* spp., modified from Packham (1962) in the light of new work in this paper based on the study of the external rhabdosomal morphology. 1, *G. nikitini* lineage; 2, *G. mazovoensis* lineage; 3, *G. tamariscus acutus* lineage; 4, *G. tamariscus linearis* lineage; 5, *G. tamariscus distans* lineage.

maintained without change. Thus, the median septum is always present and is undulating to zig-zag; and the thecae, apertures and hoods remain basically unaltered. Only the dimensions change. It is clear that several forms are closely related, but stratigraphic occurrence becomes the only reasonable indicator of evolution on present evidence. In short, *Metaclimacograptus* exemplifies conservative lineages, in direct contrast to *Glyptograptus*, which shows considerable plasticity, species diversity, and numerous cladogenetic derivatives. In *Metaclimacograptus* there appear to be no overall trends and no evolutionary derivatives of the genus.

The origins of the genera *Glyptograptus* and *Metaclimacograptus* themselves are perhaps rooted in the late Ordovician. *Glyptograptus s.s.* and *Metaclimacograptus s.s.* both occur in the *persculptus* Biozone of the uppermost Ordovician (Rickards *et al.* 1977). *Metaclimacograptus* may have been derived from a *Normalograptus* by introduction of an undulating median septum which allowed closer packing of thecae and the possibility of thecal introversion.

Normalograptids are represented in the Orenburg fauna by three new species: *N. legrandi*, *N. melchiny* and *N. sobolevskayae* (Text-figs 14–17, 19, 26). Each is a minute form with high thecal spacing and a narrow rhabdosome. It is impossible at present to relate them to any previously described forms. They occur after the main peaks of *N. normalis* and *N. angustus*, at the beginning of the period when it might be considered that *Normalograptus* went into decline. They could, therefore, be diminutive, short-lived end members of normalograptid lineages. Alternatively, as is possible with the diminutive glyptograptids in this paper, they may represent specialised palaeobiogeographical races. It should be remembered, however, that they do occur with normally proportioned species such as *P. innotatus* (Text-fig. 30).

Representatives of Pattern I, first defined in an evolutionary context by Koren' and Rickards (1996), are in need of clearer definition. We describe several forms in this paper, but more material is needed to identify

three of them, which are left under open nomenclature (*Sudburigraptus* sp. 1–3). But it does seem likely that *Sudburigraptus*, which ranges from the *persculptus* Biozone into the middle Llandovery, contains the stock which gave rise to *Agetograptus*, *Rivagraptus* and *Parapetalolithus* (see Koren' and Rickards 1996).

The biserials described in this paper not only indicate an unsuspected biodiversity in the *vesiculosus* Biozone but also cause us to rethink the evolutionary lineages of *Glyptograptus* especially. Our work suggests that careful examination of the *acuminatus* and *atavus* biozones might yield unexpected results in terms of the diversity of diminutive species of biserials.

#### CORTICAL BANDAGES

This paper provides the first detailed descriptions of cortical bandages in early Silurian biserial graptolites. The only previous studies (Crowther and Rickards 1977; Crowther 1981) on *P. innotatus* were based on specimens from our Mazovo locality.

The cortical bandages of *Glyptograptus telarius* sp. nov. (Plate 2; Text-fig. 8) are the most striking of all the species described herein. We use the term 'railtrack' to define bandages which have conspicuously thickened edges, and relatively thin centres, so that the bandage-edges, parallel to each other, resemble miniscule railway tracks criss-crossing the peridermal surfaces. The only other case known of railtrack bandages is the Ordovician species *Orthograptus gracilis* (Roemer) (e.g. Crowther 1981).

The bandages of *G. telarius* raise the possibility that the cortical bandages may have species-specific features, and may thus add to the measurable biocharacters of a species. It has been argued elsewhere (Crowther and Rickards 1977; Crowther 1981; Sudbury 1991; Rigby 1994) that the bandages are related to individual thecae, to individual thecal size, and possibly to the size of the secretory organ, the preoral disc. So one might expect an increase in size along the rhabdosome, and a tendency to radiate from individual thecae. However, when the bandages are compared from similar rhabdosomal positions it does seem possible that each species has characteristic bandages: they will differ in length and width dimensions; on the number of fibres visible within them; on whether their edges are scarp-like or tapered; on their curvature; on their terminations; on the presence or absence of enveloping membrane; on the presence of pits and granules; and on their pattern of distribution (Table 1).

It should be emphasized that the fibres visible commonly along the lengths of bandages may not actually be individual collagen fibrils; hence, we used the descriptive term fibre or striation depending on whether there is much relief to them (fibres) or not (striations) but may represent bundles of collagen fibrils. The question of scale can really only be resolved by ultrathin sections or very large SEM enlargements, neither of which is possible on all material.

Table 1 shows our measurements of the bandages in the species in this collection. Although the differences may appear small, they are surprisingly constant. Moreover, the bandages often have an overall texture which is distinctive, but which at present we find immeasurable.

Membrane or sheet fabrics, which often surround bandages, enveloping them in a thin layer, are not always detectable; again it is a problem of both preservation and resolution. Nevertheless, we have identified granular and pitted textures, in places in the process of flaking away from the fibres, so that the presence of a membrane fabric seems likely. We are now inclined to regard the pits in the membrane fabrics as the SEM equivalents of the vesicles (?fat bodies) described in various papers (e.g. Towe and Urbanek 1972; Crowther 1981). They are in exactly the same position and are of exactly the same dimension. Of course, the presence of numerous fat bodies within the periderm of the graptoloid clearly has implications for the buoyancy of the organism, but that matter is beyond the scope of the present work.

In one species, *Normalograptus sobolevskayae* sp. nov. (Text-fig. 23C–D), there is a peculiar striated texture beneath obvious bandages which may be related to neither bandages nor fuselli. Unless this represents some kind of basal layer to the cortex or part of a bandage, deeply buried, and lacking a membrane, we can offer as yet no interpretation. The full areal extent of it is not known.

In another species, *Metaclimacograptus* cf. *undulatus* (Kurck) (Text-fig. 34), the bandages are deposited over the (temporary) thecal apertures of growing thecae. Whilst it is commonplace to find bandages growing over the lips of completed thecae, adding to the endocortex and, often, thickening and rounding the lips, this is the first record of cortical deposits draped over a growing thecal tube. The same specimens

TABLE 1. Summary of bandage structure and ultrastructure, details of which are given in the appropriate systematic descriptions below. Scarp: describes whether the long edge of the bandage is well delineated and scarp-edged, whether it is not, or whether it is tapered; ending: describes nature of the ends of the bandages; membrane: describes nature of the sheet membrane fabric, if present, enveloping each bandage; fibres: describes number or nature of fibres or striations (see text on cortical bandages) parallel to the length of each bandage; other: describes any additional comments on the nature of the bandages.

Species	bandage structure								
	width	length	scarp	curvature	ending	membrane	orientation	fibres	other
<i>G. t. praecursor</i> subsp. nov.			no				mostly		thin
<i>G. mazovoensis</i> sp. nov.	0.021–0.025		no			axial	axial	thin	
<i>G. nikitini</i> sp. nov.	0.107–0.13	>0.38	yes	broadly curved	rounded	pitted	? criss-cross	60–70	
<i>G. pavlinovi</i> sp. nov.	0.033–0.036	>0.022	probably	broadly curved		? granular	varied	numerous	
<i>G. telarius</i> sp. nov.	0.025	>0.25		wavy		granular	axial	10	railtrack
<i>G. zimai</i> sp. nov.	0.045–0.049	>0.21	no	straight			axial		thin
<i>Pseudoglytograptus?</i> sp.			no				axial		? thin
<i>C. vesiculosus</i> (Nicholson)	0.08	>0.24	yes				varied		
<i>N. legrandi</i> sp. nov.	0.024–0.04	0.10–0.26	yes	varied	rounded or rectangular			18–25	
<i>N. melchini</i> sp. nov.	0.34–0.38	0.072–0.110		banana-shaped	rounded	present		numerous, fine	
<i>N. sobolevskayae</i>	0.32–0.38	0.12–0.16	yes	gently curved	rectangular	pitted & granular			
<i>Sudburigraptus</i> sp. 2	0.054–0.064	>0.38	probably tapering		rounded	present, pitted		faint	
<i>Sudburigraptus</i> sp. 3	0.037–0.041	>0.20		gently curved					
<i>P. innotatus</i> (Nicholson)	0.008–0.051	0.10–0.26	yes sigmoidal	gently	rounded	absent	some orientation		
<i>M. hughesi</i> (Nicholson)	0.047–0.050	>0.15	yes	straight		? pitted & granular	varied		
<i>M. cf. undulatus</i> (Kurck)	0.046–0.048	0.162–>0.174	no			? absent	criss-crossed		
<i>M. bjerreskovae</i> sp. nov.	0.065–0.070	0.15	yes		bluntly rounded		varied	numerous	
<i>Metaclimacograptus?</i> sp.	? 0.0013	>0.14	yes	gently curved	?	? absent	varied	radiate from apertures	

(Text-fig. 34A) shows what appear to be bandages almost parallel to the fuselli, but it is just possible that this is the same fuselli lineation referred to below in the case of several species (see next section).

It is possible, though in need of further study, that cortical bandages may have some value in higher taxonomy than at species level. For example, in this work, all the species of *Glyptograptus* where bandages have been detected seem to have a preponderance of longitudinal or axial bandage arrangement that is broadly parallel to the rhabdosome's axis. Whilst this is often true of metasicular bandages in graptolites, in the instances of these *Glyptograptus* species it applies to the whole rhabdosome. However, in the *Normalograptus* species in this paper the bandages are certainly arranged in more criss-cross patterns, except when on metasiculae or when deposited on the thecal ventral walls when they are also sometimes subparallel. Anything which helps to distinguish between Silurian glyptograptids and normalograptids is worth pursuing further.

The cortical bandages play an important role in the growth of the virgella. Whilst other studies have shown that the virgella is cored with fuselli, it is certain that it is thickened and strengthened, and fused with the downgrowing portion of  $th_1^1$  by the addition of bandages. Near the base of the virgella the bandages may be helical in arrangement, wrapping around the base of the spine and thickening it (Text-fig. 31B). Farther along the virgella the bandages tend to be deposited along the length of the spine, often producing a ridge or seam where adjacent bandages join (Text-figs 21B, 25B).

A final point concerns the opposite ends of the bandages, both ends being rarely seen because of the extensive overlapping of bandages. In one species, *P. innotatus* (Nicholson), one end of the bandage is nicely rounded whereas the other is bluntly, almost rectangularly, terminated. Perhaps this indicates the direction of movement of the preoral disc, the ragged end being the point of lift-off after completion of the bandage which began with the rounded end. *P. innotatus* also confirms the work herein on *M. cf. undulatus* in that temporary apertures of incompletely grown thecae may well have bandages draped over their edges, contributing at a very early stage of development of the colony to the endocortex. Clearly this observation should be visible in TEM studies, but we are not aware that this is the case. In light microscope studies such a rapid ending to a bandage should also be visible, and we have observed it on Crowther's (1978) pictures of *O. gracilis*.

#### FUSELLI

Fuselli are deposited without stages of incremental growth. They are secreted as completed entities. Rickards *et al.* (1971) illustrated, but did not interpret, faint striations parallel to the margins of the fuselli, on the external surface of the fuselli. Subsequently Rickards and Dumican (1984) interpreted striations normal to the fusellar margins as misinterpreted (by Rickards *et al.* 1971) bandages. However, in this work we have identified three cases in which a clear fibre or striation structure is present on the fuselli, and which is parallel to the length of fuselli. The species are: *Glyptograptus telarius* sp. nov., *Normalograptus? sobolevksyae* sp. nov., and *Metaclimacograptus cf. undulatus* (Kurck). This may also be the case in *Paraclimacograptus innotatus* (Nicholson). In *Cystograptus vesiculosus* (Nicholson) striations occur normal to the length of the fuselli.

As there is no evidence of growth increments in fusellar deposition in any graptolites, the striations presumably represent movement of the secretory organ in a direction parallel to the length of a fusellus as it was deposited. If so, it perhaps implies a much faster rate of deposition than the eight hours needed by extant hemichordates for a similar task, otherwise chance alone would determine that some half-finished fuselli would be found on growing tips, and they do not seem to be. It seems unlikely that all these examples can be attributed to the presence of cortical bandages exactly parallel to the fusellae.

A further discovery concerns the secretion of the genicular hoods in *Paraclimacograptus innotatus* (Nicholson) and *Metaclimacograptus orcus* Koren' and Rickards. It is clear that the genicular hood associated with the geniculum of  $th(n+1)$  was secreted by the zooid in  $th(n)$  and was completed, along with the infragenicular wall of  $th(n+1)$  before the thecal tube of the latter was constructed (Text-fig. 30B). (In this single sense secretion is similar to the metathecal hood of some *Monograptus s.s.* species.) The infragenicular wall and genicular hood of  $th(n+1)$  served as a platform along which the thecal tube of  $th(n+1)$  grew.

This is in marked contrast to the interpretation of Bulman (1970, p. V62) who concluded that the distal portion of the interthecal septum was secreted by  $th(n+1)$ . Patently this cannot be the case in the two species quoted here. How far such a secretory mode can be extended to other geniculate Silurian biserials is uncertain at present. Bulman (1970) also referred to those monograptids where the whole of the interthecal septum can only be secreted by  $th(n)$ . Thorsteinsson (1955) averred that in some cyrtograptids the interthecal septum is secreted only by  $th(n+1)$ . However, if Rigby (1994) is correct in her analogies of the activities of the zooids of extant hemichordates with those of graptolites, there is clearly considerable flexibility as to which zooid or zooids secreted what part of the periderm. Perhaps this is what the graptolite growth patterns are showing?

#### A NOTE ON THECAL SPACING MEASUREMENTS

Historically, thecal spacing measurements have been taken by counting the number of thecae in a 5 mm or 10 mm unit length, more commonly the latter. The measurement was then expressed as 'number of thecae per cm' or 'number of thecae in 10 mm'. Packham (1962) questioned the usefulness of this method because it failed, often, to note the rapid changes of thecal spacing (and hence size) near the proximal end of especially small biserial species. Packham's alternative was to measure the ventrally exposed length of 1–3 thecae and then calculate the spacing for this section in terms of thecae per 10 mm or 5 mm. It has the merit of being broadly comparable to the older technique, rendering even quite old measurements usable, and yet at the same time recording smaller changes along the stipe. This is the method we prefer, and we have used it throughout this paper. However, in deference to the preferred use by some workers of the 2TRD (Howe 1983) measuring system, we have also given 2TRD figures where we deem these to be relevant. Howe's technique does not differ greatly from Packham's except that most users do not recalculate for  $n$  thecae per 10 mm, leaving the exposed ventral length of two thecae as a reading. We feel that this does not facilitate comparison with earlier methods.

#### SYSTEMATIC PALAEOLOGY

Order GRAPTULOIDEA Lapworth, 1875

Superfamily DIPLOGRAPTACEA Lapworth, 1873 (emend. Fortey and Cooper, 1986)

Family GLYPTOGRAPTIDAE Mitchell, 1987

Subfamily GLYPTOGRAPTINAE Mitchell, 1987

Genus GLYPTOGRAPTUS Lapworth, 1873 (emend. Koren' and Rickards, 1996)

*Type species.* By original designation, *Diplograptus tamariscus* Nicholson, 1868; Llandoverly, Scotland.

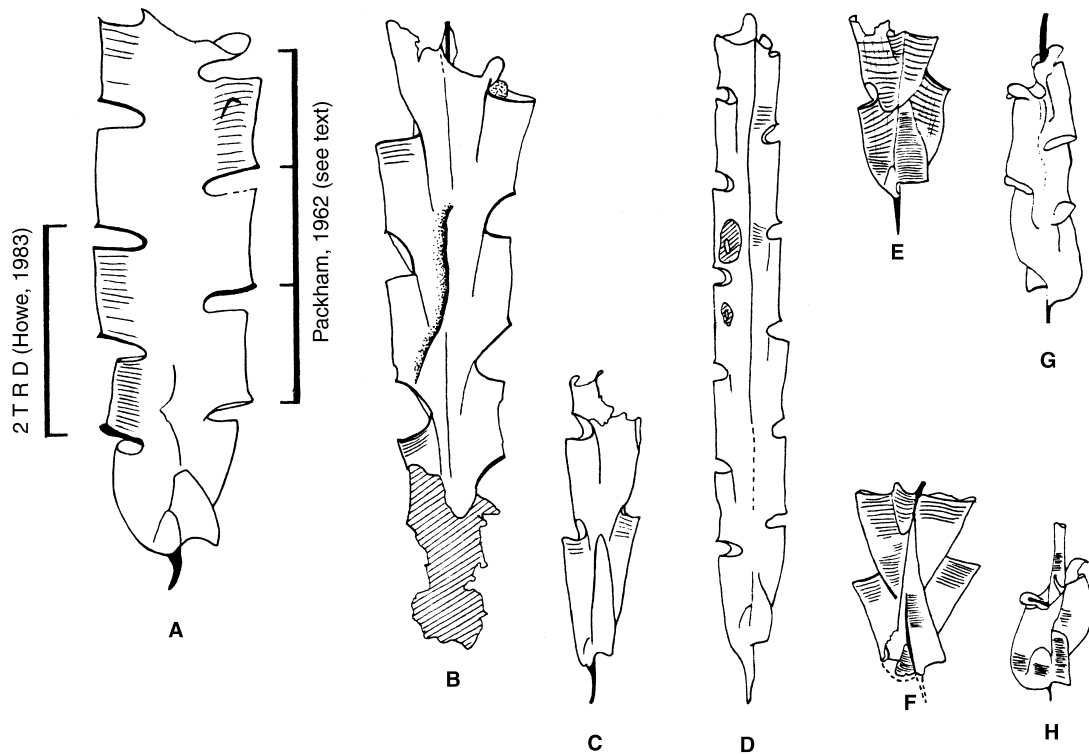
*Diagnosis.* Proximal development of *tamariscus* (I) Pattern: thecae with sigmoidal curvature varying from gentle to sharp ('climacograptid'); supra-genicular wall vertical in some, to sloping outwards more frequently; apertures generally everted but may be horizontal; may be septate, partially septate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

*Remarks.* Some of the following glyptograptids fall readily into the generic diagnosis, some are close to the *G. tamariscus* group of species, and some are amongst the tiniest glyptograptids known and amongst the smallest graptoloids. *G. nikitini* sp. nov. and *G. pavlinovi* sp. nov. both have almost normalograptid thecae proximally (Pl. 1, figs 2–3, 5) and in this sense resemble some previously described glyptograptids such as *G. incertus sensu* Churkin and Carter 1970 (Loydell 1992).

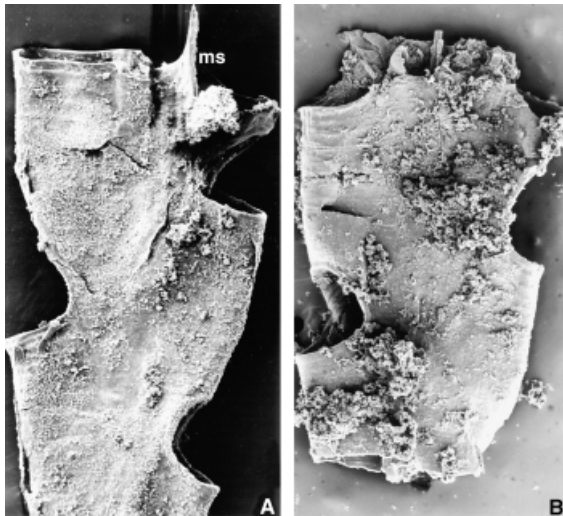
*Glyptograptus tamariscus praecursor* subsp. nov.

Text-figures 4B, 5

*Derivation of name.* To indicate that this subspecies is an early form in the *G. tamariscus* lineages.

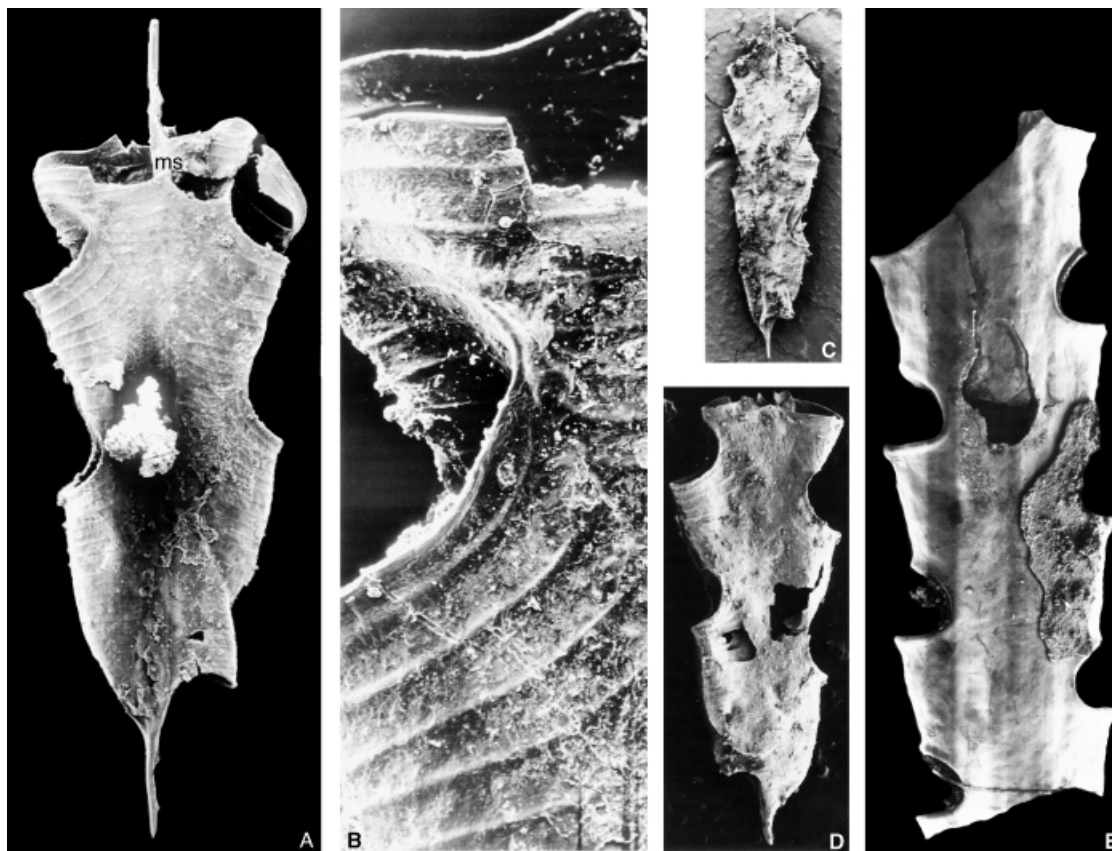


TEXT-FIG. 4. A, *Metaclimacograptus hughesi* (Nicholson), SM A108584; for explanation of Howe (1983) and Packham (1962) thecal measuring techniques, see text. B, *Glyptograptus tamariscus praecursor* subsp. nov., holotype, X.25756, three-dimensional specimen close to proximal end. C, *Glyptograptus* sp. 2, X.25818. D, *Normalograptus melchini* sp. nov., holotype, X.25817. E, *Sudburigraptus* cf. *eberleini* (Churkin and Carter), X.25819. F, *Sudburigraptus* aff. *berleini* (Churkin and Carter), X.25820. G-H, *Metaclimacograptus orcus* Koren' and Rickards, respectively, X.25821 and 25822. All figures  $\times 25$ .



TEXT-FIG. 5. *Glyptograptus tamariscus praecursor* subsp. nov. SEM micrographs of slightly flattened fragments with broken proximal ends showing long supragenicular walls and strongly alternating thecae; ms, median septum. A, X.25757; B, X.25758; both  $\times 62$ .





TEXT-FIG. 6. A–D, *Glyptograptus mazovoensis* sp. nov. SEM micrographs. A, holotype, X.25759, obverse view of a young colony showing median septum (ms), flowing thecal geniculum, and everted apertures;  $\times 72$ . B, SEM detail of a young colony showing strongly ridged fusellar margins and parallel striae in between;  $\times 300$ . C, SM A108589, obverse view of a young colony flattened and showing artificial 'orthograptid' appearance of thecae;  $\times 20$ . D, X.25761, reverse view of a young colony with lateral wall covered with numerous bandages;  $\times 40$ . E, *Glyptograptus nikitini* sp. nov., X.25762, fragment of colony with broken proximal end showing extremely thick cortex which entirely masks fuselli;  $\times 40$ .

*Holotype.* SM X25750, Text-figure 4B.

*Material.* Three specimens, one in full relief, two partially flattened, all lacking a proximal end, although the three-dimensional specimen is close.

*Diagnosis.* *tamariscus*-like glyptograptid with 13–16 thecae in 10 mm, and a dorso-ventral width of 0.45–0.82 mm; long excavations, with a supragenicular:infragenicular wall ratio of 2 or 3:1; geniculum rimmed; thecal angle 5–15 degrees; septate.

*Description.* The thecae are strongly alternating, slightly everted aperturally (declination from the horizontal 5–30 degrees) and with relatively long excavations so that the supragenicular:infragenicular wall ratio is 2 or 3:1. The geniculum itself is flowing but with a rim which is distinctly thickened (Text-fig. 5B). The thecal spacing in the three specimens is slightly different, being 16, 14 and 13, but the exact position on the rhabdosome is not known. The angle of thecal inclination is very low on the most proximal thecae seen (5 degrees) but may be as much as 15 degrees more distally. The specimen in relief shows straight infragenicular walls (Text-fig. 4B) but the two slightly flattened specimens are faintly convex (Text-fig. 5A–B). The number of fuselli on the supragenicular wall is about 14–18. Each

specimen has an indication of a median septum. One specimen shows faint traces of bandages which mostly appear to be aligned parallel to the length of the rhabdosome.

*Remarks.* This form is perhaps the closest of the Urals specimens to the *G. tamariscus* group as redefined by Packham (1962) and, like *G. nikitini*, is closest to *G. t. tamariscus* form B. It is not suggested, on current evidence, that *G. t. praecursor* is the certain ancestor of the later explosion of *G. tamariscus* subspp., but either it or *G. nikitini* are possible ancestors of lineage 1 (Text-fig. 3).

*Glyptograptus mazovoensis* sp. nov.

Text-figure 6A-D

*Derivation of name.* After Mazovo, the village from where the graptolite collections were made.

*Holotype.* SM X25759, Text-figure 6A.

*Material.* Five specimens, partially three-dimensional, including early growth stages and fragments of mature but broken proximal ends.

*Diagnosis.* Small *tamariscus*-group glyptograptid with a dorso-ventral width of 0.52–0.80 mm, and a thecal spacing of 14–16 in 10 mm; apertures strongly everted, moderately alternating; rhabdosome septate from third thecal pair; all thecae with flowing geniculum.

*Description.* None of the specimens shows the apex of the sicula, but its position must be above the level of the aperture of  $th^2$ . The sicular aperture is slightly flared (Text-fig. 6A), and has an apertural diameter of 0.15–0.20 mm. In obverse view it is visible for 0.40–0.48 mm and in reverse view for 0.17 mm in the one specimen where this is measurable. The sicular aperture is furnished with a stout, spike-like virgella 0.25–0.36 mm long, and is distinctly concave.

$Th^1$  grows downwards for 0.36 mm, turning upwards 0.11 mm below the sicular aperture and then growing for 0.62–0.90 mm. Its aperture is strongly everted (Text-fig. 6A), declined from the horizontal at up to 60 degrees. About 23 fuselli comprise the upward-growing part of  $th^1$ , and as the aperture is approached these mirror clearly the eventual apertural eversion: during growth of the  $th^1$  tube the aperture will be more or less horizontal until five fuselli from the final apertural position, when they rapidly change, fusellus by fusellus, to the everted state. Subsequent thecae show similar growth development. Fusellar margins on all thecae are quite strongly ridged, and between the ridges are at least 15 parallel striae (Text-fig. 6B).  $Th^2$  has a length of 0.44–0.59 mm visible in obverse view. The thecae are relatively short, broad tubes:  $th^2$ , for example, has apertures 0.22 mm wide and lengths around 0.51 mm, giving a 2:1 ratio. All thecae have a flowing geniculum (Text-fig. 6D), the supragenicular wall being 0.25 mm long and the infragenicular wall 0.18 mm. The supragenicular wall:infragenicular wall ratio is 1.4:1.0. This reflects the considerable eversion of the thecal aperture. Fuselli on the supragenicular wall number 9–11.

Thecal spacing is high, 14–16 in 10 mm (2TRDs, 1.18–1.47) and thecal overlap one-third. The angle of thecal inclination is 5–10 degrees on  $th^1/1^2$  and 20–30 degrees thereafter. There are 11–12 fuselli on the  $th^2$  metatheca.

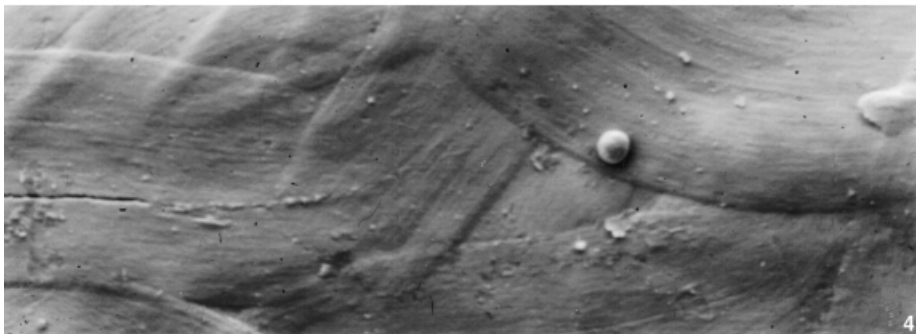
The overall rhabdosomal aspect is of a small glyptograptid with a slightly tapering proximal end, conspicuously

EXPLANATION OF PLATE 1

SEM micrographs

Figs 1–2. *Glyptograptus nikitini* sp. nov. 1, detail of Text-figure 6E showing wide, irregularly overlapping bandages on the lateral wall of the colony; note also ragged appearance of rounded terminations (T) and distinct lateral margins of bandages with parallel fibrils (?) between them;  $\times 522$ . 2, X.25803, holotype, proximal end of broken colony with strongly geniculate thecae of normalograptid appearance;  $\times 40$ .

Figs 3–5. *Glyptograptus pavlinovi* sp. nov. 3, X. 25804, proximal fragment of the growing colony with five pairs of thecae completed, obverse view;  $\times 20$ . 4, further magnification of 3 showing wide, short, bandages broadly curved and frequently overlapping each other; note that fuselli are not visible;  $\times 500$ . 5, holotype, X.25805, reverse view of the mature colony showing weakly biform thecae;  $\times 20$ .



KOREN' and RICKARDS, *Glyptograptus*

everted thecal apertures, and a rhabdosomal length of less than 3 mm. The dorso-ventral rhabdosomal width is: at  $th1^1$ , 0.55–0.66 mm;  $th2^1$ , 0.55–0.77 mm;  $th3^1$ , 0.80 mm.

Bandages are present, more or less parallel to the axis of the rhabdosome, but are very delicate and, presumably, thin, 0.021–0.025 mm wide. Longitudinal or axial bandages have been detected on the ventro-lateral sides of the metathecae (Text-fig. 6A). Striae between and parallel to the fusellar ridges are puzzling and do not seem to be bandages at all (see section on fuselli above). Upon flattening (Text-fig. 6C) *G. mazovoensis* may take on an orthograptid profile, something which has been pointed out previously in other glyptograptid species (Hutt *et al.* 1970). Clearly, great care is needed in dealing with flattened representations of both *Glyptograptus* and *Sudburigraptus*.

*Remarks.* *G. mazovoensis* sp. nov. is a more 'normal' Silurian glyptograptid in the sense of dimensions, and *G. tamariscus varians* Packham (1962) is probably the closest species, certainly in respect of the overall rhabdosomal aspect (see also Text-fig. 3). *G. mazovoensis* sp. nov. differs, however, on several counts, notably in having a higher thecal spacing (14–16 cf. 10–14) and shorter thecae (0.44–0.59 mm cf. 0.75–1.5 mm for  $th1^1/th1^2$ ). Were it not for these striking measurement differences *G. mazovoensis* could easily be mistaken for the stratigraphically later form (*cyphus-gregarius* biozones); it may be an evolutionary ancestor.

*G. mazovoensis* sp. nov. resembles *G. praecursor* in one respect only, namely in the presence of subdued ridges or striae parallel to the fuselli margins: in all other measurements it is markedly different.

*Glyptograptus nikitini* sp. nov.

Plate 1, figures 1–2; Text-figure 6E

*Derivation of name.* In honour of the late Dr I. I. Nikitin who discovered the Mazovo locality.

*Holotype.* SM X25803, Plate 1, figure 2.

*Material.* Twelve specimens showing early growth stage and more distal thecae.

*Diagnosis.* Small glyptograptid with almost normalograptid thecae for first three pairs; distal thecae with inclined supragenicular walls; geniculum sharp throughout; dorsoventral width 0.52 mm proximally to 0.95 mm distally; thecal spacing 14–11 in 10 mm.

*Description.* The proximal thecae are difficult to distinguish from those of normalograptids because the supragenicular wall is essentially vertical (Pl. 1, fig. 2); the geniculum itself is sharp and possibly thickened. This gives the appearance, superficially only, of the supragenicular wall sloping slightly inwards. The apertures are strongly everted and there is a pronounced apertural lip. Therefore, as the supragenicular wall approaches this position it leans outwards in a manner which is more glyptograptid. The distal thecae show remarkably similar thecae, apertures, and geniculum to those proximally, but the supragenicular wall slopes outwards for its whole length (Text-fig. 6E). The supragenicular wall:infragenicular wall ratio is 1.5:1.0, indicating the considerable axial length of the apertural excavation. The excavation:dorso-ventral width ratio is 1:4. Thecal evertion is slightly greater in the proximal thecae, being about 35 degrees from the horizontal, compared with 20 degrees distally.

The sicular length is not seen, but the sicula is visible on the reverse side for 0.22 mm. The sicular aperture is almost horizontal and has a width of 0.16 mm, and bears a stiffly recurved virgella c. 0.57 mm long.  $Th1^1$  and  $th1^2$  both grow upwards for 0.70 mm, inclined outwards at about 10–15 degrees. Distal thecae are inclined outward at 15–20 degrees. Thecal overlap is about one-half.

Conspicuous but flat bandages, with clearly defined margins, are present (Pl. 1, fig. 1). Bandage widths vary from 0.107 to 0.13 mm, lengths are >0.38 mm, and the ends are hemispherically rounded. Within each bandage there are 60–70 fibrils visible, but whether these are individual fibrils, or fibrillar bundles of collagen, cannot be determined. The bandages are broadly curved along their lengths, but do not show preferred orientations with respect to individual thecae. They embrace the apertural margins of the thecae. Both specimens exhibit a thick cortical bandaging which greatly subdues the relief and visibility of the fuselli. One rounded end of the bandages has a ragged appearance in detail, as though this was the lift-off point of the secreting organ. The opposite end is more rectilinear in outline. Pitted sheet fabric membranes have been detected on the bandages of the lateral rhabdosome walls.

*Remarks.* This species is very similar to *Glyptograptus pavlinovi* (Pl. 1, figs 3–5), but differs in its lower thecal spacing (11–14 cf. 15–19 in 10 mm; 2TRDs 1.42–1.80 cf. 1.05–1.35). In other respects they are similar, especially in the change of proximal to distal thecae, the angles of inclination, and the nature of the thecal excavation and thecal eversion. It seems likely that these glyptograptids are in the process of separating evolutionarily from normalograptids, the main proliferation of which precedes and co-exists with them.

*G. nikitini* and *G. pavlinovi* are unlike any other glyptograptids in this fauna in that they are biform and have a sharp geniculum. In general dimensions *G. nikitini* resembles *G. t. tamariscus s.l.* in rhabdosomal size and thecal spacing, and some of the forms illustrated by Packham (1962) as *G. t. tamariscus* form B do have a pronounced geniculum on the proximal thecae and distal thecae with outwardly inclined supragenicular walls. Possible evolutionary relationships are discussed in the section on evolution above.

The biform arrangement of the thecae in both *G. nikitini* sp. nov. and *G. pavlinovi* sp. nov. recalls that of *G. incertus* Elles and Wood, 1907, although the latter is a much larger species. *G. nikitini* also resembles *G. avitus* Davies, 1929 in having a rhabdosome only slightly narrower, a not dissimilar thecal spacing, and in having sharply geniculate thecae. It is more likely that Davies' species is an ancestor of *G. nikitini* rather than of *G. t. tamariscus* A as suggested tentatively by Packham (1962).

*Glyptograptus pavlinovi* sp. nov.

Plate 1, figures 3–5

*Derivation of name.* In honour of the late Prof. V. N. Pavlinov, a pioneer worker on the graptolite-bearing deposits in the southern Urals.

*Holotype.* SM X25805, Plate 1, figure 5.

*Material.* Thirteen specimens, including several early growth stages.

*Diagnosis.* Small, tapering glyptograptid with almost normalograptid proximal thecae for first two to three pairs; distal thecae inclined outwards; geniculum sharp throughout; dorso-ventral width 0.44–0.90 mm distally; thecal spacing 15–19 in 10 mm.

*Description.* The sicula has a length of 1.0–1.2 mm, of which 0.25 mm comprises the prosicula, and the sicular apex reaches the level of the aperture of  $th1^1$ . The sicular apertural region is visible in obverse view for 0.42–0.75 mm and the aperture itself has a diameter of 0.13–0.20 mm. The metasicula is visible in reverse view for 0.15–0.20 mm. The sicular aperture is more or less horizontal and is furnished with a sharp, spine-like virgella 0.25–0.45 mm long (Pl. 1, fig. 3).

$Th1^1$  grows downwards for 0.30–0.35 mm, extending below the sicular aperture for 0.10 mm, before turning upwards, at an angle of 10 degrees, for 0.54–0.57 mm.  $Th1^2$  grows upwards for 0.44–0.65 mm, its aperture markedly above that of  $th1^1$ . Both apertures, and all subsequently, are everted and declined from the horizontal at 10–20 degrees (Plate 1, fig. 5). The rhabdosomal dorso-ventral width at  $th1^1$  is 0.40–0.47 mm, and at  $th1^2$  0.45–0.52 mm; this gradually increases to 0.90 mm at  $th7$ . Thecal excavations:rhabdosomal width ratio is 1:4.

The thecal spacing is 15–19 in 10 mm (2TRDs of 1.00–1.35), and the thecal apertures are moderately alternating. The median septum is complete after the second thecal pair. Thecal excavations are defined by the everted apertures and by a pronounced geniculum. The supragenicular walls are straight, but seem slightly concave above the geniculum, reflecting the heavy nature of the latter; and as they are more outward-leaning just below the thecal aperture, the overall aspect is glyptograptid rather than normalograptid. The more distal thecae have the supragenicular wall outwardly inclined at 20–30 degrees.

In many parts of the rhabdosome the fuselli are entirely masked by thick cortical deposits consisting of several layers of flat, broadly curved bandages. These are 0.033–0.036 mm wide and more than 0.22 mm long. They have sharply distinct lateral margins with numerous parallel fibres between. They tend to criss-cross at varying angles (Pl. 1, fig. 4).

*Remarks.* The similarities and few but striking differences from *G. nikitini* have been commented upon above under the latter species. It is possible that they are distinct morphs of the same species. There is no

overlap at all in the thecal spacing variation, the two forms having quite different spacings and the bandages having different dimensions (width in *G. pavlinovi* is 0.036 mm and in *G. nikitini* 0.13 mm). However, the overall appearance and some other dimensions are closely similar. The biform nature of *G. pavlinovi* and *G. nikitini* could give rise to problems of identification upon flattening, when they might possibly resemble minute *Diplograptus* species.

*Glyptograptus telarius* sp. nov.

Plate 2, Text-figures 7–9

*Derivation of name.* Latin *telarius*, a web, referring to the cross-hatching of fuselli and railtrack bandages.

*Holotype.* SM X25763, Plate 2, figures 1–2.

*Material.* Fifteen specimens, various growth stages in relief.

*Diagnosis.* Very small glyptograptid, less than 5 mm long, and with a maximum dorso-ventral width of 0.55 mm in three dimensions, with a high thecal spacing up to 28 in 10 mm (2TRD 0.70–0.80); first thecal pair characteristically wider dorso-ventrally than subsequent thecal pairs; septate; bandages of railtrack type, mostly subparallel to rhabdosome length.

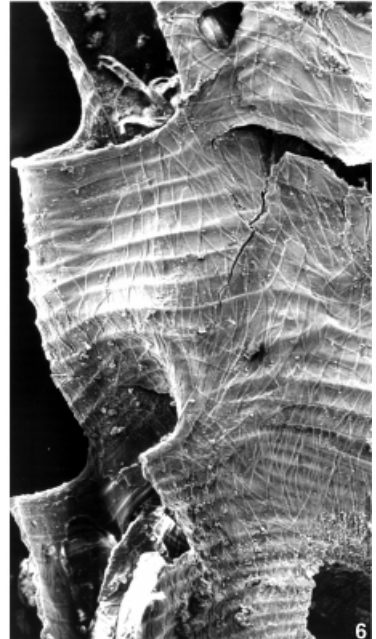
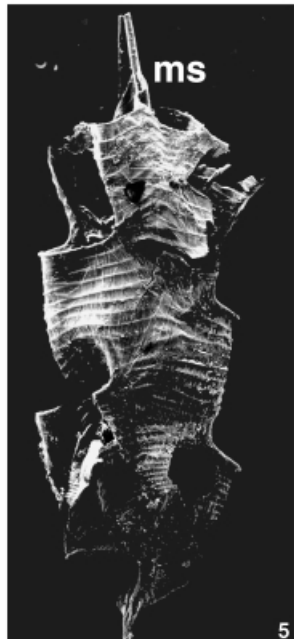
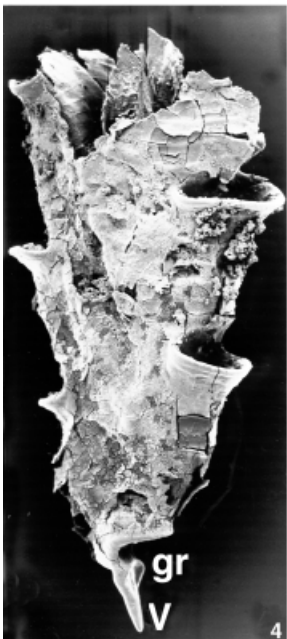
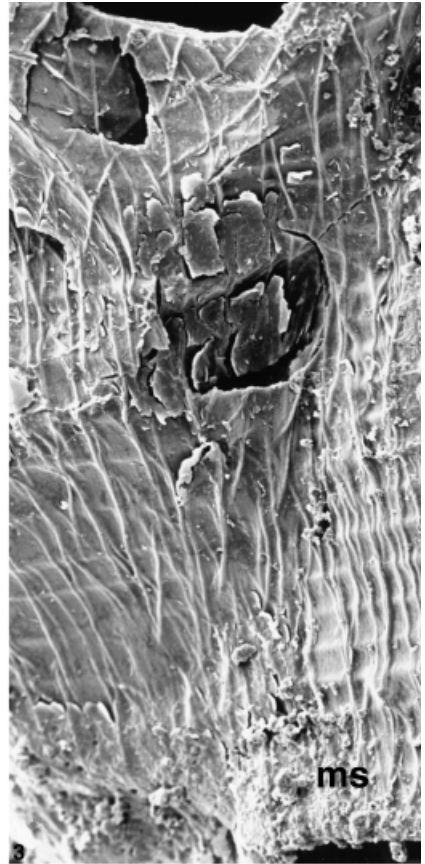
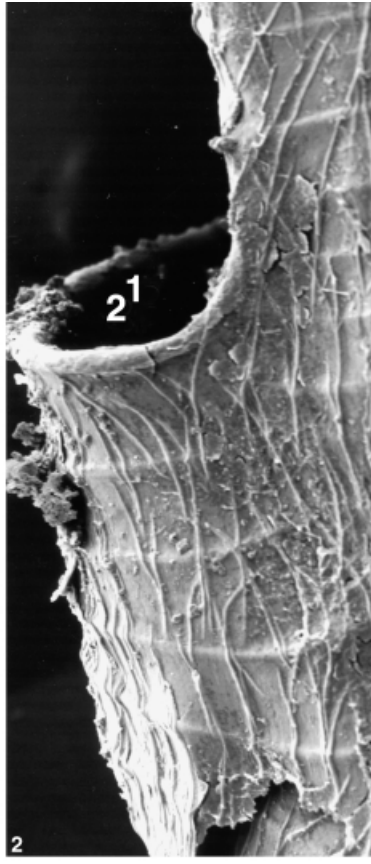
*Description.* The sicula is not seen in its entirety, being obscured by later thecal growth, but the apex is probably at about the level of the second pair of thecae, giving it an approximate length of 0.70 mm. The sicular aperture is relatively wide, at 0.17–0.24 mm. The metasicula is visible in obverse view for 0.35 mm and in reverse view for 0.30 mm, and is slightly flared. The apertural rim is almost horizontal. The virgella is short, 0.10–0.20 mm, but quite stout and commonly directed slightly across the aperture of the sicula; the angle from the axis ranges from 0–30 degrees (Pl. 2, figs 4–5), which may be unrelated to the down-growing portion of  $th1^1$ . There is also an indistinct dorsal groove along the proximal part of the virgella (Pl. 2, fig. 5).

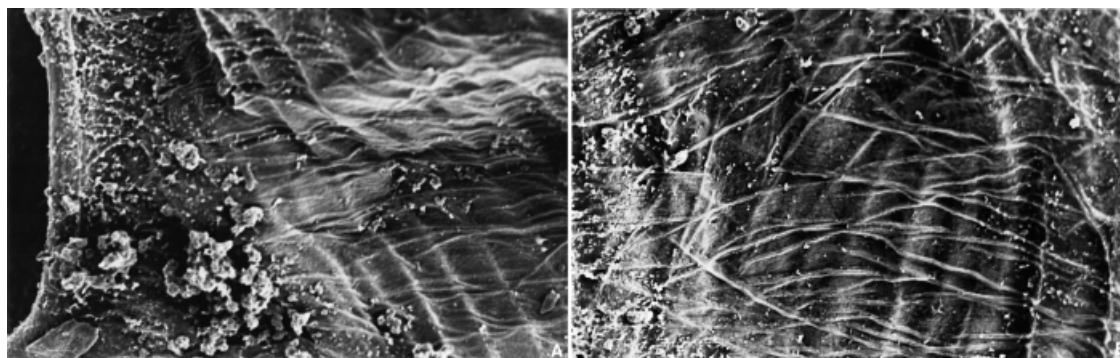
The initial down-growing portion of  $th1^1$  is not seen, but its distal extremity reaches to 0.05–0.10 mm below the sicular apertural rim before turning upwards. The ventral wall of  $th1^1$  is inclined to the rhabdosomal axis at 20–30 degrees, as is that of  $th1^2$ . The thecal apertures vary from almost horizontal and slightly everted, being in the latter case declined from the horizontal at 10–40 degrees, more usually 10–20 degrees. Thecal lengths are approximately 0.38 mm;  $th1^2$ , the most easily measured, varies from 0.35–0.41 mm. Thecal overlap is less than one-third the thecal length.

The thecal apertures are slightly everted and expanded, have thickened rims, and in some cases there is a slight reduction in proximo-distal width of the fuselli as the rim is approached. The presence of a rim suggests that growth of the metatheca is complete. In several specimens the rim is very thick, overhanging the free ventral and ventro-lateral walls somewhat (Pl. 2, figs 2, 6). Occasionally, the ventral apertural margin shows a slight saddle. Thickening of the rim is almost certainly caused by bandage additions which follow the curve of the rim itself. Fuselli are widely spaced, increasing from the metasicula to the more distal parts of the colony, but on  $th2^1$ , about half way along the colony, the

EXPLANATION OF PLATE 2

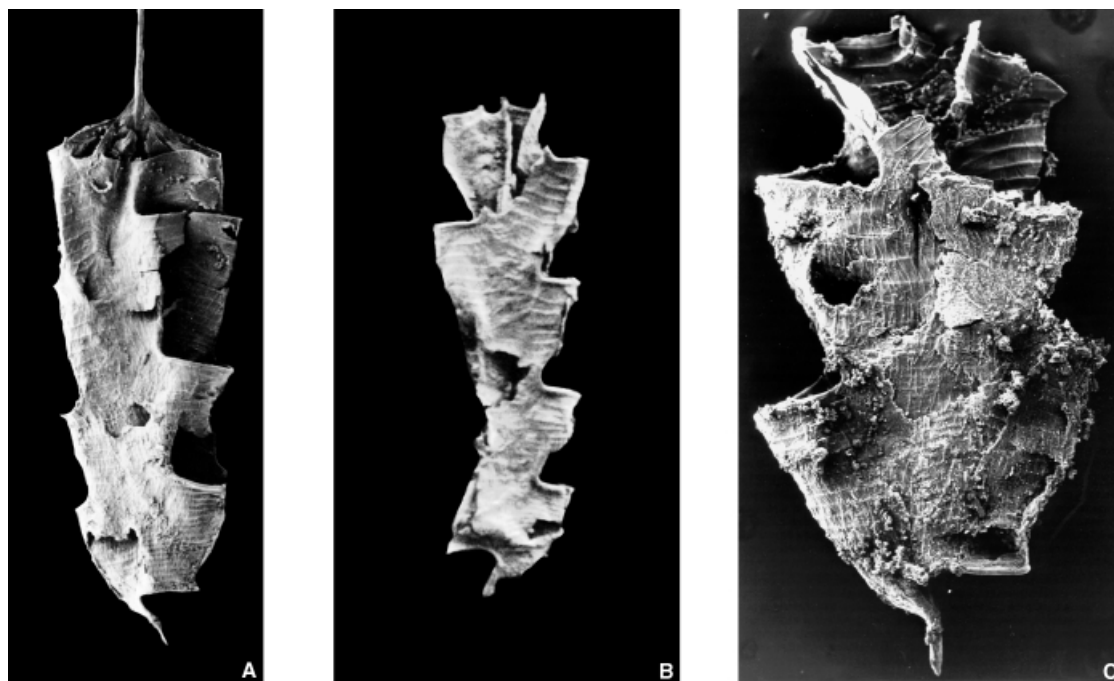
Figs 1–6. *Glyptograptus telarius* sp. nov. SEM micrographs. 1, holotype, X. 25763, obverse view of a young colony;  $\times 170$ . 2, SEM detail of Text-figure 8A showing ‘railtrack’ bandages overlapping each other and crossing fuselli at right angles or high angles on the lateral, sub-apertural wall of  $th2^1$ ;  $\times 445$ . 3, SEM detail of 1 showing lateral walls of metasicula (ms) and  $th1^1$  with frequently overlapping longitudinal bandages running across fuselli,  $\times 461$ . 4, X.25764, ventro-lateral view of broken proximal end showing slightly expanded and everted thecal apertures with thickened rims; note the peculiar outgrowth (gr) and groove at the base of free virgella (v);  $\times 126$ . 5, X.25765, reverse view of a young colony showing median septum (ms) and groove on the dorsal side of virgella at its base;  $\times 91$ . 6, SEM detail of 5 showing mostly longitudinal broadly curved bandages running over the ventro-lateral wall and overgrowing thecal apertures; note that longitudinal bandages are absent on the zigzag structure close to the thecal aperture, where only fine horizontal striations are seen;  $\times 178$ .





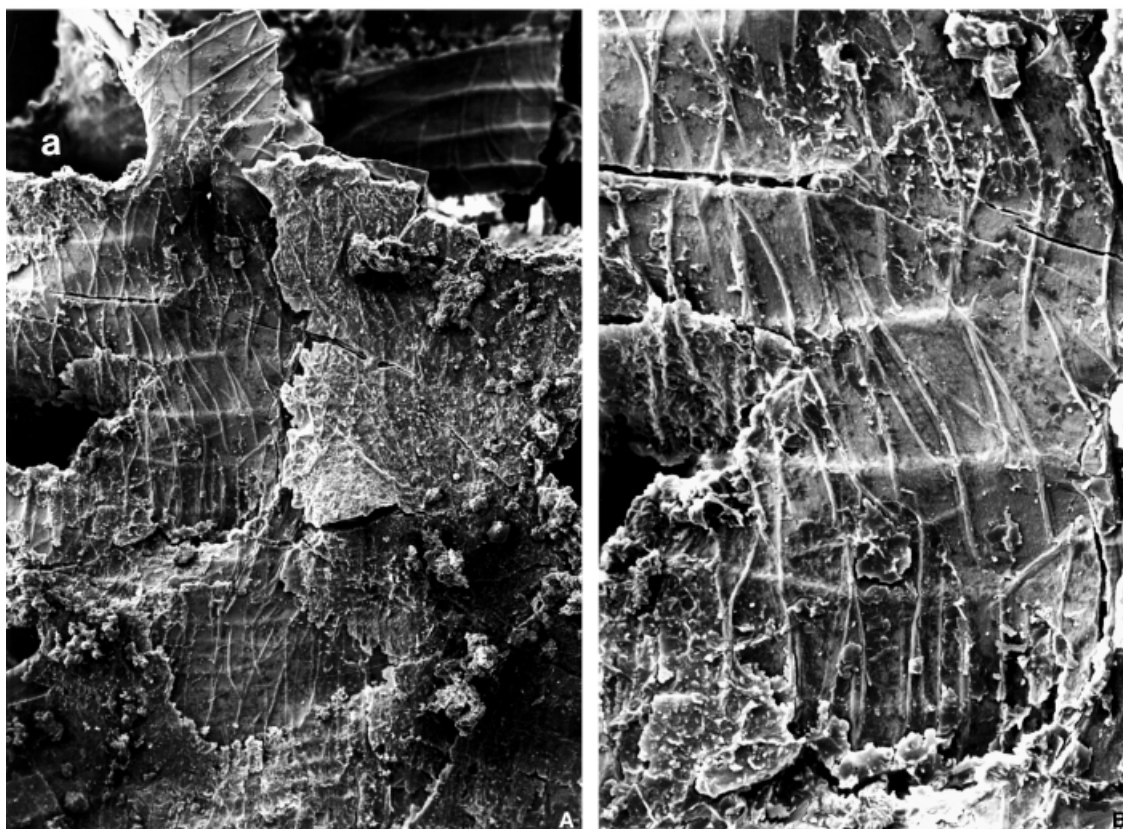
TEXT-FIG. 7. SEM micrographs of *Glyptograptus telarius* sp. nov., details of Plate 2, figure 1, holotype X.25763. A, micrograph showing lateral side of metasicula covered with longitudinal frequently overlapping bandages;  $\times 364$ . B, numerous randomly overlapping curved bandages obscuring fuselli on lateral side of  $th2^1$ ; note fine parallel striae between thickened lateral margins of individual bandages;  $\times 391$ .

number of fuselli on the free ventral wall varies from 9–11. There is a fibrillar texture, visible in several places, within the width of the fusellus and parallel to its margins (Pl. 2, fig. 6). Each fusellar growth band margin is ridge-like, giving the rhabdosome a corrugated appearance (and implies that the dovetailing of fusellar fabric envelopes is robust) especially in reflected light of a light microscope examination. There is a flowing geniculum on most specimens, and on a few the geniculum is very weak: the free ventral walls of  $th2^1$  *et seq.* are inclined at about 10–20 degrees, that is



TEXT-FIG. 8. *Glyptograptus telarius* sp. nov. SEM micrographs. A, X.25766, reverse view of slightly tilted young colony showing well preserved median septum;  $\times 40$ . B, X.25767, proximal part of broken colony showing flowing thecal geniculum;  $\times 20$ . C, X.25768, slightly flattened proximal fragment showing high and widely-spaced fuselli partly obscured by numerous longitudinal bandages of railtrack appearance;  $\times 120$ .





TEXT-FIG. 9. SEM micrographs of *Glyptograptus telarius* sp. nov., details of Text-figure 8c, showing fusellar and cortical structure on lateral side of colony. A, bandages crossing fuselli normally or obliquely and running over  $th2^1$  apertural margin (a = aperture) and  $th3^1$  genicular rim;  $\times 177$ . B, detail of A showing unconformity in overlapping bandages within different layers;  $\times 444$ .

slightly less than the figure for  $th1^1$  and  $th1^2$ . On flattened specimens it may be anticipated that the apparent geniculation would increase, as does the dorso-ventral width (to 0.60–0.65 mm). The rhabdosome is septate, possibly fully septate, from the third thecal pair. Specimens developed beyond the fourth thecal pair are not known in this material.

The whole colony has conspicuous railtrack bandages (Text-fig. 8A–B). These are sparser at the growing end of the colony, but they do reach the growing end, even where thecae are incompletely grown. They unquestionably reach the thickened thecal apertural rims and overgrow them. The vast majority of bandages are broadly parallel to the length of the colony (i.e. longitudinal or axial) and are not obviously related to individual thecae, but some do run parallel to the fuselli. There is no radiation of bandages from thecal apertures, but they do have wavy curvature and criss-cross each other at low angles giving the appearance of bifurcating thickened edges.

Bandages increase in width from the proximal end to the more distal thecae, being on the whole slightly narrower than the fuselli which they overlie on any particular theca. Because of the number of bandages and their degree of overlap, bandage length cannot be measured easily, but bandage width varies from 0.019 mm proximally to  $>0.025$  mm on the more distal thecae. Each bandage is characterised by thickened rims at the edges, the fibrous material between being very thin, although with up to ten faint fibres parallel to the long edges of the bandages. Remnants of granular sheet fabric bounding the cortical bandages have been seen on the lateral wall of the metasicula of one of the specimens (Text-fig. 9A). It consists of a granular base with small, irregular holes.

Even in early growth stages, with three thecae incomplete, bandages may be three layers thick. In some thecae there is little or no bandage covering on the zigzag septum where this is subapertural. Whether this is widespread in the

species we have been unable to ascertain. There are slight changes from one part of the colony to another. Thus, on the lateral rhabdosomal walls the bandages are rather more chaotic than the axially arranged ones elsewhere. On the metascicula they are longitudinally arranged, cross each other at low angles, and contribute directly to an endocortex inside the metascicular aperture.

*Remarks.* *G. telarius* sp. nov. is the smallest glyptograptid known, and its thecal size and spacing is more reminiscent of dendroids than of graptoloids. Probably it has the closest thecal spacing known of any graptoloid. Another unique feature is that the dorso-ventral stipe width at the level of  $th1^1/th1^2$  exceeds that at subsequent thecae. The railroad bandages are known in only one other graptolite, namely *Orthograptus gracilis* (Roemer) (see Crowther and Rickards 1977).

These features serve readily to distinguish *G. telarius* from all previously described biserial graptolites, including the other small species described below. In particular, none of the other glyptograptids in this paper has railroad bandages, and they differ on other counts too: *G. mazovoensis* has a much lower thecal spacing (14–16, cf. 28); *G. nikitini* also has a lower thecal spacing (14–11); *G. pavlinovi* has bifurcated thecal structure; *G. zimai* has a different supragenicular: infragenicular wall ratio (5:1 cf. 1.5:1); *G. t. praecursor* has a lower thecal spacing (16–13 in 10 mm) and a low supragenicular: infragenicular wall ratio (5:1 cf. 2–3:1). *G. telarius* sp. nov. has the overall rhabdosomal aspect of the *G. tamariscus* (Nicholson) group (see Packham 1962 for summary), which is commonly represented from the *cyphus* Biozone and higher. The possible evolutionary relationships of the Uralian glyptograptid to the *G. tamariscus* group is discussed above in the section on evolution (Text-fig. 3).

*Glyptograptus zimai* sp. nov.

Text-figures 10, 11C–D

*Derivation of name.* In honour of the late Dr M. Zima, distinguished graptolite worker from Kirgizstan.

*Holotype.* SM X25772, Text-figure 11c.

*Material.* Four specimens, early growth stages and more distal fragments, one of the latter more or less flattened.

*Diagnosis.* Uniform, small glyptograptid with geniculate thecae; the dorso-ventral width 0.40–0.65 mm (relief), 0.73 mm (flattened); thecal spacing 15–20 in 10 mm (2TRDs 1.0–1.31); narrow, tapering rhabdosome; septate; relatively long supragenicular wall inclined at 15–20 degrees; thecal overlap one-third; thecal apertures horizontal.

*Description.* The sicular length is unknown, but the free metascicular part is visible for 0.22 mm in reverse view, and the sicular aperture (0.14 mm) is furnished with a relatively long, thin virgella of 0.55 mm (Text-fig. 11c).  $Th1^1$  grows upwards for 0.53 mm and  $th1^2$  for 0.55 mm, dorso-ventral widths at these apertures being respectively 0.42 mm and 0.45 mm. The dorso-ventral width at  $th2^1$  is 0.55 mm, and more distally 0.65 mm (relief) and 0.73 mm (flattened).

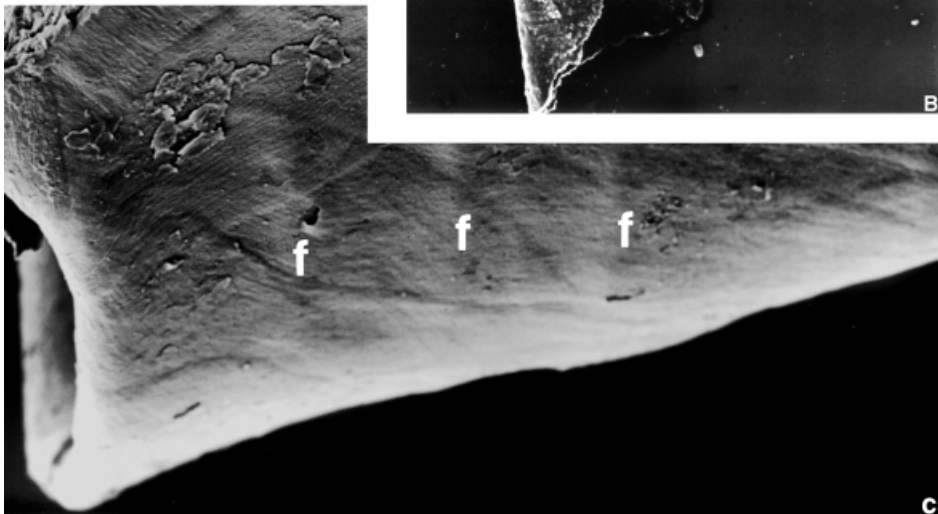
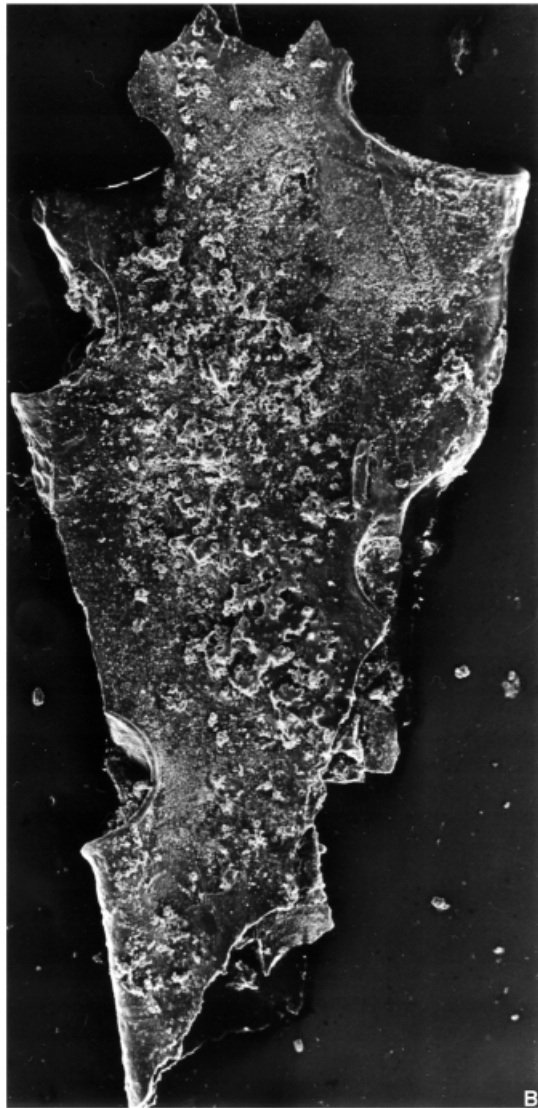
Supragenicular walls 0.44–0.55 mm; infragenicular walls 0.10–0.13 mm, giving a ratio of about <5:1. Supragenicular walls comprise 18–20 fuselli. Thecal apertures are more or less horizontal or with slight eversion (Text-fig. 10A) and they are overhung in part by a sharp geniculum; in one specimen a thickened apertural rim connects to the geniculum (Text-fig. 10B).

A further specimen is very similar to the above-described specimens but differs in one respect, namely in having longer upward-growing parts of  $th1^1$  and  $th1^2$ , respectively 0.66 mm and 0.75 mm. The thecal spacing at 14.5 in 10 mm is lower than the proximal ends of *G. zimai*: we refer this specimen (X25912) to *G. aff. zimai*.

Bandages are present on *G. zimai* (Text-fig. 10C). These are longer than 0.21 mm and have widths of 0.045–0.049 mm. All the bandages are thin and smooth, and those at lower levels are often seen pressed through. The bandages are comparatively straight and are mostly subparallel to the rhabdosomal axis, although some radiate from the thecal apertures (Text-fig. 11D).

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TEXT-FIG. 10. SEM micrographs of *Glyptograptus zimai* sp. nov. A, X. 25806, proximal fragment with no sicula;  $\times 36$ . B, X.25807, fragmentary and almost flattened specimen showing thecal rim wall;  $\times 51$ . C, detail of A showing fuselli (f) and several layers of overlapping bandages running over thecal aperture of the last theca to the left ( $th3^2$  ?);  $\times 342$ .



*Remarks.* *G. zimai* differs from *G. nikitini* in the uniform nature of the thecae and lack of vertical supragenicular walls on the proximal thecae. There is a general resemblance to *G. tamariscus varians* Packham from which it differs in its higher thecal spacing.

*Glyptograptus* sp. 1

Text-figure 11A

*Material.* A single early growth stage with only two thecae developed, in relief.

*Description.* The sicula is 1.35 mm long (prosicula 0.25 mm, with an aperture of 0.006 mm) and has an aperture 0.16 mm wide, with a short but broken virgella. Prosicular longitudinal fibres are visible near the apex of the sicula, but the prosicula/metasicula boundary is unclear. The exposed metasicular portion is 0.75 mm in reverse view, and will be more exposed than that in obverse view. Th1<sup>1</sup> grows below the horizontal sicular aperture for 0.10 mm before turning upwards for 0.87–0.88 mm. Th1<sup>2</sup> is not completely grown but has an incomplete length of almost 1 mm (its prothecal part is damaged). The overall proximal end has a slightly pointed appearance. The dorso-ventral width at the th1<sup>1</sup> aperture is 0.50 mm; it appears as though the thecae may be strongly alternating. The sicula is visible in reverse view for 0.80 mm. Overlapping cortical bandages occur on the obverse lateral wall, being especially numerous in the region of the common canal and on the proximal part of the exposed metasicula. At the latter site they obscure the fuselli. The bandages are long, flat, longitudinally arranged, and broadly curved.

*Remarks.* Again, this form resembles some of the *tamariscus* group of species, possibly most closely *G. t. varians* Packham and *G. t. acutus* Packham in the lengths and dispositions of th1<sup>1</sup> and th1<sup>2</sup>. The long th1<sup>1</sup> and th1<sup>2</sup> distinguish this form from others in the same assemblage described herein. There is a superficial resemblance of this proximal end to *Rhaphidograptus toernquisti* (Elles and Wood) but the latter has broadly climacograptid thecae: in fact the superficial resemblance really reflects the fact that the proximal end has a pointed appearance with th1<sup>1</sup> and th1<sup>2</sup> growing upwards and outwards rapidly. The main difference between *G. sp. 1* and *G. t. varians* and *G. t. acutus* is that the sicula is more exposed in reverse view.

*Glyptograptus* sp. 2

Text-figure 11B

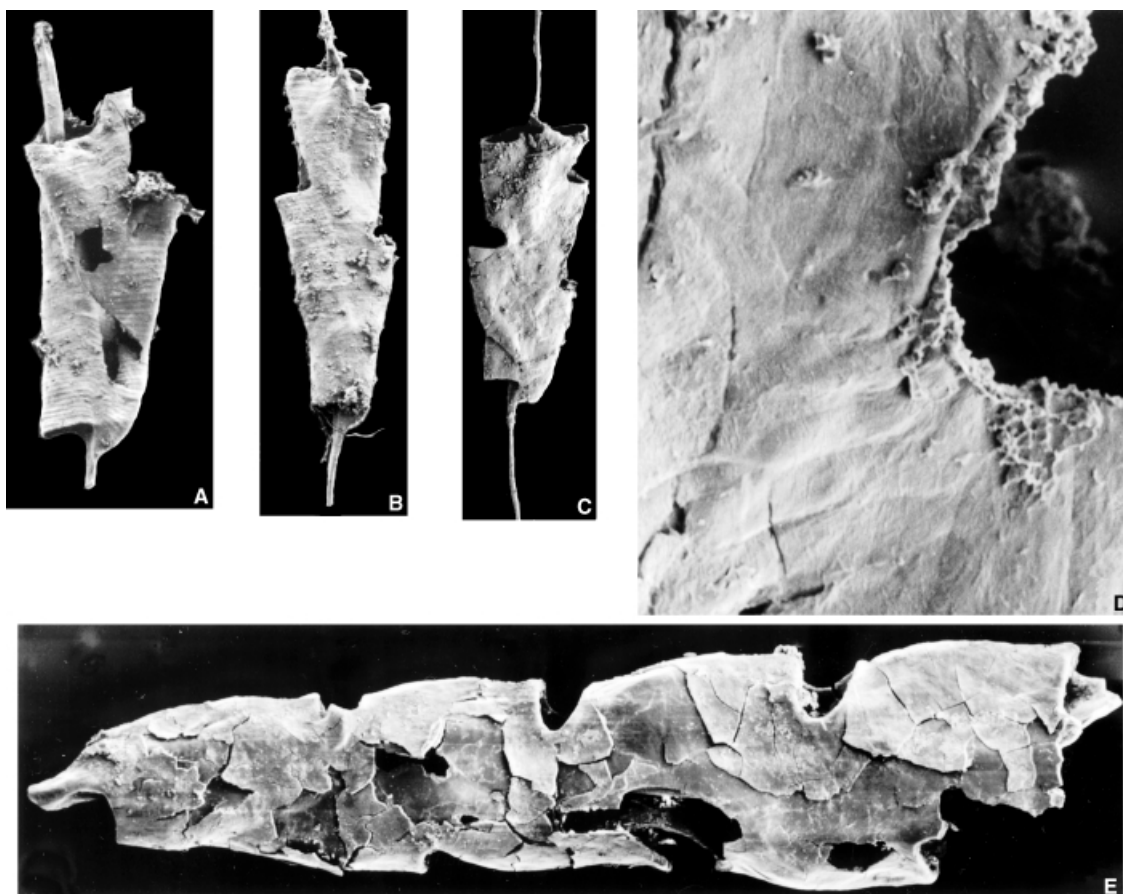
*Material.* A single, well-preserved, three-dimensional early growth stage with three complete thecae and two incomplete thecae, as an SEM preparation, and a specimen preserved in glycerine permitting obverse and reverse views (four thecae developed).

*Description.* The sicular apex is overgrown by later thecae but it is visible in reverse view for 0.20 mm and in obverse view for 0.60 mm, and has an apertural width of 0.11 mm with a virgella 0.20–0.38 mm long. Th1<sup>1</sup> grows downwards for 0.35 mm reaching below the sicular aperture for 0.08 mm before turning upwards for 0.65 mm. Th1<sup>2</sup> grows upwards for 0.70 mm, and the apertures of th1<sup>1</sup> and th1<sup>2</sup> are horizontal. The dorso-ventral width at the level of th1<sup>1</sup> is 0.38–0.39 mm, and at the level of th2<sup>1</sup> is 0.40 mm. The thecal spacing is 15 in 10 mm (2TRD 1.3 mm). The overall appearance of the proximal end is a narrow, tapering, even pointed species, with straight thecae possessing a small geniculum positioned quite low down so that the supragenicular wall (0.42 mm) is relatively long with a supragenicular/infragenicular ratio of about 5:1. The rhabdosome is septate from the third thecal pair. Growth fuselli are visible in places and number 15 on the metatheca of th2<sup>2</sup>.

*Remarks.* *G. sp. 2* differs from *G. zimai* in having longer th1<sup>1</sup> and th1<sup>2</sup> which grow straighter upwards. It is also narrower than *G. zimai*.

Genus PSEUDOGLYPTOGRAPTUS Bulman and Rickards, 1968

*Type species.* By original designation, *Glyptograptus (Pseudoglyptograptus) vas* Bulman and Rickards, 1968, Llandovery, northern England.



TEXT-FIG. 11. A, *Glyptograptus* sp. 1. SEM micrographs. A, X.25769, young colony with sicula visible for most of its length, reverse view;  $\times 40$ . B, *Glyptograptus* sp. 2, X.25770, growing colony at the stage of the third pair of thecae, reverse view;  $\times 40$ . C–D, *Glyptograptus zimai* sp. nov. C, X.25772, holotype, young rhabdosome at the stage of third and fourth pair of growing thecae, reverse view;  $\times 32$ . D, SEM detail of C showing apertural part of  $th_2^1$  with numerous cortical bandages running to its aperture;  $\times 480$ . E, *Pseudoglyptograptus?* sp., X.25771, adult colony broken at the level of fourth pair of thecae, obverse view;  $\times 60$ .

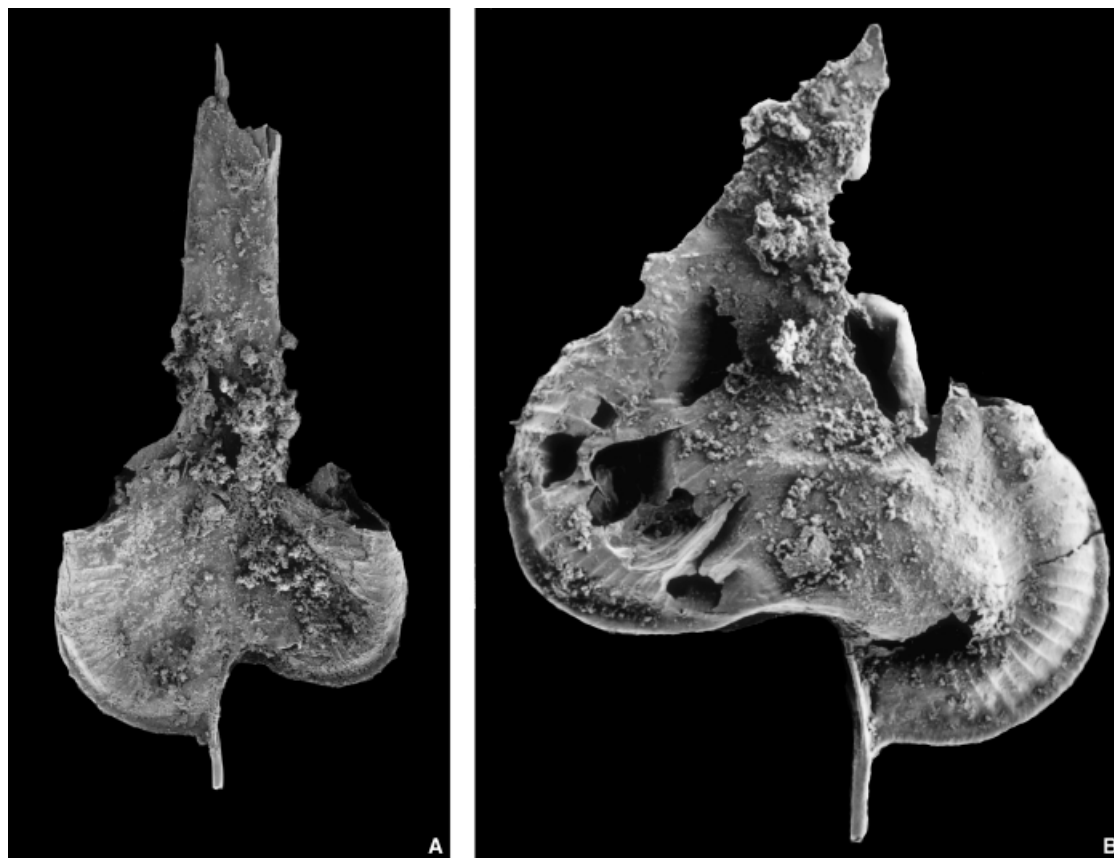
*Diagnosis.* Glyptograptid distinguished by concavo-convex supragenicular wall, strongly everted apertures, and a subapertural constriction, sometimes transverse.

*Pseudoglyptograptus?* sp.

Text-figure 11E

*Material.* A single, well-preserved rhabdosome in full relief, obverse view, three pairs of thecae well developed as well as a complete  $th_4^1$ .

*Description.* The most striking features are the gently tapering rhabdosome, the horizontal thecal apertures, and the gently convex supragenicular walls becoming slightly concave just below the thecal apertures. The view exhibits the sicula for 0.42 mm above an aperture 0.13–0.14 mm wide. There is a robust virgella, broken after 0.15 mm.  $Th_1^1$  grows below the horizontal sicular aperture for 0.12 mm before turning upwards for 0.56–0.57 mm.  $Th_1^2$  grows upwards for a similar distance, although in obverse view its origin is obscured.



TEXT-FIG. 12. *Cystograptus vesiculosus* (Nicholson); fragments of young colonies with almost completed first pair of thecae; SEM micrographs. A, X.25773, obverse view;  $\times 60$ . B, X.25774, reverse view;  $\times 53$ .

The dorso-ventral width at  $th1^1$  is 0.39 mm, at  $th2^1$ , 0.44 mm and at  $th3^1$ , 0.52 mm. At  $th4^1$  the dorso-ventral width is estimated at 0.58 mm. These dimensions define the gently tapering nature of the rhabdosome.

Thecal spacing is 17–18 in 10 mm (2TRDs 1.07, 1.10 at  $th1^1/th2^1$  and  $th2^1/3^1$  respectively). Thecal excavations are 0.11 mm wide and 0.10 mm long ( $th3^1$  aperture), and they occupy one-quarter of the rhabdosomal dorso-ventral width. The geniculum is sharply rimmed, but overall has a flowing rather than an angular aspect.

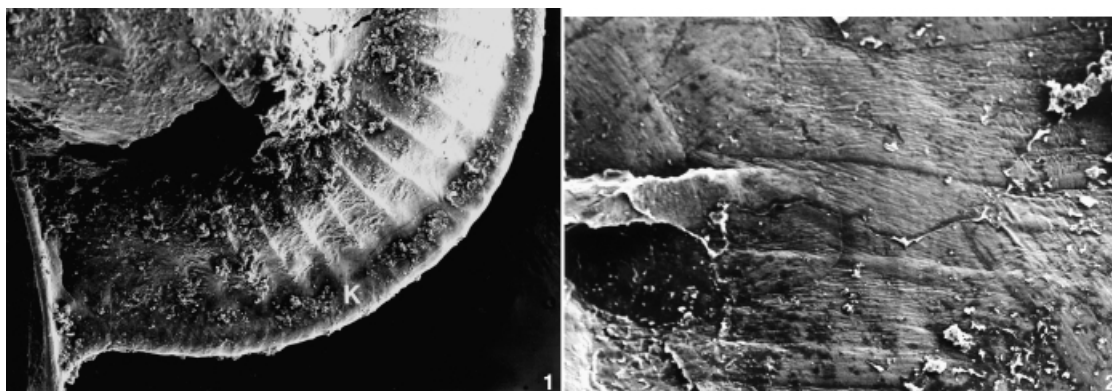
There are faint suggestions of bandages in the thick, flaking cortex, and these are broadly along the lengths of the thecae. Fuselli are almost totally obscured, but seem spaced at about 12 per metatheca, as seen on  $th2^1$ .

*Remarks.* This is a minute pseudoglyptograptid? with close thecal spacing, quite distinct from all the other forms described in this paper in the nature of the metathecae. There are small but clear similarities with the genus *Pseudoglyptograptus* Bulman and Rickards (1968), which post-dates this form, being typical of the mid-Llandovery.

#### Genus CYSTOGRAPTUS Hundt, 1942 (emend. Rickards, 1970)

*Type species.* Subsequently designated by Jones and Rickards, 1967, *Diplograptus vesiculosus* Nicholson, 1868, Llandovery, Scotland.

*Diagnosis.* Diplograptid with long, overlapping, doubly sigmoidal thecae; thecal apertures everted, facing ventrally; rhabdosomal cross-section rectangular; sicula and  $th1^1$  very long; often possessing nemal vanes.



TEXT-FIG. 13. SEM micrographs of *Cystograptus vesiculosus* (Nicholson). A, fragment of specimen in Text-figure 12B, X.25774, the lowermost part of  $th1^1$  showing high fusellar ridges, cortical bandages running over keel (k);  $\times 117$ . B, detail of A showing overlapping cortical bandages; note scarp-edged lateral margins and broadly rounded ends;  $\times 285$ .

*Cystograptus vesiculosus* (Nicholson) *s.l.*

Text-figures 12–13

- 1868 *Diplograptus vesiculosus* Nicholson, p. 57, pl. 3, fig. 11.  
 1907 *Diplograptus* (*Orthograptus*) *vesiculosus* Nicholson; Elles and Wood, p. 229, pl. 28, fig. 8a–d; text-fig. 151a–f.  
 1967 *Cystograptus vesiculosus* (Nicholson); Jones and Rickards, text-figs 3d, 6, 8a–d.  
 1974 *Cystograptus vesiculosus* (Nicholson, 1868); Hutt, p. 45, pl. 4, fig. 15; pl. 5, figs 4–5; text-fig. 9, figs 4–5.  
 1982 *Cystograptus vesiculosus* (Nicholson, 1868); Urbanek, Koren' and Mierzejewski, p. 207, figs 1–21.  
 1985 *Cystograptus vesiculosus* (Nicholson); Storch, p. 96, pl. 2, figs 1, 5, 7; pl. 4, figs 2, 7–8; text-fig. 3E–H.  
 1996 *Cystograptus vesiculosus* (Nicholson, 1868); Koren' and Rickards, pl. 3, figs 4–10.

*Material.* Ten isolated specimens, one mounted for SEM in obverse view, one in reverse; both are early growth stages with  $th1^1$  and  $th1^2$  partly grown and partly broken. Numerous other fragments of sicula and thecae.

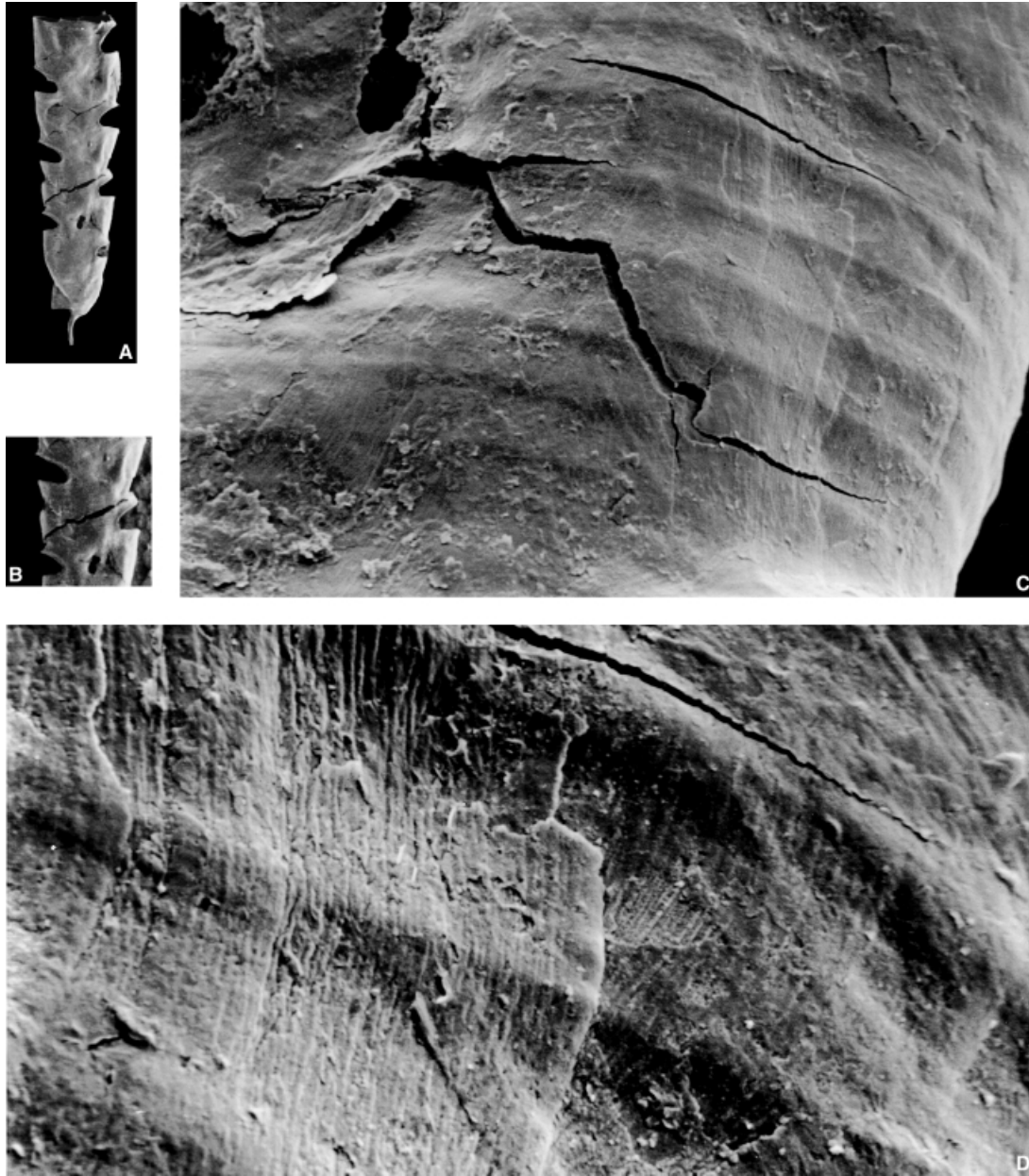
*Description.* The rhabdosomal width at the level of the first thecal pair is 1.13 mm, although the anticipated apertural retroversion and subsequent 'geniculum' are not developed in this growth stage. In  $th1^1$  22–23 fuselli are developed, and a similar number in that portion of  $th1^2$  seen. No growth lines are visible on the metasacula. The sicular aperture is concave, 0.20 mm wide, and  $th1^1$  extends below its level by 0.42 mm before turning upwards.

A very prominent keel is developed along the central part of the ventral walls of both  $th1^1$  and  $1^2$  (Text-figs 12–13A). The keel is sharp, laterally flattened, and 0.05 mm high, but diminishing to zero aperturally (remembering that the thecae are incomplete and the final aperture not reached). The overall curvature of both  $th1^1$  and  $th1^2$  is semicircular but, presumably, when completed would show the double sigmoidal curvature of the species.

At this stage of growth the 'apertures' are strongly everted, which presages the ultimate ogee curvature of the thecal tubes.

The fuselli are high, conspicuous ridges, in spite of an extensive covering of cortex. The cortex is conspicuously bandaged, each bandage being 0.08 mm wide and at least 0.24 mm long; frequent overlaps make exact measurement difficult. The bandage edges are sharp but not especially thickened. Coarse, parallel fibres are visible within them, parallel to their lengths, but are not easily counted. Each fibre may represent a bundle of collagen fibrils normally detectable in ultrathin slices. Bandages cross the thecal ventral keels at various angles, and the general disposition of bandages seems varied.

There are two peculiarities on the specimens. The first concerns the base of the virgella. It would seem that there is a thickened rib on both the obverse and reverse sides of  $th1^1$ ; these two ribs embrace the very basal/proximal part of the



TEXT-FIG. 14. SEM micrographs of *Normalograptus legrandi* sp. nov. A, X.25808, holotype, colony broken at the level of fifth pair of thecae, reverse view;  $\times 20$ . B-C, details of A showing aperture of  $th2^2$ , geniculum and supragenicular wall of  $th2^1$  with randomly-overlapping bandages; B  $\times 30$ ; C,  $\times 480$ . D, detail of C showing fusellar ridges crossed by longitudinal bandages; note also pitted sheet fabric enveloping individual bandages;  $\times 1800$ .

virgella, which remains as a thin rod between the said ribs. Thinner periderm certainly connects the ribs to each other and to the virgella (Text-fig. 13A).

The second strange feature is seen as  $th1^1$  turns upwards: there are fine ridges/striations aligned normal to the fuselli boundaries, but which are unrelated to the cortical bandages. This feature is discussed further in the section on fuselli above.



*Remarks.* The ridges/striations normal to the fuselli may be similar to the texture described by Rickards *et al.* (1971) in *Monograptus* (a structure which was subsequently considered to be fragments of bandages; Rickards and Dumican 1984). In the case of *Cystograptus* it seems to have no real relationship to the bandages. Possibly it is some kind of membranous layer overlying the fuselli. Fragments of nematularia (the vaned virgular modifications) have previously been described (Urbanek *et al.* 1982), especially the ultrastructure. No bandages were detected on the nematularium.

#### Genus NORMALOGRAPTUS Legrand, 1987

*Type species.* By original designation, *Climacograptus scarlaris* var. *normalis* Lapworth, 1877, Llandovery, Scotland.

*Diagnosis.* Proximal development of *normalis* (H) Pattern; thecae with sharp sigmoidal curvature and conspicuous geniculum; infragenicular wall inclined at more than 45 degrees from the vertical; supragenicular wall more or less vertical; rhabdosomes septate, partially septate or aseptate; apertures usually more or less horizontal; thecal and sicular spinosity rare; sicula usually less than 2 mm long; cortical bandages possibly more randomly orientated than in some groups.

#### *Normalograptus legrandi* sp. nov.

Plate 3; Text-figures 14–17

*Derivation of name.* In honour of Dr P. Legrand.

*Holotype.* SM X25808, Text-figure 14A.

*Material.* Five specimens in relief, mostly early growth stages with the sicula and first 2–4 pairs of thecae.

*Diagnosis.* Diminutive normalograptid with a dorso-ventral width of 0.45–0.52 mm, and a maximum distal dorso-ventral width (at th<sup>4/5</sup>) of 0.60 mm, a thecal spacing of 24–19 in 10 mm; minute sicula 0.82–0.96 mm long; supragenicular walls inclined outwards at <5 degrees.

*Description.* The rhabdosome is characterized by its minute size, rounded proximal end, and supragenicular walls which slope outwards very gently, usually at <5 degrees (Text-fig. 14A).

The sicula is 0.82–0.96 mm long and has an aperture 0.12–0.16 mm wide. Th<sup>1</sup> grows downwards for 0.26–0.28 mm, and upwards for 0.45–0.66 mm, reaching to 0.06–0.08 mm below the sicular aperture. Th<sup>2</sup> grows upwards for 0.48–0.66 mm (the lower figures in obverse views). The sicular apertural region is visible in reverse view for 0.12–0.15 mm and in obverse view for 0.41–0.55 mm. The virgella is short and needle-like, some 0.14–0.20 mm long.

The dorso-ventral width at th<sup>1</sup> is 0.40–0.58 mm; at th<sup>2</sup>, 0.50–0.58 mm; at th<sup>3</sup>, 0.55 mm and at th<sup>4</sup>, 0.60 mm. The thecal apertures are broadly horizontal and the thecal excavations 0.10–0.15 mm deep by 0.08–0.13 mm long, forming about one-fifth to one-sixth the dorso-ventral width of the rhabdosome. The supragenicular:infragenicular wall ratio is 3.5:1. The supragenicular walls are in some cases almost vertical after the first two pairs of thecae or may slope outwards at <5 degrees. The geniculum is always sharp and sometimes thickly rimmed, even around the apertural lip.

The rhabdosomes are heavily bandaged over clear fuselli, which number 14–15 on the supragenicular wall of th<sup>2</sup> and 15–19 on the metatheca of th<sup>1</sup>. The bandages seem constant in width for one specimen, but vary sharply from specimen to specimen: the widths are of the same order as the widths of the fuselli (Text-fig. 14C–D). Some examples of bandage width are as follows: 0.02, 0.025, 0.027, 0.03, 0.035, 0.037, 0.042 mm. Bandages are more or less straight, generally curved, or even wavy, and of very varied distribution, only locally parallel where they traverse an apertural lip (Text-fig. 15). Some parallel groupings along the length of the metasicula continue down the length of the virgella, wrapping around it (Pl. 3, fig. 3; Text-fig. 15B). The lateral margins of the bandages are clearly distinguished but not unusually thickened. Bandage lengths are not easy to measure, given their frequent overlap, but some are: 0.10, 0.13, 0.17, 0.20, 0.23, 0.24, 0.25, 0.26 mm. The bandage ends can be rounded or rectangular, and within them, parallel to the

long edges, are fibres possibly representing fibril bundles of collagen (Text-figs 16–17). These latter number 18–25, but are not easy to count. In some places (Text-fig. 14c) the sheet fabric has broken away, revealing probable individual collagen fibrils with their annulation preserved. Sheet fabric is often present, and consists of irregular pits in a granular background.

*Remarks.* *N. legrandi* sp. nov. is one of the tiniest species referred to the genus. In overall appearance it recalls *N. angustus* Perner or *N. mirnyensis* (Obut and Sobolevskaya), but differs from both in its high thecal spacing (e.g. in a 5-mm length of *N. mirnyensis* the original description established 6.5–7.5 thecae, compared with nine in *N. legrandi* sp. nov.). The new species also has a consistently shorter virgella, smaller sicula (half the length) and a shorter  $th1^1$ . The thecae are quite different from those of *N. melchini* sp. nov., described next, especially in the contrasting excavations and nature of the supragenicular wall. *N. melchini* also has an even narrower rhabdosome and is probably the narrowest known normalograptid.

*Normalograptus melchini* sp. nov.

Text-figures 4D, 19–21

*Derivation of name.* In honour of Dr M. Melchin.

*Holotype.* SM X25817, Text-figure 4D.

*Material.* Eighteen specimens in relief, mostly with 2–4 thecal pairs developed.

*Diagnosis.* Unusually slender, parallel-sided normalograptid with minute thecal excavations, strongly alternating thecae, which may be slightly introverted, and elongate supragenicular walls; supragenicular:infragenicular wall ratio >6:1; thecal spacing 15–20 in 10 mm; rhabdosomal width 0.32–0.46 mm.

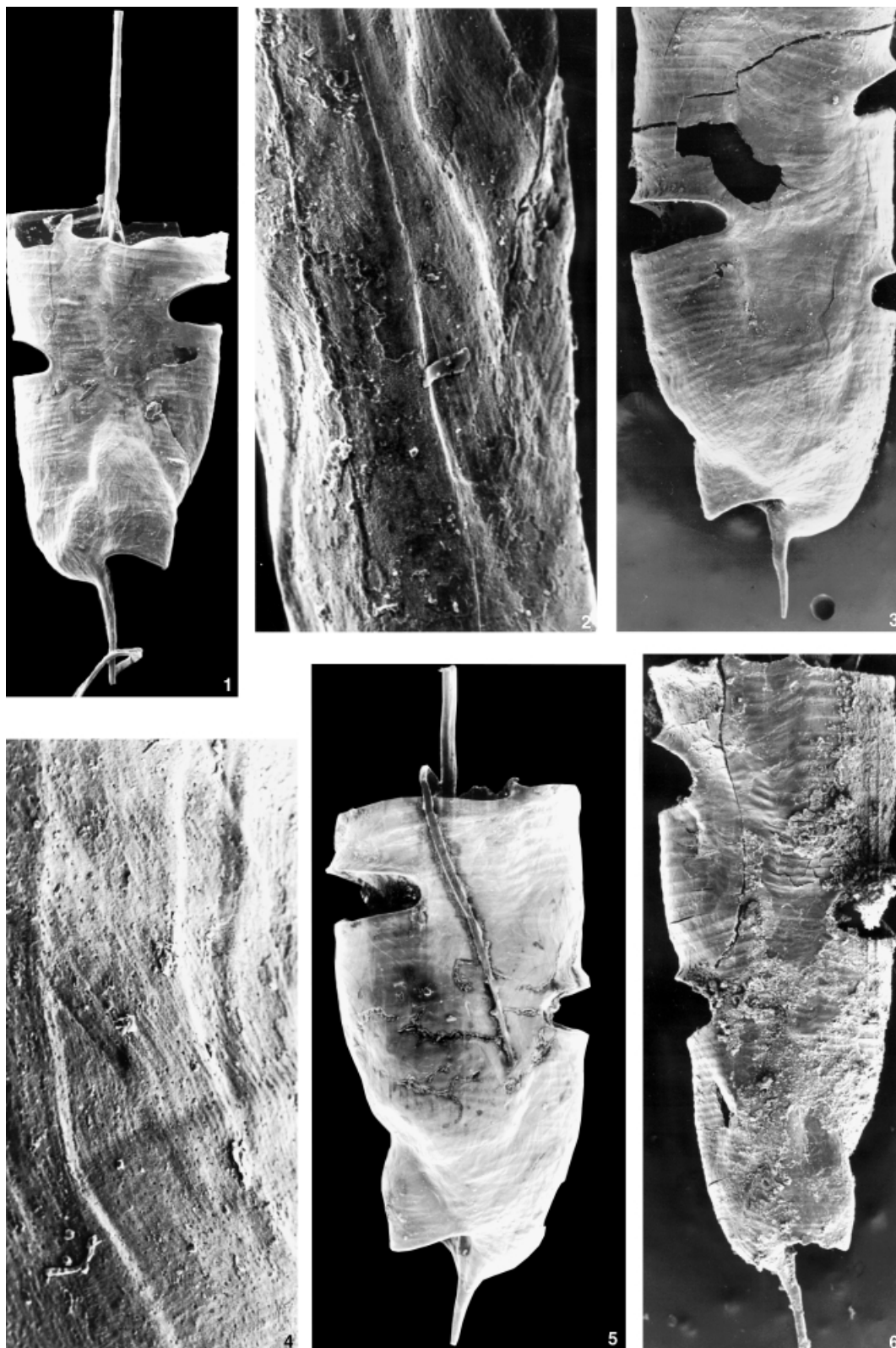
*Description.* The sicula is probably about 0.80–1.08 mm long although it is almost wholly covered in the apertural region, approximately 0.12–0.22 mm wide, being visible in reverse view, and 0.30–0.51 mm in obverse view (Text-fig. 20). The sicular aperture is 0.09–0.12 mm broad; the virgella is robust, short and spike-like, but mostly broken in our material, the exceptions ranging from 0.27–0.45 mm long.

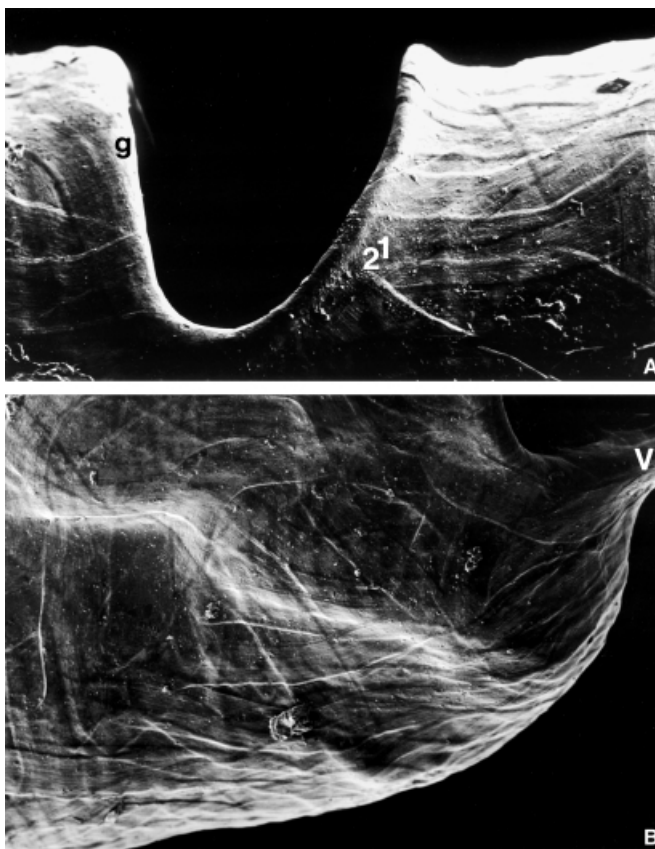
$th1^1$  turns upwards 0.02 mm below the horizontal sicular aperture, and grows upwards for 0.52–0.68 mm, and  $th1^2$  has a length of 0.54–0.64 mm. For a rhabdosome of these dimensions, therefore,  $th1^1$  and  $1^2$  are relatively long. The dorso-ventral rhabdosomal width at the level of the aperture of  $th1^2$  is 0.31–0.40 mm; at  $th2^1$ , 0.35–0.46 mm; at  $th3^1$ , 0.38–0.40 mm. After the first thecal pair there is very little rhabdosomal taper and it remains parallel-sided at more or less 0.40 mm. The rhabdosomal cross section is oval rather than round, and this is certainly an original, unflattened, feature.

The supragenicular:infragenicular wall ratio is >6:1, the excavations being minute and occupying about one-seventh the dorso-ventral width of the colony (Text-fig. 20). The excavation depth is of the order of 0.04–0.08 mm, and

EXPLANATION OF PLATE 3

Figs 1–6. *Normalograptus legrandi* sp. nov. SEM micrographs. 1, X.25775, young colony at the stage of second pair of thecae, showing numerous cortical bandages extending up to the growing end as seen on lateral side of rhabdosome;  $\times 85$ . 2, proximal part of free virgella displaying longitudinal bandages and pitted sheet fabric;  $\times 25,000$ . 3, X.25776, young colony and three pairs of thecae showing sharp fusellar ridges and thick cortical bandages to the growing end, reverse view; the diagonal rod is an artefact;  $\times 100$ . 4, detail of 3, showing longitudinal bandages and pitted sheet fabric on supragenicular wall of  $th21$ ;  $\times 2310$ . 5, X.25777, young colony with two pairs of incomplete thecae, reverse view;  $\times 100$ . 6, X.25778, young colony with three incomplete pairs of thecae, obverse view;  $\times 90$ .





TEXT-FIG. 15. SEM micrographs of *Normalograptus legrandi* sp. nov. A, detail of specimen on Plate 3, figure 1, X.25775, showing overlapping bandages running over the  $th1^1$  aperture and geniculum (g) of  $th2^1$ ;  $\times 396$ . B, detail of specimen as above showing several layers of cortical bandages on the lateral wall of the  $th1^1$  downward- and upward-growing portions, as well as on subapertural part of metasicula; v, virgella;  $\times 246$ .

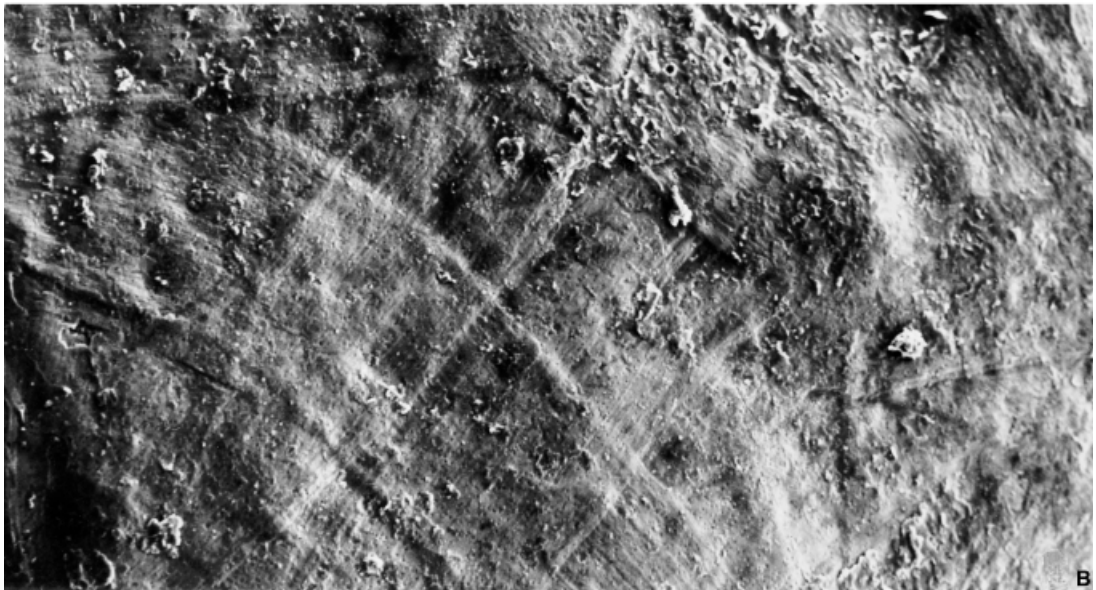
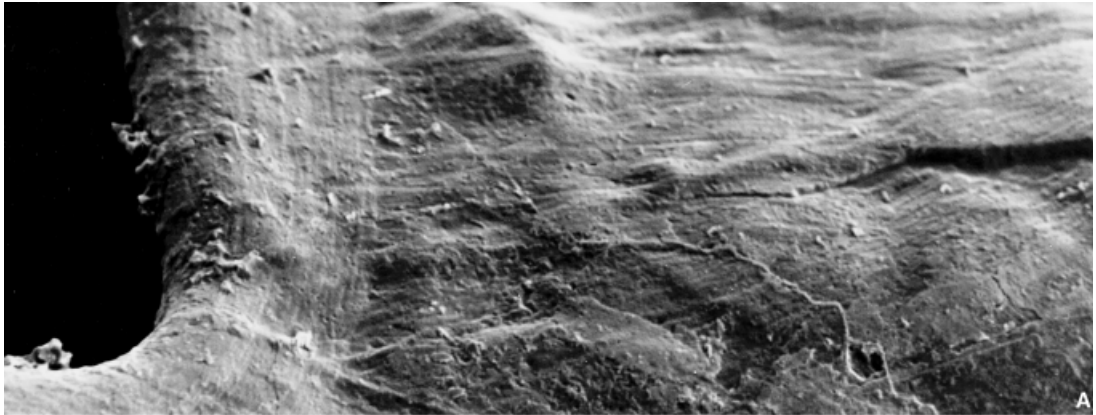
the length 0.06 mm, the apertural lips being either horizontal or very slightly introverted. Each geniculum seems to be completed before that theca continues further growth, so that the apertural region is quickly hooded by the succeeding theca.

Thecal spacing is 15–20 in 10 mm (2TRDs 1.02–1.36 mm) and the apertures strongly alternating, separated by long, vertical, supragenicular walls. The rhabdosome is septate from the third thecal pair, although the degree of bandaging usually obscures its appearance on the lateral walls.

The rhabdosomes are well bandaged, bandage widths being 0.034–0.038 mm, and lengths 0.072–0.11 mm, so that they are relatively wide and short with neatly rounded ends. Curvature varies from almost straight to slightly curved (banana-shaped) (Text-figs 19, 21B). Some radiate from the thecal apertures (Text-fig. 19A), and on the lateral walls of the thecae they have a more random distribution (Text-fig. 21B). Each bandage appears to be encased in a membranous layer, which is flaking off in places.

The bandages are slightly longer where  $th1^1$  turns upwards along the virgella, and they grow downward along the virgella. Fibres (? fibrils) within the bandages are finer and less distinctive than those of the other species in this fauna, but they are more numerous.

**Remarks.** This is the most distinctive normalograptid known, and its combination of narrowness, minute semicircular excavations, and long supragenicular walls, serves to distinguish it from any previously described forms. Only in thecal spacing does *N. melchini* sp. nov., resemble *N. legrandi* sp. nov., and even then the overlap in measurement of this feature is small.



TEXT-FIG. 16. SEM micrographs of *Normalograptus legrandi* sp. nov. A, detail of Plate 3, figure 5, X.25776, showing horizontal and longitudinal bandages on  $th_2^1$  apertural margin and on its lateral wall;  $\times 717$ . B, detail of Plate 3, figure 5 showing frequently, and irregular, overlapping bandages on lateral wall of  $th_1^2$ ;  $\times 967$ .

*Normalograptus sobolevskayae* sp. nov.

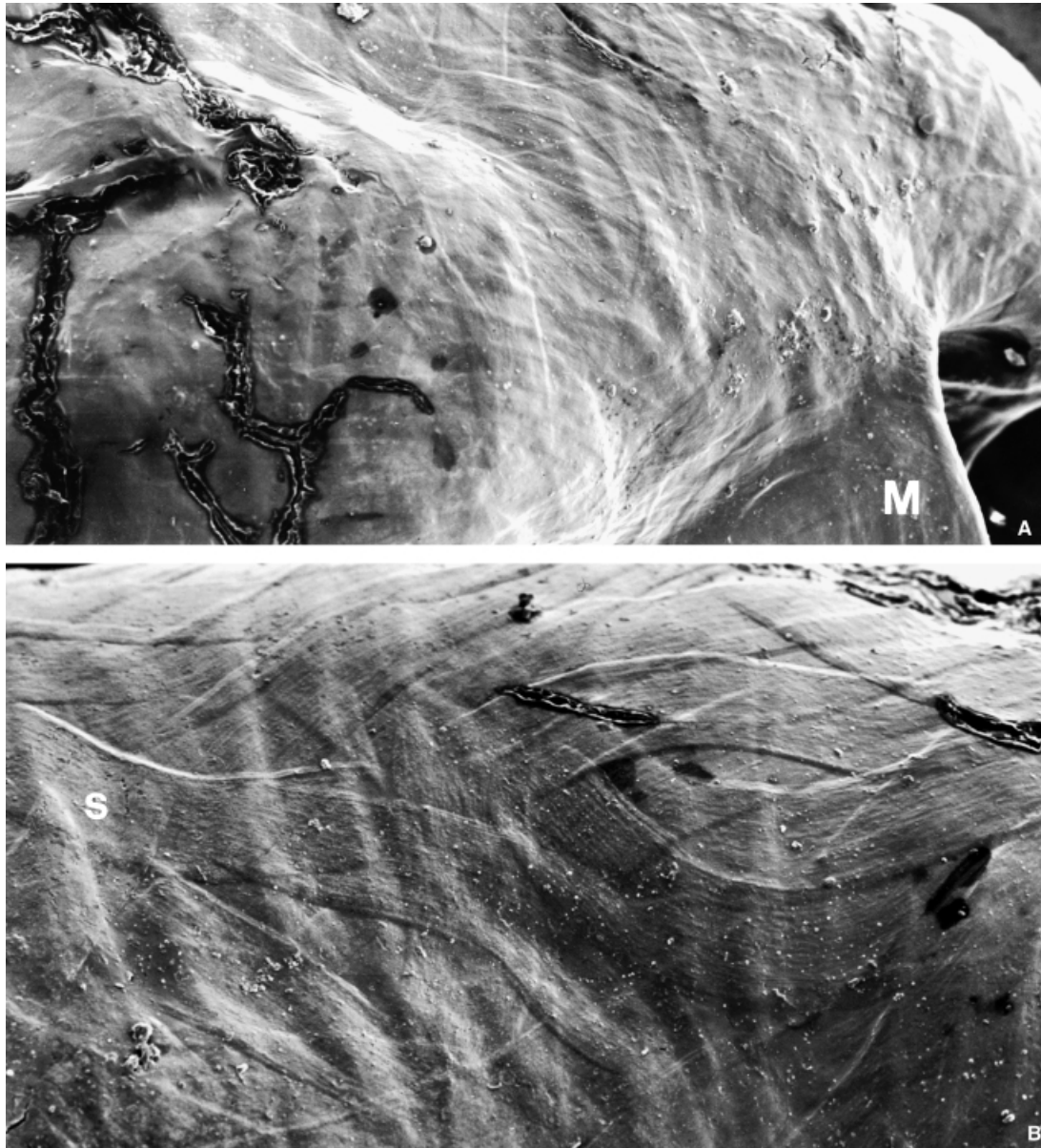
Text-figures 22–26

*Derivation of name.* In honour of Dr Rimma Sobolevskaya.

*Holotype.* SM X25784; Text-figure 22c.

*Material.* Eleven specimens showing various developmental stages from the first to the fourth thecal pairs.

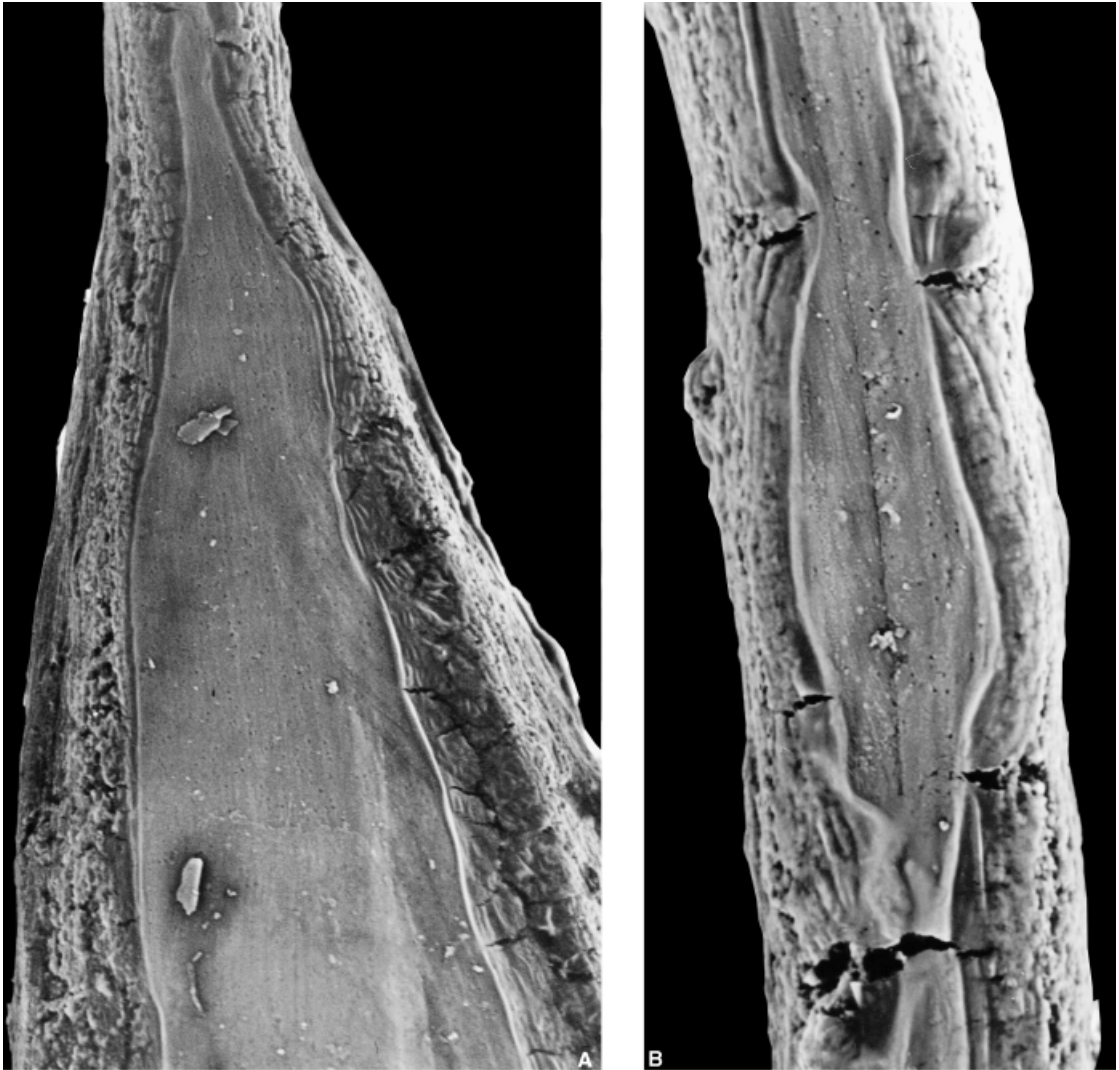
*Diagnosis.* Minute normalograptid, 0.37–0.55 mm wide, with a thecal spacing of 15–21 in 10 mm; septate; alternating thecae; supragenicular walls vertical to slightly inclined outwards; short, moderately deep excavations.



TEXT-FIG. 17. SEM micrographs of *Normalograptus legrandi* sp. nov. A, detail of specimen on Plate 3, figure 2, X.25777, showing cortical bandages on lateral wall of  $th1^1$  and partly on subapertural part of metasicula (M); note their irregular overlapping and banana-shaped outline;  $\times 430$ . B, detail of showing  $th2^1$  supragenicular wall covered with scarp-edged bandages; note parallel fibres between their margins and pitted sheet fabric (s);  $\times 525$ .

*Description.* The sicula has a length of 0.87 mm, its apex reaching close to the level of the aperture of  $th2^1$ . In obverse view it is exposed for 0.48–0.54 mm (Text-fig. 22A), and in reverse view for 0.23–0.28 mm (Text-fig. 22E). The sicular aperture is 0.11–0.17 mm wide and is furnished with a relatively long, spike-like, virgella 0.15–0.45 mm long. The sicular aperture is horizontal or with a slight dorsal tongue (Text-fig. 22E–G).

The proximal end is tapering, almost pointed in some specimens, caused by the supragenicular walls leaning slightly



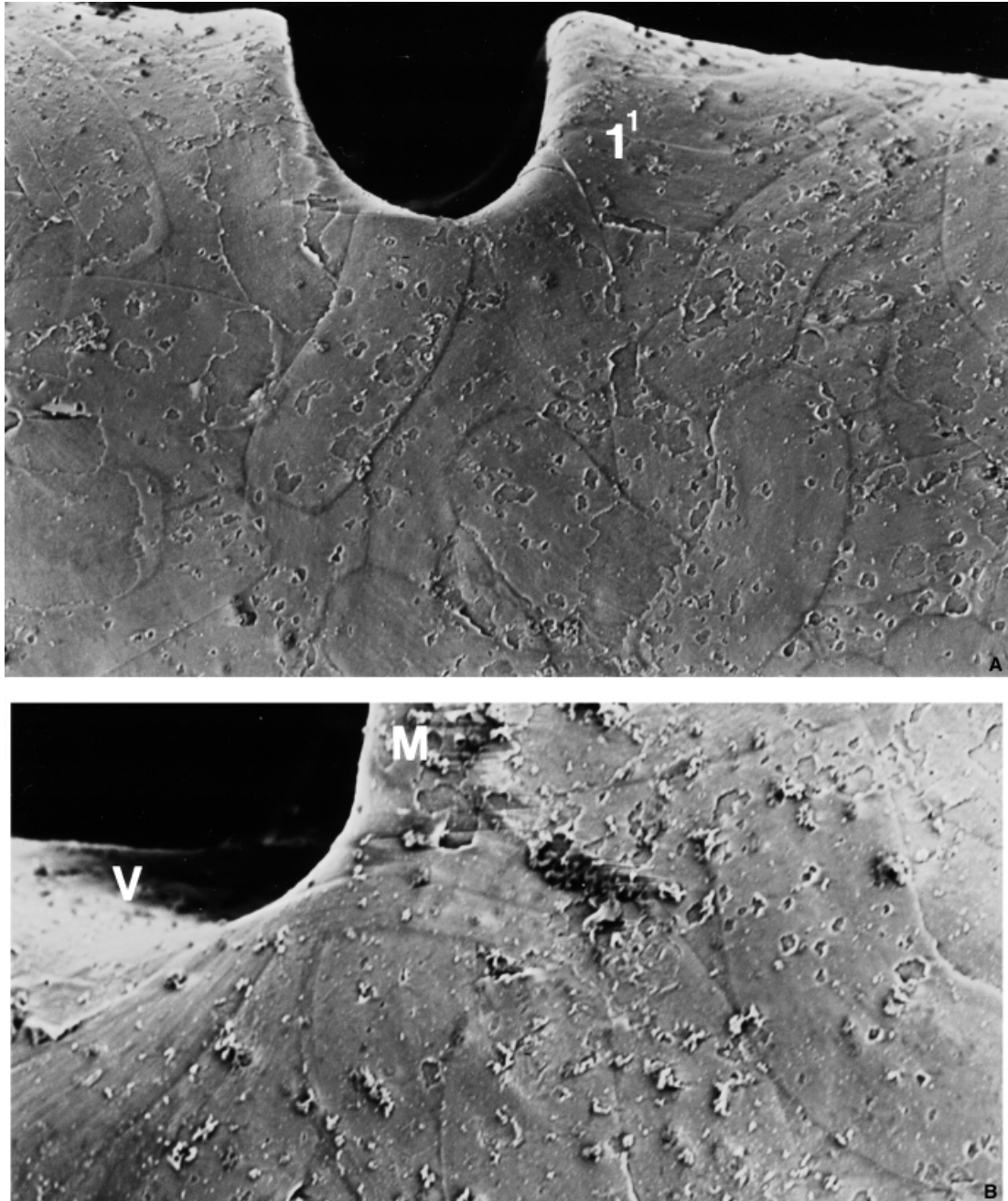
TEXT-FIG. 18. *Normalograptus legrandi* sp. nov., SEM micrographs; X.25779, prosicula tip (A) and nema (B);  $\times 2280$ .

outwards.  $th1^1$  grows downwards for 0.22–0.25 mm and reaches some 0.065–0.10 mm below the sicular aperture, before turning upwards for 0.50–0.68 mm. The upward growing  $th1^2$  has a length of 0.45–0.78 mm. The dorso-ventral width of the rhabdosome is, at the level of the aperture of  $th1^1$ , 0.37–0.46 mm;  $th2^1$ , 0.41–0.53 mm;  $th3^1$ , 0.50–0.58 mm; and  $th4^1$ , one specimen only, 0.55 mm. The thecal spacing is 15–21 in 10 mm (2TRDs, 0.95–1.29 mm).

Thecal excavations have a depth of 0.09–0.12 mm and a length of 0.07–0.17 mm that is broadly semicircular. As a proportion of the rhabdosome width at any one point they have the ratio of approximately 1:5. The supra-genicular wall is relatively long, with a supra-genicular:infragenicular wall ratio of 6 or 7:1. Two specimens, possibly referable to *N. cf. sobolevskayae*, have ratios of 4 or 5:1, but in all other dimensions compare closely with the types. The genicular rim is well marked in most of the specimens by a slight thickening (Text-fig. 22C–D). The rhabdosome is septate, the septum beginning opposite the mid-point of the supra-genicular wall of  $th3^2$ .

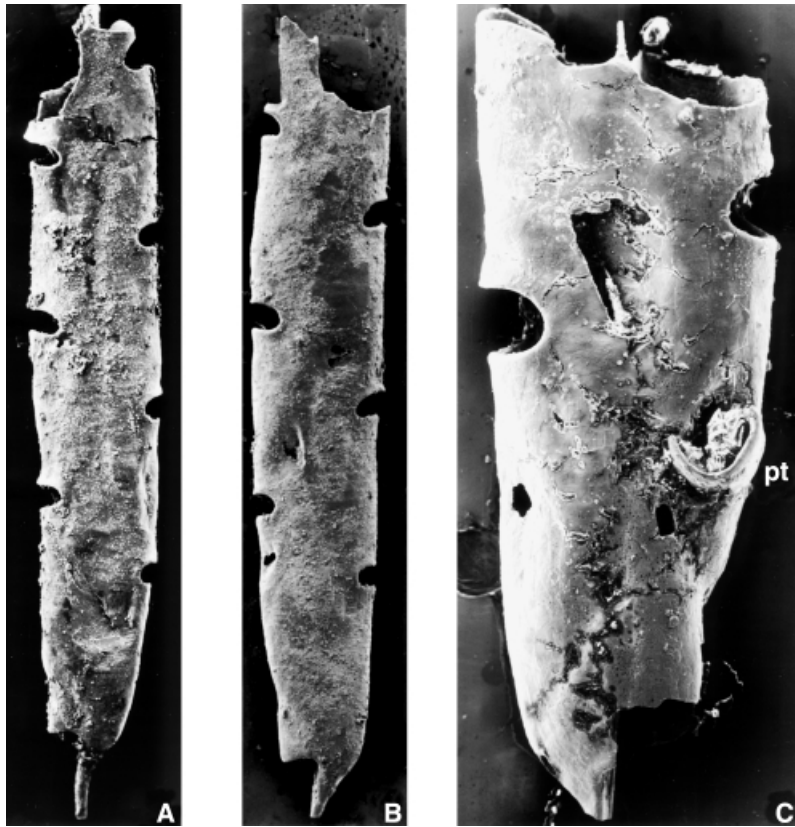
Bandages are well developed in this species, often almost obscuring the fuselli, and banana-shaped (Text-fig. 23C–D). On the metasicula they occur longitudinally but also obliquely, the latter possibly being the later ones.





TEXT-FIG. 19. SEM micrographs of *Normalograptus melchini* sp. nov., X.25809; details of irregularly overlapping banana-shaped cortical bandages on the lateral wall of the proximal part of the adult colony; parallel striae or fibres are hardly visible because of thick sheet fabric enveloping individual bandages. A, apertural and genicular rims of th1<sup>1</sup> and th2<sup>1</sup>;  $\times 470$ . B, subapertural part of metascicula (M) and inner part of virgella (v);  $\times 830$ .



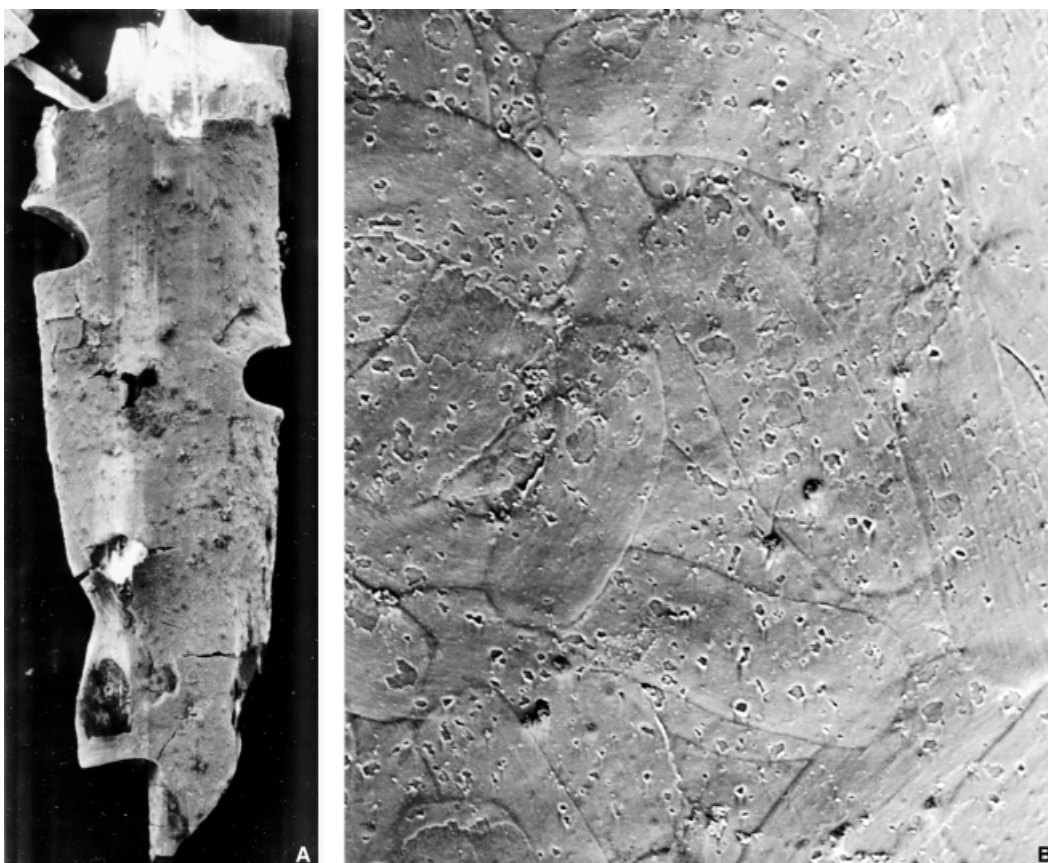


TEXT-FIG. 20. *Normalograptus melchini* sp. nov., SEM micrographs. A–B, fragments of adult rhabdosomes broken at the level of fourth pair of thecae, reverse view. A, X.25780;  $\times 83$ . B, X.25781;  $\times 83$ . C, X.25782, young colony with two incomplete pairs of thecae covered by overlapping cortical bandages; note 'pseudotheca' (pt) with rimmed apertural margin formed on (?through) the lateral wall of  $th1^2$ ;  $\times 89$ .

The bandages strongly coat and thicken the virgella, mostly growing longitudinally (sometimes with a clear seam at bandage edges) but near the base of the virgella they are often wrapped around it, thickening and smoothing its junction with both the sicular aperture and the down-growing portion of  $th1^1$  (Text-fig. 25B). All bandages have clearly defined margins and are probably of the type described by Crowther (1981) as scarp-edged (see, for example, Text-fig. 23D). On the obverse lateral walls of  $th1^1$  a lower layer of bandages is roughly parallel to the fuselli, and an outer layer is broadly at right angles to the fuselli, very roughly parallel to the rhabdosomal axis.

By the time the reverse side of  $th2^2$  metatheca is reached, the bandage orientation is very variable with frequent overlapping of bandages. The ends of these rather short (?) bandages are bluntly rounded or unrounded, rectilinear. Where bandages overlap the geniculum they run both parallel to it and across it, giving the appearance of a thickening and strengthening structure. The metasicula is seen to have several layers of bandages in some specimens, and the earliest seem to be longitudinal, the later, possibly thicker and wider bandages are more random, cover  $th1^1$  as well (Text-fig. 23B), and are presumably related to bandaging of the rhabdosome as a whole, not just the metasicula. There is one peculiar fabric (Text-fig. 23D) underlying the bandages as illustrated, but normal to the fuselli. It is composed of minute striations, with one or two coarser striae: we can offer no ultrastructural/depositional explanation for this at present, unless it represents a cortical bandage deposition without the normal enveloping sheet fabric.

Many bandages show internal fibres parallel to their length. These may represent the bundles of collagen fibrils seen in ultrathin slices. Sheet fabric is well preserved and consists of a granular texture with frequent pits (Text-fig. 26B–D). Where bandage measurements have been possible they are as follows: length in mm, 0.12, 0.13, 0.15, 0.16; width in mm, 0.032, 0.032, 0.033, 0.33, 0.034, 0.036, 0.038, 0.040.

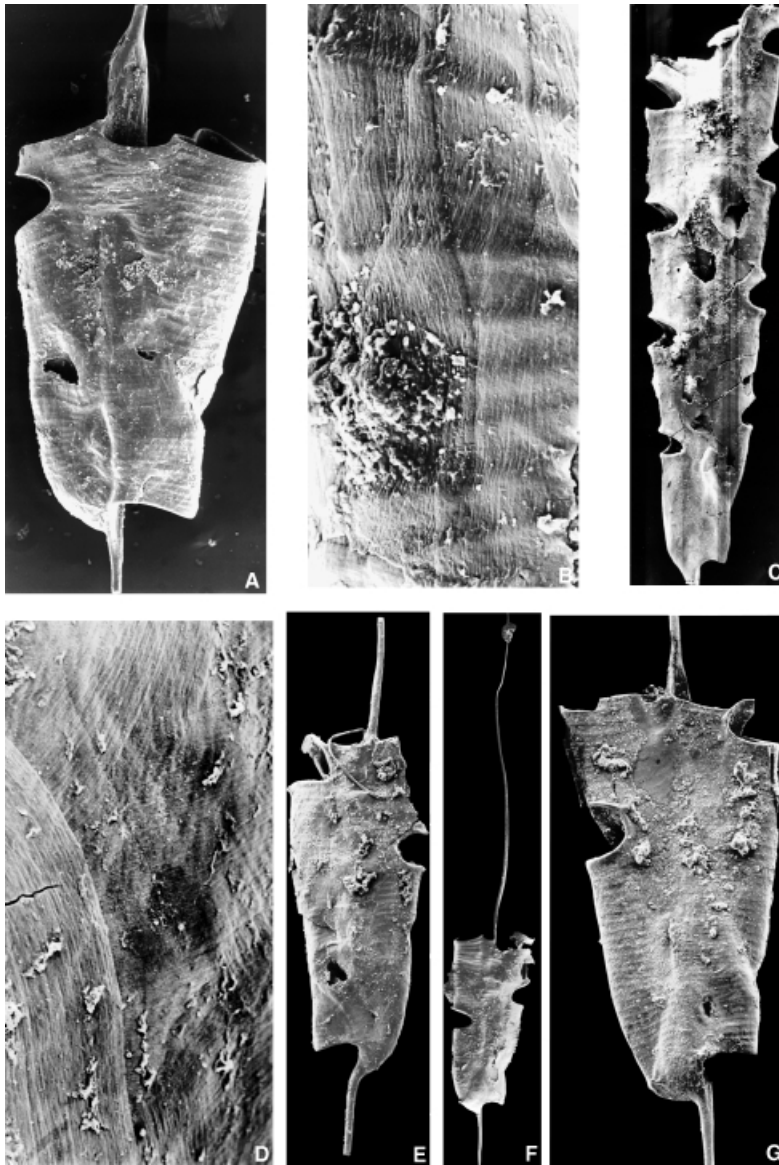


TEXT-FIG. 21. *Normalograptus melchini* sp. nov., SEM micrographs. A, X.25933, proximal fragment broken at the level of second pair of thecae, reverse view;  $\times 200$ . B, detail of the specimen in Text-figure 19, X.25809, showing lateral wall of th1<sup>2</sup> with short and broad 'banana-shaped' bandages randomly overlapping; note also clearly visible parallel striae (fibrils?) between lateral margins of bandages where sheet fabric has flaked off;  $\times 550$ .

*Remarks.* In general appearance *N. sobolevskayae* sp. nov. resembles superficially *N. rectangularis* (McCoy) but is of totally different dimensions. There is also a similarity to *N. mirnyensis* (Obut and Sobolevskaya) from which *N. sobolevskayae* differs in its higher thecal spacing (15–21 in 10 mm, cf. 13–15 in 10 mm). The relative lengths of the supragenicular walls are also greater in *N. sobolevskayae*, and the rhabdosome is slightly narrower. Two specimens (X.26243–4; not figured) do have similar supragenicular walls to those of *N. mirnyensis*, but the thecal spacing is still as high as in *N. sobolevskayae*, at 20 in 10 mm (2TRD of 1 mm), and we prefer to retain these forms, with caution, as *N. cf. sobolevskayae*. *N. legrandi* sp. nov. has similar overall dimensions but a more rounded proximal end, a higher thecal spacing, and a shorter virgella. The supragenicular:infragenicular wall ratio is quite different in the two forms (3.5:1, cf. 6 or 7:1). Nevertheless the evolutionary relationship between *N. sobolevskayae* and *N. legrandi* with *N. mirnyensis* is distinctly possible.

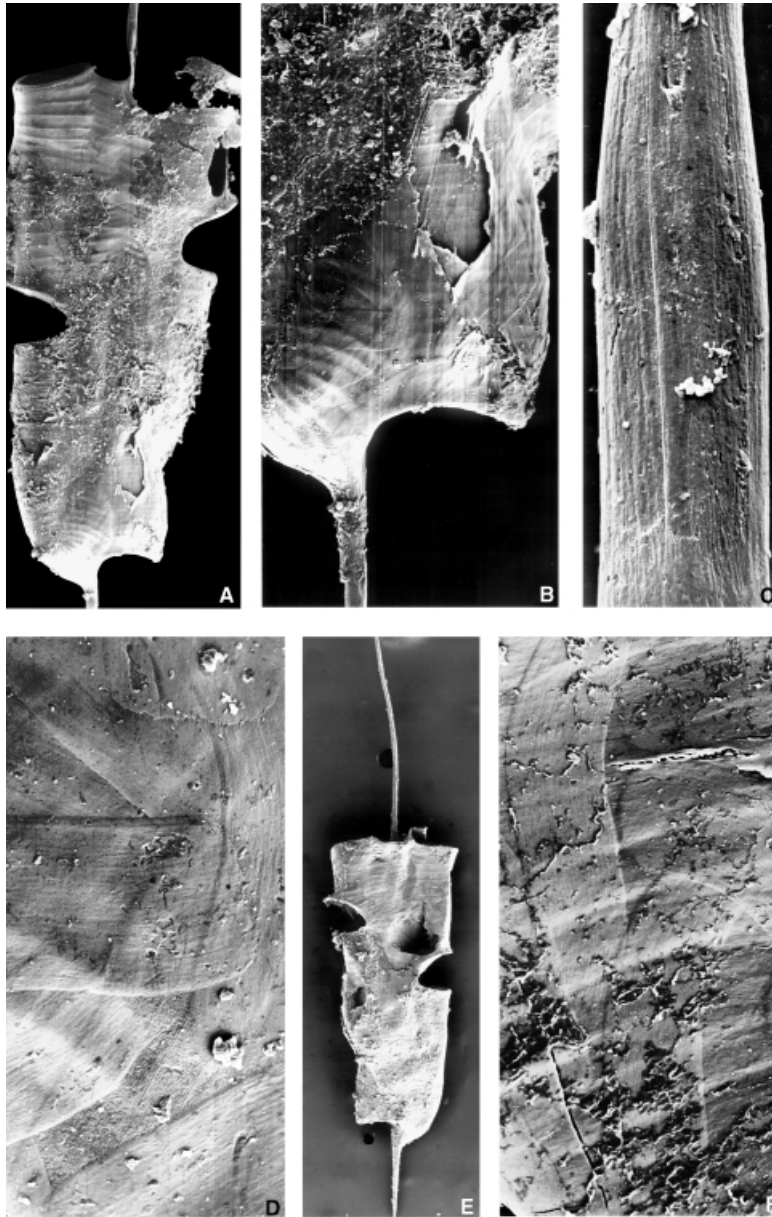
#### Genus SUDBURIGRAPTUS Koren' and Rickards, 1996

*Type species.* *Orthograptus eberleini* Churkin and Carter, 1970, from the *vesiculosus* and *cyphus* biozones; by original designation.

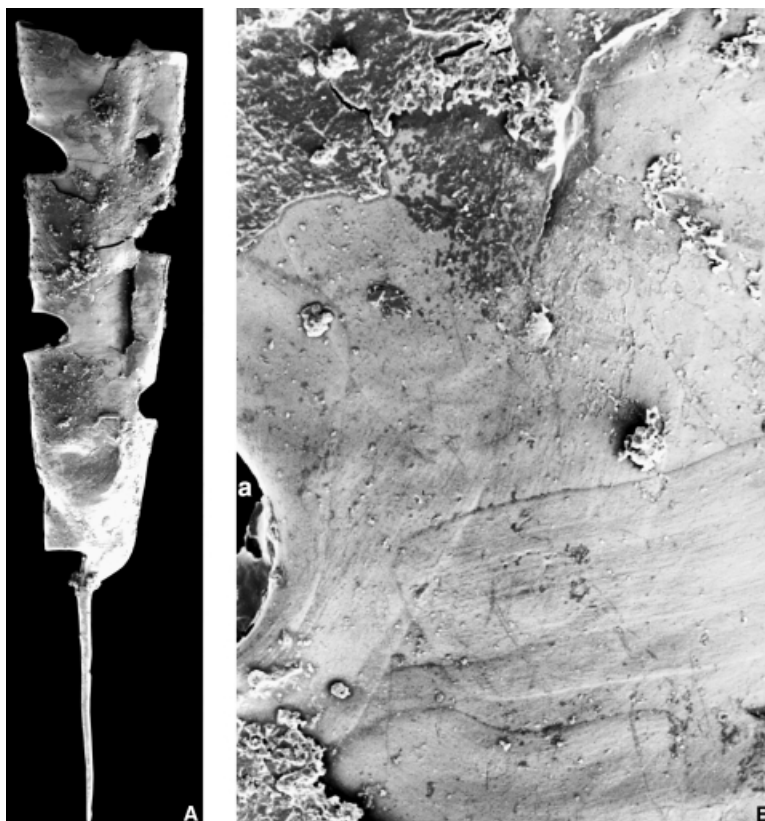


TEXT-FIG. 22. A-G, *Normalograptus sobolevskayae* sp. nov., SEM micrographs. A, X.25783, young colony at the stage of second pair of growing thecae; note cortical bandages running over the 'temporary' apertural margins of thecae; obverse view;  $\times 101$ . B, detail of A showing outer layer of predominantly longitudinal bandages running across fuselli on lateral wall of  $th1^1$ ; note sharp-ridged, parallel fibres and barely noticeable pitted sheet fabric;  $\times 829$ . C, X.25784, holotype, adult colony broken at the level of the fifth pair of thecae, obverse view;  $\times 42$ . D, detail of C showing bandages on the lateral side of the metascicula;  $\times 1190$ . E-F, young colonies, second pair of thecae partly completed. E, X.25785, reverse view;  $\times 59$ . F, X.25786, obverse view;  $\times 28$ . G, X.25787, obverse view;  $\times 91$ .

*Diagnosis.* Small, non-spinose biserials with rather *tamariscus* (I) Pattern than *normalis* (H) 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. 23. *Normalograptus sobolevskayae* sp. nov., SEM micrographs. A, X.25788, young colony with two pairs of thecae showing the beginning of median septum, obverse view;  $\times 79$ . B, detail of A showing extreme proximal end of the colony with at least two separate layers of cortical bandages seen on metasicula;  $\times 199$ . C, detail of B showing distal portion of virgella covered with longitudinal bandages and pitted sheet fabric;  $\times 861$ . D, further detail of B showing fuselli and overlapping bandages of scarp-edged type covered with pitted sheet fabric on the lateral wall of the down-growing portion of  $th1^1$ ; note also in the lower part of the micrograph, a bandage that is not covered with sheet fabric;  $\times 2261$ . E, X.25789, young colony with two pairs of thecae incomplete, reverse view;  $\times 45$ . F, detail of E showing long, banana-shaped bandages crossing fuselli on lateral wall of  $th2^2$ ;  $\times 553$ .



TEXT-FIG. 24. *Normalograptus sobolevskayae* sp. nov., SEM micrographs. A, X.25790, young rhabdosome with third pair of thecae almost completed, reverse view;  $\times 27$ . B, detail of A showing irregularly overlapping bandages on the lateral side of rhabdosome near th1<sup>2</sup> aperture (a);  $\times 455$ .

*Remarks.* These are rare and inconspicuous forms occurring from the *acuminatus* to *cyphus* biozones, 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 simpler development and loss of spines. They differ from *Pseudorthograptus* in being only virgellate rather than pseudancorate (*sensu* Koren' and Rickards 1996), 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 addition to those described below: *Orthograptus* sp. (Rickards 1988); *Orthograptus? attenuatus* Rickards, 1970; *Orthograptus abbreviatus* Elles and Wood (*sensu* Hutt 1974, pars); *Orthograptus abbreviatus* (Elles and Wood 1907, pars).

*Sudburigraptus* cf. *eberleini* (Churkin and Carter, 1970)

Text-figure 4E

*Material.* Two certain specimens, one more doubtful, each with one or two thecae only, but all in full relief.

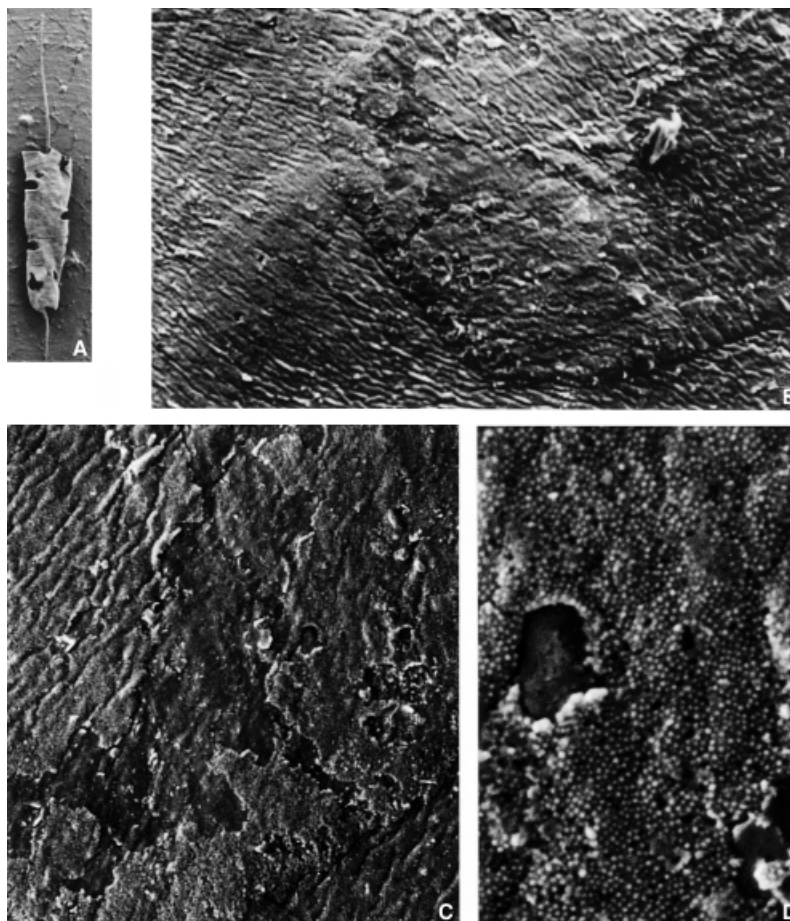


TEXT-FIG. 25. *Normalograptus sobolevskayae* sp. nov., SEM micrographs. A, X.25791, young colony with three pairs of thecae incompletely developed, showing base of median septum, obverse view;  $\times 45$ . B, detail of A showing lowermost part of  $th1^1$ , virgella (v) and sicular apertural rim (r) covered with overlapping bandages;  $\times 595$ .

*Description.* The sicula is 0.70–0.80 mm long, with an aperture 0.18 mm wide, and a virgella 0.20–0.30 mm long. The sicula is visible in obverse view for 0.40–0.60 mm, but in reverse view for less than 0.10 mm.  $th1^1$  grows upwards for 0.50 mm, and  $th1^2$  has a length of 0.45–0.48 mm. At the level of the aperture of  $th1^1$  the dorso-ventral width is 0.50–0.60 mm, and at  $th2^1$ , 0.55 mm. The thecal apertures are everted, and the free ventral thecal walls straight, except in the case of the more doubtful specimen when they are very slightly concave. Thecal spacing is 10 in 10 mm (2TRD, 2 mm). No median septum has been detected on any of the specimens.

One specimen (SM X25819) has numerous cortical bandages arranged longitudinally on all the early thecae ( $th1^1$ – $2^2$ ). It has not been studied under SEM as it is very delicate; hence, accurate measurements have not been made of bandage length and width.

*Remarks.* *S. cf. eberleini* differs from the form we describe below as *S. aff. eberleini* in that the sicula is almost wholly overgrown by the early thecae, revealing in obverse view only 0.40 mm of the metasicula in the definite specimens, as opposed to 0.77 mm in *S. aff. eberleini*. The latter also has a more robust proximal end with  $th1^1$  and  $1^2$  diverging at a higher angle, and with concave free ventral walls. The rather problematical specimen of *S. cf. eberleini* has slight similarities with *S. aff. eberleini* in that the sicula is slightly more exposed (0.60 mm) and the free ventral walls very slightly concave, but in most other characters it is closer to *S. cf. eberleini*. *S. aff. eberleini* has a high thecal spacing of 16 in 10 mm.



TEXT-FIG. 26. SEM micrographs of *Normalograptus sobolevskayae* sp. nov. A, X.25810, holotype, young rhabdosome with three incomplete pairs of thecae, obverse view;  $\times 28$ . B, detail of A showing bluntly rounded end of individual bandage on lateral wall of subapertural part of  $th1^1$ ; note wrinkled surface of cortical layer which may well be a taphonomic feature;  $\times 1312$ . C, detail of B showing partly preserved granular sheet fabric;  $\times 2625$ . D, detail of C showing granular layer;  $\times 10,500$ .

*Sudburigraptus* aff. *eberleini* (Churkin and Carter, 1970)

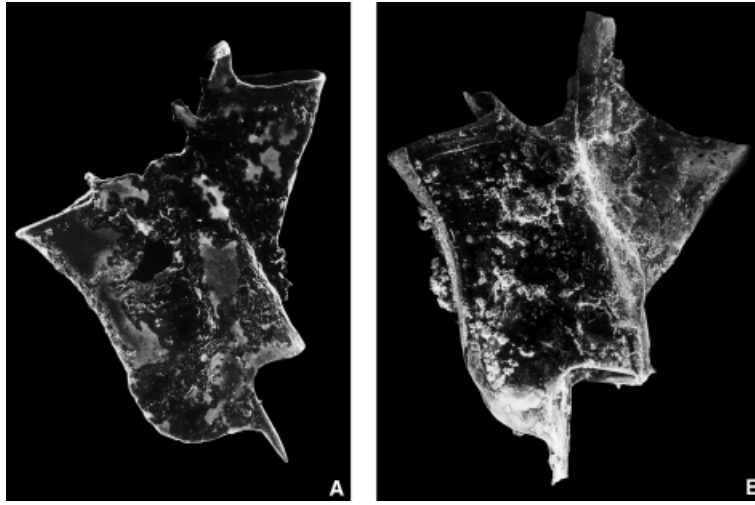
Text-figure 4F

aff. 1970 *Orthograptus eberleini* Churkin and Carter, pp. 29–30; pl. 3, fig. 2; text-fig. 12A–B.

*Material.* Two specimens, slightly flattened, showing two or three pairs of thecae developed, the larger specimen being a growth stage, the smaller specimen being distally broken.

*Description.* The sicula is very short, 0.62–0.77 mm, and fully exposed in obverse view.  $Th1^1$  grows downwards for 0.26 mm, half of which length is below the horizontal sicular aperture. The virgella is more than 0.18 mm long, short and spike-like, but broken in one of the two specimens. The sicular aperture is 0.15 mm wide.

$Th1^1$  grows upwards for 0.58–0.67 mm, and  $th1^2$  for 0.45–0.52 mm.  $Th1^1$  and  $1^2$  diverge at some 40–50 degrees and the free ventral walls are markedly concave. The thecal angle of inclination is 20–30 degrees, usually nearer the latter figure.



TEXT-FIG. 27. *Sudburigraptus* sp. 1., SEM micrographs, young rhabdosomes at the stage of the first pair of almost completed thecae, obverse side. A, X.25811;  $\times 100$ . B, X.25812;  $\times 128$ .

The dorso-ventral width at the level of the aperture of  $th1^1$  is 0.57–0.77 mm; at  $th2^1$ , 0.84 mm; and at  $th3^1$  approximately 1 mm. The thecal spacing is 16 in 10 mm (2TRD, 1.23 mm) and the thecal tubes are relatively straight tubes, three times as long as wide with overlap about one-third the thecal length. The thecal apertures are everted with respect to the rhabdosomal axis, reflecting the relatively high-angled thecal inclination. Metathecal growth lines ( $th2^2$ ) number 23.

*Remarks.* The differences between this form and *S. cf. eberleini* are discussed in the previous description. Five further problematical specimens (Plate 4, Text-fig. 27) have the overall appearance of *S. aff. eberleini* but a rather different shape and different dimensions.  $Th1^1$  and  $1^2$  have markedly concave walls, not unlike *Petalolithus*, and the thecal apertures are more strongly alternating. The dorso-ventral width at  $th1^1$  is no more than 0.50 mm, and the thecal spacing is 16–20 in 10 mm. This form we refer to only as *Sudburigraptus* sp. 1, which is figured herein but not fully described. It is close to *S. aff. eberleini* but is almost certainly a different species.

*Sudburigraptus* sp. 1

Plate 4, figures 1–3; Text-figure 27

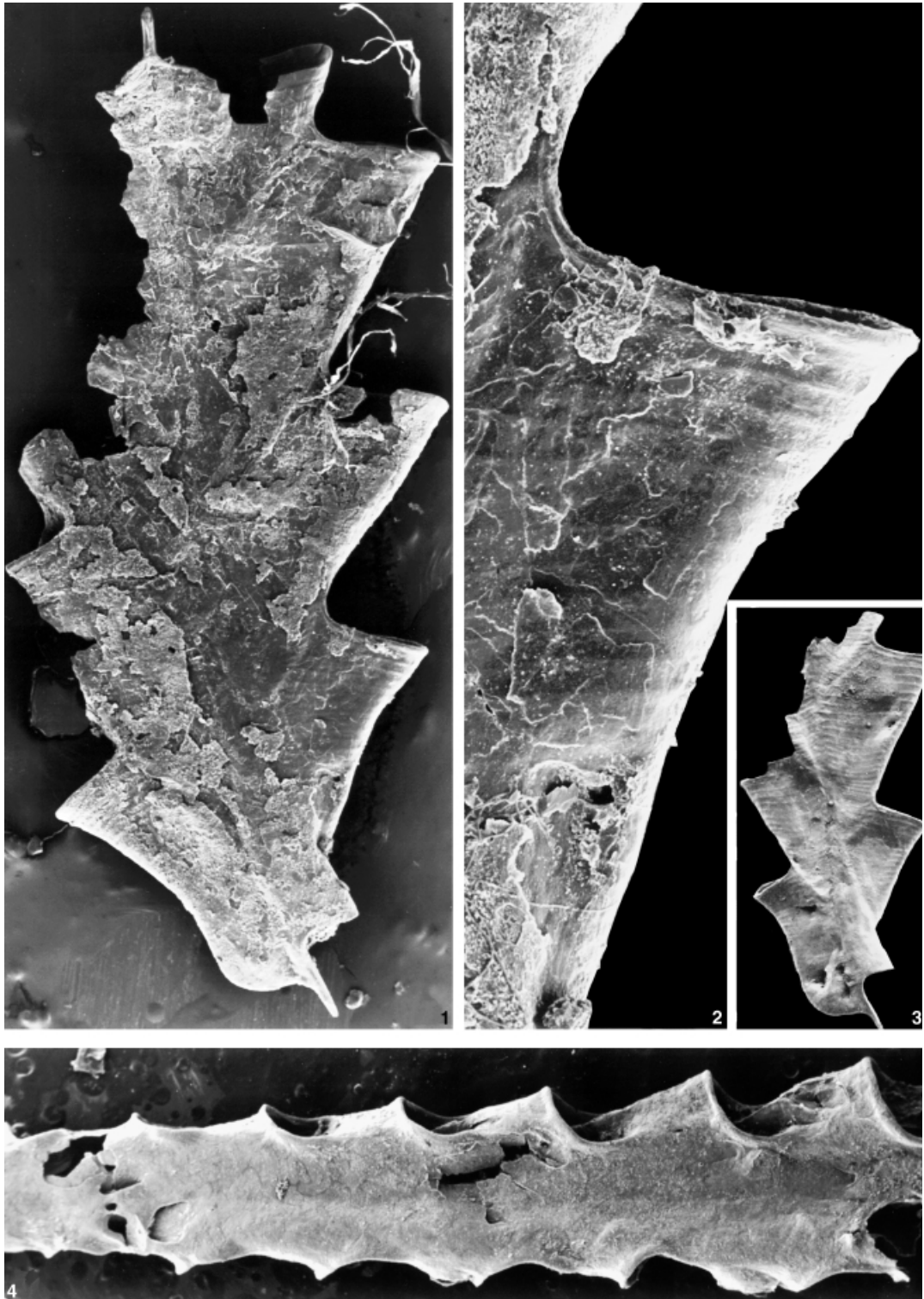
(Not described: see remarks following previous description.)

EXPLANATION OF PLATE 4

Figs 1–3. *Sudburigraptus* sp. 1, SEM micrographs. 1, X.25792, young colony broken along first thecal series, obverse view;  $\times 65$ . 2, detail of 1 showing  $th1^2$ ;  $\times 235$ . 3, SM A108587, colony broken at the level of third pair of thecae;  $\times 40$ .

Fig. 4. *Sudburigraptus* sp. 2, SEM micrograph, X.25794, adult colony broken at the extreme proximal end, obverse view with partly broken apertural part of sicula;  $\times 34$ .





KOREN' and RICKARDS, *Sudburigraptus*

*Sudburigraptus* sp. 2

Plate 4, figure 4

*Material.* A single well-preserved though incomplete specimen, in full relief; the extreme proximal and distal ends broken, but with eight pairs of thecae in 5.2 mm.

*Description.* Gradually tapering rhabdosome 0.54 mm wide proximally, 0.59 mm at th<sup>2</sup>; 0.70 mm at th<sup>3</sup>; 0.76 mm at th<sup>4</sup> and 0.78 mm at th<sup>5</sup> and 1 mm at th<sup>7</sup>; thecal spacing 15.5–16 (2TRD 1.23 mm) proximally and 13 in 10 mm at the distal end; thecae are straight tubes with everted apertures and strongly thickened apertural lips; interthecal septum concave to ventral side; sicula exposed in obverse view for at least 0.65 mm taking it above the level of the aperture of th<sup>1</sup>. Thecal overlap approximately one-third; thecal inclination about 20 degrees. Rhabdosome thickly bandaged, which completely obscures the fuselli; orientation is quite varied, but tends to be longitudinal on the ventro-lateral walls and in the subapertural parts of the thecae; lateral rhabdosomal walls show more random orientation of bandages; bandage margins distinct, in places slightly tapering; bandage ends are rounded; fibres/striations parallel to length of bandages are faint and fine; sheet fabric may be present, and large pits occur in the outer layers; bandage widths 0.054–0.064 mm; lengths more than 0.32–0.38 mm (both ends rarely seen).

*Remarks.* *Sudburigraptus* sp. 2 has broader bandages than any other species in this fauna, and has more closely spaced fibres/striations. From *S. eberleini* s.l., *S. sp. 2* also differs in having strongly everted and thickened apertural margins. It has a higher thecal spacing than *S. cf. eberleini*. *Sudburigraptus* sp. 3 lacks the everted apertures of *S. sp. 2*.

*Sudburigraptus* sp. 3

Text-figure 28

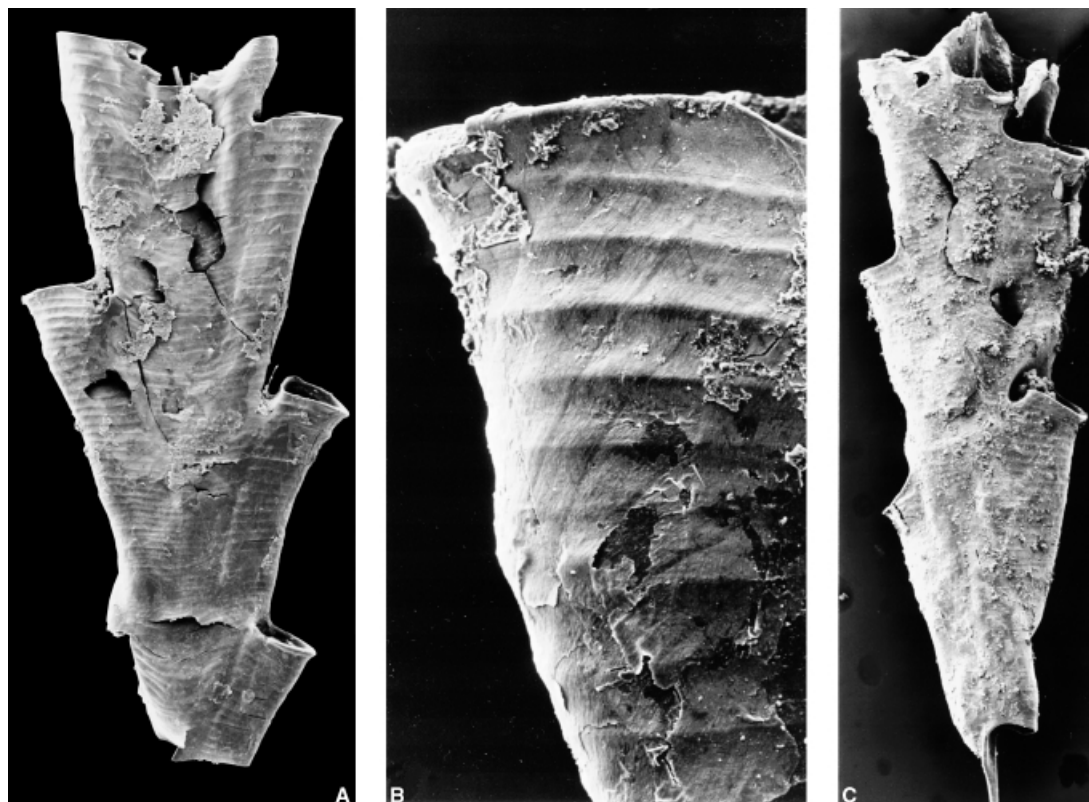
*Material.* Two specimens, one a proximal end with five thecae preserved, one of a more distal fragment also with five thecae; both in relief and well preserved.

*Description.* The sicula is exposed for 0.46 mm in obverse view, the aperture almost horizontal, and a short but broken virgella is spine-like in shape. Th<sup>1</sup> has a downward-growing portion of 0.22 mm, and then grows upward for 0.58 mm; the upward growth and, hence, length of th<sup>2</sup> is 0.51 mm. The thecal apertures are strongly alternating, spaced at 16–17 in 10 mm (2TRD, 1.19 mm), and overlapping about one-third. The dorso-ventral width of the rhabdosome is 0.42 mm at th<sup>1</sup> and 0.50 mm at th<sup>2</sup>. It is uncertain whether one proximal end is septate but the other certainly is (Text-fig. 28C); and the full length cannot be measured; it appears to be long and narrow.

Th<sup>2</sup> has a small, dorsal, apertural notch, seemingly unmatched on the reverse side, and th<sup>2</sup> shows a faint suggestion of this notch, again only on the obverse side of the aperture (Text-fig. 28B). The free ventral walls of the thecae are straight, except for a slight bending near the ventral apertural lip. The angle of inclination is about 15 degrees. The thecae are simple tubes with strongly everted apertures.

The more distal fragment has very similar thecae, again displaying notches on two thecae (in one actually causing metathecal isolation; Text-fig. 28A), but the thecal spacing is much lower at 12 in 10 mm (2TRD, 1.69 mm) and the dorso-ventral width is 0.89 mm. This fragment is certainly aseptate in this view (though whether obverse or reverse cannot be determined). Thecal overlap is about one-third, and angle of inclination about 20 degrees, whilst the number of metathecal fuselli is 24–26, a figure not dissimilar to those of the proximal fragment (20–26). Bandages are well-displayed and variously oriented on the lateral rhabdosomal walls (Text-fig. 28A). They are gently curved: lengths cannot be measured but widths of 0.03–0.041 mm have been obtained. On the lateral walls of the thecae themselves bandages are more parallel, cross fuselli obliquely, and some are certainly longer than 0.20 mm (Text-fig. 28A).

*Remarks.* It is possible that the proximal and distal fragments are referable to the same species, the large dimensions of the distal thecae reflecting a fairly long rhabdosome. The overall aspect of the rhabdosome and thecae recalls especially *Pseudorthograptus mutabilis* (see Koren' and Rickards 1996), and the notches recorded in *Sudburigraptus* sp. 3 may reflect the slight tendency to thecal isolation seen in some pseudorthograptids or dimorphograptids. *S. sp. 3* is, however, much smaller than these forms, and stratigraphically lower, and they lack, so far as we can tell, virgellar modifications. However, *Pseudorthograptus* may well originate from such forms. There is also a certain resemblance of the thecae to



TEXT-FIG. 28. *Sudburigraptus* sp. 3, SEM micrographs. A, X.25795, fragment of colony showing fuselli and overlapping bandages over the whole lateral wall inclusive of the growing end;  $\times 56$ . B, detail of A showing sharp fusellar ridges overlain by bandages on the lateral wall of the first complete theca on the left;  $\times 520$ . C, X.25796, young colony with three pairs of thecae almost completed, and median septum; note also dorso-ventral notch on the aperture of  $th1^2$ ;  $\times 30$ .

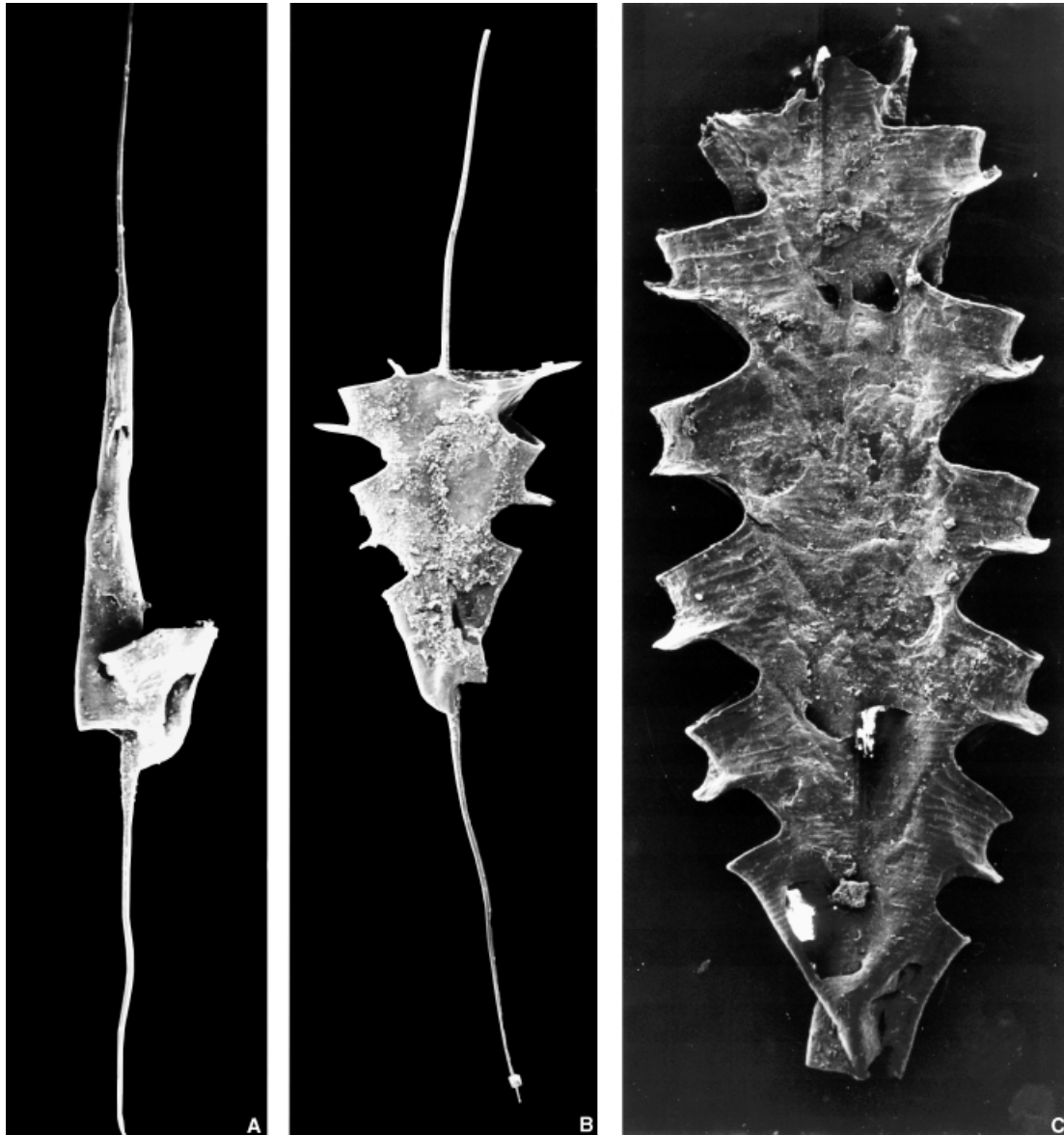
*Dimorphograptus* (*Bulmanograptus*) Přibyl *s.l.*, and *Dimorphograptus* spp. certainly occur at the site (but have not been isolated), but *Sudburigraptus* sp. 3 has no uniserial portion.

The two specimens (X25795 and X25796) are united under *Sudburigraptus* sp. 3 on the grounds of general appearance, dimensions, and the notching of some thecae. However, it is possible that they should be referred to separate species of *Sudburigraptus*, the one partially septate, the other septate.

#### Genus PARACLIMACOGRAPTUS Přibyl, 1947

*Type species.* By original designation *Climacograptus innotatus* Nicholson, 1869, Llandoverly, Scotland.

*Diagnosis.* Pattern of proximal development *tamariscus* (I) type; short downward-growing part to  $th1^1$ ;  $th1^1$  and  $th1^2$  strongly upward-growing and widely diverging from each other so that the proximal end is pointed; thecae strongly geniculate; geniculum with large genicular hood of fusellar tissue, formed before next thecal tube is laid down; thecal excavations large, semicircular; apertures horizontal or everted; supragenicular wall vertical, short, little longer than length of excavation; rhabdosomes septate or aseptate, ?partially septate.



TEXT-FIG. 29. *Paraclimacograptus innotatus* (Nicholson), SEM micrographs. A, X.25797, developmental stage, early growth of the first pair of thecae, reverse view;  $\times 56$ . B, X.25798, young rhabdosome with the third and fourth pairs of thecae; note also the early formation of the hood of  $th_3^2$ ; obverse view;  $\times 34$ . C, X.25799, adult rhabdosome, reverse view;  $\times 52$ .

*Paraclimacograptus innotatus* (Nicholson, 1869)

Text-figures 29–30

- 1869 *Climacograptus innotatus* Nicholson, p. 238, pl. 11, figs 16–17.  
 1906 *Climacograptus innotatus* Nicholson; Elles and Wood, p. 212, pl. 27, fig. 10a–c; text-fig. 143a–b.  
 1970 *Climacograptus innotatus innotatus* Nicholson 1869; Rickards, p. 31, pl. 2, fig. 11.



TEXT-FIG. 30. SEM micrographs of *Paraclimacograptus innotatus* (Nicholson). A, X.25813, short, broad bandages of different orientation on subapertural part of metasicula and over its aperture (a); note also distinct lateral margins and broadly rounded ends of individual bandages;  $\times 830$ . B, X.25814, underside of thecal hood, showing fusellar structure; f, fusellar edges;  $\times 1145$ .

- 1974 *Climacograptus innotatus innotatus* Nicholson 1869; Hutt, pp. 21–22, pl. 1, figs 6–7, 12; text-fig. 8, fig. 7 (see for full synonymy).  
 1977 *Climacograptus innotatus innotatus* Nicholson 1869; Crowther and Rickards, p. 19, pl. 4, fig. 3.  
 1981 *Climacograptus innotatus innotatus* (Nicholson 1869); Crowther, p. 88, pl. 13, figs 4–7.

*Material.* More than 70 specimens showing all stages of growth.

*Description.* Fusiform rhabdosome dominated by sharply tapering proximal end, robust thecae, large semicircular excavations, and genicular hoods of fuselli, coated with cortical bandages. Dorso-ventral width at  $th1^1$  (excluding hoods) 0.32–0.68 mm; at  $th1^2$ , 0.46–0.80 mm;  $th13$ , 0.72–0.82 mm;  $th1^4$ , 0.84 mm;  $th1^5$ , 0.87 mm; angle of divergence of  $th1^1$  and  $1^2$ , 30–50 degrees; downward growth length of  $th1^1$ , 0.19–0.26 mm; upward growth of  $th1^1$ , 0.40–0.57 mm; distance of  $th1^1$  below sicular aperture, 0.07–0.09 mm; length of  $th1^2$ , 0.30–0.64 mm; sicular length, 0.83–1.10 mm; prosicula length, 0.44–0.45 mm; sicular apertural width, 0.09–0.15 mm; virgella up to 1.42 mm; sicular exposure from overgrowth of  $th1^1$  and  $th1^2$ , 0.11–0.67 mm; excavation: dorso-ventral width ratio, 1:3 or 4; length of genicular hoods, 0.06–0.16 mm; genicular hood of  $th(n+1)$  built by zooid of  $th n$ ; ratio of thecal length:width, 1:2 or 3; ratio supragenicular: infragenicular wall, 1:2; thecal spacing 20–24 at level  $th1^{1/2^1}$ ; 22–28 at level of  $th2^{1/3^1}$ ; thecal overlap <S.

Bandages well seen in several areas, notably the prosicular apex junction with the nema, metasicular lateral wall (Text-fig. 30B), genicular hoods, and lateral rhabdosomal walls; all short and gently curved, with rounded ends. Near the base of the nema, and the base of the metasicula, is a single layer of longitudinally arranged bandages; sometimes they overlap each other at a low angle.

On  $th1^1$  some bandages parallel the aperture and yet others overlap the rim at varying angles; these are at a markedly high angle, 90 degrees in some instances, to the longitudinal bandages on the early prothecal part of  $th1^2$ . In this region, too, some bandages are seen radiating from the sicular aperture, so presumably the siculozooid is partly responsible for their laying low down on  $th1^1$ . Several layers are detectable on  $th1^1$ , overall with a random orientation. These bandages have a width of 0.033–0.035 mm and a length of 0.10 mm. They are scarp-edged with rounded ends at one end, and tapered, rather ragged endings at the other. This suggests that the zooid secreted from the rounded end to the ragged end, which is the lift-off position. In all these bandages, fibres are seen parallel to the long edges.

In the region of the genicular hoods cortical bandages are secreted on the hood before the fuselli of  $th(n+1)$  were laid down. The upper surface of the hood has at least two layers of bandages: a lower layer longitudinally arranged and an upper layer where the bandages go across the hood to the next supragenicular wall, reinforcing the angle between the latter and the hood base. At this stage the outer edge of the hood is still relatively thinly layered with bandages. The bandages crossing the angle between hood and supragenicular wall are 0.051 mm wide, plastered across the angle itself, and sometimes finish irregularly upon the supragenicular wall.

In several instances the cortical bandages wrap over the thecal apertural rim before the thecal tube is completed, that is over a temporary aperture. This does not seem to have been observed previously in any species, except in this paper [see also *Metaclimacograptus cf. undulatus* (Kurck)].

#### Family METACLIMACOGRAPTIDAE Koren' and Rickards, 1996

##### Genus METACLIMAGOGAPTUS Bulman and Rickards, 1968 (emend. Koren' and Rickards, 1995)

*Type species.* By original designation, *Diplograptus hughesi* Nicholson, 1869; Llandovery, Lake District, England.

*Diagnosis* (revised). Minute rhabdosomes, usually less than 10 mm long, and less than 1.20 mm wide; proximal development *normalis* (H) Pattern; thecae tightly packed, usually strongly alternating about an undulating or rounded zigzag median septum; excavations deep, sometimes introverted, sometimes overhung with genicular hood; supragenicular wall may be straight, but more commonly 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 of folding into the protheca, and the sharp zigzag of the Ordovician genus.

#### *Metaclimacograptus hughesi* (Nicholson, 1869)

Text-figures 4A, 31–32

- 1869 *Diplograptus hughesi* Nicholson, p. 235, pl. 11, figs 9–10.  
 1968 *P. (Metaclimacograptus) hughesi* (Nicholson); Bulman and Rickards, pp. 3–6, text-figs a–c.  
 1991 *Metaclimacograptus hughesi* (Nicholson, 1869); Loydell, p. 675, pl. 2, figs 3–4, 6, 9, 12.  
 1995 *Metaclimacograptus hughesi* (Nicholson, 1869); Koren' and Rickards, pl. 14, figs 9–14, text-fig. 23A (see for full synonymy).

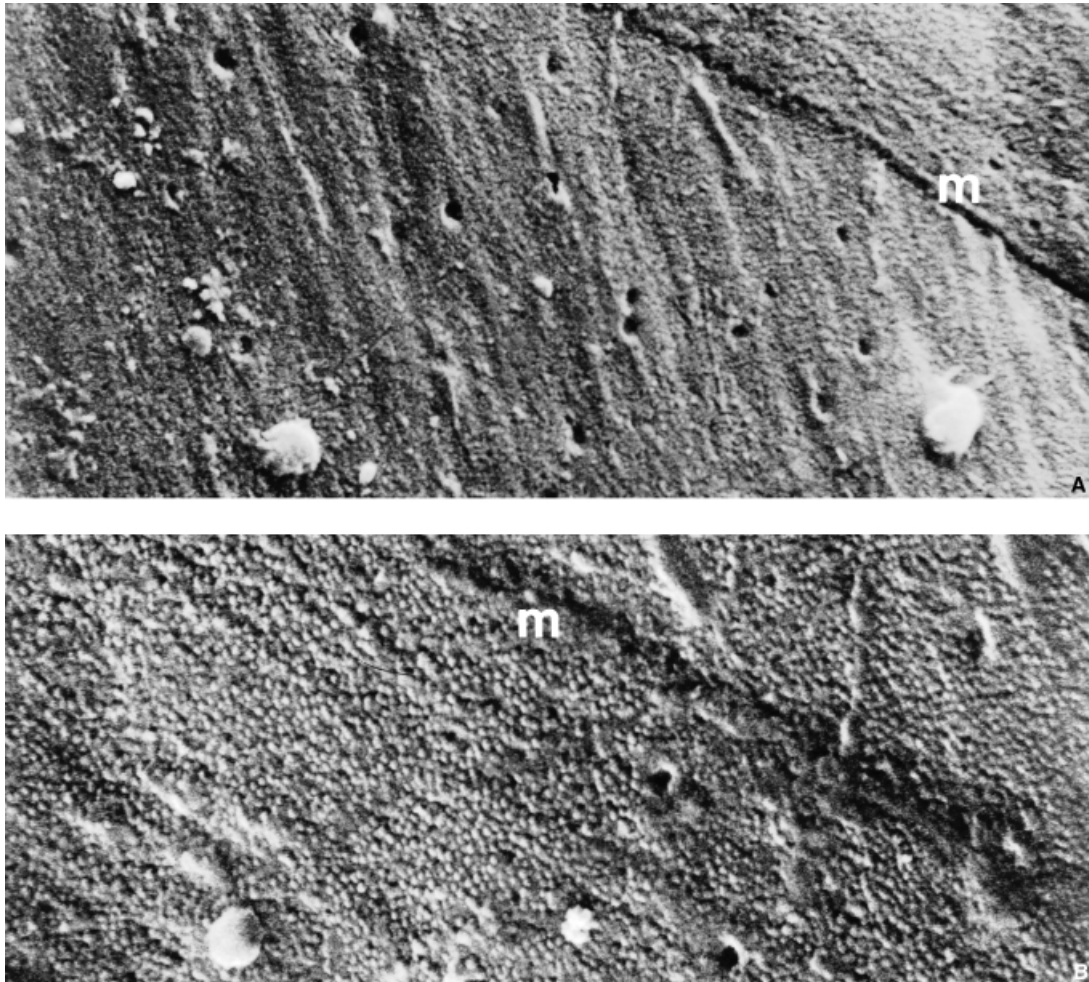


TEXT-FIG. 31. SEM micrographs of *Metaclimacograptus hughesi* (Nicholson). A, X.2515, adult rhabdosome broken at the level of fifth pair of thecae, obverse view;  $\times 30$ . B, detail of A showing base of free virgella covered with horizontal and longitudinal bandages;  $\times 1880$ . C, detail of B showing granular sheet fabric and larger pits (p);  $\times 15,000$ .

*Material.* Two fully three-dimensional specimens.

*Description.* Specimen, 2.80 mm long, with five pairs of thecae to damaged but growing end;  $th1^1$  barely extends, in its down-growing part, below the sicular aperture; dorso-ventral width at  $th1^1$ , 0.63 mm; at  $th2^1$ , 0.65 mm; at  $th3^1$ , 0.75 mm and at  $th4^1$ , 0.80 mm; rhabdosome has round cross section and is parallel-sided; genicular rims are pronounced with short, hood-like outgrowths, and they extend ventrally for 0.04 mm further than the preceding apertural rim (Text-figs 4A, 31A); thecal excavations deep (0.20 mm) and short (0.08–0.09 mm), occupying about





TEXT-FIG. 32. SEM micrographs of *Metaclimacograptus hughesi* (Nicholson). A, detail of Text-figure 31A showing granular and irregular pitted structure of sheet fabric; note lateral margin (m) of individual bandage in the upper right corner, and subcircular pit distribution;  $\times 7500$ . B, detail of A;  $\times 15,000$ .

one-third of the dorso-ventral rhabdosomal width; supragenicular walls are 0.52–0.53 mm long, infragenicular walls 0.075 mm long, giving a ratio of 7:1; thecal spacing 15.5–17.5 in 10 mm (2TRDs, 1.12, 1.25);  $th1^1$  downgrowing portion is 0.25 mm, and the upward-growing part 0.55 mm; the sicula is exposed for 0.42–0.43 mm in obverse view; sicular aperture 0.18–0.19 mm; virgella short and stout, obliquely directed, 0.16 mm long (Text-fig. 31A–B). Bandages 0.047–0.050 mm wide,  $>0.15$  mm long, more or less straight, scarp-edged, of varied orientation, and with pitted and granular sheet fabric membranes (Text-figs 31C, 32).

*Remarks.* This is an extremely important record of the species, being the first below the *cyphus* Biozone. The dimensions are closely similar to previous descriptions, especially to the review by Bulman and Rickards (1968). The only difference we can detect is that the thecal spacing is slightly higher for comparable parts of the rhabdosome (16 cf. 15.5–17.5). Other measurements fall well within the range for *M. hughesi* and the overall appearance of the specimen is quite typical.



*Metaclimacograptus bjerreskovae* sp. nov.

Plate 5, figures 1–2

*Derivation of name.* In honour of Dr M. Bjerreskov.

*Holotype and only specimen.* SM X25800, Plate 5, figures 1–2. A single, well-preserved, three-dimensional specimen with a thick cortical layer; broken at the level of the fourth thecal pair.

*Description.* A minute, slim, pointed rhabdosome, the last point emphasized by a long, robust and straight virgella 2.40 mm long (incomplete), which is longer than the preserved portion of rhabdosome (2.30 mm).  $th1^1$  grows downward below the sicular aperture for 0.12 mm: the sicular aperture is exposed in obverse view for 0.32 mm. The upward-growing part of  $th1^1$  is 0.79 mm. The upward-growing part of  $th1^2$  is partly obscured aperturally, but is of similar length to the upward-growing part of  $th1^1$ . The thecal apertures are strongly alternating.

Dorso-ventral width at the  $th1^1$  aperture is 0.36 mm and this gradually increases to 0.46 mm at  $th3^1$ . Thecal spacing is 14.5–17 in 10 mm (2TRDs 1.17 mm, 1.32 mm). Thecal excavations are short (0.06–0.07 mm) and deep (0.05–0.06 mm) and the apertures introverted. The overhanging geniculum is sharp but has no outgrowths of any kind. It overhangs the preceding theca such that the geniculum is 0.06 mm further from the rhabdosomal axis. The supragenicular walls are 0.53–0.56 mm and the supragenicular:infragenicular wall ratio is 5:1. The supragenicular walls, therefore, appear relatively long, and they are distinctly convex. No apertural rims are present.

The rhabdosome has a thick coating of cortical bandages which are relatively wide, at 0.065–0.070 mm, and have a length of 0.15 mm. The long sides have scarp edges. Numerous fine fibres are visible within them, and the bandage ends, where visible, are bluntly rounded. There is no preferred orientation, but it is clear that they coat the whole of the apertural region and contribute to the endocortex as well as the exocortex.

*Remarks.* This is an unusual metaclimacograptid with an astonishingly robust and long virgella relative to the colony size. The thecae are also rather long, and the supragenicular:infragenicular wall ratio high. The only other metaclimacograptid with such a pronounced virgella is *M. fidus* Koren' and Mikhaylova (1980) from the *acuminatus* Biozone of Kazakhstan, but this form is much larger than *M. bjerreskovae* sp. nov.

*Metaclimacograptus orcus* Koren' and Rickards, 1995

Plate 5, figures 5–7; Text-figure 4G–H

1995 *Metaclimacograptus orcus* Koren' and Rickards, pl. 15, figs 8–9; text-fig. 22F

*Material.* Six specimens, almost in full relief, other fragments.

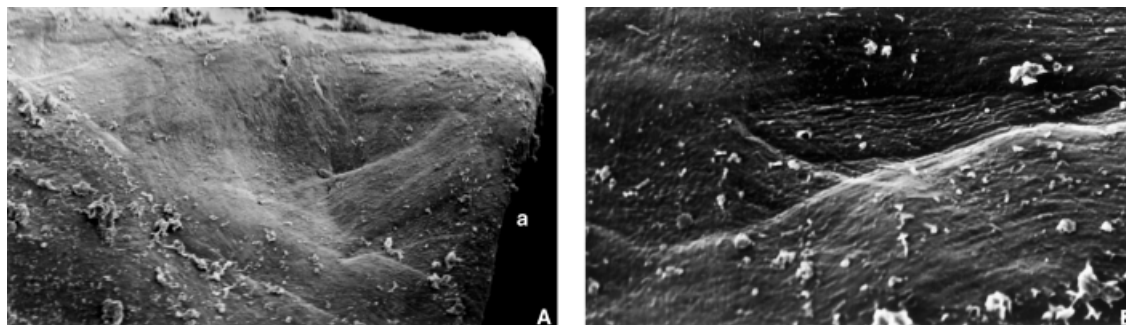
*Description.* Minute metaclimacid, 1.5–2.5 mm long, possibly with as few as 5–7 thecae developed; dorso-ventral width 0.35–0.42 mm; distal diminution in width occurs and greatest width may be at level of  $th1^1/1^2$ ; thecal spacing 20–28 in 10 mm.

The sicula is 0.90–1.0 mm long, and has an aperture 0.09–0.14 mm wide, possessing a short dorsal tongue. The sicula is exposed for 0.10–0.13 mm in reverse view and 0.40–0.45 mm in obverse view. The virgella may reach 0.3 mm in length and is directed slightly across the sicular aperture. The down-growing portion of  $th1^1$  is not clearly seen (0.22 mm) but it turns upwards at about the level of the sicular aperture or up to 0.08 mm below, and then grows upward for 0.40–0.49 mm;  $th1^2$  has a length of 0.55–0.56 mm.  $th1^1$  is almost bulbous in outline. The dorso-ventral width at the level of the aperture of  $th1^1$  is 0.30–0.42 mm and this is often the maximum width of the colony, or even at the midpoint of  $th1^1$ . Some rhabdosomes are parallel-sided but others show a diminution in width distally.

Thecal apertures are strongly alternating, and deep, slit-like excavations occupy almost half the dorso-ventral width. They are slightly introverted and are overhung by a sharp geniculum: excavation depth is 0.12–0.18 mm and the length 0.04 mm.

Two of the characteristic rhabdosomal features are the broad proximal end (relative to mesial and distal parts) with its bulbous  $th1^1$ , and the manner in which the genicular hood forms, completely overhanging the exposed aperture before the next metatheca is formed. It is also clear from several growing tips that there is little room for development of another theca.

*Remarks.* This form differs from the original description only in two respects: (1) an even higher thecal spacing; (2) less convex supragenicular walls. The thecal spacing figures do overlap with the original



TEXT-FIG. 33. SEM photographs of *Metaclimacograptus* cf. *undulatus* (Kurck), details of Plate 1, figure 3. A, cortical bandages on lateral wall of subapertural part of  $th1^2$ ; a = aperture;  $\times 115$ . B, randomly-overlapping bandages on lateral wall of  $th1^1$ ; note also their sharply-edged lateral margins and prominent parallel fibres;  $\times 470$ .

material, which was from the Kos-Istek region of western Kazakhstan (Sakmara Formation). The thecae are moderately convex in the Mazovo material, and it is possible that the degree of convexity is influenced by the preservation of the original, which are internal moulds of blue opaline silica. In most respects the specimens from the two regions agree closely.

*Metaclimacograptus* cf. *undulatus* (Kurck, 1882)

Plate 5, figures 3–4; Text-figures 33–34

*Material.* Five specimens, in three dimensions.

*Diagnosis.* Relatively robust metaclimacograptid with rounded proximal end and parallel-sided rhabdosome; median septum from third thecal pair; slit-like apertures, distinctly introverted; dorso-ventral width 0.57–0.67 mm; thecal spacing 19–20 in 10 mm; very short virgella.

*Description.* The sicula is exposed in obverse view for 0.29 mm.  $Th1^1$  grows downwards for 0.23 mm, going below the horizontal sicular aperture for 0.10 mm before turning upwards for 0.57 mm.  $Th1^2$  has a length of 0.46 mm as seen in

EXPLANATION OF PLATE 5

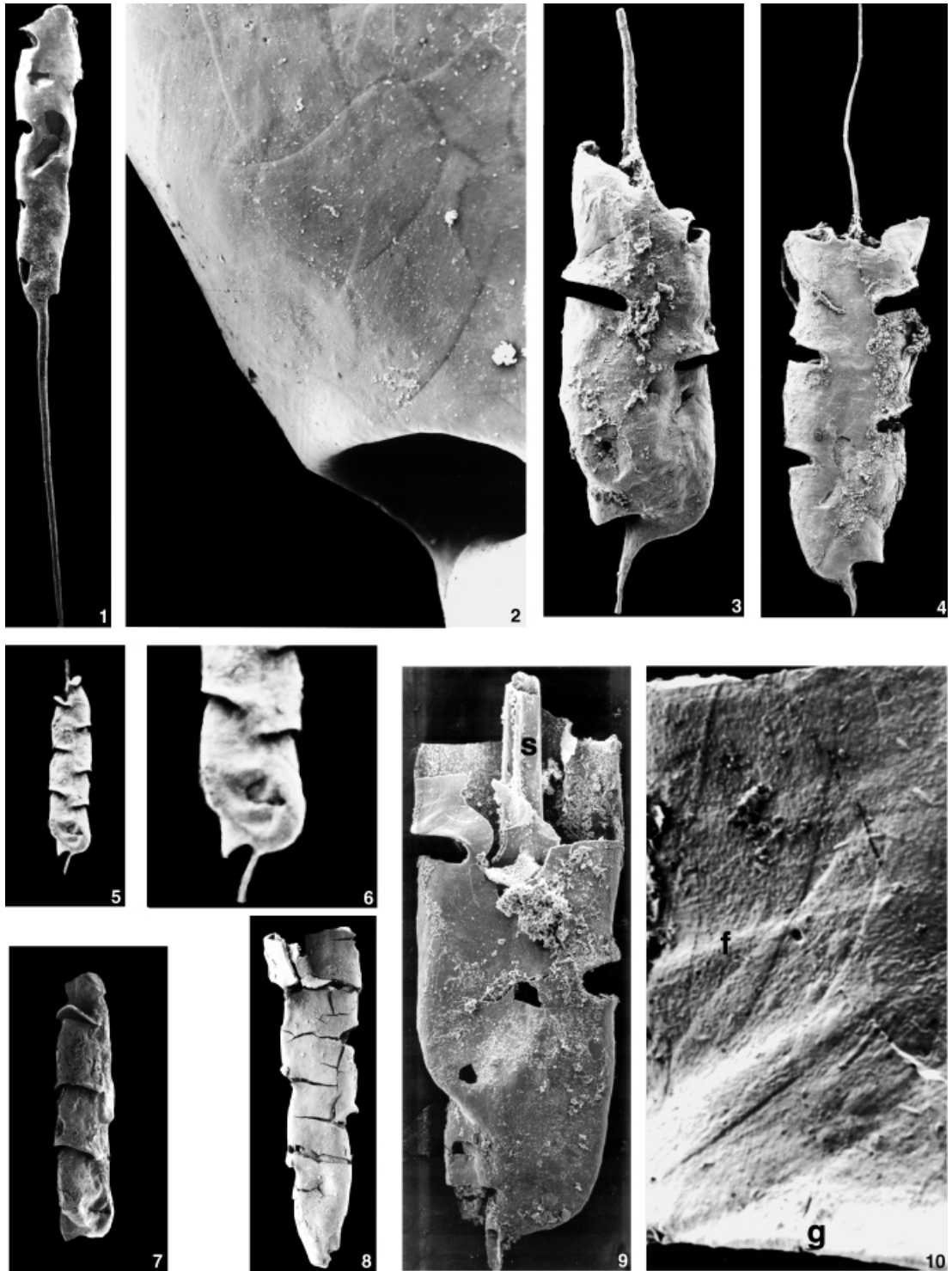
Figs 1–2. *Metaclimacograptus bjerreskovae* sp. nov., SEM micrographs. 1, X.25800, holotype, adult rhabdosome broken at the level of fourth pair of thecae; note also long and stout virgella;  $\times 34$ . 2, detail of specimen in Fig. 1 showing  $th1^1$  aperture and supragenicular wall of  $th2^1$  covered with frequently-overlapping banana-shaped bandages; note also pitted sheet fabric;  $\times 460$ .

Figs 3–4. *Metaclimacograptus* cf. *undulatus* (Kurck), SEM micrographs. 3, X.25934, young colony at the stage of the third pair of thecae, reverse view;  $\times 85$ . 4, X.25935, young colony with three pairs of thecae almost completed, obverse view;  $\times 52$ .

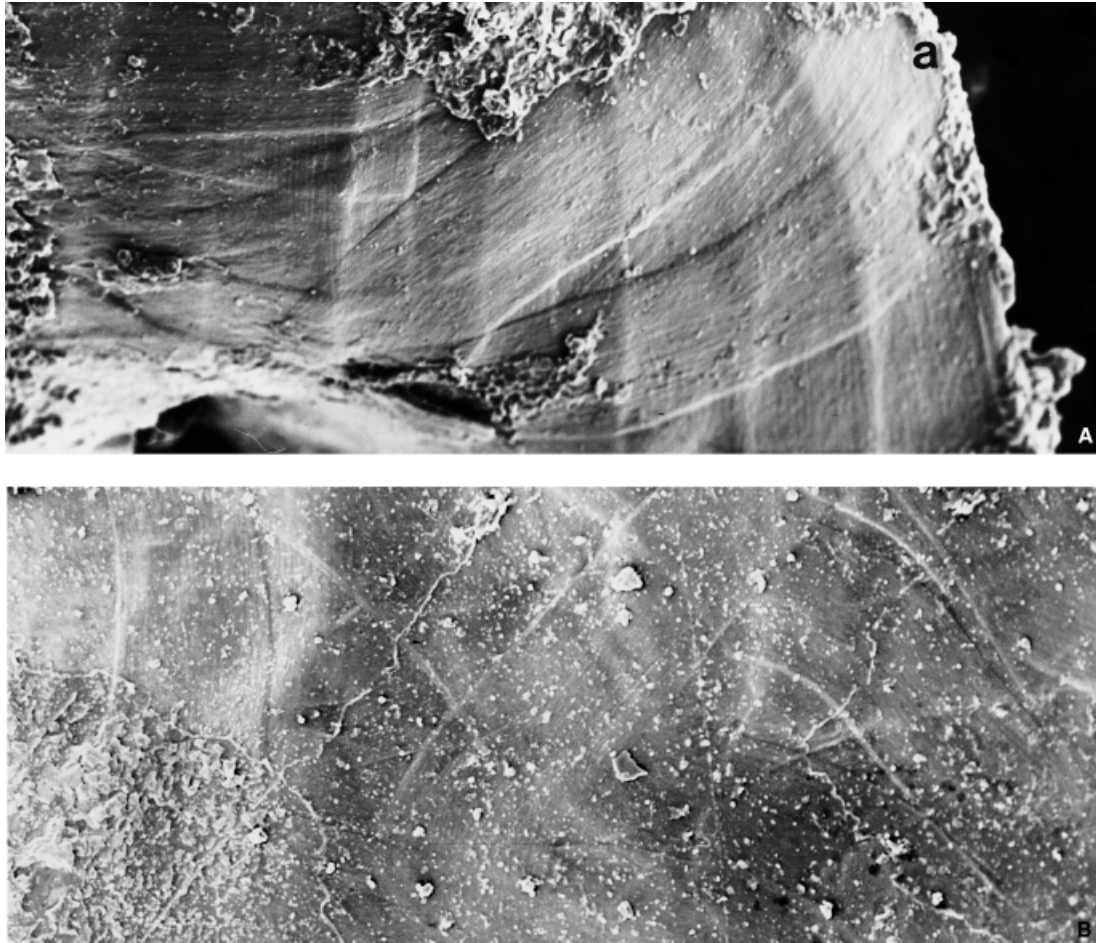
Figs 5–7. *Metaclimacograptus orcus* Koren' and Rickards, SEM micrographs. 5, X.25801, colony with four pairs of thecae incomplete, reverse view;  $\times 20$ . 6, detail of 5. 7, same specimen, ventral view of the second row of thecae; note median septum;  $\times 40$ .

Fig. 8. *Climacograptus* sp., SEM micrograph, SM A108628, three-dimensional specimen with pyrite infill, heavily cracked, thick periderm, showing typical concavo-convex supragenicular walls;  $\times 40$ .

Figs 9–10. *Metaclimacograptus?* sp., SEM micrographs. 9, X.25802, proximal fragment of colony broken at the level of the second pair of thecae, reverse view; s, sicula,  $\times 145$ . 10, detail of 9 showing bandages crossing fuselli (f) at different angles and crossing the geniculum (g) of  $th2^2$ ;  $\times 1440$ .



KOREN' and RICKARDS, diplograptids



TEXT-FIG. 34. SEM micrographs of *Metaclimacograptus* cf. *undulatus* (Kurck), details of Plate 23, figure 4. A, X.25935, cortical bandages running both parallel to fuselli and crossing them on the lateral wall of  $th3^2$  and going over its 'temporary' apertural rim (a);  $\times 515$ . B, cortical bandages on  $th1^2$  lateral wall;  $\times 430$ .

obverse view. The sicular aperture has a diameter of 0.12–0.15 mm, is horizontal or with a slight dorsal tongue, and has a virgella of 0.25 mm (Pl. 5, figs 3–4).

The subapertural parts of  $th1^1$  and  $1^2$  are already parallel to the rhabdosomal axis, and the dorso-ventral width at the apertures of  $th1^1$  and  $1^2$  are, respectively, 0.52–0.57 mm and 0.59 mm; at  $th2^1$ , 0.60–0.62 mm; and at  $th3^1$ , 0.67 mm. The thecal excavations are about 0.10–0.20 mm wide and 0.07–0.08 mm long, i.e. slit-like. The apertural lips and geniculae are a little thickened, and the apertures introverted. The median septum is present from the level of the third pair of thecae, but its position on the lateral rhabdosomal walls cannot be seen, largely because of thick cortex.

On the supragenicular walls of the thecae fuselli are clearly visible and number about 13. Bandage covering is, however, considerable, and even where thecal tubes are incomplete (e.g.  $th3^2$ ) bandages are generally arranged in a criss-cross fashion (Text-fig. 34B) with frequent overlapping so that layers may be three deep. Dimensions are: length 0.162–>0.174 mm; width, 0.046–0.048 mm. In the subapertural regions bandages are laid down both across the fuselli and parallel to them (Text-fig. 34A). The fuselli, like the bandages, may show a fibre-like or striated structure parallel to their lengths but very inconspicuous. Whilst in the case of bandages these are presumably fibrils, or bundles of fibrils, of collagen, in the case of the fuselli striations their nature is not known. The bandages do not have raised edges and may not have a membrane or sheet fabric coating.

*Remarks.* In general dimensions this form is close to *M. undulatus* (Kurck) from which it differs in the absence of strongly developed genicular hoods overhanging the thecal apertures.

*Metaclimacograptus?* sp.

Plate 5, figures 9–10

*Material.* Two well-preserved, three-dimensional proximal ends, one with a broken extremity, each showing little more than three thecae.

*Description.* The proximal end is rather rounded with the sicula exposed in reverse view quite conspicuously, for 0.16 mm above an aperture with a (horizontal) diameter of 0.09 mm. The sicula itself is probably 0.94 mm or a little longer. The late metathecal parts of both  $th1^1$  and  $th1^2$  are upward-growing, parallel to the rhabdosomal axis, and the rhabdosome is parallel-sided. Dorso-ventral widths are, at  $th1^1$ , 0.36 mm, and at  $th2^1$ , 0.37 mm.  $Th1^1$  grows down below the sicular aperture for 0.10 mm and then upwards for 0.45 mm.  $Th1^2$  is 0.48 mm long measured in obverse view. Thecal apertures are strongly alternating, introverted beneath a conspicuous geniculum which is robustly flange-like but without outgrowths. Excavations are 0.05–0.09 mm deep, and 0.03–0.05 mm long.

Thecal spacing is 20–22 in 10 mm (2TRDs, 0.92–0.93 mm). The virgella is stout, short and straight. The rhabdosome is copiously bandaged making fuselli difficult to see on one specimen (although there may be 15 fuselli on the metatheca of  $th2^1$  in the other specimen). The bandages are scarp-edged, of varied orientations where seen, but possibly radiating from the thecal apertures. Other measurements are not possible.

One specimen has a suggestion of part of a zigzag median septum, whilst the other suggests that the geniculum was completed before growth of the succeeding metatheca.

*Remarks.* There is a superficial resemblance to *Normalograptus* but the slight apertural introversion and the trace of a zigzag median septum belies this. *Metaclimacograptus?* sp. has the rhabdosomal form of *M. hughesi* (Nicholson) but a far higher thecal spacing. The supragenicular walls are too long for *M. undulatus* (Kurck) and, again, the thecal spacing is rather high. From *M. orcus* Koren' and Rickards it differs in having no rounding of the supragenicular wall, whilst *M. bjerreskovae* sp. nov. has too low a thecal spacing, rounding of the supragenicular wall, and a virgella of totally different proportions. Of the *Metaclimacograptus* spp. described by Koren' and Rickards (1995), *M.?* sp. differs from *M. khabakovi* Koren' and Rickards and *M. khvorovi* Koren' and Rickards in being much more slender.

Genus CLINOCLIMACOGRAPTUS Bulman and Rickards, 1968

*Type species.* By original designation, *Pseudoclimacograptus (Clinoclimacograptus) retroversus* Bulman and Rickards, Llandovery, Sweden and Britain.

*Diagnosis.* Climacograptid with proximally convex and distally concave supragenicular walls; geniculum more or less rounded; thecal apertures strongly everted, facing more or less ventrally; median septum gently undulating in the proximal region, more or less straight distally.

*Remarks.* This genus is difficult to identify in flattened material when the outline tends to approach *Normalograptus* (see Bulman and Rickards 1968; Rickards 1972, for details).

*Clinoclimacograptus* sp.

Plate 5, figure 8

*Material.* A single specimen in relief with thick cortical tissue obscuring fuselli, SM A108628.

*Description.* Part of the sicular aperture may be broken, but it is visible in reverse view for about 0.15 mm. The dorso-ventral width at the level of  $th1^1$  is 0.40 mm and at the level of  $th2^1$  0.40 mm. The maximum dorso-ventral width is 0.55 mm, at the distal end of the narrowly tapering rhabdosome. Because the supragenicular walls are markedly

concavo-convex the maximum dorso-ventral width at any one thecal level is at the convex part of the supragenicular wall, in this case 0.50 mm at  $th_3^1$ . The geniculum is relatively sharp with a short hood, and it extends ventrally beyond the level of the preceding apertural lip by 0.10 mm.  $Th_1^1$  grows upwards for 0.65 mm and  $th_1^2$  for approximately 0.62 mm. Thecal spacing is 14–16 in 10 mm (2TRD 1.2–1.4 mm).

*Remarks.* This form differs from *C. retroversus* Bulman and Rickards only in having a slightly higher thecal spacing (14–16 cf. 10–13 in 10 mm). This is the stratigraphically earliest record of *Clinoclimacograptus*.

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