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Late Wenlock and Ludlow (Silurian) Plectograptinae (Retiolitid Graptolites), Cape Phillips Formation, Arctic Canada

by

Alfred C. Lenz

Paleontological Research Institution
1259 Trumansburg Road
Ithaca, New York, 14850 U.S.A.

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LATE WENLOCK AND LUDLOW (SILURIAN) PLECTOGRAPTINAE (RETIOLITID GRAPTOLITES), CAPE PHILLIPS FORMATION, ARCTIC CANADA

by

A. C. LENZ

Department of Geology
University of Western Ontario
London, Ontario, N6A 5B7
CANADA

ABSTRACT

A rich fauna of beautifully preserved, isolated and uncompressed late Wenlock and early Ludlow retiolitids of the Subfamily Plectograptinae were recovered through acid dissolution of limestone nodules in the Cape Phillips Formation, central Arctic Islands. The fauna ranges in age from the late Wenlock *Cyrtograptus lundgreni–Monograptus testis* Zone to the mid-Ludlow *Saetograptus fritschi linearis* Zone.

The fauna consists of seven genera/subgenera, *Agastograptus, Gothograptus, Holoretiolites, Paraplectograptus, Plectograptus* (*Plectograptus*), *Plectograptus* (*Sokolovograptus*), and *Spinograptus*; and sixteen species: *Agastograptus clathrospinosus* (Eisenack), *Agastograptus quadratus*, n. sp., *Gothograptus nassa* (Holm)[1], *Gothograptus chainos*, n. sp., *Gothograptus eisenacki* (Obut and Sobolevskaya)[2], *Gothograptus marsupium*, n. sp., *Gothograptus*? sp., *Holoretiolites mancki* (Münch), *Paraplectograptus eiseli* (Manck)[3], *Paraplectograptus praemacilentus* (Bouček and Münch), *Paraplectograptus sagenus*, n. sp., *Plectograptus* (*Plectograptus*) *macilentus* (Törnquist)[4], *Plectograptus* (*Sokolovograptus*) *textor* Bouček and Münch, *Plectograptus* (*Sokolovograptus*?) sp., *Spinograptus apoxys*, n. sp., and *Spinograptus nevadensis* (Berry and Murphy). *Spinograptus spinosus* (Wood) and *Balticograptus* are recognized in only flattened form, are rare and poorly preserved, and are not described.

Biostratigraphic ranges of the taxa, as known from the Arctic occurrences, are as follows: *Plectograptus* (*Sokolovograptus*) and *Paraplectograptus* begin in the late Llandovery and range to the end of the *Cyrtograptus lundgreni– Monograptus testis* Zone; *Spinograptus nevadensis* ranges through the *Cyrtograptus perneri–Monograptus opimus* and the *Cyrtograptus lundgreni–Monograptus testis* zones; *Gothograptus eisenacki, Gothograptus marsupium*, and *Gothograptus*? sp. appear in, and are confined to, the *Cyrtograptus lundgreni–Monograptus testis* Zone, while *Gothograptus nassa* and *Gothograptus chainos* are restricted to the latest Wenlock "*Pristiograptus*" *ludensis* Zone; *Agastograptus clathrospinosus* begins slightly below the *Cyrtograptus lundgreni–Monograptus testis* Zone and extends into the *Lobograptus progenitor* Zone; *Spinograptus spinosus*[5] ranges from the "*Pristiograptus*" *ludensis* Zone through the early Ludlow *Lobograptus progenitor* Zone; *Agastograptus quadratus*, n. sp. is confined to the *Lobograptus progenitor* Zone; and *Holoretiolities mancki* and *Plectograptus* (*Plectograptus*) *macilentus* range through the *Lobograptus progenitor* and *Saetograptus fritschi linearis* zones.

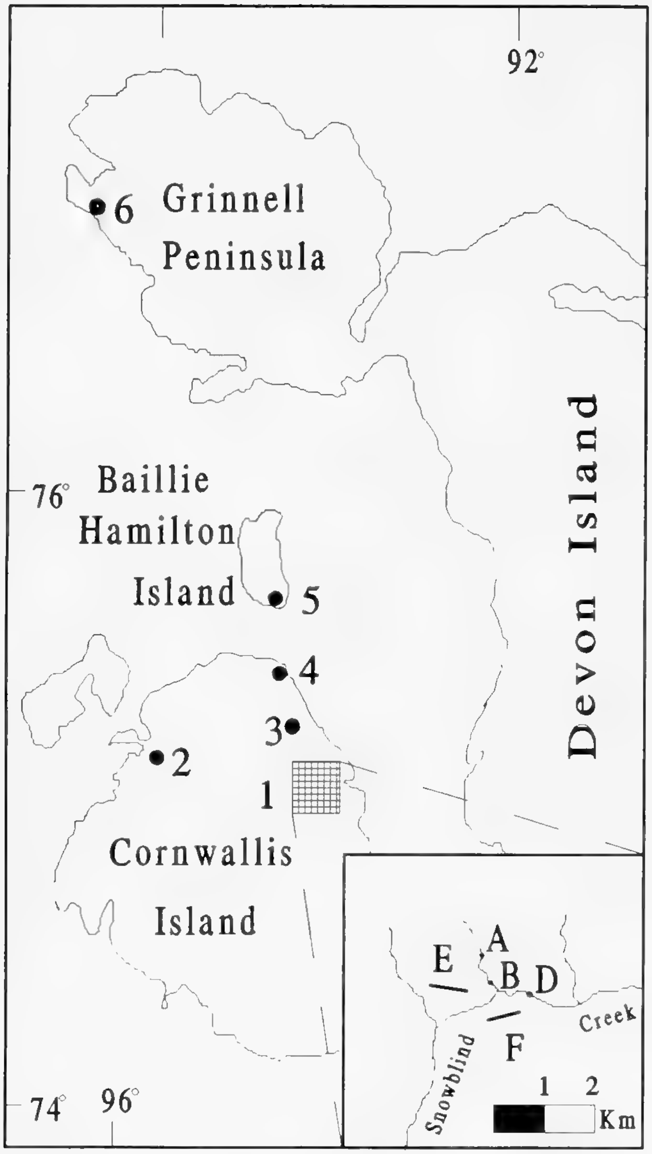
Morphological characteristics of the long-ranging taxa *Paraplectograptus* and *Plectograptus* (*Sokolovograptus*) suggest they are the progenitors of two late Wenlock and early Ludlow subgroups: the first being those in which the virgula is attached throughout, or to some distal part of the rhabdosome; the second being those in which the virgula is free distally. Representatives of both groups ranged through to the early or mid-Ludlow, prior to the final extinction of the plectograptines.

INTRODUCTION

Retiolitids, including the plectograptines, by virtue of the reduction of their skeletal elements to a series of narrow lists, are among the most beautiful groups of graptolites. Because of this much-reduced skeleton, and the small size and fragility of many of the taxa, they are relatively rarely preserved, even as flattened films on shale. They have, therefore, been among the least understood groups of graptolites. The recovery of isolated, uncompressed specimens, particularly from the Arctic, has recently contributed much to the understanding of the overall morphology, growth, and development and, to some extent, the evolutionary development of the retiolitids (Lenz and Melchin, 1987a, 1987b).

The Cape Phillips Formation of the Canadian Arctic Islands has long been recognized for its superb preservation of graptolites, including retiolitids, in limestone nodules (Thorsteinsson, 1958). My recent work on these upper Wenlock and Ludlow shales and their enclosed nodules led to the recovery of sixteen species of plectograptine retiolitids, all uncompressed. The collecting localities from which these specimens were recovered are shown in Text-figures 1 and 2. The late Wenlock and Ludlow forms are specifically focussed on because plectograptines in that part of the stratigraphic column are much less known or understood than those of the late Llandovery. During the late Wenlock and Ludlow, an unprecedented evolutionary diversification occurred among the plectograptines, prior

[1] Uncommon and found only in flattened form.
[2] Abundant.
[3] Rare.
[4] Rare.
[5] Found only in flattened form and not described.



Text-figure 1.—Index map showing collecting localities. The inset shows details of sections from which samples were collected in the Snowblind Creek area (loc. 1) during the 1990 field season.

to their extinction in mid-Ludlow time. This diversification of the plectograptines during the latest Wenlock and earliest Ludlow coincided with a distinct drop in monograptid diversity.

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Financial support has been through a Natural Sciences and Engineering Research Council (Canada) operating grant, and logistical support in Arctic Canada has been through the Polar Continental Shelf Project.

PREVIOUS STUDIES

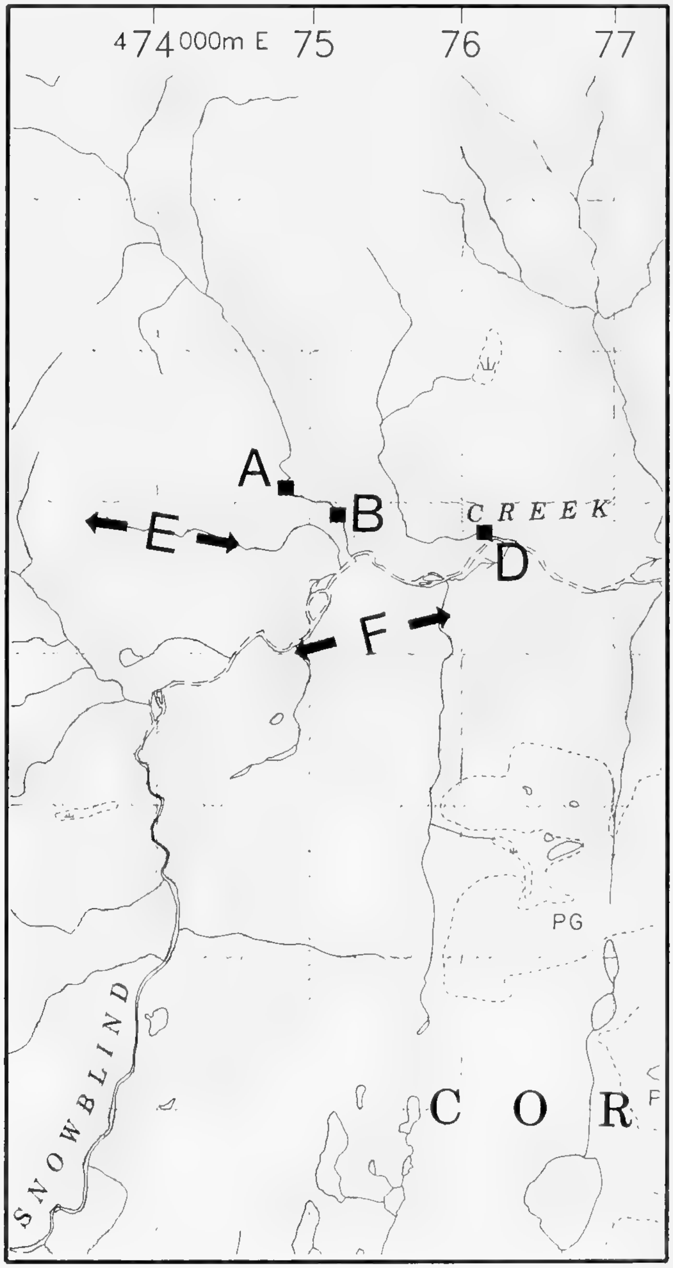
Silurian retiolitids were noted among the graptolite faunas recovered from limestone nodules in the Cape Phillips Formation of Cornwallis Island by Thorsteinsson (1958); none, however, was illustrated. A small fauna of flattened Wenlock and Ludlow plectograptine graptolites from the same general region was described and illustrated in Lenz (1978), and a single Ludlow species was illustrated in Jackson, Lenz, and Pedder (1978). Subsequently, all genera of isolated and uncompressed Silurian retiolitids recognized at that time were discussed and illustrated in Lenz and Melchin (1987a), and to a minor extent in Lenz and Melchin (1987b). Finally, a few taxa of Arctic Silurian retiolitids, most commonly of the *Retiolites geinitzianus* type, have been illustrated in papers devoted to growth and development, or the nature of the skeletal elements of the retiolitids (Kirk, 1973; Bates and Kirk, 1978, 1984, 1986; Crowther, 1981). Although it does not illustrate Arctic retiolitids, the paper of Berry and Murphy (1975) on Silurian and Devonian graptolites of Nevada is also relevant.

Elsewhere in the world, studies of uncompressed and isolated Wenlock and Ludlow retiolitids include: isolated specimens of *Stomatograptus* Tullberg, 1883 and *Gothograptus nassa* (Holm, 1890) by Holm (1890), and of *Gothograptus nassa* by Wiman (1896), both from Gotland; the pioneering studies of Eisenack (1935, 1951) on the Silurian, particularly Ludlow, glacial erratics of northern Germany, which yield a number of beautifully preserved taxa; Obut and Sobolevskaya's (1965) studies of isolated specimens of *Gothograptus eisenacki* Obut and Sobolevskaya, 1965; Obut and Zaslavskaya's (1976) study of isolated material of *Retiolites* Barrande, 1850, *Pseudoretiolites* Bouček and Münch, 1944, and *Sokolovograptus* Obut and Zaslavskaya, 1976 from boreholes in Siberia; and finally, the important study of Obut and Zaslavskaya (1983, and its English translation [1986]), which discussed Silurian retiolitid classification and recognized as new the genus *Agastograptus* Obut and Zaslavskaya, 1983.

TECHNIQUES FOR RECOVERY OF GRAPTOLITES FROM NODULES

Because they commonly have a thin siliceous coating, nodules are broken open to aid in the acid-digestion process. For best recovery of graptolites, particularly the delicate types, acid dissolution must be very slow, using only 1–2% HCl[6], with small amounts of acid being added daily or more often. Periodically, the surface of the acid is skimmed gently with a 60–100 mesh stainless steel sieve to collect graptolites floating on the surface. Most graptolites float because of the CO_2 bubbles inside or clinging to the rhabdosomes. The graptolites in the sieve are then rinsed very gently in hot water to wash away clays or other fine particles as well as some of the organic matter derived from the nodules[7]. The residue is then gently washed in absolute alcohol to remove all traces of the oily organics, following which it is washed into small, tightly-closed jars and stored in absolute alcohol. The graptolites may be stored this way indefinitely. A very fine hair brush is subsequently used to pick and transfer specimens.

When the dissolution of the nodule is complete, and the surface has been skimmed one more time, the entire contents of the container are poured slowly and gently through a 60–100 mesh sieve, until the bottom sediments are just beginning to accumulate on the sieve. After this, the washing procedure outlined above is repeated.



Text-figure 2.—A portion of the Separation Point Mapsheet 58 G/2 (scale 1:50,000), showing the Snowblind Creek area (loc. 1) in relation to local topography. Contour interval = 10 m. Letters designate sections from which samples were collected during the 1990 field season.

Most graptolites from any one nodule will float to the surface and will be recovered by skimming. Some, and often many, specimens will, however, sink, particularly those containing pyrite. It is important, therefore, to examine the residues on the bottom of the container. In rare cases, nearly monospecific assemblages have been recovered almost entirely from the bottom residue.

Depending on the size of the nodule or amount of

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[6] Acetic or other organic acids are even more gentle, but require much more time.

[7] Nodules from the Cape Phillips Formation contain a large amount of "oily" organics.

nodular material being digested, the processes described above may be repeated several times before dissolution is complete. Some clay-rich nodules will readily dissolve only to the point where the clays become so thick as to totally impede dissolution; a further problem arises in this case because graptolites may remain lodged in the clays. If the clay layers are thin, periodic scrubbing of the nodules will permit additional dissolution and further recovery of graptolites. At times, however, the clay content is too great, and the nodule must be discarded.

BIOSTRATIGRAPHY

Wenlock, Ludlow, and Pridoli graptolite sequences of the Arctic Islands have been the focus of study for several years. As a result, recent zonal schemes based on flattened graptolite material for the Wenlock (Lenz and Melchin, 1990, 1991) and for the Ludlow (Lenz, 1990) are readily usable. The zones discussed below are a composite of those defined in these studies: the species names used to define the zones are those of Lenz and Melchin (1991).

WENLOCK

Cyrtograptus centrifugus–Cyrtograptus insectus Zone

The zone is recognized by the appearance of either of the two index species. *Monograptus* cf. *M. flexilis* (Elles, 1900) appears in the zone, but extends beyond, as does *Monograptus flemingi* (Salter, 1852).

Monograptus instrenuus–Cyrtograptus kolobus Zone

Most commonly, the zone is recognized by the first appearance of *Monograptus instrenuus* Lenz and Melchin, 1991, and this is reinforced by the occurrences of *Cyrtograptus kolobus* Lenz and Melchin, 1991, *Cyrtograptus preclarus* Lenz, 1988b [rare], as well as possibly by *Pristiograptus meneghini* (Gortani, 1922).

Cyrtograptus perneri–Monograptus opimus Zone

The appearance of either of the index species indicates the base of the zone. *Cyrtograptus pseudomancki* Lenz and Melchin, 1991, is restricted to the zone, and *Cyrtograptus multiramis* Törnquist, 1910 attains its acme in this zone, but ranges into the overlying zone.

Cyrtograptus lundgreni–Monograptus testis Zone

This is the earliest zone of relevance to this study. The index species are very characteristic of the zone, but important other elements include *Cyrtograptus radians* Törnquist, 1887 and *Cyrtograptus hamatus* (Baily, 1861). Plectograptines include *Paraplectograptus* Přibyl, 1948 (three species), *Spinograptus* spp., *Plectograptus* (*Sokolovograptus*) spp., *Gothograptus eisenacki* Obut and Sobolevskaya, 1965, *Gothograptus marsupium*, n. sp., and *Agastograptus clathrospinosus* (Eisenack, 1951).

"*Pristiograptus*" *ludensis* Zone

The composition of the zone is markedly different from that of the underlying zones. "*Pristiograptus*" *ludensis* (Murchison [*sensu* Wood, 1900]), "*Pristiograptus*" *sherrardae* (Sherwin, 1975), and "*Pristiograptus*" *praedeubeli* (Jaeger, 1990), are typical. *Gothograptus nassa*, *Gothograptus chainos*, n. sp., and *Agastograptus clathrospinosus*, among the plectograptines, are also found in the zone, the first two being restricted to the zone.

LUDLOW

Lobograptus progenitor Zone

Characteristic of the zone are *Lobograptus progenitor* Urbanek, 1966, *Pseudomonoclimacis dalejensis* (Bouček, 1936), and the first appearance of *Bohemograptus bohemicus bohemicus* (Barrande, 1850). Plectograptines include *Spinograptus spinosus* (Wood, 1900), *Holoretiolites* Eisenack, 1951, *Agastograptus* spp., and *Balticograptus* Bouček and Münch, 1952. *Spinograptus* Bouček and Münch, 1952 and *Balticograptus* are found in flattened form only, and are not well-preserved.

Saetograptus fritschi linearis Zone

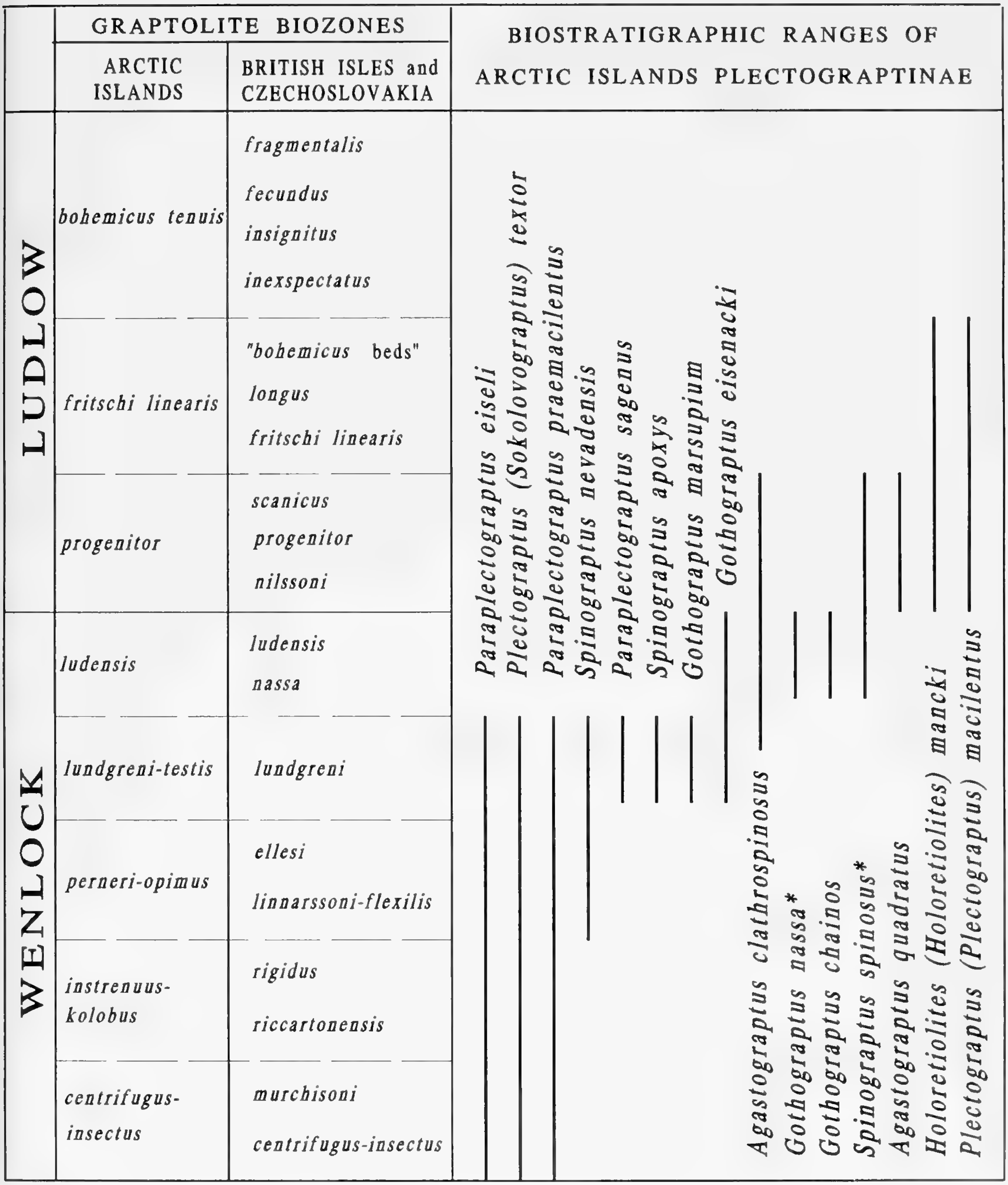
The first appearance of the index species in association with *Monograptus ceratus* Lenz, 1988a is diagnostic. The fauna is of low diversity, although *Pseudomonoclimacis dalejensis* is common in the interval, and *Bohemograptus bohemicus bohemicus* continues through the zone. *Holoretiolites mancki* (Münch, 1931) and *Plectograptus* (*Plectograptus*) *macilentus* (Törnquist, 1887) are the only plectograptines in the zone.

Bohemograptus bohemicus tenuis Zone

The first appearance in abundance of the index species is the primary indicator of the zone. The zonal equivalent elsewhere contains several other species of *Bohemograptus* Přibyl, 1967. The zone appears to be devoid of plectograptines.

ZONAL CORRELATION

The suggested correlation of the Arctic Islands Wenlock and Ludlow strata with a composite of zones from Great Britain (Rickards, 1976) and Czechoslovakia (Přibyl, 1983; Jaeger, 1986) is shown on Text-figure 3. For more detailed discussions of the correlations, see Lenz (1990) and Lenz and Melchin (1991). Biostratigraphic ranges of the plectograptine species described herein are shown in same figure. Zonal assignments and zonal ranges shown for the plectograptine species



Text-figure 3.—Wenlock and Ludlow graptolite biozonations of the Arctic Islands (after Lenz, 1990, and Lenz and Melchin, 1991), in comparison with a composite of the biozones of the British Isles and Czechoslovakia (after Rickards, 1976; Přibyl, 1983; and Jaeger, 1986), and the biostratigraphic ranges of plectograptine retiolitids recognized in the Arctic Islands. Species marked with an asterisk are found only in flattened form on bedding planes in shale. Excluded from the chart are taxa recognized only at the generic level.

are based on the position of graptolite-bearing nodules relative to the adjacent, subjacent, and/or superjacent graptolites flattened on shale surfaces.

PHYLOGENY AND PHYLOGENETIC CLASSIFICATION

It has long been believed that Ordovician retiolitids are unrelated, phyletically, to Silurian forms (see Rickards, Hutt, and Berry, 1977; Rigby, 1986; Mitchell, 1987, for up-to-date references), and it is only the Silurian taxa in the Family Retiolitidae that are relevant in this study. Furthermore, Silurian retiolitids have been subdivided, largely for convenience, into early Silurian Retiolitinae and later Silurian Plectograptinae (Bouček and Münch, 1952; Bulman, 1970). With the advent of electron microscopy, and the recognition of a distinctly different micro-ornament on the skeletal elements in the two subfamilies (Lenz and Melchin, 1987a), there is now a sounder basis for formal recognition of the two subfamilies. Thus, all taxa with a pustulose micro-ornament are assigned to the Subfamily Plectograptinae, while those earlier forms with a parallel linear pattern are members of the Subfamly Retiolitinae.

Relatively little has been written of the evolution of the Silurian retiolitids. Bouček and Münch (1952), for example, say nothing of the ultimate origin of the two subfamilies, except to tentatively suggest that they are derived independently. Bulman (1970) is even more vague, and only suggests a derivation of the family members from one or more lines of diplograptids. Rickards, Hutt, and Berry (1977) point to the similarity between petalograptids and Silurian retiolitids and suggest a phylogenetic relationship. They further suggest that taxa such as *Plectograptus*? *bouceki* Rickards, 1967 [= *Plectograptus* (*Sokolovograptus*) *bouceki* Rickards, 1967] might be ancestral to plectograptines. Bates and Kirk (1984) point out the strong similarity between the ancorae of petalograptids and those of the retiolitids, and suggest that the retiolitid clathrium is derived from further development of the ancoral structures. They, however, make no comment on the derivation of the two subfamilies. Mitchell (1987) and Melchin and Mitchell (1991) consider that the "pattern I" development is characteristic of the retiolitids, and propose that the early skeletal framework of retiolitids and the ancoral processes of petalograptids and "*Orthograptus*" *obuti* Rickards and Koren, 1974, are homologous structures. Some workers, then, accept the concept of the derivation of Silurian retiolitids from one or more petalograptid ancestors. The problem, however, is compounded by the fact that the post-coronal orifices (discussed below) are ancora-related structures, and not true thecae, which are sicula-derived structures.

Turning to the Plectograptinae (*i.e.*, essentially late Llandovery to Ludlow retiolitids), the group, as already noted, is united by the common occurrence of pustulose micro-ornament, a feature therefore considered to be primitive. The origin of the group, however, is in doubt. Rickards, Hutt, and Berry (1977), as well as Bouček and Münch (1952), considered the group most likely to be derived separately from the Retiolininae. I do not accept that view: the reasons are twofold. First, a continuous record of retiolitines and plectograptines exists in Arctic Canada; and second, there appear to be at least two primitive features linking the plectograptines directly with *Retiolites* Barrande, 1850 or closely related retiolitines. A prosicula is commonly present in *Retiolites* (Lenz and Melchin, 1987a); is apparently present, though rare, in the long-ranging *Plectograptus* (*Sokolovograptus*) Obut and Zaslavskaya, 1976; and has been observed for the first time herein in *Paraplectograptus* Přibyl, 1948. Equally importantly, both *Retiolites* and all plectograptines have a simple, four-pronged ancora in which two opposed branches usually join with the lists forming the base of the post-coronal orifices, the other pair of prongs being involved in development of the corona. Such primary (plesiomorphic) astogenetic structures surely provide an adequate link between the two subfamilies. On the other hand, the appearance of the pustulose micro-ornament is apparently sudden and without transition.

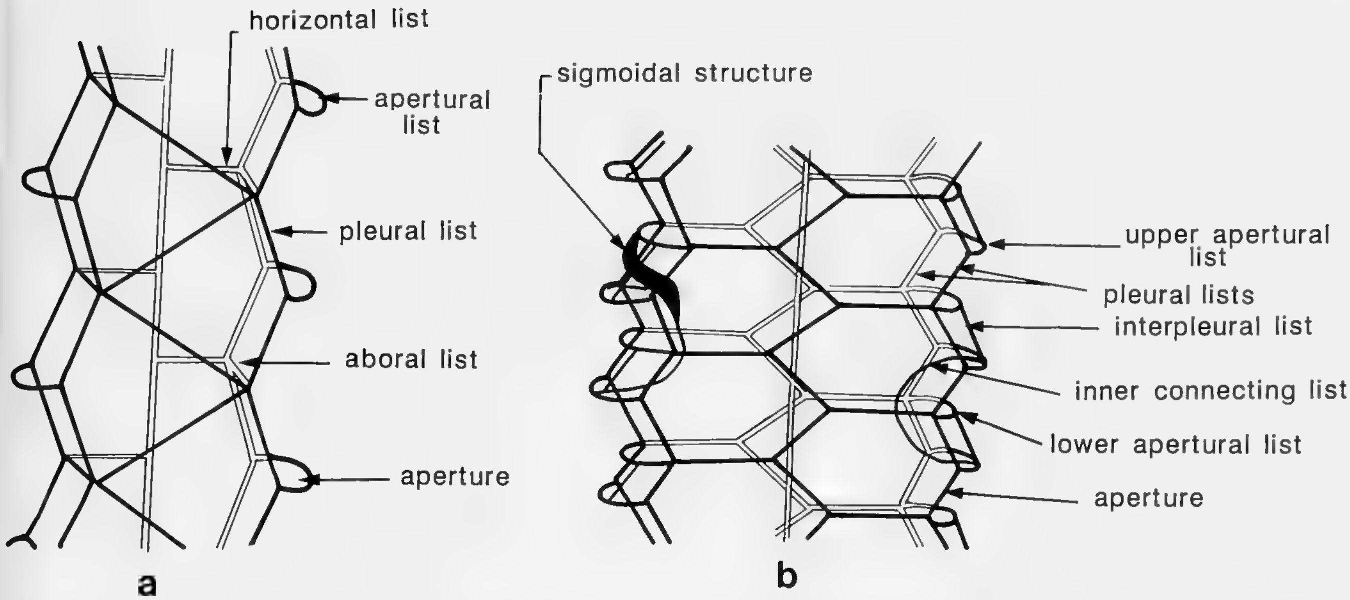
Beyond that level, the picture is less clear. However, two distinct morphotypes are present in the late Llandovery: the *Paraplectograptus* type, in which the virgula is incorporated into the skeletal wall or into the distal part of the rhabdosome in younger forms; and the *Plectograptus* (*Sokolovograptus*) type in which the virgula is free throughout (see Text-fig. 4). These morphotypes consitute good ancestral models for two subgroups of later Silurian plectograptines (the *Plectograptus* Subgroup and the *Paraplectograptus* Subgroup of this study). Geochronologically, the progenitors of the two subgroups appear in the late Llandovery, but do not undergo major diversification until the late Wenlock (see Table 1, p. 24).

If it is accepted that there are two distinct subgroups, the ramifications are important; namely, that at or about the time of final extinction of the plectograptines, species of both subgroups were present, making the extinction even more profound.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

Graptolites, being an extinct group, are difficult to compare with living, colonial organisms, and consequently there are no analogs to indicate the degree of inter- and intra-specific variation common among spe-



Text-figure 4.—Diagrammatic composite sketch of morphological components in (**a**) *Paraplectograptus*-type plectograptines, and (**b**) *Plectograptus*-type plectograptines. Most terms are those standardardized in Bulman (1938, 1970); new morphological terms are *sigmoidal structure*, *interpleural list*, and *inner connecting list*.

cies. Furthermore, the vast majority of graptolites are preserved as flattened, two-dimensional objects on shale surfaces, a fact that sometimes makes taxonomic studies difficult. In rare instances, however, such as in the present study, graptolites are enclosed as uncompressed, three-dimensional objects in limestone nodules, and may be released by acid dissolution.

The recovery of these freed, uncompressed specimens of Silurian retiolitids represents a unique opportunity to better understand the astogeny, classification, morphological variation, and evolution of the group. Most genera and some species of retiolitids have been illustrated in isolated, uncompressed form by earlier workers, so that the morphologic criteria of most genera are well understood. Paradoxically, the superb preservation of such specimens creates a problem in the recognition of, and comparison with, species and even genera that are preserved in the more common, flattened mode. As examples, the distinctions between *Paraplectograptus* Přibyl, 1948 and *Plectograptus* Moberg and Törnquist, 1909 (*sensu stricto*); *Spinograptus* Bouček and Münch, 1952 and *Agastograptus* Obut and Zaslavskaya, 1983; and *Holoretiolites* Eisenack, 1951 and *Balticograptus* Bouček and Münch, 1952 are difficult, and at times impossible, to make in flattened forms.

In this study, the Plectograptinae have been divided into two informal subgroups: those with the virgula attached throughout or to the distal part of the rhabdosome, and those in which the virgula is totally free beyond its ancoral attachment. As such, the formal recognition of two subgroups at the Tribe level, or the elevation of the Subfamily Plectograptinae to the Family level might seem justified. However, until the large group of Silurian retiolitids, including the plectograptines, is studied *in toto*, the informal division seems justified.

Morphological criteria used in the recognition of genera are primarily qualitative ones; they include degree of attachment, if any, of the virgula; profile of the rhabdosome, and whether it remains parallel-sided or narrows distally; the presence or absence of an appendix; gross construction of the rhabdosome, particularly the nature of the primary clathria; shape and profile of the thecal walls; nature of the thecal aperture; and the presence or absence of thecal spines or spinoreticuli.

The routine recovery of large numbers of immature to mature specimens from any one horizon or nodule permits the recognition of all growth stages, and thus eliminates most of the problems in misidentification of early growth stages. Furthermore, these growth stages record the progressive increase in density and the change in mesh size and shape of the secondary skeleton, the reticulum. Both mesh size and shape can vary considerably from species to species. Intraspecific variation is high, even allowing for changes during maturation of the rhabdosome, and admittedly there is a degree of subjectivity. In this study, all specimens recovered from a single nodule or from a series of nodules from the same stratum, which share most characters, are considered to represent the same species. The existence of large numbers of specimens permits ready comparison of material from different sections and stratigraphic levels. In most cases, therefore, the differences between species recognized in this study are fairly clearcut and unequivocal. The exception to this is a group of species of *Paraplectograptus*: *P. eiseli* Manck, 1917, *P. praemacilentus* (Bouček and Münch, 1952), an undescribed species from older strata illustrated in Lenz and Melchin (1987a), and *P. sagenus*, n. sp., all of which show degrees of overlap. The differences among these species are outlined in the discussion of *P. praemacilentus*.

Measurements of rhabdosomal features such as length, width, and thecal spacing were made directly from SEM photographs. Size comparators are defined as follows: small = 1–3 mm; medium/moderate = 3–7 mm; and large = >7 mm.

Synonymies used herein are not exhaustive; instead they comprise the original author and a varying number of subsequent authors, all of which are considered to be of taxonomic importance.

Morphology and Morphological Terminology

The retiolitid rhabdosome meshwork requires some terminology beyond that normally used in the *Treatise* (Bulman, 1970) for fully sclerotized forms such as monograptids and diplograptids. Skeletal-element terminology as used specifically for retiolitids by Bulman (1938) and Rickards (1967) is adapted herein, and newly named skeletal elements are shown on Text-figure 4. Because of the strikingly different development in those taxa with a virgula attached throughout the length of the rhabdosome (*e.g.*, *Paraplectograptus* Přibyl, 1948), in comparison with those in which the virgula is free throughout (*e.g.*, *Plectograptus* Moberg and Törnquist, 1909), or attached only at the distalmost end of the rhabdosome (*e.g.*, *Gothograptus* Frech, 1897), a uniform terminology applicable to all retiolitids/plectograptines is not possible.

In this study, in which some new species and several taxa not previously or adequately known in uncompressed form are described, several new morphological terms are employed. The most commonly occurring, newly named structures are thin, vertically oriented lists connecting the lower apertural list of one theca to the upper apertural list of the preceding one, and termed herein *interpleural lists* (see Text-fig. 4). A second new structure consists of a thin, internal, threadlike, inwardly curved list joining the upper apertural list of one theca to that of the preceding or succeeding theca. This is given the name *inner connecting list* (Pl. 17, fig. 5; Pl. 18, fig. 6). Finally, a structure seen thus far in only a single species, *Spinograptus apoxys*, n. sp., is a solidly sclerotized, sigmoidally curved, bladelike structure connected to the lower apertural list of one theca, and curving inward to connect with the inner connecting list of the underlying theca. This is termed the *sigmoidal structure* (Pl. 18, fig. 5).

Traditionally, morphological terms applied to retiolitids have been those used in more "conventional" graptolites such as the diplograptids. The reason for this is easy to comprehend: large retiolitids such as *Retiolites* Barrande, 1850 (*s. l.*) and *Stomatograptus* Tullberg, 1883, with their heavy, dense, meshwork reticulum, and the rare "sheeting-over" of the entire meshwork by a thin periderm, plus the presence of ephemeral, fully or partly sclerotized thecal "floors" (see Lenz and Melchin, 1987b), make it an easy step to apply such terms as *theca*, *thecal wall*, *thecal floor*, by extrapolation from the fully sclerotized diplograptids. The continuation of this extrapolation from heavily reticulated to lightly or not-at-all reticulated retiolitids (*e.g.*, *Holoretiolites* Eisenack, 1951) appears logical.

A feature common to all plectograptines is their early developmental stage (see p. 13). Typically, the two short, opposing branches of the ancora each divide into a pair of considerably longer and distally curving branches, each pair diverging at an angle of about 60° (Pl. 1, fig. 2; Pl. 5, fig. 10; Pl. 13, fig. 8). One opposing pair of ancoral branches whose alignment is parallel to and intimately connected with the development of the subsequent thecal apertures, attaches directly to the lists forming the "base" of left and right openings (the *post-coronal orifices* of this study). These openings define the top of the corona (see openings above strongly curved coronal lists in Pl. 5, fig. 10). The second opposing pair of ancoral branches, which are oriented at an angle of about 60° to the plane of the rhabdosomal axis, generally undergo further splitting and are mainly involved in the further development of the corona (see stereopairs on Pl. 14, figs. 5, 6).

The left and right openings, herein termed *post-coronal orifices*, are superficially similar to thecal apertures (see opening above strongly curved list in lower right corner of Pl. 3, figs. 5, 7; openings above lowermost left and right lists in Pl. 4, fig. 7; Pl. 5, fig. 10; Pl. 9, figs. 8, 9). It is clear, however, from the examination of plectograptines such as several species of *Gothograptus*, and by extrapolation from older retiolitines such as *Pseudoretiolites* Bouček and Münch, 1944 and *Pseudoplegmatograptus* Přibyl, 1948, which preserve the prosicula and which have elaborately developed internal structures, that the first true thecae (*i.e.*, thecae 1^1 and 1^2) are the first openings distal of the post-coronal orifices. In *Gothograptus eisenacki* Obut and Sobolevskaya, 1965, for example, the floor of theca 1^2 clearly extends below and inside of the post-coronal orifice[8].

[8] I thank Bates and Kirk for pointing this out.

It appears, therefore, that the post-coronal orifices are features of the ancora, whereas thecae 1^1 and 1^2 derive directly from the region where the sicula was, as is typical in all diplograptids; *i.e.*, they are homologues.

The fully or partially sclerotized prosicula is a structure that gradually disappears in the evolution of the Retiolitidae. Earlier taxa such as *Pseudoretiolites* and *Pseudoplegmatograptus* consistently retain the prosicula, as does the later *Stomatograptus*. *Retiolites* relatively often retains a prosicula, prosicular threads, or a prosicular "ring" (Lenz and Melchin, 1987a). The plectograptines, on the other hand, seldom show any trace of a prosicula, although Obut and Zaslavskaya (1976) illustrated immature specimens of *Plectograptus* (*Sokolovograptus*) *parens* (Obut and Zaslavskaya, 1976) that retain fragments or threads of a prosicula, as do rare specimens of *Paraplectograptus* illustrated herein (Pl. 13, figs. 5–10). The presence of sicular remnants in other plectograptines is more problematic. Bates and Kirk (written commun., 1990), however, are confident that they can recognize vestiges of the prosicula and the prosicular ring, and are therefore able to distinguish between the sicula-derived virgella and the post-sicular virgula. This helps in the understanding of the early growth stages, and recognition of thecae 1^1 and 1^2. However, in the absence of any vestige of the sicula, the term 'virgula' is consistently used for the entire rodlike structure in the following taxonomic section.

Throughout, conventional terms such as theca, clathrium, reticulum, are used, even though it is recognized, as implied above, that some of the structures may not be homologous. While revisions of morphological terms as applied to Silurian retiolitids are probably necessary, this should only be done in light of a thorough study of all Silurian retiolitids, rather than from the viewpoint of only the plectograptines.

There has been much discussion of life orientations of graptolites (Kirk, 1990 and numerous citations therein; Rigby and Rickards, 1990). In this study, the traditional "ancora-down" position is used, and terms such as *up*, *down*, *proximal*, and *distal* are employed in the traditional sense [*i.e.*, *Treatise* (Bulman, 1970)].

ABBREVIATIONS OF REPOSITORY INSTITUTIONS

Described specimens, with one exception, are housed in the type collection of the Geological Survey of Canada, Ottawa, and are assigned Survey (GSC) numbers. A single specimen of *Gothograptus nassa* (Holm, 1890) on loan from the Riksmuseum, Stockholm, Sweden, carries the acronym RM. The other repository noted is University of California, Riverside, designated by the acronym UCR.

SYSTEMATICS

Order **GRAPTOLOIDEA** Lapworth *in* Hopkinson and Lapworth, 1875

Family **RETIOLITIDAE** Lapworth, 1873

Subfamily **PLECTOGRAPTINAE** Bouček and Münch, 1952

Diagnosis[9].—Clathria well-developed, sometimes with reticula, lacinia absent; development with ancora stage; one opposed pair of ancoral branches joins lists of post-coronal orifices, the other pair oriented at angle to plane of rhabdosome and involved in development of corona; proximal end of rhabdosome may be somewhat inflated (corona), may narrow distally, and in some genera terminates in slender tubular appendix. Virgula free or incorporated into ventral wall. Lists pustulose on outside surfaces. Seams of the clathria and reticula face in and out, respectively.

Plectograptus Subgroup[10]

Genus **PLECTOGRAPTUS** Moberg and Törnquist, 1909

Type species.—*Retiolites macilentus* Törnquist, 1887. Early Ludlow *colonus* shales, Germany.

Remarks.—This genus is characterized by possession of a rhabdosome that is rectangular in cross-section, generally parallel-sided, although forms that increase or decrease in width distally are known, and by a clathrium of subhexagonal meshes, with or without some minor reticulum, and a central, free virgula.

Two more or less distinct morphologic groups exist; one group, characterized by the genotype, typically lacks or has only minor reticulum, and the skeletal framework is well-ordered. This group constitutes *Plectograptus* (*Plectograptus*); the second group possesses a more disorderly skeleton and variable amounts of reticulum; following the practice of Lenz and Melchin (1987a), these forms are assigned to *Plectograptus* (*Sokolovograptus*)[11].

Subgenus **PLECTOGRAPTUS** Moberg and Törnquist, 1909

Plectograptus (*Plectograptus*) *macilentus* (Törnquist, 1887)
Plate 1, figures 6–8

Retiolites macilentus Törnquist, 1887, p. 491, fig. 3.

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[9] Modified after Lenz and Melchin (1987a).

[10] Includes *Plectograptus* (*Plectograptus*) Moberg and Törnquist, 1909, *Plectograptus* (*Sokolovograptus*) Obut and Zaslavskaya, 1976, and possibly *Agastograptus* Obut and Zaslavskaya, 1983.

[11] This is in contrast to Obut and Zaslavskaya (1976, 1986), who defined *Sokolovograptus* as a separate genus.

Plectograptus macilentus (Törnquist). Moberg and Törnquist, 1909, p. 13, pl. 1, figs. 1–12; Bouček and Münch, 1952, p. 120, pl. 1, figs. 1–4; text-figs. 1e, 6a, 7a–f; Jackson, Lenz, and Pedder, 1978, pl. 2, figs. 10–12.
Retiolites (*Plectograptus*) *tetracanthus* Eisenack, 1951, p. 140, pl. 23, figs. 6–8; pl. 24, fig. 8; pl. 25, fig. 9; text-figs. 4, 5.

Material.—A single, fragmentary isolated specimen from locality 1, section B; one from locality 1, section SBC 4, 7 m; six fragments from a single nodule at locality 3. Illustrated specimens consist of GSC 103981–103983.

Occurrence.—Early Ludlow, *Lobograptus progenitor* and *Saetograptus fritschi linearis* zones.

Description.—Rhabdosome a simple, orderly meshwork of clathria and parietal lists, on ventral and dorsal sides joined to a zigzag median list. Thecal profile climacograptid, defined by equally strongly looped lower and upper apertural lists joined by single central interpleural list. Thecal margins parallel, or inclined at angle to rhabdosomal axis. Rhabdosomal width (based on flattened specimens) ranges from 1.6–1.9 mm and thecal spacing is 5–5.5 in 5 mm. Ancora and corona simple, consisting of four long, curved lists; corona lacks rim, and a simple square opening between the ancora and the horizontal list links earliest-formed parietal lists. Two proximally directed spines emerge from ancora (Pl. 1, figs. 6, 8).

Remarks.—The simple, orderly arrangement of the clathrial and parietal lists of both ventral and dorsal sides of the rhabdosome, as well as the square, climacograptid thecal profile, are characteristic of the species. The single, central interpleural list is also typical, but is often difficult to recognize, particularly in flattened specimens, and the proximally directed ancoral spines seem unique to the species, as noted by Bouček and Münch (1952).

The small number and fragmental nature of the specimens prevents a more detailed description.

Subgenus **SOKOLOVOGRAPTUS** Obut and Zaslavskaya, 1976

Type species.—*Sokolovograptus textor* (Bouček and Münch, 1952). Mid-Wenlock *Cyrtograptus rigidus* Zone, Motol Shale, Czechoslovakia.

Plectograptus (Sokolovograptus) textor Bouček and Münch, 1952
Plate 2, figures 1–8

Plectograptus? *textor* Bouček and Münch, 1952, p. 127, text-figs. 9a–e.
?*Sokolovograptus parens* Obut and Zaslavskaya, 1976, pl. 3, figs. 1–8.
Plectograptus (*Sokolovograptus*) *textor* (Bouček and Münch). Lenz and Melchin, 1987a, pl. 3, figs. 6, 10, 13.

Material.—Nine specimens from locality 4, Cape Phillips; eight from locality 2, Rookery Creek; and two from locality 1, section E. Illustrated specimens consist of GSC 78449, 103984– 103988.

Occurrence.—Rare in late Wenlock strata, but common in the early and mid-Wenlock *Cyrtograptus centrifugus–Cyrtograptus insectus* and *Cyrtograptus perneri–Monograptus opimus* zones.

Description.—Rhabdosome rectangular in cross-section, mostly parallel-sided and up to 8 mm long, but a few specimens exhibit gradual distal widening to a maximum width up to 1.5 mm exclusive of apertural lists. Corona rounded, simple; post-coronal orifices rectangular in outline; in some specimens, region from corona to level of first theca may be somewhat bulbous and inflated, and wider than regions immediately distal of it. Virgula typically less than half length of long rhabdosomes. Clathrial and reticular skeletal elements almost indistinguishable on ventral and dorsal walls; composed of irregular polygonal, triangular, or quadrate meshes. Meshwork more dense and less orderly proximally, becoming progressively more orderly, coarser, and more quadrangular distally. Thecae generally climacograptid in profile proximally, but more orthograptid distally, about 7–8 in 5 mm. Apertural list forming thecal "lip" generally strongly arcuate (Pl. 2, fig. 2); thecal "walls" outlined by a less-curved list or by a simple, loose, reticular network (Pl. 2, fig. 5). Thecae of most-distal region are generally defined only by robust, highly curved apertural lists.

Remarks.—Obut and Zaslavskaya (1976) illustrated a delicate prosicula or partial prosicula, in the early growth stages in some of their specimens of *Sokolovograptus parens*. No hint of a prosicula has been seen in the Cape Phillips specimens.

The distinguishing features of *Plectograptus* (*Sokolovograptus*) *textor* are a disorderly clathrium and reticulum, which become less dense and more orderly distally, and thecae that are more or less distinctly orthograptid in profile distally. The species, as perceived herein, differs from the similar *Plectograptus*? *bouceki* Rickards, 1967, in being narrower, possessing less dense clathrial/reticular elements, and in lacking the extremely long and curved apertural list. It is remarkably similar to *Sokolovograptus parens* Obut and Zaslavskaya, 1976 in thecal as well as clathrial/reticular characteristics, but appears to be consistently wider. The two may be conspecific.

Plectograptus (Sokolovograptus?) species
Plate 1, figures 1–5

Material.—Two specimens from 28 m, and 24 from 68 m, at locality 1, section E. Illustrated specimens consist of GSC 103976–103980.

Occurrence.—Late Wenlock, *Cyrtograptus lundgreni– Monograptus testis* Zone.

Description.—Rhabdosome distinctly rectangular in cross-section; coronal region bowl-shaped, rhabdosome widening relatively rapidly to about level of theca 2, then gradually decreasing in width distally. Corona simple, comprised of a few sinuous lists; post-coronal orifice indistinct, square in outline. Rhabdosomal wall pleural lists more or less straight. Thecal walls consisting of long and strongly looped apertural lists (Pl. 1, fig. 5), proximal of which much less strongly curved lists outline the thecal "walls". Internal to the apertural list is an inwardly curved aboral list. Meshwork a loose, irregular arrangement of coarse clathrial lists, and finer, more regularly spaced and shaped reticular lists. Reticulum progressively denser and finer with maturity. In immature specimens, pleural, apertural, and aboral lists may extend well beyond level of clathrium/reticulum of the rhabdosomal walls, giving a ladderlike appearance to distal walls. Virgula long and free throughout, even in mature specimens.

Remarks.—This species is tentatively assigned to *Plectograptus* (*Sokolovograptus*) due, in part, to the rarity of mature specimens. Like species of *Plectograptus* (*Plectograptus*) Moberg and Törnquist, 1909, the species is rectangular in cross-section and the virgula is free throughout. It differs in possessing a disorderly clathrium and relatively dense reticulum, but its thecal lists show a distinct alternation between long and medium length, features that are typical of *Plectograptus* (*Sokolovograptus*).

The study specimens differ from those of *Plectograptus* (*Sokolovograptus*) *textor* in possessing a more dense and orderly reticulum. The reticular fabric of the species is reminiscent of *Spinograptus nevadensis* (Berry and Murphy, 1975), as are the ladderlike walls of immature specimens. The study specimens, however, totally lack spines (some specimens appear superficially to possess spines, but those structures are merely broken apertural lists).

Genus **AGASTOGRAPTUS**
Obut and Zaslavskaya, 1983

Type species.—*Agastograptus robustus* Obut and Zaslavskaya, 1983, pl. 24, fig. 1; holotype, 251/42-4/1[12]. Early Ludlow *Neodiversograptus nilssoni* Zone.

Diagnosis[13].—

Clathria clearly visible; may have reticulum and zigzag membrane in the middle of the rhabdosome. Thecal apertures with twin spinoreticuli-reticular ends formed by reticular fibres and lists turned in the direction opposite the thecal mouth. Virgula placed in the middle of the rhabdosome, apparently unattached distally (the virgula is almost always broken off close to its proximal end).

Remarks.—Obut and Zaslavskaya (1983, 1986) assign *Retiolites nevadensis* Berry and Murphy, 1975 to *Agastograptus*. Berry and Murphy (1975, p. 100), however, note only the presence of "lists that appear as spines or flanges" and do not mention any elaborations. A retention of the species within *Spinograptus* Bouček and Münch, 1952 is therefore reasonable.

The chief diagnostic characteristic of *Agastograptus* is the presence of spinoreticuli. Some species of the genus are otherwise little different from *Plectograptus* (*Plectograptus*) Moberg and Törnquist, 1909 or *Plectograptus* (*Sokolovograptus*) Obut and Zaslavskaya, 1976. Whether spinoreticuli can always be distinguished in specimens flattened on shale, and thereby prevent confusion with *Spinograptus* Bouček and Münch, 1952, remains to be seen.

Agastograptus clathrospinosus (Eisenack, 1951)
Plate 3, figures 1–7; Plate 4, figures 1–9

Retiolites clathrospinosus Eisenack, 1951, p. 139, pl. 23, figs. 1, 2a, 2b.
?*Spinograptus spinosus* (Wood). Berry and Murphy, 1975, p. 102, pl. 15, fig. 8.
Spinograptus cf. *spinosus* (Wood). Lenz, 1978, p. 636, pl. 7, figs. 3, 4.
Agastograptus clathrospinosus (Eisenack). Obut and Zaslavskaya, 1983, p. 108, pl. 25, figs. 1–3; Obut and Zaslavskaya, 1986, p. 212, figs. 2a–c.

Material.—One-hundred-ten specimens from locality 6, section SJF 145; 32 from locality 1, sections E and F. Several flattened specimens (not illustrated) have been collected in shale from north-central Bathurst Island (76°10′N; 99°10′W). Illustrated specimens consist of GSC 99150–99153, 103989– 103997.

Occurrence.—Late Wenlock. *Cyrtograptus lundgreni– Monograptus testis* and "*Pristiograptus*" *ludensis* zones, and mainly, the earliest Ludlow *Lobograptus progenitor* Zone.

Description.—Rhabdosome rectangular in cross-section, parallel-sided or widening gradually distally, maximum observed width and length 1.3 mm and 6 mm, respectively, rhabdosome apparently open at distal end. Thecae about 8 in 5 mm. Ancora of two short branches that quickly divide into four relatively long branches, one pair of which joins with basal lists of post-coronal orifices; orifices large, distinctly rectangular in outline, directed laterally. Corona of a few lists, open, broadly bowl-shaped, base of post-coronal orifice formed of long, broadly looped list that may curve proximally (Pl. 4, fig. 7). Thecal lateral walls pleural lists moderately undulose. Thecal lower apertural list strongly arcuate (Pl. 4, fig. 2); thecal "hood" that marks base of succeeding theca a strongly arcuate list, which on the proximal side may be elaborated by a few finer reticular lists. Thecal apertures arcuate in profile, directed laterally, overall thecal profile climacograptid. Thecal "hoods" bear a pair of marginally located, long spinoreticuli that are up to 1.2 mm long and contain

[12] Repository unknown; not given by Obut and Zaslavskaya (1983).
[13] From Obut and Zaslavskaya (1986, p. 210).

as many as 25 reticular fibres; spinoreticuli ranging from parallel-sided to club-shaped or spatulate, some showing evidence of continuous-sheeting peridermal tissue. Spinoreticuli occcurring primarily as "hoods" over thecal apertures, but may be present elsewhere, including on the post-coronal orifice, or on mid-regions of the rhabdosome (Pl. 3, fig. 2). Clathrial framework of interlinked and crudely alternating left and right curved lists and thinner secondary lists; reticulum very fine, absent in immature specimens, rare in mature forms. Meshes 0.07–0.08 mm across. Pustules elongated, in distinct rows.

Remarks.—Diagnostic characters of this species are the relatively long and broad spinoreticuli, and the comparatively fine and dense reticular meshwork; this meshwork being much finer and denser than in any other species of *Agastograptus* Obut and Zaslavskaya, 1983.

Spinograptus cf. *spinosus* (Wood) was reported in flattened form from the Arctic Islands (Lenz, 1978). Obut and Zaslavskaya (1983, 1986) consider this to be *Agastograptus clathrospinosus*; my reexamination of the Arctic specimens confirms this. In like manner, the broad and poorly defined "spines" of "*Spinograptus spinosus*" of Berry and Murphy (1975) strongly suggest spinoreticuli.

Agastograptus quadratus, new species
Plate 5, figures 1–10

Origin of species name.—L. *quadratus* = square, four-cornered; referring to the square, boxlike profile of the thecae.

Type specimens.—Holotype, GSC 99173; paratypes, GSC 99171, 99172, 103998, 103999.

Material.—Hundreds of specimens[14] from a single nodule at Cape Sir John Franklin, locality 6, section SJF 155.

Occurrence.—Early Ludlow. *Lobograptus progenitor* Zone.

Diagnosis.—Large species with a simple zigzag clathrial skeleton, minimal reticulum, distinctly square thecae, and short, broad spinoreticuli.

Description.—Rhabdosome 7–8 mm long, rectangular in cross-section, widening slowly from top of coronal region to about level of first three to four thecae, parallel thereafter; maximum width 1.8–2.0 mm exclusive of spinoreticuli, thecae 5–6 in 5 mm. Ancora of two moderate-length primary, and four longer secondary branches; corona simple, broad, with gently curved base; post-coronal orifices large, pentagonal in outline, directed laterally, proximal margin tongue-like (Pl. 5, fig. 10). Clathria of long, alternating left- and right-curving lists joined to more-or-less vertical pleural lists on both sides of rhabdosome. Upper apertural lists strongly arcuate, constituting a hoodlike structure of one theca and the base of the succeeding theca. Hoodlike aspect of upper apertural lists accentuated by development of marginally positioned pairs of short, broad, spatulate spinoreticuli containing up to 12 crisscrossing reticular fibres (Pl. 5, fig. 8). Lower apertural lists, corresponding to the lower apertural "lip", strongly arcuate, joined to inwardly deflected part of the pleural lists. Upper and lower apertural lists joined by a single, thin, medially placed interpleural thread (Pl. 5, fig. 7), attached to which may be a vertically oriented spinoreticulum. Thecal profile distinctly square and climacograptid, accentuated by deep, horizontally oriented thecal apertures. Reticulum absent to weakly developed, of rare crisscrossing lists joined to coarse clathrial network. Virgula apparently free throughout. All lists, including spinoreticuli and virgula, are pustulose.

Remarks.—The most striking feature of the species is the distinctly square or boxlike climacograptid profile of the thecae, with the spinoreticuli superficially resembling supragenicular hoods. Overall, the rhabdosome of the species is substantially like *Plectograptus macilentus* (Törnquist, 1887), to which spinoreticuli have been added.

Agastograptus quadratus differs from *Agastograptus robustus* Obut and Zaslavskaya, 1983 in possessing a less orderly zigzag clathrium and, most distinctly, in its boxlike thecae, the latter feature also readily separating it from *Agastograptus munchi* (Eisenack, 1951). *Agastograptus balticus* (Eisenack, 1951), while bearing spinoreticuli, is otherwise much more like *Gothograptus* Frech, 1897, especially species like *Gothograptus nassa* (Holm, 1890), which bear thecal hoods.

The species is somewhat like "*Retiolites*" *wimani* Eisenack, 1951 in its simple clathrium, but the thecal "walls" of that species are inclined at a moderately high angle to the rhabdosomal axis, and its pleural lists are much more strongly undulose.

Paraplectograptus Subgroup[15]

Genus **GOTHOGRAPTUS** Frech, 1897

Type species.—*Retiolites nassa* Holm, 1890, pl. 2, figs. 12, 13 (holotype)[16]. Late Wenlock *nassa* Zone, Eksta beds, Gotland, Sweden.

Diagnosis.—Corona rounded, width may be equal to maximum rhabdosomal width. Coronal meshwork

[14] Because the specimens are so entangled, it is impossible to give a precise number.

[15] Includes *Gothograptus*, *Holoretiolites* Eisenack, 1951, *Paraplectograptus* Přibyl, 1948, and *Spinograptus* Bouček and Münch, 1952 (described in this study), as well as *Balticograptus* Bouček and Münch, 1952 (not described).

[16] Repository unknown; not given by Holm (1890).

made finer through addition of reticular lists, although not every species has a well-developed reticulum. Rhabdosomes of most species narrow distally. Clathrial pattern complex and somewhat irregular; reticulum often well-developed, becoming more dense with maturity. Thecae long with climacograptid, glyptograptid, or pseudoglyptograptid profile, apertures directed laterally, distally, or proximo-laterally. Rhabdosome commonly terminated by a tubular appendix with fine meshes, or at least with a distally attached and fairly robust virgula. Virgula may be free through substantial part of rhabdosomal length, then moves to ventral side and is incorporated into skeletal framework, generally continuing beyond tubular appendix.

Gothograptus nassa (Holm, 1890)
Plate 6, figures 1–3, 5

Retiolites nassa Holm, 1890, p. 25, pl. 2, figs. 12–14; Wiman, 1896, pl. 11, figs. 1, 4–6, 8–14; *non* figs. 2, 3, 7.
Retiolites (*Gothograptus*) *nassa* Holm. Elles and Wood, 1908, p. 343, pl. 34, figs. 15a–d; text-fig. 225.
Gothograptus nassa (Holm). Bouček and Münch, 1952, p. 112, pl. 1, figs. 9–11; text-figs. 2a–i, 3a–d; Paškevičius, 1974, pl. 14, figs. 1, 2; Berry and Murphy, 1975, p. 101, pl. 15, fig. 2; Lenz and Melchin, 1987b, figs. 4a–e; *non* Lenz, 1978, p. 635, pl. 6, fig. 5 [= *Gothograptus chainos*, n. sp.].

Type specimens.—Not formally designated in Holm (1890).

Material.—Fifteen moderately preserved flattened specimens on shale from north-central Bathurst Island (76°10′N; 99°10′W).

Occurrence.—Latest Wenlock "*Pristiograptus*" *ludensis* Zone.

Description[17].—Rhabdosome about 1 cm long, exclusive of appendix. Maximum width of 1.3–1.6 mm attained in proximal region, margins remaining parallel throughout most of length or, more commonly, gradually narrowing distally. Distal end abruptly narrowed, continuing as parallel-sided appendix. Meshwork of rhabdosomal walls dense, meshes square or rectangular. Thecal apertures obscured by sclerotized, lunate, proximally projecting thecal hoods that are present throughout length of rhabdosome. Thecal spacing about six in 5 mm.

Remarks.—The large size and uniquely developed sclerotized thecal hoods throughout the length of the rhabdosome are characteristic of the species.

Gothograptus chainos, new species
Plate 7, figures 1–12

Gothograptus nassa Lenz, 1978, p. 635, pl. 6, fig. 5.

Derivation of name.—Gr. *chainos* = open mouth, wide gape; referring to the gaping, hoodless, thecal apertures.

Type specimens.—Holotype, GSC 104004; paratypes, GSC 104001–104003; 104005–104009.

Material.—Thirty-three well-preserved specimens from locality 1, section F 39, Snowblind Creek. Illustrated specimens consist of GSC 104001–104009.

Occurrence.—Latest Wenlock "*Pristiograptus*" *ludensis* Zone.

Diagnosis.—Rhabdosome small, rounded in cross-section; meshwork dense, almost entirely of clathrial lists. Thecal apertures open and with a yawning appearance, relatively deep, rims of thecae thickened, totally without hoods. Virgula free throughout, but attached to distal end, and incorporated into well-developed tubular appendix.

Description.—Rhabdosome small, width 0.9–1.1mm, rounded to ovate in cross-section, maximum length 5 mm. Corona rounded, bowl-shaped. Rhabdosome widens slowly from top of corona to first theca and then width constant or decreasing slightly thereafter. Rarely, maximum width attained and maintained just anterior to top of corona; rhabdosome decreases in width toward distal end, then abruptly narrows and develops tubular appendix. Rhabdosomal walls straight to gently undulose. Ancoral and coronal lists thickened in mature specimens, coronal brim may be somewhat lip-like; post-coronal orifice ovate to rounded, with a thickened rim (Pl. 7, figs. 6, 12). Meshwork coarse and dense in mature specimens, individual meshes subrounded to polygonal in outline, about 0.2 mm in diameter, composed almost entirely of clathria in which list "seams" face inward; reticulum represented only by rare, scattered hair-like lists. Thecal apertures prominent, with gaping, mouth-like outline, surrounded by thickened rims; proximal side of thecal lip straight, that of the distal side arched (Pl. 7, fig. 4); thecae totally devoid of hoods. Thecal size and depth generally increasing distally, occupying ⅕ to ¼ rhabdosomal width; thecae about five in 5 mm. Virgula free throughout all but distal end of rhabdosome, and incorporated into well-developed tubular appendix. Appendix consists of nema and a tubular meshwork of clathrial lists; nema extends beyond end of appendix.

Remarks.—Superficially, the species bears considerable resemblance to the typical, but somewhat immature specimens of *Gothograptus nassa* (Holm, 1890) (*i.e.*, those without thecal hoods). Differences between the two species are as follows: 1, thecal apertures of *Gothograptus chainos* project laterally, while those of *Gothograptus nassa* project more or less proximally, and tend to overhang the thecal walls; 2, *Gothograptus chainos* lacks thecal hoods, even in the most mature specimens; 3, rhabdosomal walls of *Gothograptus chainos* are straight to gently undulose, while those of *Gothograptus nassa* are markedly undulose, in part because

[17] Based on specimens flattened on shale.

of the overhanging thecal apertures; and 4, the virgula of *Gothograptus chainos* is entirely free throughout all except the distal end of the rhabdosome, whereas in *Gothograptus nassa*, it is an integral part of the skeleton throughout.

The new species is more like an undescribed species from Germany (photographs kindly sent by H. Jaeger) in rhabdosomal shape and theca apertural outline, but differs in totally lacking thecal hoods and, most importantly, in possessing a virgula that is free through all but the distalmost part of the rhabdosome.

Gothograptus eisenacki Obut and Sobolevskaya, 1965
Plate 8, figures 1–9; Plate 9, figures 1–9

Gothograptus eisenacki Obut and Sobolevskaya, 1965, p. 41, pl. 3, figs. 5, 6; Lenz and Melchin, 1987a, pl. 2, figs. 5, 13, 14; pl. 3, figs. 1, 8.

Type specimens.—Obut and Sobolevskaya, 1965, pl. 3, fig. 5 (holotype, 1087a/24[18]). Late Wenlock *Monograptus testis* Zone, central Taimyr, Russia.

Material.—Sixty-nine specimens from locality 1, section E; three from locality 1, section 10C, 48 from locality 1, section 10D, 20 from locality 1, section 10D?, and 53 from locality 2, Rookery Creek. Illustrated specimens consist of GSC 78440, 78446, 99146–99149, 104011–104018.

Occurrence.—*Cyrtograptus lundgreni–Monograptus testis* and "*Pristiograptus*" *ludensis* zones.

Description.—Rhabdosome round to ovate in cross-section, small, seldom more than 0.7–0.8 mm in maximum width, but variable in length; length seldom more than 3 mm, but a single incomplete specimen illustrated herein and in Lenz and Melchin (1987a) probably exceeded 5 mm. Rounded, complex, bulbous coronal region; post-coronal orifices broadly lunate in outline; large dorsal and ventral openings on theca 1^2 side of rhabdosome (Pl. 8, fig. 1). Maximum width of rhabdosome attained about midlength of theca 1^1; width narrowing distally; rhabdosome generally terminating in a tubular appendix or, in immature specimens, in a distally attached virgula. Total thecal number varies considerably, depending on length of rhabdosome, from as few as two per side to sometimes four and, in one case seven per side. Thecae distinct, even in immature specimens; walls strongly rounded in cross-section and markedly undulose in profile, formed of relatively fine meshwork of clathrium and finer reticulum. Thecal walls long, that of one theca generally projecting inside and below apertural lip of previous theca; floor of theca 1^2 extends inside corona almost to base of ancora. Thecal profile more-or-less pseudoglyptograptid in profile. Main skeleton a relatively coarse clathrium of long, more-or-less alternately left- and right-curving, arcuate lists, between which is the relatively dense reticulum. Reticulum added progressively, so that immature specimens are relatively coarsely meshed while mature specimens are finely and heavily meshed. Virgula free and central through main part of rhabdosome, distally joined by horizontal lists to clathrium. Distal end of mature specimens with variable length, cylindrical, fine-meshed, spirally developed, tubular appendix that incorporates the virgula on one side; free virgula may extend some distance beyond end of appendix. In immature specimens, appendix may not be developed.

Remarks.—The most striking feature of this species is its variable length, and consequently the total number of thecae. Thecal number ranges from two to seven in specimens from Arctic Canada, and Kozlowska-Dawidziuk (1990) illustrates specimens from Poland with up to ten thecae per side; in all other ways long and short specimens are identical. The rhabdosomal length and thecal number apparently bear no relationship to maturity, since the appearance of the appendix in essence marks the end of lengthening. No pattern such as progressive lengthening or shortening through time, nor of dimorphism, is apparent; considerable variation may occur in any one collection.

Gothograptus eisenacki is, because of its size, shape and unique thecal profile, readily distinguishable from all other species of *Gothograptus* Frech, 1897.

Gothograptus marsupium, new species
Plate 10, figures 1–9; Plate 11, figures 1–8

Derivation of name.—L. *marsupium* = pouch, bag, purse; referring to the pouch-like shape of the thecae.

Type specimens.—Holotype, GSC 104024; paratypes, GSC 99174–99176, 104019–104023; 104025–104030.

Material.—Two-hundred-fifteen specimens from locality 1, section E; six from locality 1, section SBC 10C; 15 from locality 1, section 10D; and four from locality 2, Rookery Creek. Illustrated specimens consist of GSC 99174–99176, 104019– 104030.

Occurrence.—Late Wenlock *Cyrtograptus lundgreni– Monograptus testis* Zone.

Diagnosis.—Rhabdosome ovoid-rectangular in cross-section, corona open and tapering, thecae undulose, pouch-like, skeletal meshwork fine and relatively delicate, distal end weakly to moderately narrowing, apparently without appendix, but with a long virgula attached to, and extending well beyond distal part of rhabdosome.

Description.—Rhabdosome ovoid-rectangular in cross-section, coronal region V-shaped to rounded, maximum width 1.2–1.4 mm across first two thecae, parallel-sided or gently tapering through the distance

[18] Repository unknown; not given by Obut and Sobolevskaya (1965).

of the next one or two pairs of thecae, consistently narrowing thereafter, sometimes rapidly; distal end may be very narrow. Virgula consistently attached to distal region by one or several lists (Pl. 10, fig. 4), sometimes extending as a simple rod for a distance equal to the total length of the rhabdosome. Two to rarely five, most commonly three thecae on each side. Corona simple, open; post-coronal orifices ovate to rectangular. Large rounded ventral and dorsal openings present on theca 1^2 side of rhabdosome (Pl. 10, figs. 3, 6). Main skeletal framework of pleural lists that zigzag prominently; thecal lip apertural list situated approximately at medially incurved part of the pleural list. Median part of outer wall of thecae curved and markedly bulging outwards (Pl. 10, fig. 7; pl. 11, fig. 7), formed of finer, intermeshed secondary lists, the density of which increases with maturity. Internally, a curved inner connecting list may join the medial region of one thecal network to that of the previous theca (Pl. 10, fig. 7). Thecae long, with an overall pronounced sigmoidal or even pseudoclimacograptid profile; floor of theca 1^2 extended below level of top of corona. Thecae about six in 5 mm. Distalmost thecae consist only of primary clathrial framework. Virgula free and central until about level of thecae 3 to 5, then joined by one to several horizontal lists to a clathrial list, distal of which it is free, and may be very long, equal to length of rhabdosome; no evidence of tubular appendix as in *Gothograptus nassa* (Holm, 1890) or *Gothograptus eisenacki* Obut and Sobolevskaya, 1965. Skeletal meshes polygonal, meshwork moderately fine, progressively finer with maturity. Meshwork, with the exception of an open coronal region, more dense proximally. Main skeletal framework clathrial, all finer skeletal lists reticular, progressive addition of reticulum leads to progessively finer meshwork of more mature specimens.

Remarks.—Although lacking any evidence of a distal tubular appendix, the morphologic features of this species, such as pronounced distal narrowing of the rhabdosome, anchoring of the virgula to the distal part of the rhabdosome, curved and complex thecal structures, and large, proximal ventral and dorsal openings, are clearly those of *Gothograptus* Frech, 1897.

This species is distinguished from *Gothograptus nassa* by its more rectangular cross-sectional shape, sigmoidal thecal profile, coarser reticulum and lack of thecal hoods, and by the fact that thecal openings are directed distally. From *Gothograptus eisenacki* it is readily distinguished by its much greater size (Pl. 11, fig. 8), rectangularity, and relatively coarser reticulum; however, the similarity in thecal profile is notable. It is like *Gothograptus intermedius* Bouček and Münch, 1952 in general form, but differs from that species in greater amount of reticulum (although it is possible that maturation would add a greater amount of reticular tissue to that species) and, most importantly, a different thecal profile and apertural orientation.

In the zigzag nature of its outer wall, with the thecal apertures developed in the most medially curved part of the pleural lists, and the absence of a tubular appendix, *Gothograptus marsupium* is like *Gothograptus pseudospinosus* (Eisenack, 1951) and *Gothograptus kozlowskii* Kozlowska-Dawidziuk, 1990; both of these species, however, possess spinelike thecal structures and their meshwork is finer and more uniform.

Gothograptus? species
Plate 6, figures 4, 6–8

Material.—Six specimens, most apparently immature, from locality 1, section SBC 10B. Illustrated specimens consist of GSC 99177–99179, 104000.

Occurrence.—Late Wenlock *Cyrtograptus lundgreni-Monograptus testis* Zone.

Description.—Rhabdosome moderate-sized, maximum length 3.5 mm, ovate in cross-section, maximum width of 0.9–1.1 mm near proximal end, then of constant width or gradually narrowing distally. Virgula free, length equal to that of rhabdosome in some specimens. Corona bowl-shaped, moderately complex; post-coronal orifices lunate in outline (Pl. 6, fig. 8); moderate-sized, kidney-shaped ventral and dorsal openings present above corona. Pleural lists of thecae zigzag, the short, medially projecting portion joining strongly curved apertural lists, and the long outward-projecting pleural lists forming thecal lateral margins. Thecal walls formed of a complex and interlocking meshwork of lists that may extend below (more proximal of) level of lip of preceding theca, giving thecae a distinct glyptograptid profile, with apertures opening in a distolateral direction (Pl. 6, figs. 4, 7). Thecal walls of both thecae 1^1 and 1^2 extend below top of coronal rim. Thecal spacing difficult to measure, about six to seven in 5 mm. Ventral and dorsal sides of rhabdosome covered with meshwork, but clathrium and reticulum difficult to distinguish. Density of meshwork decreases distally on ventral and dorsal walls as well as on thecal walls.

Remarks.—The generic assignment of this species is questionable. Like the type species of *Gothograptus* Frech, 1897, it is ovate in cross-section, may decrease in width distally, and possesses complex, curved and long thecal walls; on the other hand, in none of the specimens is the virgula seen to join with the skeleton. Whether this is real, or merely due to immaturity or incompleteness of the material, is unclear.

This species differs from *Gothograptus marsupium*, n. sp., the most similar form, in its ovate cross-section, more irregular and slightly coarser meshwork and, particularly, in that its thecal apertures open distolaterally. From immature specimens of *Gothograptus nassa*

(Holm, 1890) (see Lenz and Melchin, 1987b), it differs in possessing a finer and more complex meshwork, and having differently shaped and oriented thecae.

Genus **HOLORETIOLITES** Eisenack, 1951

Type species.—Retiolites mancki Münch, 1931[19].

Occurrence.—Early Ludlow *colonus* beds, Baltic limestones, Germany.

Diagnosis[20].—Rhabdosome small. Corona always developed, mediolar part cylindrical, quadrilateral, or conically narrowing distally. Virgula in corona and extending to about mediolar region, central. Not known distally. Narrow, cylindrical appendix in some species. Skeleton of clathrium only [*Holoretiolites* (*Holoretiolites*)] or clathrium and reticulum [*Holoretiolites* (*Balticograptus*) Bouček and Münch, 1952].

Remarks.—Bulman (1970, p. 131) places *Balticograptus* in synonymy with *Holoretiolites*. However, because of the well-developed reticulum in *Balticograptus*, it seems preferable to follow Bouček and Münch (1952) in making it a subgenus of *Holoretiolites*. This is analogous to the relationship between *Plectograptus* (*Plectograptus*) Moberg and Törnquist, 1909 and *Plectograptus* (*Sokolovograptus*) Obut and Zaslavskaya, 1976.

The close similarity in mode of rhabdosomal construction, including the manner of development of the first two thecae directly from ancoral lists (Eisenack, 1951, text-fig. 10), termination in a distal appendix, as well as stratigraphic position, suggest that *Holoretiolites* is directly derived from *Gothograptus*.

Subgenus **HOLORETIOLITES** Eisenack, 1951

Holoretiolites (Holoretiolites) mancki (Münch, 1931)
Plate 12, figures 1–12

Retiolites mancki Münch, 1931, p. 35, figs. 1–13; Eisenack, 1935, pl. 4, fig. 15; pl. 7, fig. 2.
Holoretiolites (*Holoretiolites*) *mancki* (Münch). Bouček and Münch, 1952, text-fig. 4a.

Material.—Thirty-three specimens from locality 1, section SBC 4, 7 m; five from locality 1, section B; two from locality 1, section SBC 8E, and 24 from locality 3, section MCM. Illustrated specimens consist of GSC 99167–99170, 104031–104033.

Occurrence.—Early Ludlow *Lobograptus progenitor* and *Saetograptus fritschi linearis* zones.

Description.—Rhabdosome rounded in cross-section, 2.5–3.0 mm long (including tubular appendix), maximum width about 0.6 mm across theca 1, tapering gradually distally, maximum thecal number three to four per side, distal end terminated by a short tubular appendix. Virgular maximum length about ⅓ that of rhabdosome. Corona simple, open, bowl-shaped; postcoronal orifices large, pentagonal in outline, directed laterally. Skeletal clathrium zigzag, of curved, left- and right-alternating lists, forming pentagonally shaped meshes on both ventral and dorsal sides of rhabdosome. Reticulum not present. Thecal lower apertural lip a short, gently curved list; upper apertural lip thecal hoods comprise long, overhanging, strongly arcuate lists (Pl. 12, fig. 5). Arcuate list joined to lower apertural list of succeeding theca by single medially placed interpleural list. Thecal apertures directed proximo-laterally. Distally, clathrial elements converge and fuse with terminal, variable-length, spiralled, fine-meshed tubular appendix (Pl. 12, figs. 2, 10, 11), beyond which an unsupported nema may extend. No evidence of virgula seen in appendix.

Remarks.—Holoretiolites (*Holoretiolites*) *mancki* is distinguished from the only other known species of the subgenus, *Holoretiolites* (*Holoretiolites*) *simplex* (Eisenack, 1935), by being relatively much longer, more gently tapering toward the distal end, and by possessing a terminal appendix, unlike the simple, sharp point seen in the latter species. All specimens recovered in this study readily fall into the definition of *Holoretiolites* (*Holoretiolites*) *mancki*, although Lenz and Melchin (1987a) described a single specimen tentatively identified as *Holoretiolites* (*Holoretiolites*) *simplex* from the same section.

Berry and Murphy (1975) report *Holoretiolites* from Nevada. Their specimens are not sufficiently well-preserved to compare with other species, although two of their illustrated specimens with long, gently tapering rhabdosomes and a light skeletal framework are suggestive of *Holoretiolites* (*Holoretiolites*) *mancki*.

Genus **PARAPLECTOGRAPTUS** Přibyl, 1948[21]

Type species.—Retiolites eiseli Manck, 1917. Repository and catalogue number unknown.

Occurrence.—Late Wenlock *Monograptus testis* Zone, Germany.

Diagnosis[22].—Corona simple, rhomboid, square in cross-section. Rhabdosome walls (clathrium) sharply angular. Virgula incorporated in, and part of, ventral wall throughout. Horizontal lists arise alternately on left and right side of virgula and join outer walls. Dorsal wall either of zigzag pleural lists connecting directly to outer walls, or with short horizontal lists connecting pleural lists and outer walls. Reticulum always makes up dorsal wall, may or may not be present on ventral wall of rhabdosome, is light or dense, generally finer than clathrium, and may or may not be uniformly

[19] Repository unknown; not given by Münch (1931).
[20] Modified after Bouček and Münch (1952).
[21] = *Pseudoplectograptus* Obut and Zaslavskaya, 1983.
[22] Modified from Lenz and Melchin (1987a).

distributed. Prosicula, represented mostly by threads and a complete apertural region (Pl. 13, figs. 5–10), rarely seen.

Remarks.—As noted in Lenz and Melchin (1987a), the definition of *Paraplectograptus* was expanded to encompass forms that may have a moderately dense reticulum, so long as the virgula is an integral part of the ventral clathrial wall throughout. This definition is further extended herein, considering the dense reticulum in *Paraplectograptus sagenus*, n. sp. This appears to be justified by a gradation among three species: *Paraplectograptus eiseli* (Manck, 1917) (almost no reticulum), *Paraplectograptus praemacilentus* (Bouček and Münch, 1952) (moderate amount of reticulum), and *Paraplectograptus sagenus*, n. sp. (dense reticulum). Furthermore, and as already outlined in Lenz and Melchin (1987a), there is good reason for suggesting that the virgula of the type species, *Paraplectograptus praemacilentus*, is incorporated into the skeletal wall; thus, the need for a new genus (*Pseudoplectograptus* Obut and Zaslavskaya, 1983) for *Paraplectograptus praemacilentus* is removed. *Paraplectograptus* is unique among the plectograptines in that it is the only genus whose virgula is continuously part of the ventral skeletal structure of all species.

Of particular interest is the nature of the clathrium and reticulum. The corona, pleural lists, aboral lists, virgula, and its attached horizontal lists are entirely clathrial. On the other hand, the skeletal lists of the entire dorsal wall of the rhabdosome, and those elements ventral to the virgula are reticulum. This feature appears to be unique among the plectograptines. A feature of further interest is the rare occurrence of a vestigial prosicula. The rare presence of a prosicula has been recognized in a single small collection from a talus nodule of probable early Wenlock age (zonal assignment uncertain) (Pl. 13, figs. 5–10). Because all specimens are immature, species identification is not possible.

Paraplectograptus eiseli (Manck, 1917)
Plate 13, figures 1–4

Retiolites eiseli Manck, 1917, p. 338, text-figs. 1–5; Hundt, 1924, p. 81, pl. 11, fig. 26; pl. 12, figs. 7–10.
Paraplectograptus eiseli (Manck). Bouček and Münch, 1952, p. 136, pl. 1, fig. 8; text-figs. 11a–h; Lenz and Melchin, 1987a, pl. 3, figs. 4, 11?, 12.

Material.—Twelve specimens from locality 1, section E; four from locality 1, section SBC 10D; and six from locality 4, section CP 850, Cape Phillips. Illustrated specimens consist of GSC 78450, 104034–104036.

Occurrence.—Late Llandovery to late Wenlock *Cyrtograptus lundgreni–Monograptus testis* Zone [rare].

Description.—Rhabdosome relatively long and narrow, relatively square in cross-section; skeletal framework orderly, of predominantly clathrial lists. Corona square, simple; post-coronal orifices pentagonal in outline, directed laterally. Virgula joins to alternating left and right horizontal (parietal) lists, which in turn join pleural and apertural lists. Dorsal side with zigzag list that alternately joins directly to pleural lists; resulting meshwork distinctly triangular (Pl. 13, fig. 2). Apertural lists prominently curved, marking the apertural lip. Reticulum present or absent on ventral wall, orderly and simple on dorsal wall; secondary reticulum, when present, scattered over rhabdosome. Rhabdosome 0.7–0.9 mm wide, thecal spacing six to seven in 5 mm.

Remarks.—This species, which is rare in the study collections, has been listed by Thorsteinsson (1958) as occurring at 20 stratigraphic levels collections from locality 4 in strata ranging in age from late Llandovery to late Wenlock, but these have not as yet been illustrated.

Paraplectograptus praemacilentus
(Bouček and Münch, 1952)
Plate 14, figures 1–6

?*Retiolites tenuis* Eisenack, 1951, p. 131, pl. 21, figs. 1–13; pl. 22, figs. 1–3; text-figs. 1, 2.
Plectograptus praemacilentus Bouček and Münch, 1952, p. 124, pl. 1, fig. 5; text-figs. 8a–d; Lenz, 1978, p. 635, pl. 6, figs. 4, 8, 10, 11.
?*Gothograptus tenuis* Obut and Sobolevskaya, 1965, p. 40, pl. 3, figs. 1–4.
Paraplectograptus praemacilentus (Bouček and Münch). Lenz and Melchin, 1987a, p. 166, pl. 3, figs. 2, 3, 5, 9.

Material.—Sixteen specimens from locality 1, section E; 23 from locality 1, section F; eight from locality 1, section SBC 10C; three from locality 1, section SBC 10D; eight from locality 2; and 32 from three collections at locality 4. Illustrated specimens consist of GSC 78441, 104041–104045.

Occurrence.—Late Llandovery to late Wenlock (Lenz and Melchin, 1987a), most common in late Llandovery and early Wenlock strata; may extend into latest Wenlock "*Pristiograptus*" *ludensis* Zone.

Description.—Rhabdosome rectangular in cross-section, 4–5 mm long with maximum width of 0.9–1.0 mm attained between thecae 1 and 3, rhabdosome parallel-sided thereafter. Corona simple, open, flat-bottomed, bowl-shaped; post-coronal orifices pentagonal in outline, directed laterally. Skeleton of zigzag clathria joined laterally, alternately to left and right horizontal parietal lists, which in turn join with the strongly zigzag pleural lists. Main skeleton-building clathrium identical on dorsal and ventral sides, with a prominently hexagonal network. Pleural lists joined by horizontal, inward-deflected aboral lists. Virgula moves to ventral side about the level of the second theca, alternately giving rise to left and right parietal lists that join aboral lists; not directly connected to zigzag clathrium. Apertural lists strongly arcuate. Secondary reticulum lightly built, scattered throughout and not forming a distinct pattern, but often retaining a crude zigzag pattern.

Remarks.—This species differs from *Paraplectograptus eiseli* (Manck, 1917) chiefly in its possession of a hexagonally arranged reticulum rather than a triangular one, as well as being more robust and possessing a moderately well-developed secondary reticulum. In overall rhabdosomal shape, it is more akin to *Paraplectograptus sagenus*, n. sp.; the latter, however, has a much more strongly developed reticulum, to the point where the medial zigzag pattern is not visible and, uniquely, possesses thecal walls.

The distinction between this species and *Paraplectograptus eiseli* may at times be subtle, since some specimens of *Paraplectograptus praemacilentus* are almost devoid of reticular lists. *Paraplectograptus praemacilentus* is more robust, with a broader corona, and its walls are typically parallel throughout the length of the rhabdosome. The prime distinction, however, is that in *Paraplectograptus eiseli*, the zigzag lists are in direct contact with the pleural lists, whereas in *Paraplectograptus praemacilentus*, short, horizontal lists are always inserted between the zigzag and pleural lists (Pl. 14, fig. 1).

Lenz and Melchin (1987a) suggested that *Retiolites tenuis* Eisenack, 1951 is an early growth stage of the mature *Paraplectograptus praemacilentus*. If true, *Paraplectograptus praemacilentus* (Bouček and Münch) would be a junior synonym of *Paraplectograptus tenuis* (Eisenack). However, the immaturity of Eisenack's specimens prevents any confident species assignment, although Eisenack's species is clearly assignable to *Paraplectograptus*, a fact already recognized by Bouček and Münch (1952).

Paraplectograptus sagenus, new species
Plate 15, figures 1–9; Plate 16, figures 1–8

Origin of species name.—L. *sagena* = fish net; referring to the well-developed skeletal meshwork of the thecal wall.

Type specimens.—Holotype, GSC 104048; paratypes, GSC 99154, 99155, 99157, 99158; 104046, 104047; 104049–104054.

Material.—Eighty-two specimens from locality 1, section E; 100 from locality 1, section SBC 10A; 130 from locality 1, section SBC 10B; and ten each from locality 1, sections SBC 10C and SBC 10D. Illustrated specimens consist of GSC 99154, 99155, 99157, 99158, 104046–104054.

Occurrence.—Late Wenlock *Cyrtograptus lundgreni– Monograptus testis* Zone.

Diagnosis.—Rhabdosome ovate in cross-section, widening gradually throughout most of length. Clathrium and reticulum difficult to distinguish, meshwork moderately dense and uniform. Thecal walls marked by complex subapertural lists.

Description.—Rhabdosome ovate in cross-section, up to 8 mm long, widening gradually from about 0.75 mm across corona to a maximum width of 1.1–1.3 mm. Thecae six to seven in 5 mm. Corona bowl-shaped, open; post-coronal orifices pentagonal in outline, directed laterally to slightly proximo-laterally. A medially placed, kidney-shaped opening, bordering on corona, present on ventral and dorsal side of rhabdosome. Main rhabdosomal skeleton of strongly zigzag marginal pleural lists and transversely connected apertural lists (Pl. 16, fig. 1). Virgula alternately giving rise to left and right bars that join to inwardly curved, inward-positioned aboral lists; these, in turn, join with pleural lists at their most medially deflected juncture. Apertural lists robust and strongly outwardly curved. Thecal walls outlined by a curved, relatively fine network of reticular lists (Pl. 15, fig. 6). Thecal profile orthograptid to glyptograptid. Thecal wall network denser in mature specimens. Reticular meshwork on ventral and dorsal surfaces relatively dense, evenly distributed, individual meshes round, square or polygonal, 0.08–0.1 mm across. Meshwork relatively uniform laterally, but less dense in distal parts of long specimens.

Remarks.—*Paraplectograptus sagenus*, n. sp. differs from *Paraplectograptus praemacilentus* (Bouček and Münch, 1952) in two features: the more dense and uniform meshwork, and the possession of a thecal wall meshwork, features that also differentiate it from *Paraplectograptus* sp. A of Lenz and Melchin (1987a). Comparison with the heavily meshed "*Plectograptus*" *lejskoviensis* Bouček, 1931 (Bouček and Münch, 1952) is difficult since that species is illustrated only by a single line-drawing. With a stated width of 3.5 mm, however, it is readily distinguished from *Paraplectograptus sagenus*.

Genus **SPINOGRAPTUS** Bouček and Münch, 1952

Type species.—*Retiolites* (*Gothograptus*) *spinosus* Wood, 1900. Repository and catalogue number of holotype unknown. Early Ludlow *Neodiversograptus nilssoni* Zone, Welsh borderland, United Kingdom.

Diagnosis[23].—Like *Plectograptus*, with well-developed reticulum and with characteristic spinelike awns arising from the two margins of the upper apertural list. Mesial transverse list lacking. Virgula distally attached to clathrium. Micro-ornamentation of elongate pustules in parallel rows.

Remarks.—The presence of a distally attached vir-

[23] Emended after Bouček and Münch (1952).

gula has not been previously reported for this genus and it is unclear whether this feature exists in the type species, *Spinograptus spinosus*. Bouček and Münch (1952, p. 133), in discussing the virgula of that species, comment "we must conclude that it is free." However, because the virgula is distally attached in the two species described herein, I assume that this is also true of the type species. This observation has important evolutionary ramifications for the genus.

Spinograptus apoxys, new species
Plate 17, figures 1–7; Plate 18, figures 1–7

Origin of species name.—Gr. *apoxys* = tapering off, becoming less; referring to the distally decreasing width of the rhabdosome.

Type specimens.—Holotype, GSC 104055; paratypes, 99164–99166, 104056–104058.

Material.—Ten specimens from locality 1, section F; six from locality 1, section 8 A, five from locality 1, section 10 C, and four from locality 1, section 10 D. Illustrated specimens consist of GSC 99164, 99166, 104055–104058.

Occurrence.—Late Wenlock *Cyrtograptus lundgreni– Monograptus testis* Zone.

Diagnosis.—Rhabdosome large, attaining maximum width at level of thecae 2 or 3, width decreasing distally; meshwork dense, uniform; thecae climacograptid, apertures large, deep. Sclerotized sigmoidal structure and stomata.

Description.—Rhabdosome rectangular in cross-section, up to 8 mm long, broadly to narrowly rounded proximally, attaining maximum width of 1.8–2.0 mm between levels of thecae 2 and 3, gradually narrowing distally, distal end apparently open. Corona rounded to V-shaped, moderately deep and complex; post-coronal orifices rectangular, directed laterally. Openings kidney-shaped, moderate-sized, proximal of base of theca 1^2 on ventral and dorsal walls of rhabdosome (Pl. 17, fig. 7). Clathrium of loose, square to polygonal lists and much finer reticulum forming a uniform meshwork whose meshes are 0.13–0.16 mm across. Stomata 0.15–0.22 mm in diameter may be present on both sides of rhabdosome and raised above level of meshwork (Pl. 17, figs. 6, 7); without thickened rims. Pleural lists alternately straight and strongly medially deflected, deflection U-shaped. Upper part of 'U' joined to distally arched upper apertural list from which project long, paired curved spines. Spines linked near bases by one or more commonly two horizontal lists, imparting the effect of a prominent thecal hood. Lower apertural lists about midway between preceding and succeeding spine pairs, joined by one or two interpleural lists, which in turn join lateral lists behind and slightly above level of thecal hood, Long thin thread, the inner connecting list, extends inward in a broad arc from the horizontal list (the upper apertural list), behind the thecal hood of one theca, to that of the preceding theca (Pl. 17, fig. 5; pl. 18, fig. 6). Solid sclerotized, vane-like sigmoidal structure (Pl. 18, fig. 5), connected to base of lower apertural list, extending downward inside the upper apertural list of the preceding theca, curving inwardly and downwardly, and finally connecting with inner connecting list (see Text-fig. 4). Thecal profile distinctly climacograptid; aperture large (Pl. 17, figs. 1, 2), almost half the thecal length, deep, directed horizontally. Virgula of mature specimens attached to skeleton distally (Pl. 17, fig. 4; pl. 18, fig. 2), but free in immature specimens.

Remarks.—Distinctive of this species are the distal narrowing of the rhabdosome, the strong climacograptid profile of the thecae and the hoodlike thecal spines. The presence of stomata, inner connecting lists, and the vane-like sigmoidal structure are unusual. An inner connecting list has previously only been seen in *Pseudoretiolites* Bouček and Münch, 1944 (Lenz and Melchin, 1987a, p. 164), but stomata are present in other retiolitids (*e.g.*, *Pseudoretiolites*, *Pseudoplegmatograptus* Přibyl, 1948, and *Stomatograptus* Tullberg, 1883). The vane-like sigmoidal structure commonly, but not invariably, appears early in the development of the rhabdosome.

Spinograptus nevadensis (Berry and Murphy, 1975)
Plate 19, figures 1–6; Plate 20, figures 1–7

Retiolites nevadensis Berry and Murphy, 1975, p. 100, pl. 15, figs. 5, 6; Lenz, 1978, p. 636, pl. 7, figs. 1, 2, 5, 6.
Agastograptus nevadensis (Berry and Murphy). Obut and Zaslavskaya, 1986, p. 210.

Type specimen.—Specimen UCR 4225/3 (Berry and Murphy, 1975, pl. 15, fig. 5). Late Wenlock *Monograptus testis* Zone.

Material.—Two specimens from locality 1, section SBC 10 B; two from locality 1, section 10 C; 12 from locality 1, section 10 D; 12 from locality 1, section 10 E; and nine from locality 1, section E 68. Illustrated specimens consist of GSC 99159–99162, 104059–104061.

Occurrence.—Late Wenlock *Cyrtograptus lundgreni– Monograptus testis* Zone.

Description.—Rhabdosome of moderate size, at least 7 mm long (flattened specimens up to 15 mm), rectangular in cross-section, maintaining constant width of 1.2–1.4 mm (exclusive of spines) for about three-quarters of length, then narrowing to a width equal to about half maximum width. Thecae four-and-one-half to five in 5 mm. Corona open, of four primary branches, each of which divides into shorter, finer secondary lists; broad, flat-bottomed and bowl-shaped (Pl. 19, fig. 1); post-coronal orifices large, rectangular to pentagonal in outline, directed laterally. Rhabdosomal

Table 1.—Matrix of morphologic features of the plectograptines. Presence of a feature is indicated by a '+', absence by '−'; '±' indicates presence or absence, depending on the species.

	Matrix of morphologic characteristics of Plectograptinae																				
	1	*2*	*3*	*4*	*5*	*6*	*7*	*8*	*9*	*10*	*11*	*12*	*13*	*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*
agastogr	−	+	+	+	−	−	+	±	±	−	±	+	−	±	±	±	−	−	−	+	+
balticogr	−	+	+	+	−	+	−	−	+	−	+	−	+	+	−	+	−	−	−	−	−
gothogr	−	+	+	+	±	±	−	−	+	±	+	−	+	±	−	+	+	−	−	−	−
holoret	−	+	+	+	−	+	−	−	+	−	+	−	+	−	+	−	+	−	−	−	−
paraplecto	+	+	+	+	+	−	−	+	−	+	−	−	−	±	−	−	−	−	−	−	−
p. (sokolov)	+	+	+	+	−	−	+	+	−	−	−	+	−	+	−	−	−	−	−	−	−
p. (plecto)	−	+	+	+	−	−	+	+	−	−	−	+	−	−	+	−	−	−	−	+	−
spinogr	−	+	+	±	−	+	−	+	−	±	−	+	−	−	−	−	+	+	+	−	−
retiolites	+	+	−	+	−	−	−	+	−	−	−	−	−	−	−	−	−	−	−	−	−

1 = prosicula; 2 = ancora with 4 main lists; 3 = rim of post-coronal orifice attached only to one pair of ancoral main branches; 4 = round pustular ornament; 5 = virgula incorporated into wall; 6 = virgula attached distally only; 7 = virgula free; 8 = rectangular cross section; 9 = round cross section; 10 = orthogr-glyptogr thecal profile; 11 = thecal rims thickened; 12 = orthogr-climacogr thecal profile; 13 = thecal walls long; 14 = reduced reticulum; 15 = no or only trace reticulum; 16 = thecal walls complex; 17 = distal appendix or terminal process; 18 = elongate pustular ornament; 19 = thecal spines; 20 = boxlike thecal profile; 21 = spinoreticuli.

walls of straight to weakly undulatory pleural lists. Clathrium comprises successive alternately left- and right-curved lists; reticulum of moderately fine, equisized, subrounded to quadrangular meshes about 0.1 mm across; reticular density increasing with maturity, uniform except at lateral margins, where meshwork more coarse. Upper apertural lists strongly curved to broadly U-shaped, with long, laterally curved paired spines at margins (Pl. 20, figs. 1, 2). Directly inward of and just inside lateral margin of rhabdosome, horizontal (aboral?) list joins pleural lists (Pl. 20, fig. 6). Lower apertural lists weakly curved, joined to abovementioned horizontal list by one or two interpleural lists. Thecal margin parallel to rhabdosomal axis. Virgula free through all but distalmost part of rhabdosome, where attached by one or two lists. In flattened specimens, virgula extends well beyond distal end of rhabdosome.

Remarks.—*Spinograptus nevadensis* is characterized by a uniform, orderly and dense meshwork, and thecal walls (pleural lists) that are essentially planar and parallel to the rhabdosomal axis for most of its length, whereas the type species, *Spinograptus spinosus* (Wood, 1900) possesses thecae with a strong orthograptid profile (Elles and Wood, 1908; Obut and Zaslavskaya, 1983, 1986). It differs from *S. apoxys*, n. sp. in being predominantly parallel-sided rather than continuously narrowing distally, and its thecal apertures are flush with the rhabdosomal wall rather than being a deep U-shaped structure.

Elles and Wood (1908, p. 345) suggest the presence of a sicula in *S. spinosus*; this has not been reported from the isolated specimens of Obut and Zaslavskaya (1986), and no hint exists in the study specimens of *S. nevadensis* or of *S. apoxys*, n. sp.

APPENDIX

COLLECTING LOCALITIES AND THEIR CONTAINED FAUNAS

The Cape Phillips Formation (Thorsteinsson, 1958), a basinal limestone and shale facies and the main graptolite-bearing unit of the region, is widespread throughout the Arctic Islands, and consequently graptolites are widely known (Melchin, 1989; Lenz and Melchin, 1990). In the central part of the Arctic Islands, and chiefly on Cornwallis Island, graptolite-bearing nodules are particularly abundant. Graptolite-bearing nodules are common in Llandovery to mid-Wenlock strata, but are much less common in upper Wenlock and Ludlow rocks. In this study, only the Snowblind Creek locality has yielded dozens of both upper Wenlock and Ludlow nodules.

Late Wenlock and Ludlow plectograptine-bearing nodules were collected from six localities (Text-fig. 1): locality 1, Snowblind Creek (75°11′N, 93°47′W); locality 2, Rookery Creek (75°22′N, 95°46′W); locality 3, unnamed creek west of Cape Manning (75°27.5′N, 94°17′W: collected by M. J. Melchin); locality 4, Cape Phillips Formation, type section (75°37′N, 94°30′W); locality 5, Baillie Hamilton Island, south shore (75°45′N, 94°22′W); and locality 6, Cape Sir John Franklin, Grinnell Peninsula (76°42.5′N, 95°53′W).

Locality 1.—Snowblind Creek, because of its rich and nearly continuous sequences of nodular faunas, is the most important locality. As a result, sections there were sampled twice, in 1988 and 1990. Five sections, labelled A, B, D, E, and F were sampled in the 1990 field season (Text-figs. 1, 2). Section C of 1990 was unfossiliferous. The same sections, when sampled previously in 1988, were labelled numerically. Table 1 shows ages, graptolite zones, and section designation equivalents for the sections sampled in the two field seasons.

Only sections E (#10) and F (#8) were long and more-or-less continuous sections, and yielded nodules throughout. Because of the difficulty in making precise stratigraphic correlations between the collections of 1988 and of 1990, faunas collected in the two years are listed and designated separately. This is justified because some species recovered in 1990 were not recovered from nodules collected in 1988, and vice versa; even within the same bed, different nodules may yield distinct faunas. Therefore, for example, a sample collected from the 41 m level in section E in 1990 is designated "SB E41", whereas a sample collected in the same place in 1988 is designated "SBC 10B".

Correlations between the section E of 1990 and section 10 of 1988 are approximately as follows: 10A = E 20 m; 10B = E 28 m; 10C = E 49 m; 10D and 10D? = E 68 m; and 10E = E 85 m.

The following collection listings proceed from oldest to youngest. Measurements are in meters above a designated section base.

Section A (of 1990) did not yield any nodular faunas, but flattened specimens of *Lobograptus progenitor* Urbanek, 1966 were recovered.

Section 5 (of 1988) yielded *Pseudomonoclimacis dalejensis* (Bouček, 1936).

Age: Ludlow, *Lobograptus progenitor* Zone.

Section B (of 1990) yielded the following:

2 m: *Holoretiolites mancki* (Münch, 1931), *Pseudomonoclimacis dalejensis* (Bouček, 1936).
3 m: *Holoretiolites mancki*.
5 m: *Holoretiolites mancki*, *Pseudomonoclimacis dalejensis*.
27 m: *Pseudomonoclimacis dalejensis*.

Section SBC 4 (of 1988) yielded the following species, preserved in flattened form:

7 m: *Bohemograptus bohemicus bohemicus* (Barrande, 1850), *Holoretiolites mancki*, *Lobograptus progenitor* Urbanek, 1966, *Monograptus ceratus* Lenz, 1988a, *Plectograptus macilentus* (Törnquist, 1887), *Pseudomonoclimacis dalejensis*.
10 m: *Bohemograptus bohemicus bohemicus*, *Pseudomonoclimacis dalejensis*.
15 m: ?*Neolobograptus* sp., *Pseudomonoclimacis dalejensis*.

Age: Ludlow, *Lobograptus progenitor* Zone.

Section D (of 1990) yielded the following:

10 m: *Saetograptus fritschi linearis* (Bouček, 1936) [flattened on shale].
75 m: *Pristiograptus* sp., *Saetograptus fritschi linearis*. [nodule]
75 m: *Bohemograptus bohemicus tenuis* (Bouček, 1936), *Monograptus ceratus*. [flattened on shale]

Section 7 (of 1988) yielded the following:

7A: *Bohemograptus bohemicus tenuis*, *Monograptus ceratus*, *Pseudomonoclimacis dalejensis*, *Saetograptus fritschi linearis*.
7B: *Saetograptus fritschi linearis*.
7C: *Pseudomonoclimacis dalejensis*, *Saetograptus fritschi linearis*.

Age: Ludlow, *Saetograptus fritschi linearis* Zone.

Section E (of 1990) yielded the following:

0 m: *Cyrtograptus* sp., *Paraplectograptus eiseli*, *Paraplectograptus praemacilentus*, *Plectograptus* (*Sokolovograptus*) *textor* (Bouček and Münch, 1952).
20 m: *Cyrtograptus hamatus* (Baily, 1861), *Paraplectograptus sagenus*, n. sp.
28 m: *Cyrtograptus hamatus*, *Monograptus priodon* (Bronn, 1835), *Paraplectograptus sagenus*, *Plectograptus* (*Sokolovograptus*?) sp.
32 m: *Cyrtograptus hamatus*, *Monograptus instrenuus* Lenz and Melchin, 1991, *Monograptus priodon*, *Paraplectograptus praemacilentus*, *Paraplectogratpus sagenus*, *Pristiograptus dubius* (Suess, 1851).
41 m: *Cyrtograptus hamatus*, *Cyrtograptus lundgreni* Tullberg, 1883?, *Gothograptus marsupium*, n. sp., *Monograptus instrenuus*, *Paraplectograptus sagenus*, n. sp.
49 m: *Gothograptus eisenacki*, *Gothograptus marsupium*, *Monograptus instrenuus*, *Paraplectograptus praemacilentus*.
53 m: *Cyrtograptus lundgreni*?, *Gothograptus eisenacki*, *Gothograptus marsupium*, *Pristiograptus dubius*.
68 m: *Agastograptus clathrospinosus*, *Monograptus instrenuus*, *Paraplectograptus sagenus*, *Plectograptus* (*Sokolovograptus*?) sp.
85 m: *Gothograptus marsupium*, *Monograptus instrenuus*, *Pristiograptus dubius*.
102 m: *Cyrtograptus lundgreni*?, *Gothograptus marsupium*, *Monograptus instrenuus*.
142 m: *Agastograptus clathrospinosus* (Eisenack, 1951), *Pristiograptus dubius*, "*Pristiograptus*" *ludensis* (Murchison [*sensu* Wood, 1900]).
153 m: *Agastograptus clathrospinosus*, "*Pristiograptus*" *ludensis*, *Pristiograptus sherrardae* (Sherwin, 1975).
155 m: "*Pristiograptus*" *ludensis*.

Age: Late Wenlock, *Cyrtograptus lundgreni–Monograptus testis* Zone [from 0 m through 102 m], and latest Wenlock, "*Pristiograptus*" *ludensis* Zone [from the 142 m, 153 m, and 155 m samples].

Section 10 (of 1988), and a nearby small isolated outcrop [sample 10D?; approximately coeval with sample 10D] yielded the following:

10A: *Cyrtograptus hamatus*, *Paraplectograptus sagenus*.
10B: *Gothograptus eisenacki*, ?*Gothograptus* sp., *Paraplectograptus sagenus*, *Spinograptus nevadensis* (Berry and Murphy, 1975).
10C: *Cyrtograptus lundgreni*, *Gothograptus eisenacki*, *Gothograptus marsupium*, *Monograptus testis* Tullberg, 1883, *Paraplectograptus praemacilentus*, *Paraplectograptus sagenus*, *Spinograptus apoxys*, n. sp., *Spinograptus nevadensis*.
10D: *Gothograptus eisenacki*, *Gothograptus marsupium*, *Monograptus testis*, *Paraplectograptus eiseli*, *Paraplectograptus praemacilentus*, *Paraplectograptus sagenus*, *Spinograptus apoxys*, *Spinograptus nevadensis*.
10D?: *Cyrtograptus* cf. *C. lundgreni*, *Gothograptus eisenacki*, *Gothograptus marsupium*, *Monograptus testis*, *Spinograptus nevadensis*.
10E: *Spinograptus nevadensis*.

Age: Late Wenlock, *Cyrtograptus lundgreni–Monograptus testis* Zone.

Section F of 1990 yielded the following:

3 m: *Cyrtograptus hamatus* (Baily, 1861), *Monograptus instrenuus* Lenz and Melchin, 1991, *Monograptus testis* Tullberg, 1883, *Paraplectograptus praemacilentus* Bouček and Münch, 1952, *Spinograptus apoxys*, n. sp.
22 m: *Cyrtograptus lundgreni* Tullberg, 1883?, *Pristiograptus praemacilentus*, *Spinograptus apoxys*.
26 m: *Cyrtograptus hamatus*.
39 m: *Gothograptus chainos*, *Pristiograptus dubius*, "*Pristiograptus*" *ludensis* (Murchison [*sensu* Wood, 1900])?.
44 m: *Agastograptus clathrospinosus* (Eisenack, 1951).
57 m: *Agastograptus clathrospinosus*, "*Pristiograptus*" *ludensis*.
62 m: *Agastograptus clathrospinosus*, "*Pristiograptus*" *ludensis*.
68 m[24]: *Cyrtograptus lundgreni*, *Monograptus instrenuus*, *Paraplectograptus praemacilentus*, *Spinograptus apoxys*.

[24] Talus sample, almost certainly out of place.

288 m: *Pseudomonoclimacis dalejensis* (Bouček, 1936).
300 m: *Monograptus ceratus* Lenz, 1988a, *Pseudomonoclimacis dalejensis.*
320 m: *Monograptus ceratus, Pseudomonoclimacis dalejensis.*
325 m: *Saetograptus fritschi linearis* (Bouček, 1936).

Age: Late Wenlock, *Cyrtograptus lundgreni–Monograptus testis* Zone [from 0 m through 26 m]; latest Wenlock, "*Pristiograptus*" *ludensis* Zone [from 39 m through 62 m, questionably 68 m]; early Ludlow, *Saetograptus fritschi linearis* Zone [from 288 m through 350 m].

Section 8 (of 1988) yielded the following:

8A: *Gothograptus eisenacki* Obut and Sobolevskaya, 1965, *Monograptus testis* Tullberg, 1883, *Paraplectograptus sagenus*, n. sp., *Spinograptus apoxys*, n. sp.
8C[25]: *Bohemograptus bohemicus tenuis* (Bouček, 1936), *Monograptus ceratus, Saetograptus* ex gr. *chimaera* (Barrande, 1850).
8E: *Agastograptus clathrospinosus, Colonograptus colonus* (Barrande, 1850), *Holoretiolities mancki* (Münch, 1931).
8F: ?*Lobograptus* sp.

Age: Late Wenlock, *Cyrtograptus lundgreni–Monograptus testis* Zone [8A]; early Ludlow, *Lobograptus progenitor* Zone [?8C–8E].

Locality 2.—Rookery Creek (field designation MRC). Only a single graptolite-bearing nodule of relevance to this study was recovered. It contains abundant *Gothograptus eisenacki* Obut and Sobolevskaya, 1965, as well as lesser numbers of *Plectograptus* (*Sokolovograptus*) *textor* (Bouček and Münch, 1952), *Gothograptus marsupium*, n. sp., and *Monograptus opimus* Lenz and Melchin, 1991.

Age: Late Wenlock, *Cyrtograptus lundgreni–Monograptus testis* Zone.

Locality 3.—Unnamed creek west of Cape Manning (field designation MCM). The single nodule collected by M. J. Melchin yielded *Bohemograptus bohemicus tenuis* (Bouček, 1936), *Holoretiolites mancki* (Münch, 1931), *Plectograptus macilentus* (Törnquist, 1887), *Pseudomonoclimacis dalejensis* (Bouček, 1936).

Age: Early Ludlow, probably *Saetograptus fritschi linearis* Zone.

Locality 4.—Cape Phillips (field designations, CP and MCP) yielded two collections of relevance to this study:

213–220 m: *Cyrtograptus* cf. *C. gracilis* Bouček, 1931, *Cyrtograptus* sp., *Monograptus firmus festinolatus* Lenz and Melchin, 1991, *Monograptus instrenuus* Lenz and Melchin, 1991.
244–250 m: *Cyrtograptus* sp., *Paraplectograptus eiseli* (Manck, 1917), *Paraplectograptus praemacilentus, Plectograptus* (*Sokolovograptus*) *textor.*

Age: Late Wenlock, *Cyrtograptus lundgreni–Monograptus testis* Zone.

[25] Possibly in part talus.

Locality 5.—Baillie Hamilton Island (field designation BH), yielded two collections relevant to this study:

42 m: *Bohemograptus bohemicus bohemicus* (Barrande, 1850), *Plectograptus macilentus* (flattened on shale).
72 m: *Lobograptus progenitor* Urbanek, 1966, *Plectograptus macilentus* (flattened on shale).

Age: Ludlow, *Lobograptus progenitor* Zone.

Locality 6[26].—Cape Sir John Franklin (field designation SJF) yielded the following:

145 m: *Agastograptus clathrospinosus* (Eisenack, 1951), *Pristiograptus dubius* (Suess, 1851), "*Pristiograptus*" *ludensis* (Murchison [*sensu* Wood, 1900])?
147 m: *Bohemograptus bohemicus bohemicus, Saetograptus roemeri* (Barrande, 1850).
148 m: *Bohemograptus bohemicus bohemicus, Lobograptus progenitor, Saetograptus roemeri*, .
149 m: *Bohemograptus bohemicus bohemicus, Lobograptus progenitor.*
154 m: *Bohemograptus bohemicus bohemicus, Plectograptus macilentus.*
155 m: *Agastograptus quadratus*, n. sp., *Bohemograptus bohemicus bohemicus.*
160 m: *Bohemograptus bohemicus bohemicus.*
163 m: *Balticograptus* sp., *Bohemograptus bohemicus bohemicus, Saetograptus roemeri.*
166 m: *Bohemograptus bohemicus bohemicus, Plectograptus macilentus.*
170 m: *Bohemograptus bohemicus bohemicus.*
172 m: *Saetograptus roemeri.*
174 m: *Bohemograptus bohemicus bohemicus, Plectograptus macilentus, Spinograptus spinosus* (Wood, 1900).

Age: Early Ludlow, *Lobograptus progenitor* Zone [147 m through 174 m].

One additional collection of flattened specimens, not shown on the index map, is relevant to this study. This is a single collection from Twilight Creek (76°10′N, 99°10′W), north-central Bathurst Island (see Lenz and Melchin, 1990), yielding: *Gothograptus nassa* (Holm, 1890), "*Pristiograptus*" *ludensis*, and "*Pristiograptus*" *sherrardae* (Sherwin, 1975).

Age: Latest Wenlock, "*Pristiograptus*" *ludensis* Zone.

[26] Locality 6 is important in that it is stratigraphically continuous and yields a good Ludlow fauna. Only at the 145 m and 155 m levels, however, were isolated specimens recovered from nodules. These nodules contained large numbers of two species of plectograptines, one new.

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PLATES

EXPLANATION OF PLATE 1

Figure — Page

1–5. ***Plectograptus* (*Sokolovograptus*?) sp.** 14

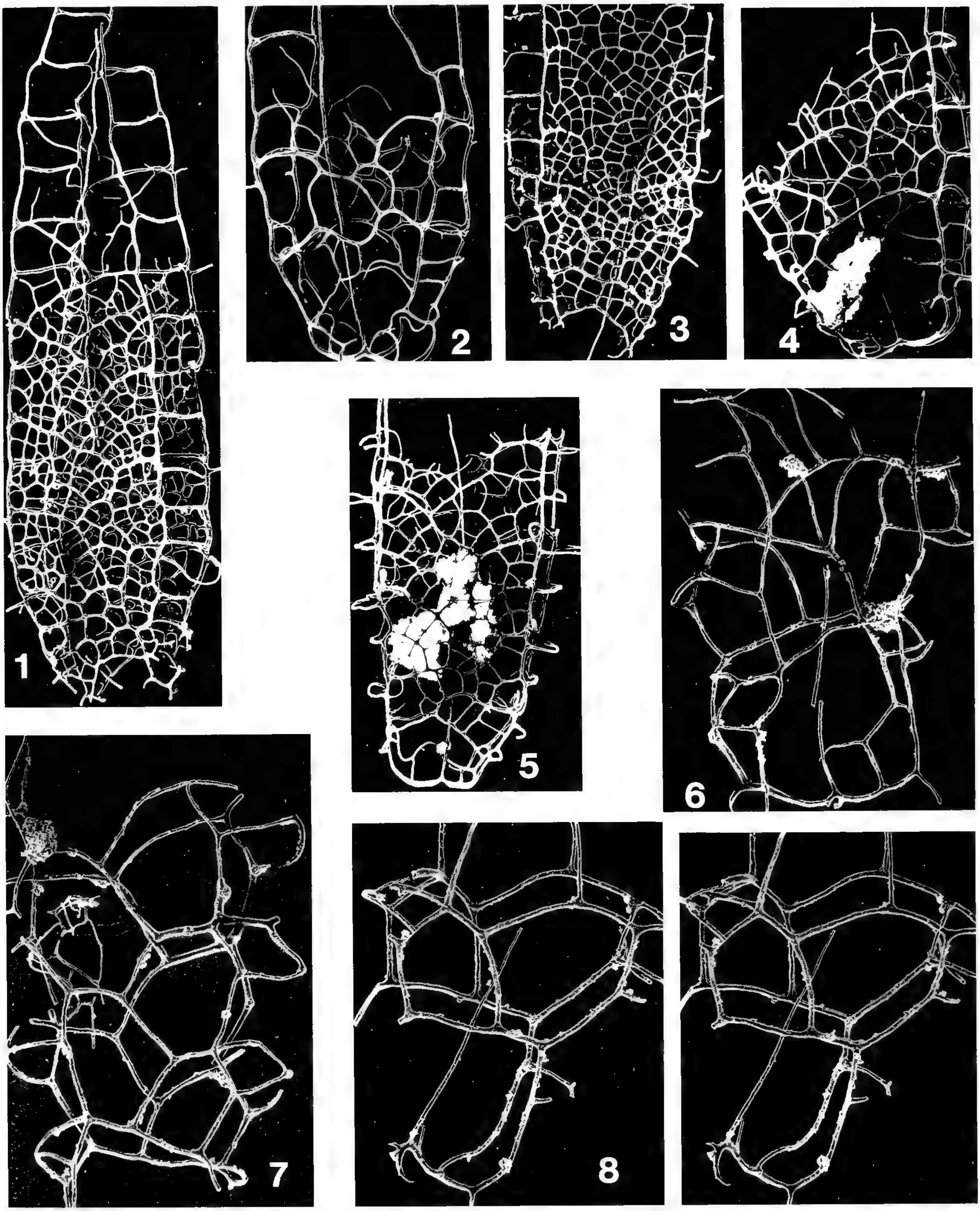
Locality 1, sections SB E68 m.

1. Large mature specimen; GSC103976, ×20.
2. Immature fragment with well preserved virgula; GSC103977, ×31.
3. Mature specimen; GSC103978, ×20.
4. Proximal end fragment; GSC103979, ×31.
5. Immature specimen with ladder-like walls; GSC103980, ×23.

6–8. ***Plectograptus* (*Plectograptus*) *macilentus*** (Törnquist). 13

Locality 1, section SB E68 m.

6. Proximal region; GSC103981, ×28.
7. Mid-region of rhabdosome; GSC103982, ×24.
8. Stereopair of proximal region; GSC103983, ×28.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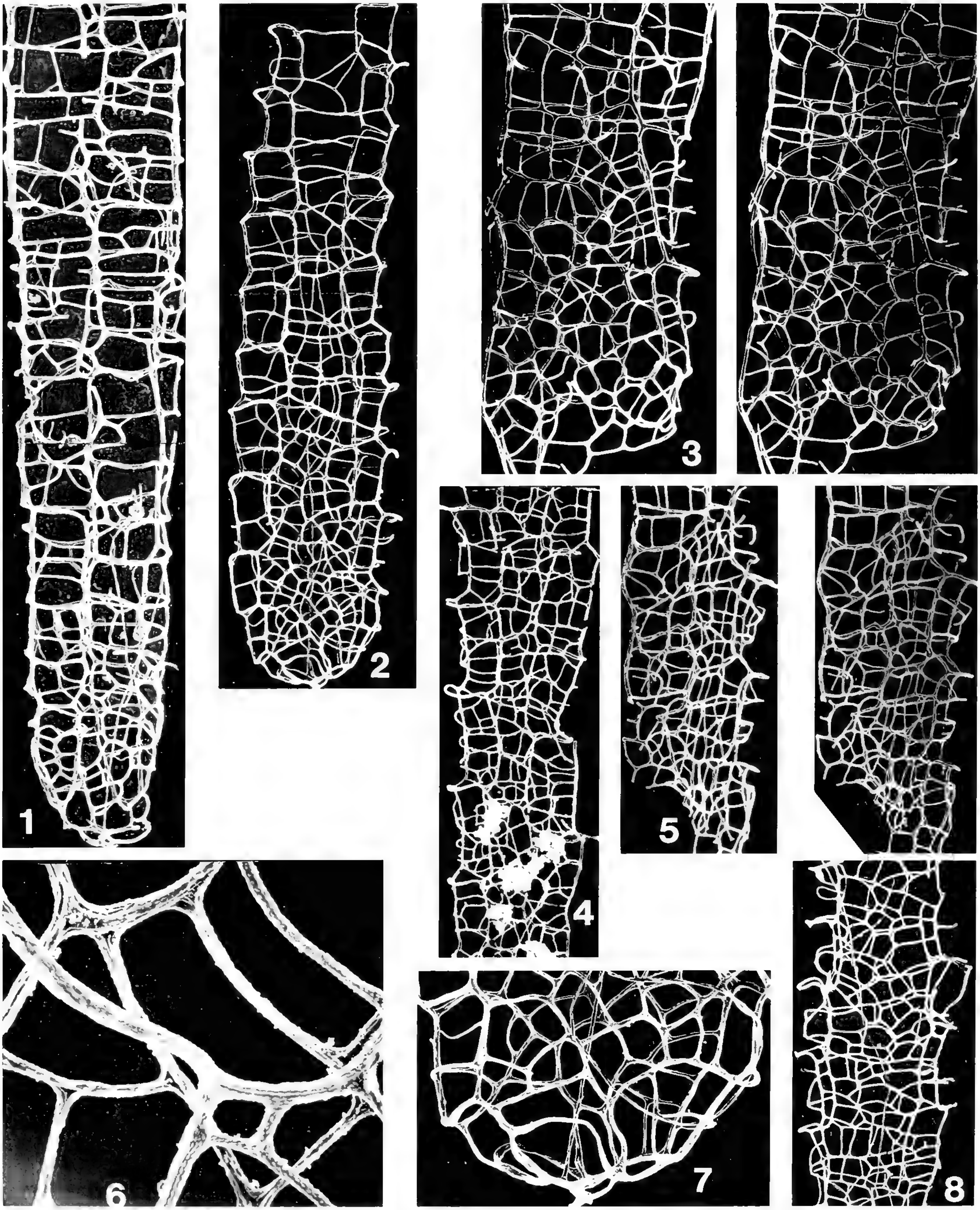
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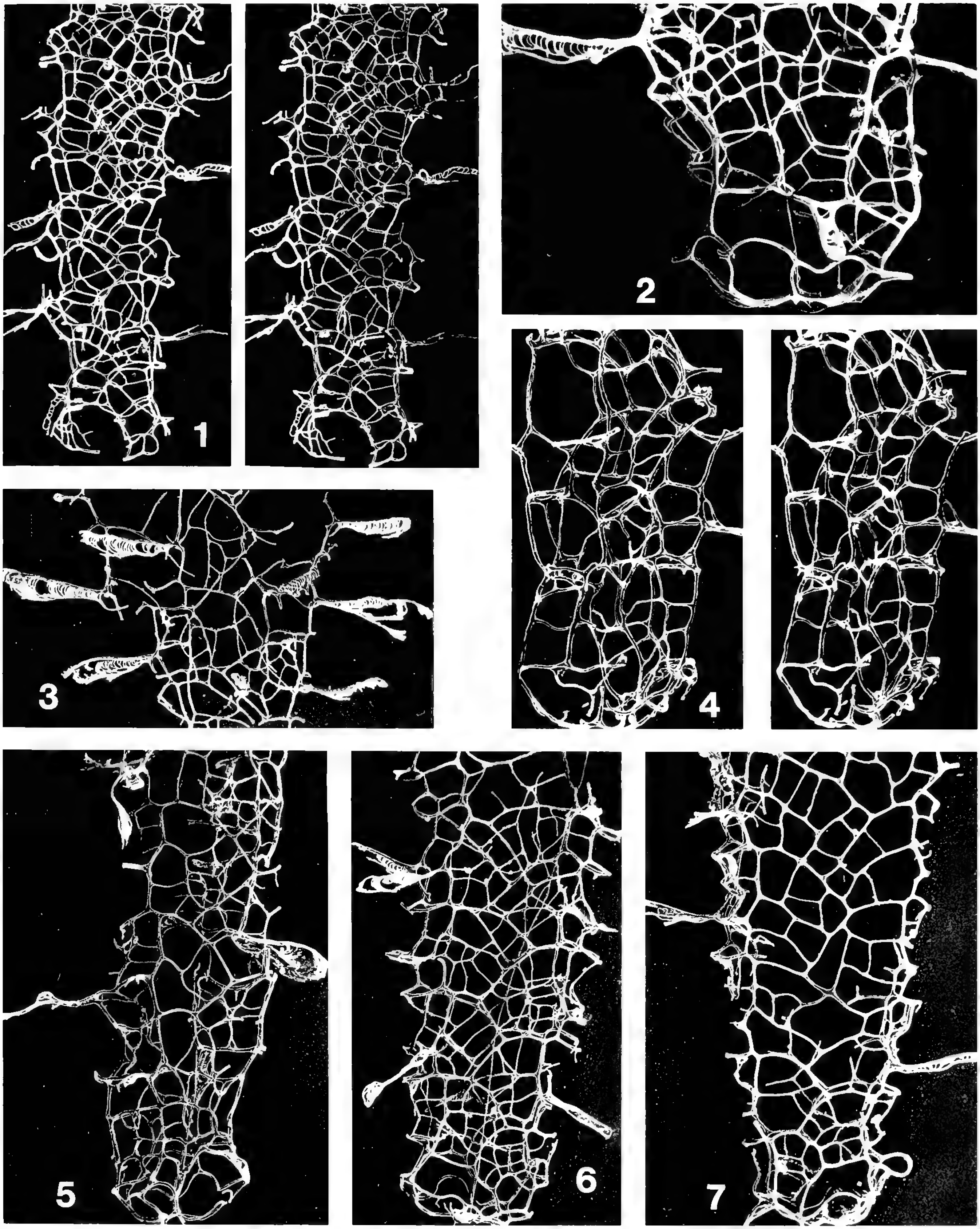
EXPLANATION OF PLATE 2

Figure Page
1–8. ***Plectograptus (Sokolovograptus) textor*** Boucek and Münch 14
1. Large specimen; locality 4, section CP390–400 (Early Wenlock); GSC78449, ×40.
2. Complete specimen; locality 1, section SB E28 m; GSC103984, ×23.
3. Stereopair of proximal region; locality 4, section CP700; GSC103985, ×35.
4. Partial specimen showing thecal characteristics; locality 1, section SBC9, GSC103986, ×20.
5. Stereopair of incomplete specimen; locality 4, section CP700; GSC103987, ×24.
6. Enlargement of thecal walls of GSC103986, ×160.
7. Proximal end of GSC103984, ×69.
8. Incomplete specimen showing thecal profile; locality 4, section CP600; GSC103988, ×20.

EXPLANATION OF PLATE 3

Figure	Page
1–9. ***Agastograptus clathrospinosus*** (Eisenack)	15

1. Fragment of a specimen with very large spinoreticuli; locality 1, section SB E142; GSC103989, ×24.
2. Immature specimen with large spinoreticuli and well preserved virgula; locality 1, section SB E142; GSC103990, ×21.
3. Proximal end fragment with large spinoreticuli; locality 1, section SB E68; GSC103991, ×18.
4. Enlargement of spinoreticulum of GSC103991, ×100.
5. Enlargement of spinoreticulum of GSC103989, ×72.
6. Mid-region of rhabdosome showing distinct zig-zag nature of the primary clathria; locality 1, section SBC8E; GSC99152, ×24.
7. Rhabdosome fragment with long spinoreticulum; locality 1, section SB E142; GSC103992, ×19.
8. Spinoreticuli of GSC99150; locality 6, section SJF145, ×56.
9. Enlargement of spinoreticulum of GSC99150, ×660.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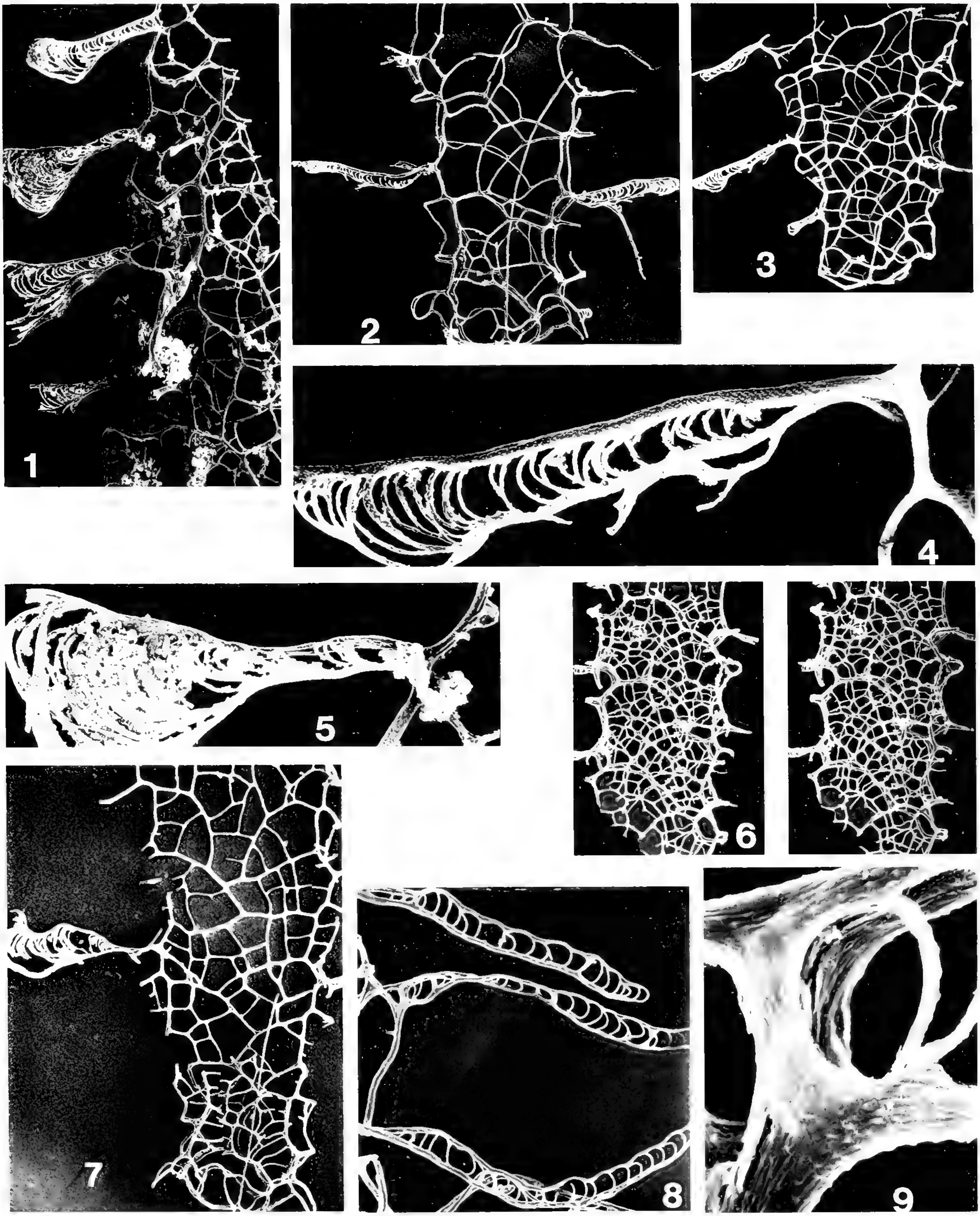
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EXPLANATION OF PLATE 4

Figure — Page

1–7. ***Agastograptus clathrospinosus*** (Eisenack) 15

1. Stereopair of GSC99151; locality 6, section SJF145, ×20.
2. Proximal end showing early spinoreticuli; locality 1, section SB E142; GSC103993, ×33.
3. Incomplete specimen with well developed spinoreticuli; locality 1, section SB E142, GSC103994, ×17.
4. Stereopair of immature specimen; locality 6, section SJF145; GSC99153, ×35.
5. Incomplete specimen; locality 1, section SB E142; GSC103995, ×19.
6. Specimen with long virgula; locality 1, section SB E142; GSC103996, ×19.
7. Proximal portion of specimen; locality 1, section SB E142; GSC103997, ×48.

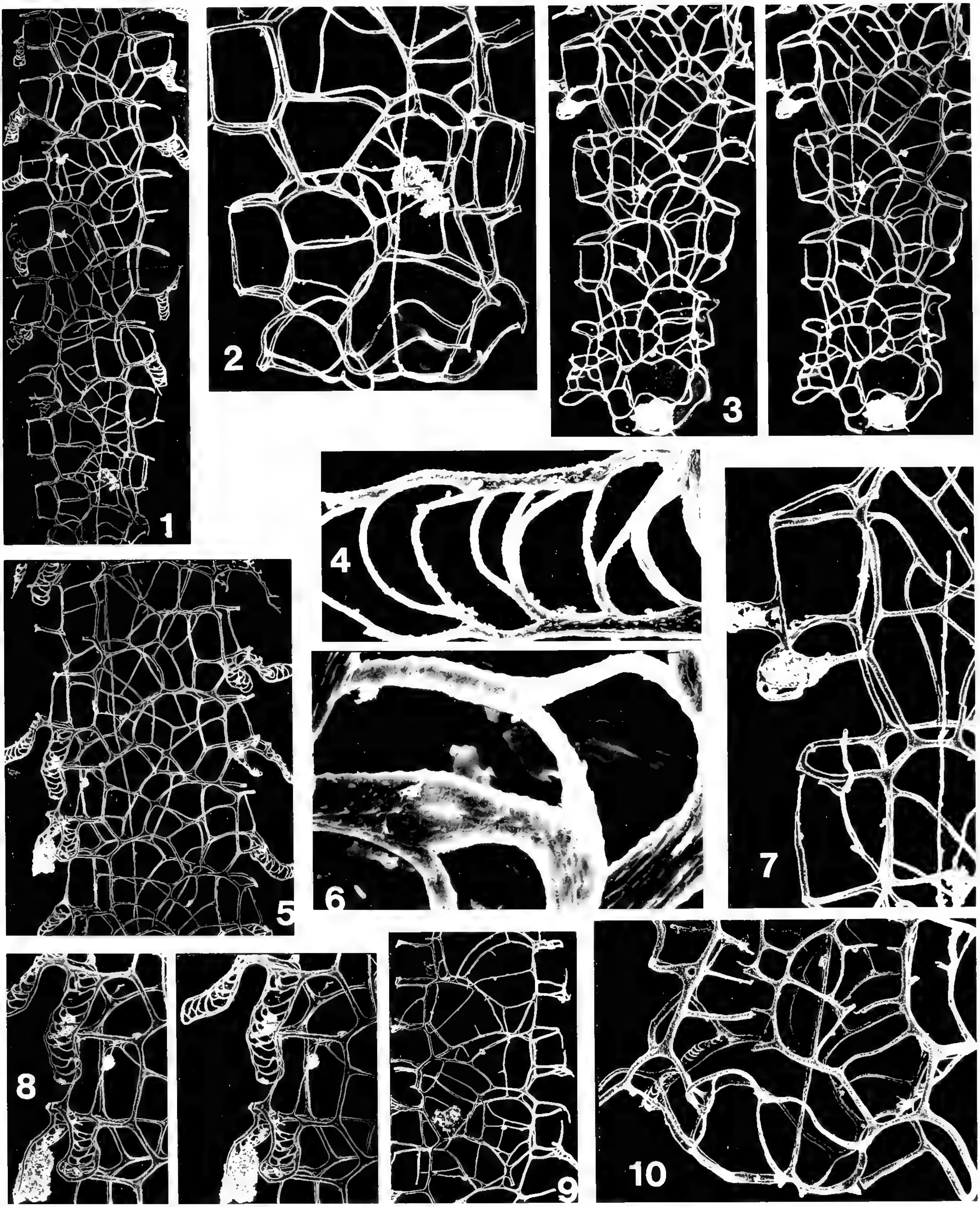
EXPLANATION OF PLATE 5

Figure Page

1–10. ***Agastograptus quadratus,*** new species 16

Locality 6, section SJF155 (except for #10).

1. Holotype specimen, GSC99173, ×16.
2. Enlargement of proximal end of holotype GSC99173, ×40.
3. Stereopair, GSC99171, ×20.
4. Enlargement of spinoreticuli of holotype GSC99173, ×240.
5. Mid-region of rhabdosome with long virgula; GSC99172, ×18.
6. Enlargement of spinoreticuli of GSC99172, ×560.
7. Thecal walls and spinoreticuli of GSC99171, ×50.
8. Stereopair of thecal walls and spinoreticuli of GSC99172, ×28.
9. Partial specimen, GSC103998, ×16.
10. Proximal end of incomplete specimen; locality 6, section SB E142, GSC103999, ×48.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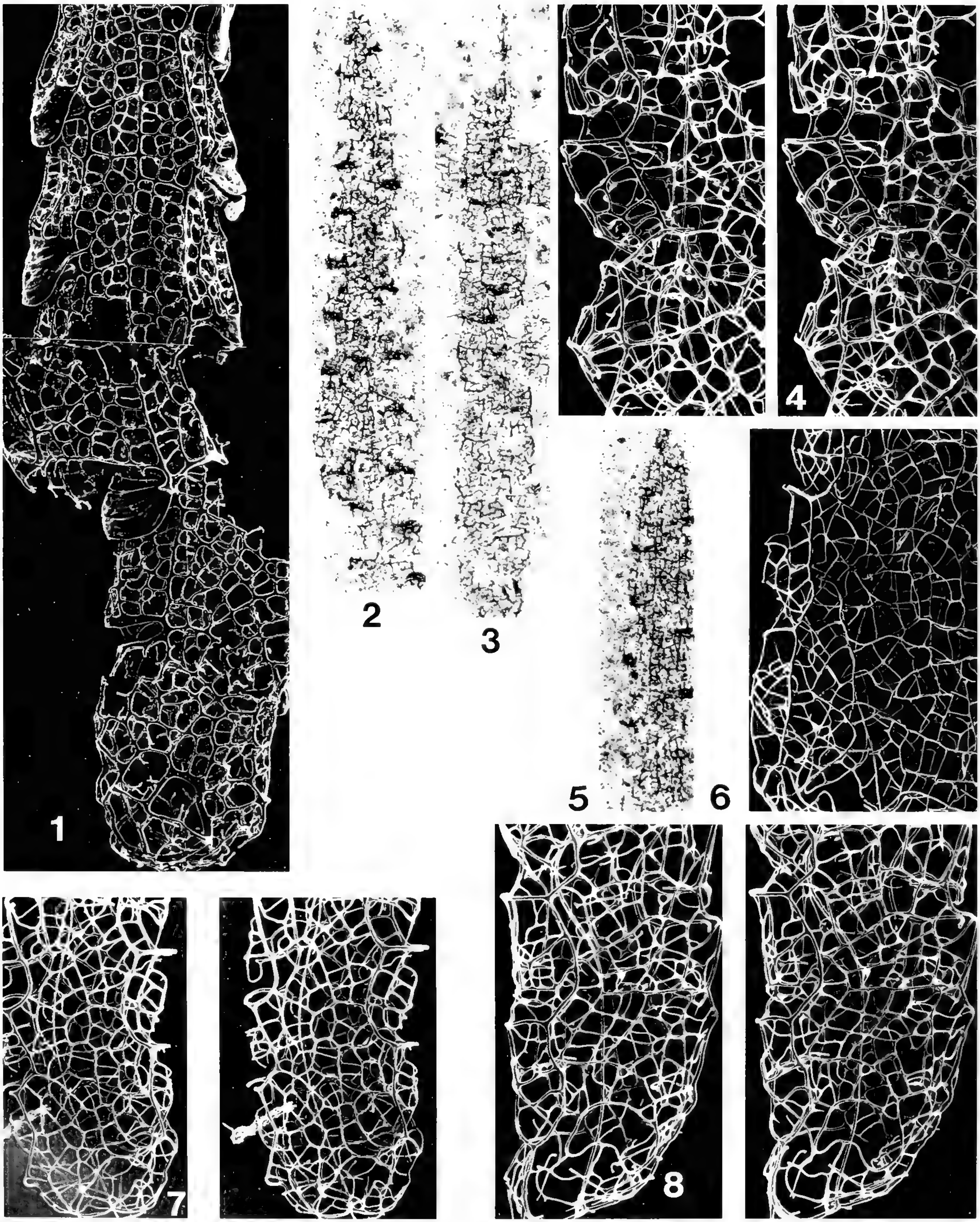
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EXPLANATION OF PLATE 6

Figure Page

1–3, 5. ***Gothograptus nassa*** (Holm) 17

1. Mature, broken specimen from Gotland showing well developed thecal hoods; RM67196, ×45.

2,3,5. Flattened specimens on shale surfaces from Twilight Creek, Bathurst Island; GSC95976, 95978 and 95977, ×14.

4, 6–8. ?***Gothograptus*** sp. 19

Locality 1, section SBC10B.

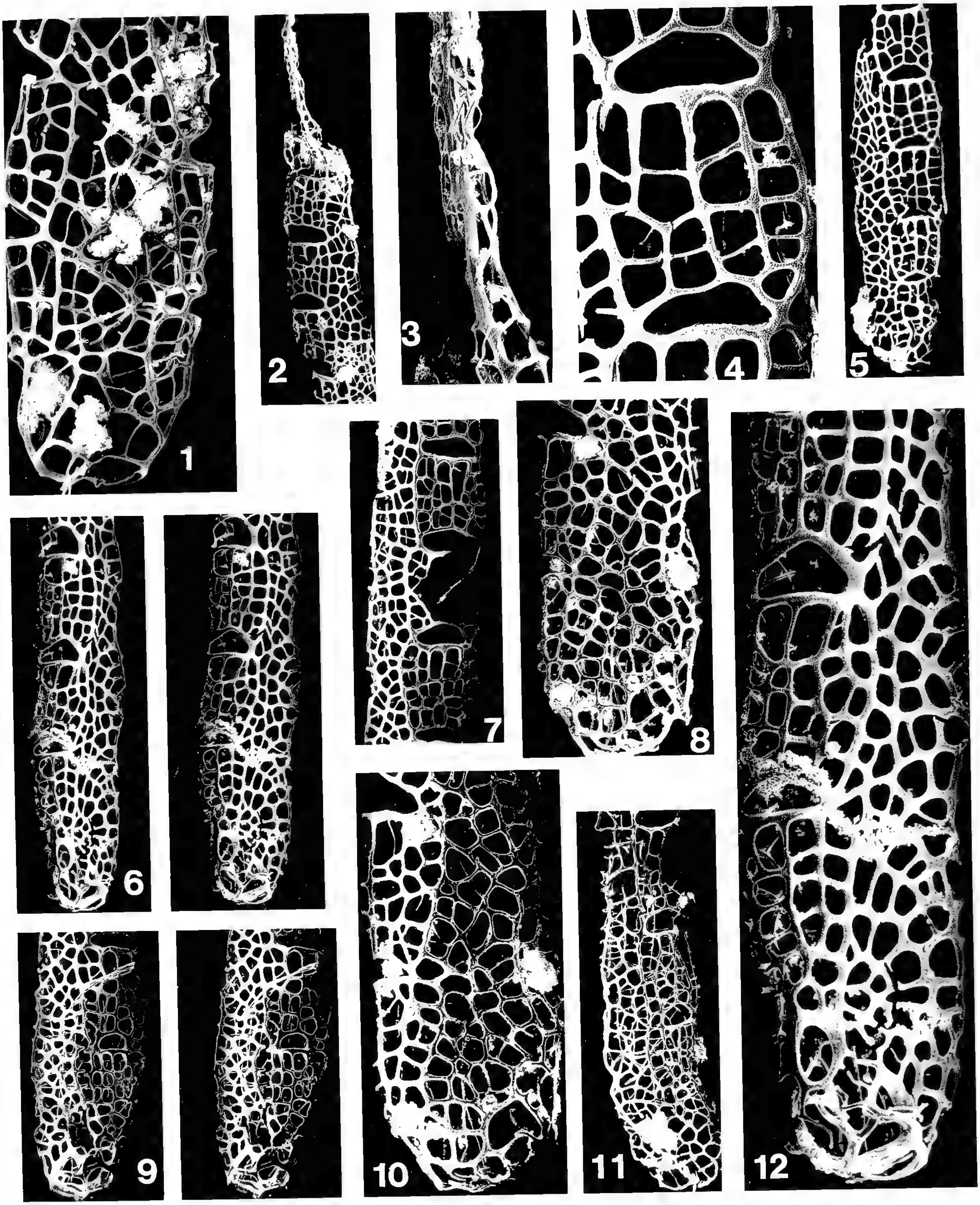
4. Stereopair of walls; GSC104000, ×40.
6. Specimen showing walls and thecae; GSC99178, ×40.
7. Stereopair of specimen with well preserved virgula; GSC99179, ×30.
8. Stereopair showing loosely curved virgula; GSC99177, ×40.

EXPLANATION OF PLATE 7

Figure Page
1–12. ***Gothograptus chainos,*** new species 17

Locality 1, section SB E39.

1. Proximal end of immature specimen; GSC104001, ×38.
2. Mature specimen with "appendix"; GSC104002, ×18.
3. Enlargement of appendix of GSC104002, ×61.
4. Enlargement of thecal apertures of GSC104003, ×58.
5. Thecal view of incomplete specimen; GSC104003, ×16.
6. Stereopair of holotype; GSC104004, ×21.
7. Thecal view of mid-region; GSC104005, ×21.
8. Proximal region; GSC104006, ×32.
9. Stereopair of mature specimen; GSC104007, ×21.
10. Proximal region; GSC104008, ×37.
11. Proximal region of immature specimen; GSC104009, ×20.
12. Enlargement of proximal region of holotype; GSC104004, ×47.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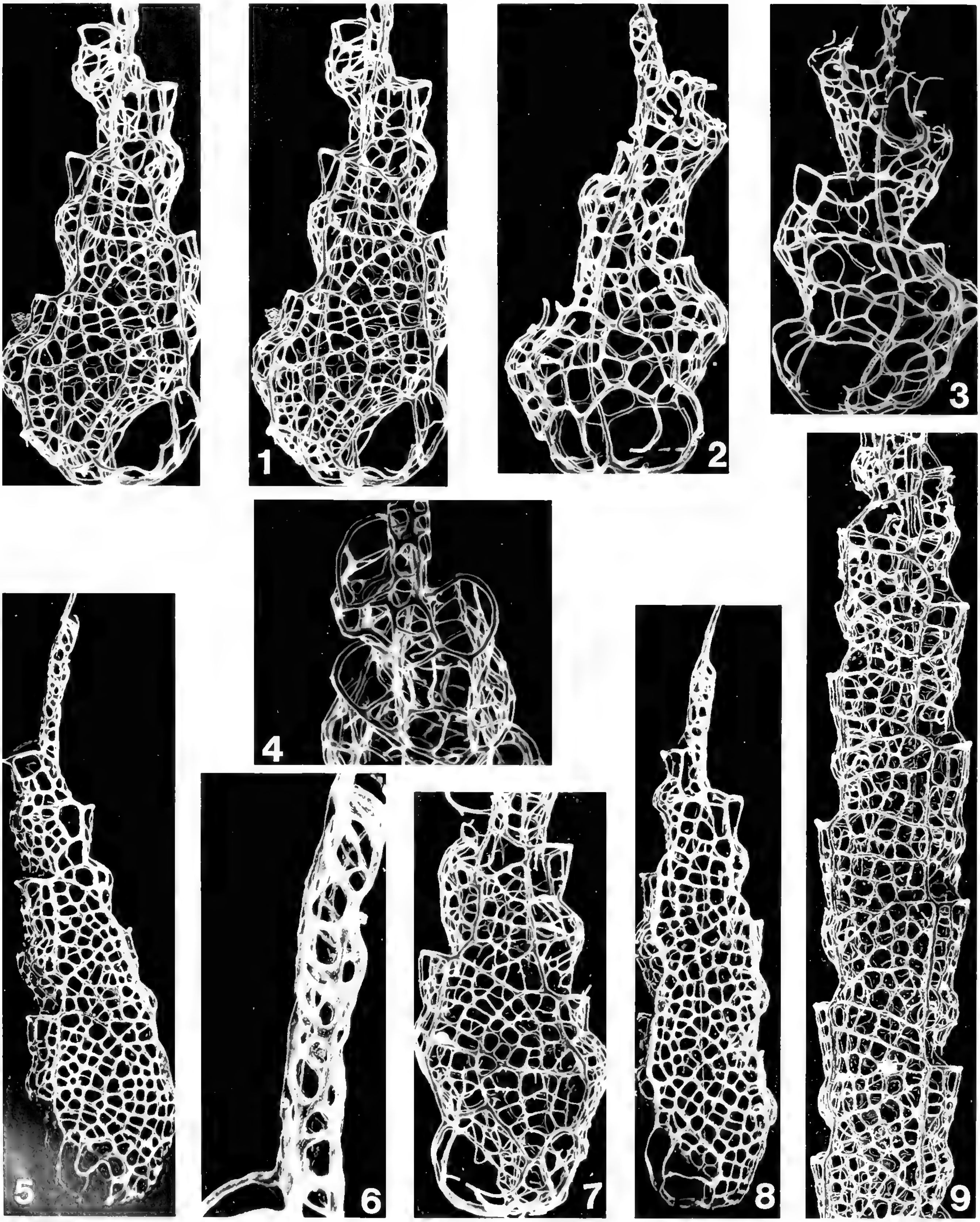
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EXPLANATION OF PLATE 8

Figure — Page

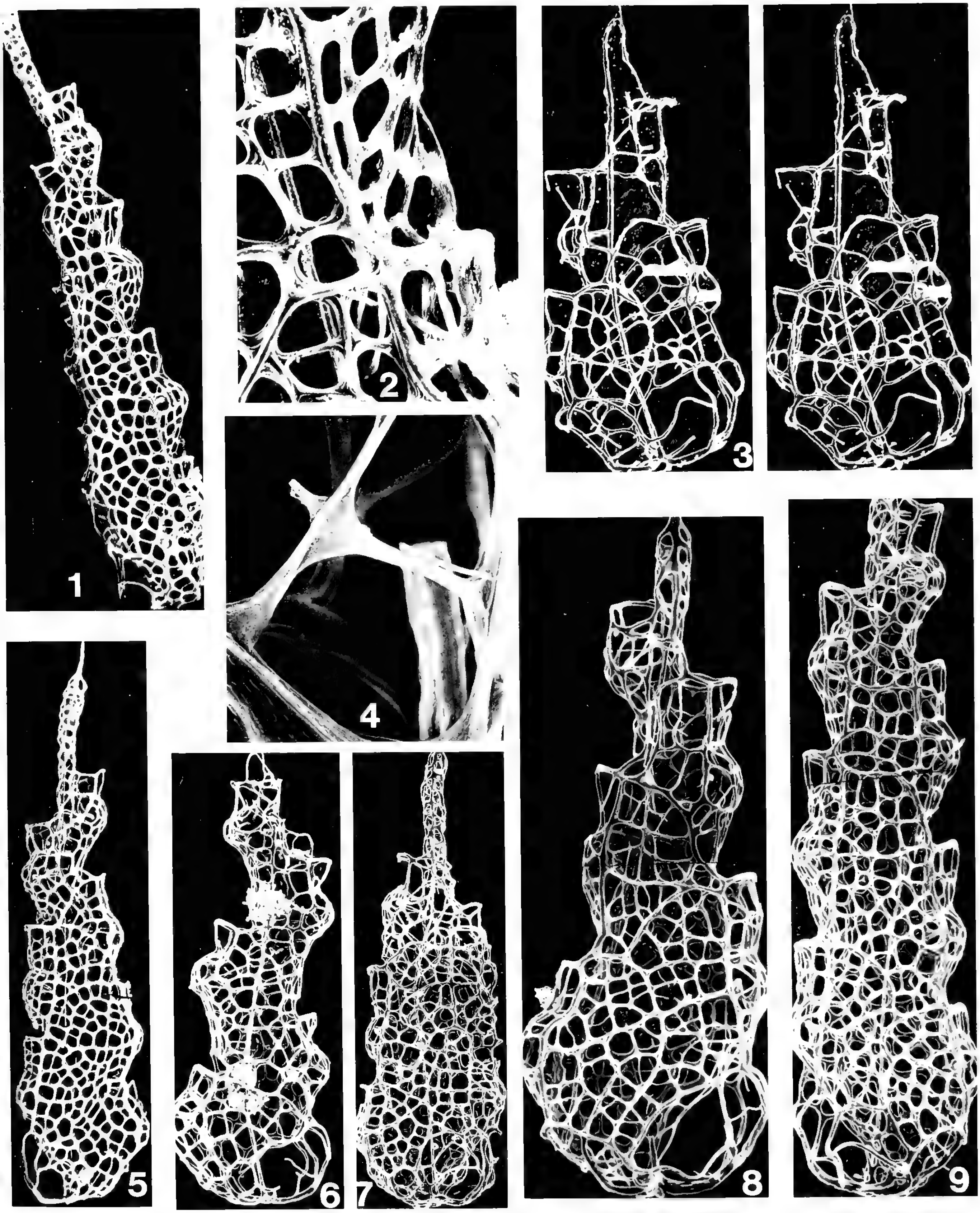
1–9. ***Gothograptus eisenacki*** Obut and Sobolevskaya 18

1. Stereopair of mature specimen; locality 2, section MRC05; GSC99148, ×60.
2. Small, near-mature specimen; locality 1, section SBC10D; GSC104011, ×50.
3. Small immature specimen; locality 1, section SBC10D; GSC99147, ×56.
4. Distal end of GSC99148, ×96.
5. Mature specimen; locality 1, section SB F68; GSC104012, ×27.
6. Enlargement of appendix of GSC104012, ×93.
7. Medium-sized, mature specimen; locality 2, section MRC05; GSC104013, ×60.
8. Mature, longer than normal specimen; locality 1, section SB F68; GSC104014, ×27.
9. Fragment of unusually long specimen; locality 2, section MRC05; GSC78440, ×40.

EXPLANATION OF PLATE 9

Figure		Page
1–9.	***Gothograptus eisenacki*** Obut and Sobolevskaya	18

1. Mature specimen, longer than normal; locality 1, section SB F68; GSC104015, ×28.
2. Enlargement of wall of GSC104015, ×139.
3. Stereopair of small, immature, but complete specimen; locality 2, section MRC05; GSC78446, ×50.
4. Enlargement of clathrial (pustulose) and reticular (seams facing out) lists of GSC104016, ×800.
5. Mature specimen; locality 1, section SB F68; GSC104017, ×24.
6. Small, immature but complete specimen; locality 1, section SBC10D; GSC99149, ×40.
7. Small, mature specimen; locality 1, section LL7 (=SB F68); GSC104018, ×40.
8. Small, mature specimen; locality 2, section MRC05; GSC104016, ×80.
9. Moderately long, mature specimen; locality 1, section LL7 (=SB F68); GSC99146, ×48.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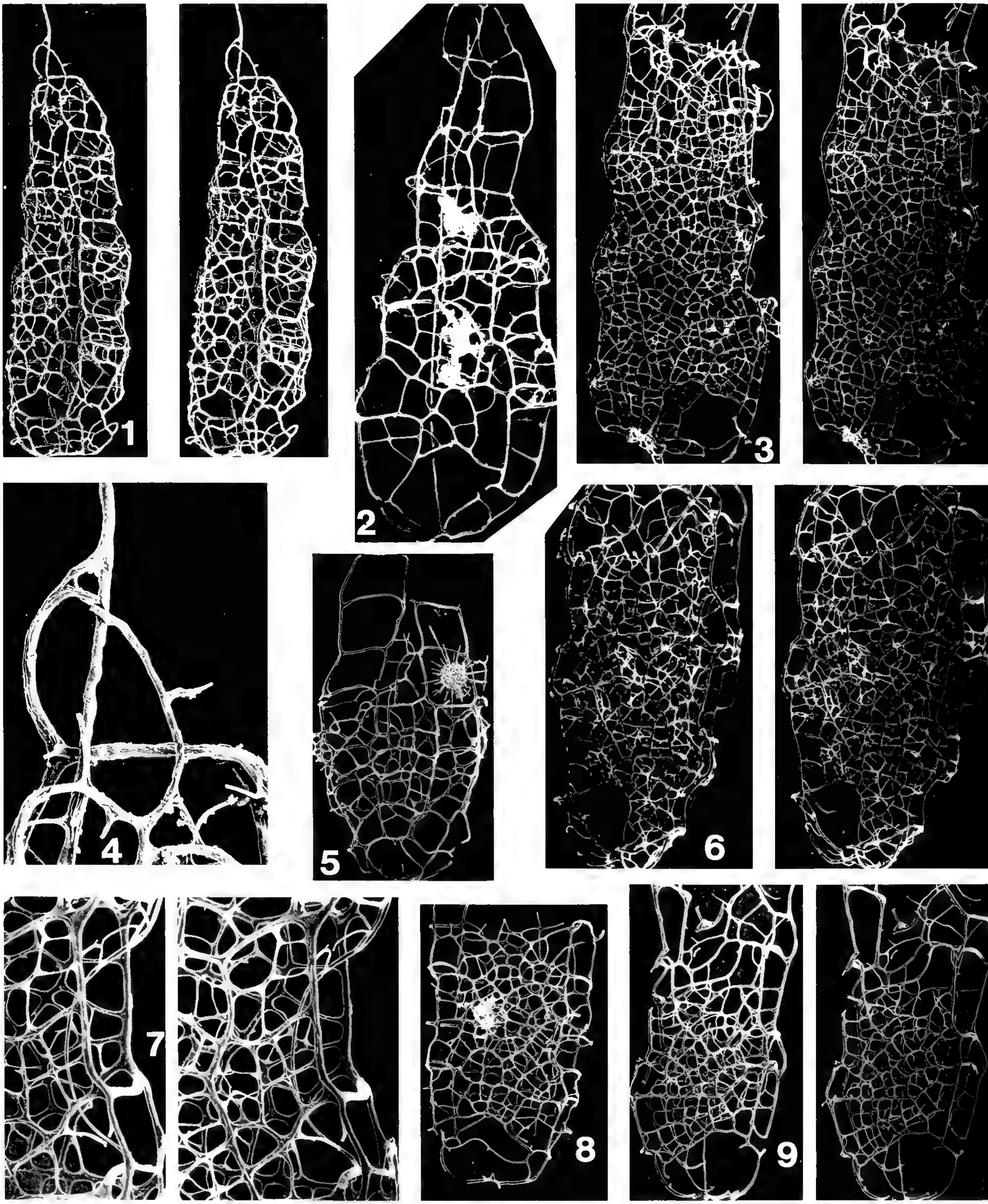
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EXPLANATION OF PLATE 10

Figure Page

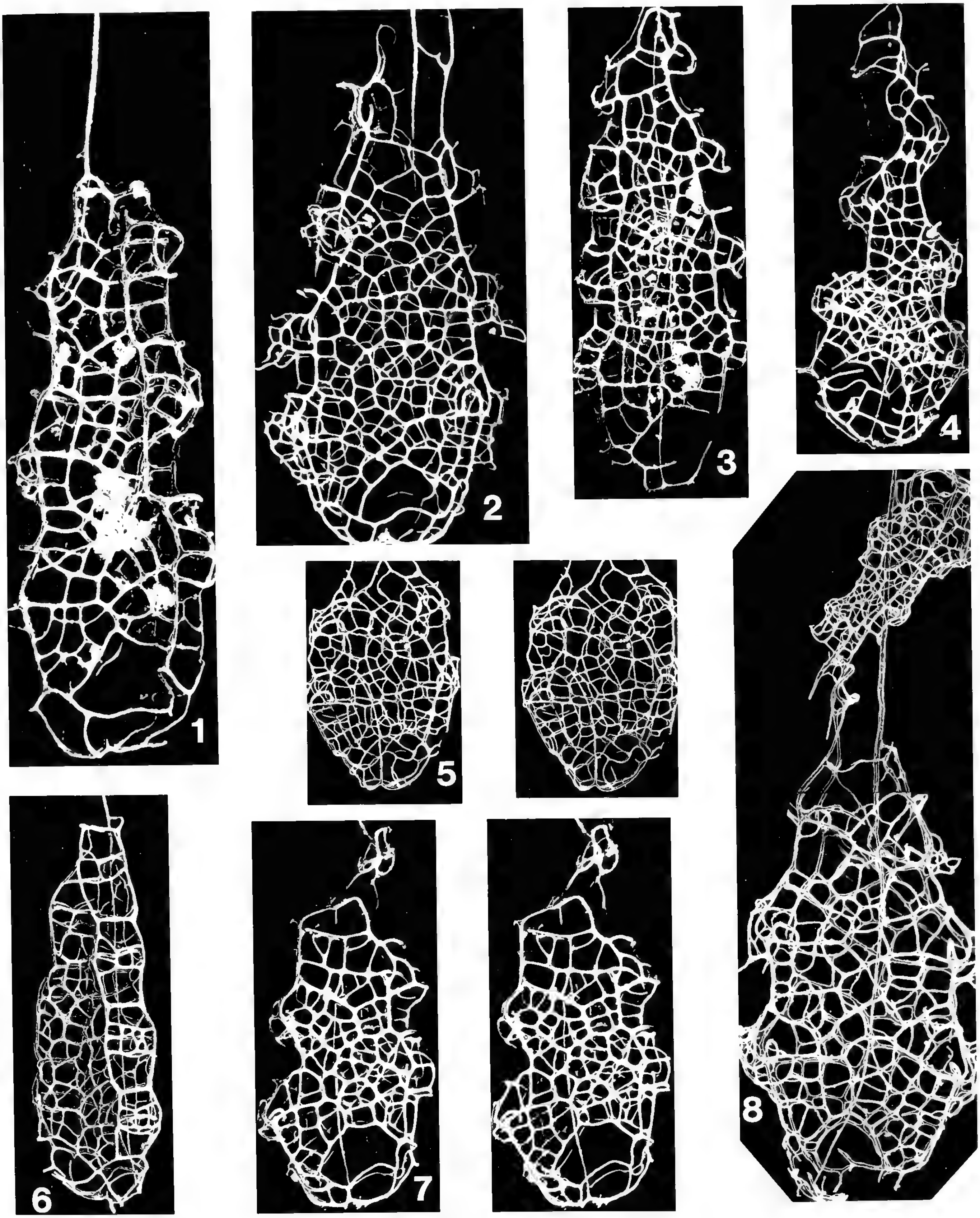
1–9. ***Gothograptus marsupium,*** new species 18

1. Stereopair of complete specimen; locality 1, section 10:3; GSC104019, ×16.
2. Immature specimen; locality 1, section SB E102; GSC104020, ×28.
3. Stereopair of mature specimen; locality 1, section SBC10D; GSC99175, ×25.
4. Enlargement of distal end of GSC104019, showing linkage of virgula and clathria, ×160.
5. Immature specimen (note radiolarian); locality 2, section MRC05; GSC99176, ×24.
6. Stereopair; locality 1, section SBC 10D; GSC99174, ×30.
7. Stereopair of GSC99174, showing thecal apertures and inner connecting list, ×64.
8. Immature specimen; locality 2, section MRC05; GSC104021, ×24.
9. Stereopair of immature specimen; locality 1, section SBC10D; GSC104022, ×24.

EXPLANATION OF PLATE 11

Figure Page
1–8. ***Gothograptus marsupium,*** new species 18

1. Complete specimen with long nema; locality 1, section SB E102; GSC104023, ×34.
2. Holotype specimen; locality 1, section SB E41; GSC104024, ×25.
3. Complete specimen; locality 1, section SB E85; GSC104025, ×22.
4. Complete but immature specimen; locality 1, section SB E85; GSC104026, ×22.
5. Stereopair of immature specimen; locality 1, section SBC10C; GSC104027, ×19.
6. Complete specimen; locality 1, section SBC10:3; GSC104028, ×16.
7. Stereopair of small, but complete specimen; locality 1, section SB E85; GSC104029, ×22.
8. Complete specimen piercing (smaller) *Gothograptus eisenacki;* locality 1, section SBC10D; GSC104030, ×28.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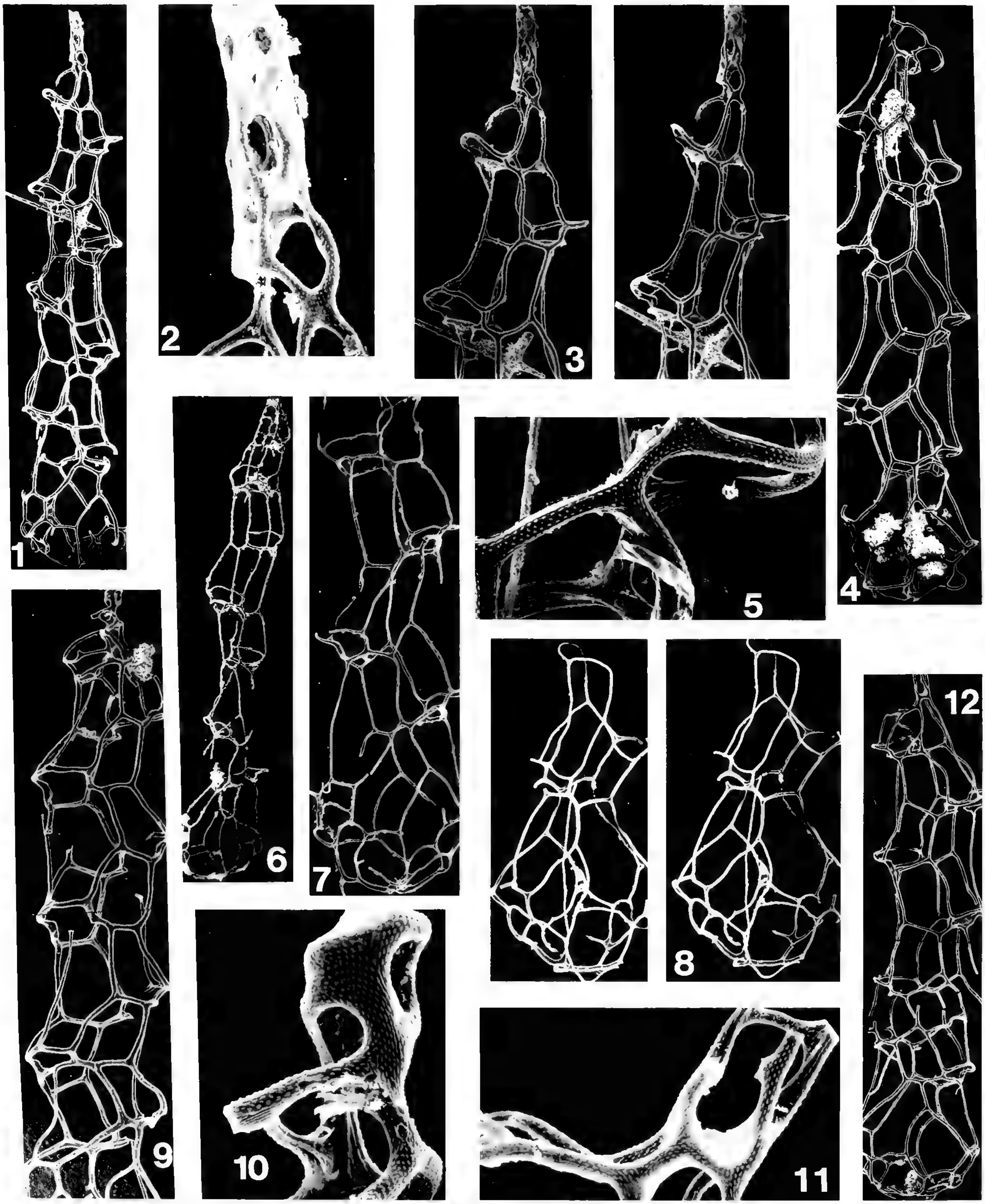
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1–12. ***Holoretiolites mancki*** (Münch) 20

1. Long specimen; locality 1, section SBC4:7; GSC99167, ×30.
2. Enlargement of "appendix" of GSC99167, ×175.
3. Stereopair of distal end of GSC99167, ×48.
4. Specimen without appendix; locality 1, section SBC4:7; GSC104031, ×48.
5. Enlargement of thecal opening of GSC104031; ×200 (note thread obscuring part of apertual lip).
6. Complete specimen; locality 3, section MCM90Y; GSC104032, ×21.
7. Incomplete specimen; locality 3, section MCM90Y; GSC104033, ×34.
8. Stereopair of immature specimen; locality 1, section SBC4:7; GSC99170, ×48.
9. Large specimen; locality 1, section SBC4:7; GSC99168, ×40.
10. Enlargement of appendix of GSC99168, ×280.
11. Enlargement of appendix of GSC99169, ×240.
12. Complete specimen; locality 1, section SBC4:7; GSC99169, ×30.

EXPLANATION OF PLATE 13

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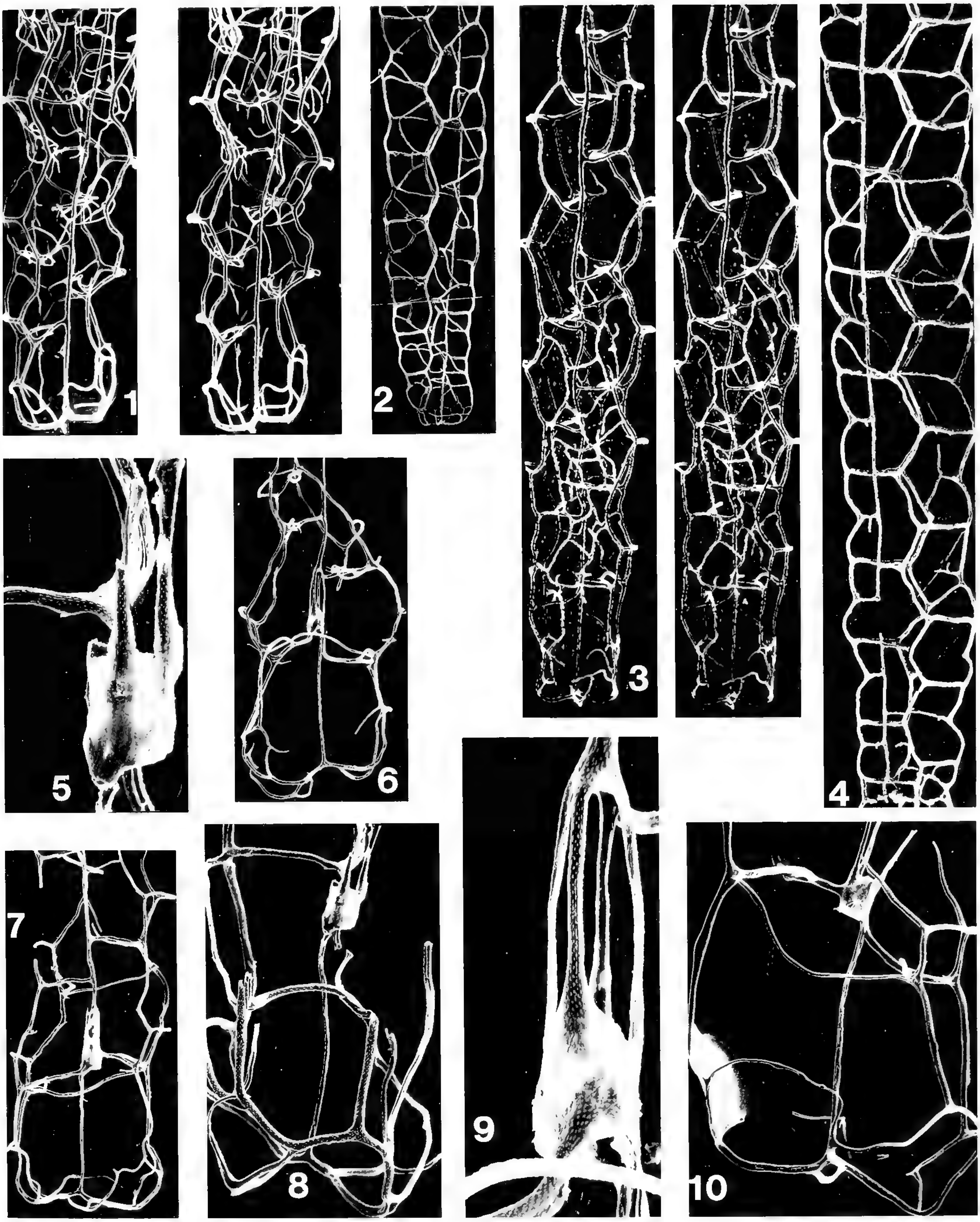
1–4. *Paraplectograptus eiseli* (Manck) 21

1. Stereopair of proximal region of a long specimen; locality 1, section SBC10D; GSC104034, ×35.
2. Specimen with only a weak reticulum; locality 1, section E 0m; GSC104035, ×11.
3. Stereopair of well preserved specimen; locality 4, section MCP152.5; GSC 78450, ×27.
4. Specimen with clathruim only; locality 1, section E Om; GSC104036, ×17.

5–10. *Paraplectograptus* sp.

Isolated nodule near locality 3; age: probably Late Llandovery or Early Wenlock.

5. Prosicular enlargement from GSC104037, ×171.
6. Well preserved specimen; GSC104038, ×34.
7. Complete, but immature specimen; GSC104039, ×34.
8. Proximal end fragment; GSC104037, ×65.
9. Prosicula of GSC104038, ×211.
10. Proximal end fragment with well preserved prosicular threads; GSC104040, ×63.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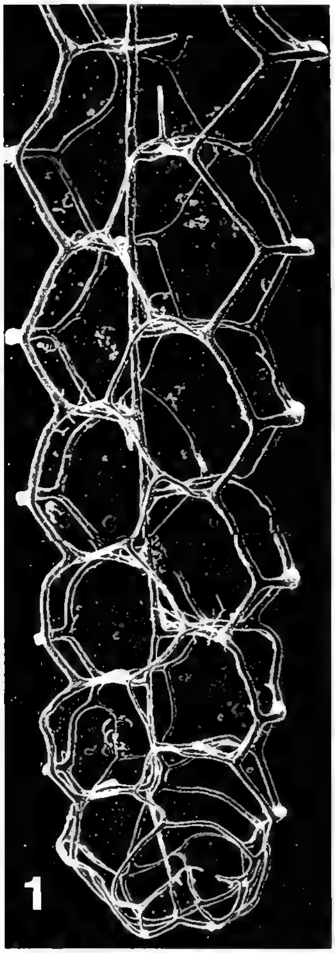
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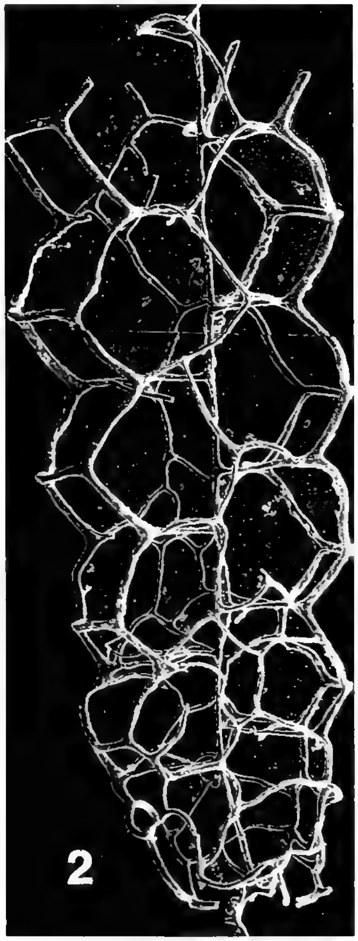
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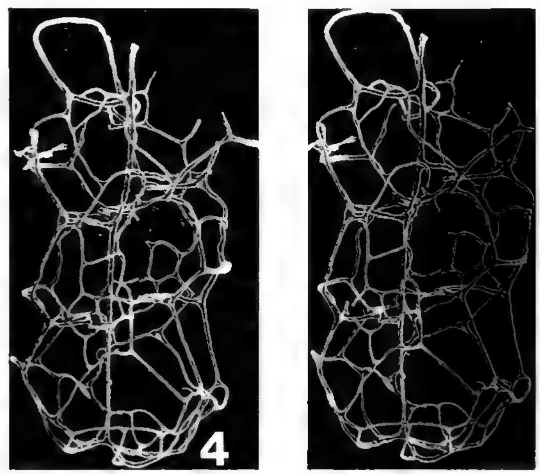
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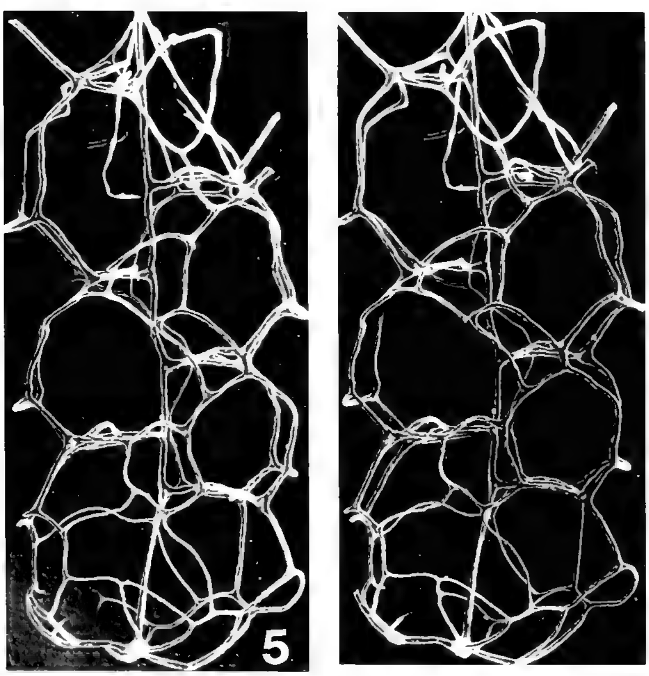
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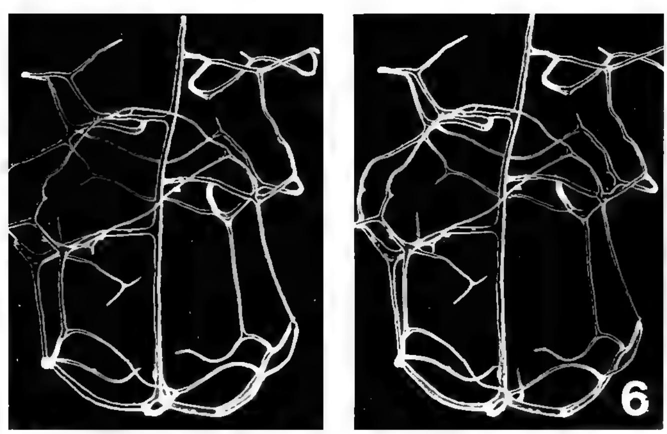
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1–6. ***Paraplectograptus praemacilentus*** (Boucek and Münch) 21

1. Large, well preserved specimen; locality 2, section MRC05; GSC78441, ×40.
2. Mature specimen; locality 4, section CP600; GSC104041, ×32.
3. Distal end view of specimen; locality 4, section CP600; GSC104042, ×48.
4. Stereopair of immature specimen; locality 4, section CP850; GSC104043, ×32.
5. Stereopair; locality 4, section CP850; GSC104044, ×40.
6. Stereopair of proximal end of immature specimen; locality 1, section SBC10C; GSC104045, ×35.

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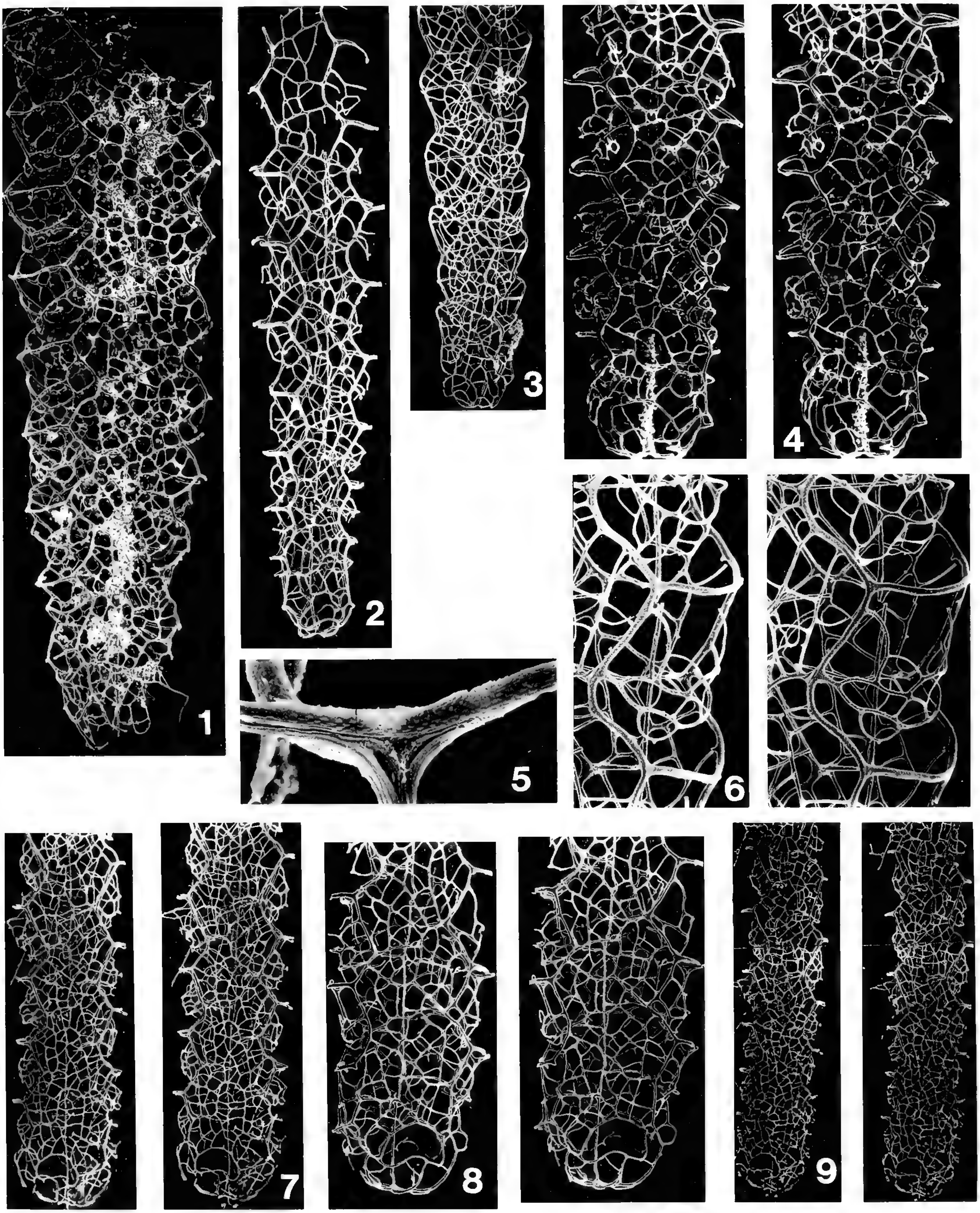
1. Large, mature specimen; locality 1, section SBC10D; GSC104046, ×24.
2. GSC99158; locality 1, section SBC10A, ×16.
3. GSC99155; locality 1, section SBC10A, ×16.
4. Stereopair; locality 1, section SBC10A; GSC104047, ×25.
5. Enlargement of lists of GSC99155, ×30.
6. Stereopair of GSC99155, showing details of thecal walls, ×48.
7. Stereopair enlargement of proximal end of holotype; locality 1, section SBC10B; GSC104048, ×20.
8. Stereopair; locality 1, section SBC10B; GSC99157, ×28.
9. Stereopair of holotype; GSC104048, ×12.



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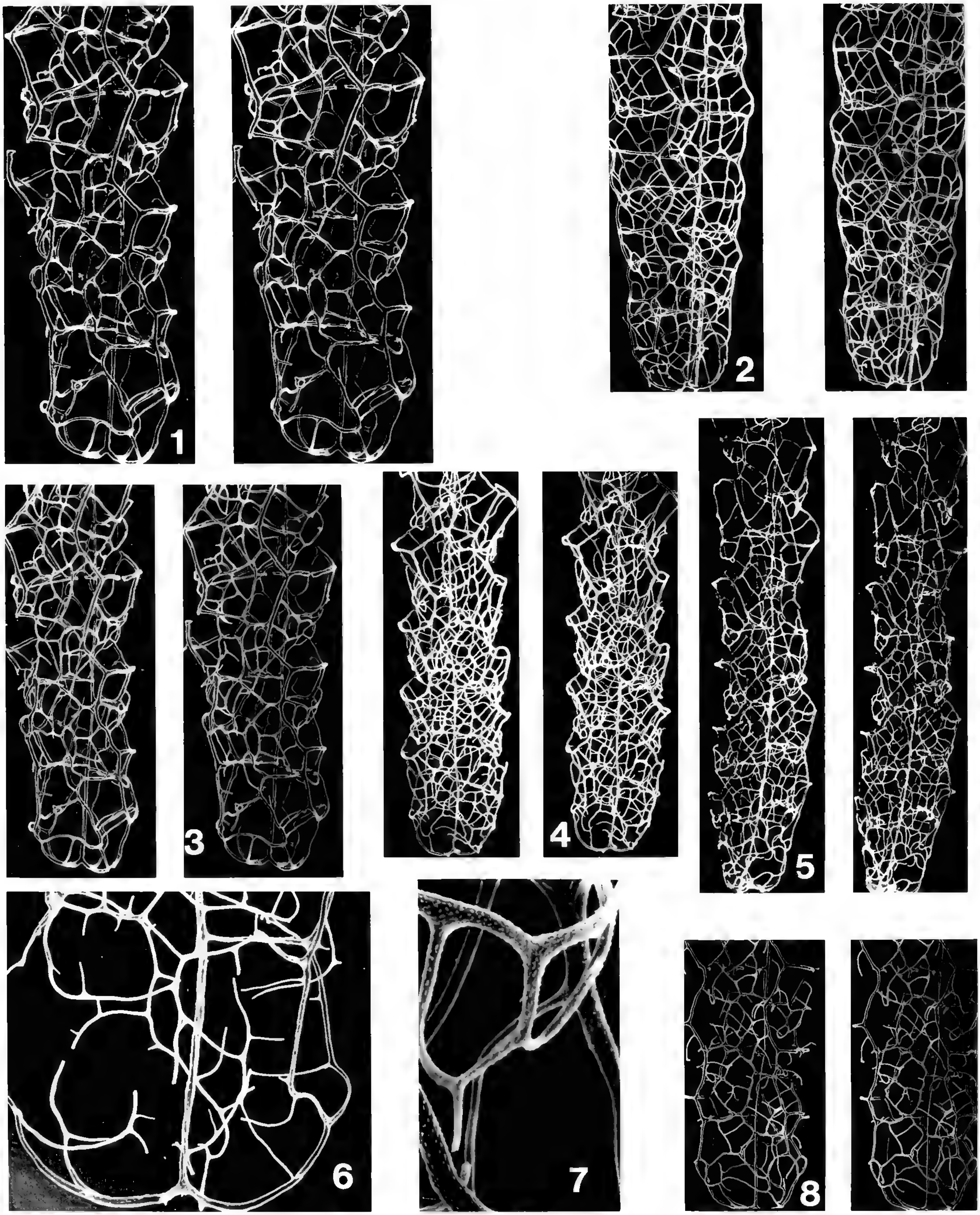
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1–8. ***Paraplectograptus sagenus,*** new species 22

1. Stereopair of immature specimen; locality 1, section SBC10A; GSC104049, ×35.
2. Stereopair; locality 1, section SBC10B; GSC99154, ×24.
3. Stereopair of immature specimen; locality 1, section SBC10A; GSC104050, ×28.
4. Stereopair of mature specimen; locality 1, section SBC10B; GSC104051, ×20.
5. Stereopair of mature specimen; locality 1, section SBC10B; GSC104052, ×22.
6. Proximal end of immature specimen; locality 1, section SBC10B; GSC104053, ×22.
7. Thecal wall lists of GSC104050, ×200.
8. Stereopair of immature specimen; locality 1, section SBC10A; GSC104054, ×27.

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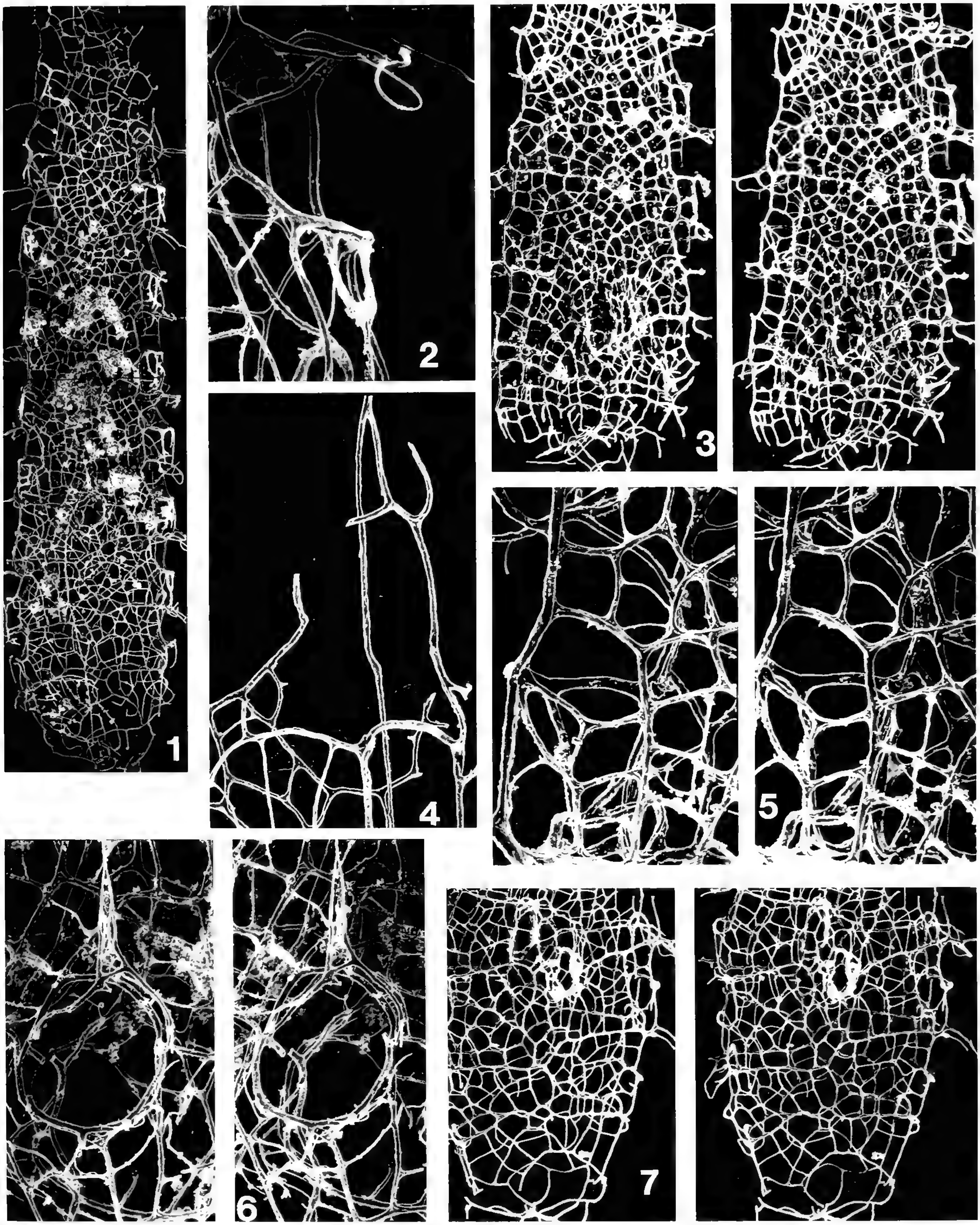
1–7.	***Spinograptus apoxys,*** new species	23

1. Holotype specimen; locality 1, section SBC10C; GSC104055, ×18.
2. Enlargement of thecal wall and inner connecting list of holotype; GSC104055, ×88.
3. Stereopair; locality 1, section SBC10D; GSC99165, ×15.
4. Distal region of fragment showing attachment of virgula to clathrium; locality 1, section SBC10D; GSC104056, ×40.
5. Stereopair enlargement of thecal walls and inner connecting lists of GSC99165, ×80.
6. Stereopair enlargement of stomata of holotype; GSC104055, ×80.
7. Stereopair of GSC99164; locality 1, section SBC10D, ×20.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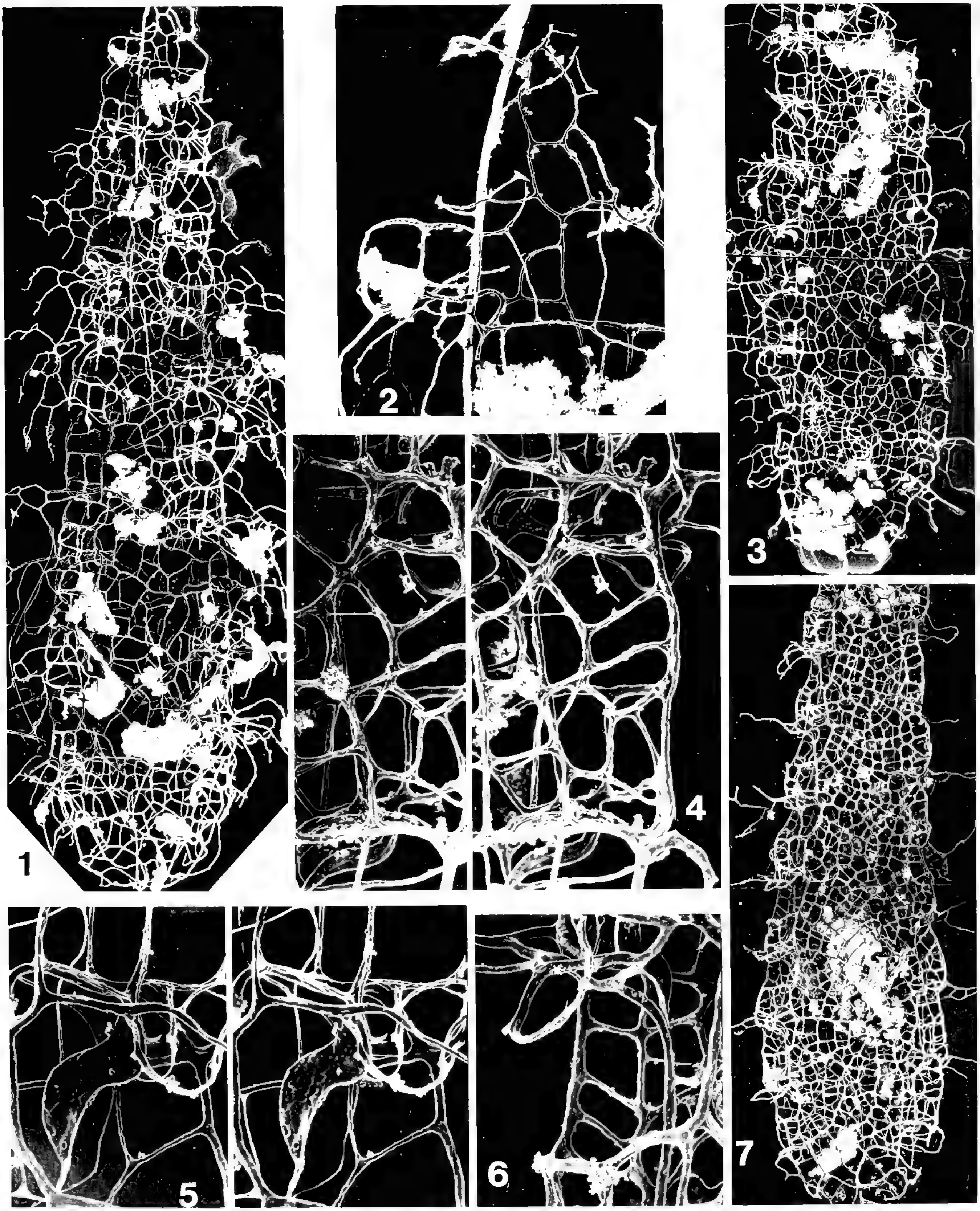
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EXPLANATION OF PLATE 18

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1–7. ***Spinograptus apoxys,*** new species 23

1. Large specimen; locality 1, section SB F3; GSC104057, ×12.
2. Enlargement of distal end of GSC104057, showing attachment of virgula to clathrium, ×38.
3. Nearly complete specimen; locality 1, section SB F3; GSC104058, ×11.
4. Stereopair enlargement of thecal region of GSC99166, showing inner connecting list and sigmoidal processes, ×55.
5. Stereopair enlargement of GSC104057, showing sigmoidal processes, ×100.
6. Enlargement of aperture of GSC99166, showing sigmoidal processes and inner connecting list, ×55.
7. Mature specimen; locality 1, section SBC10D; GSC99166, ×15.

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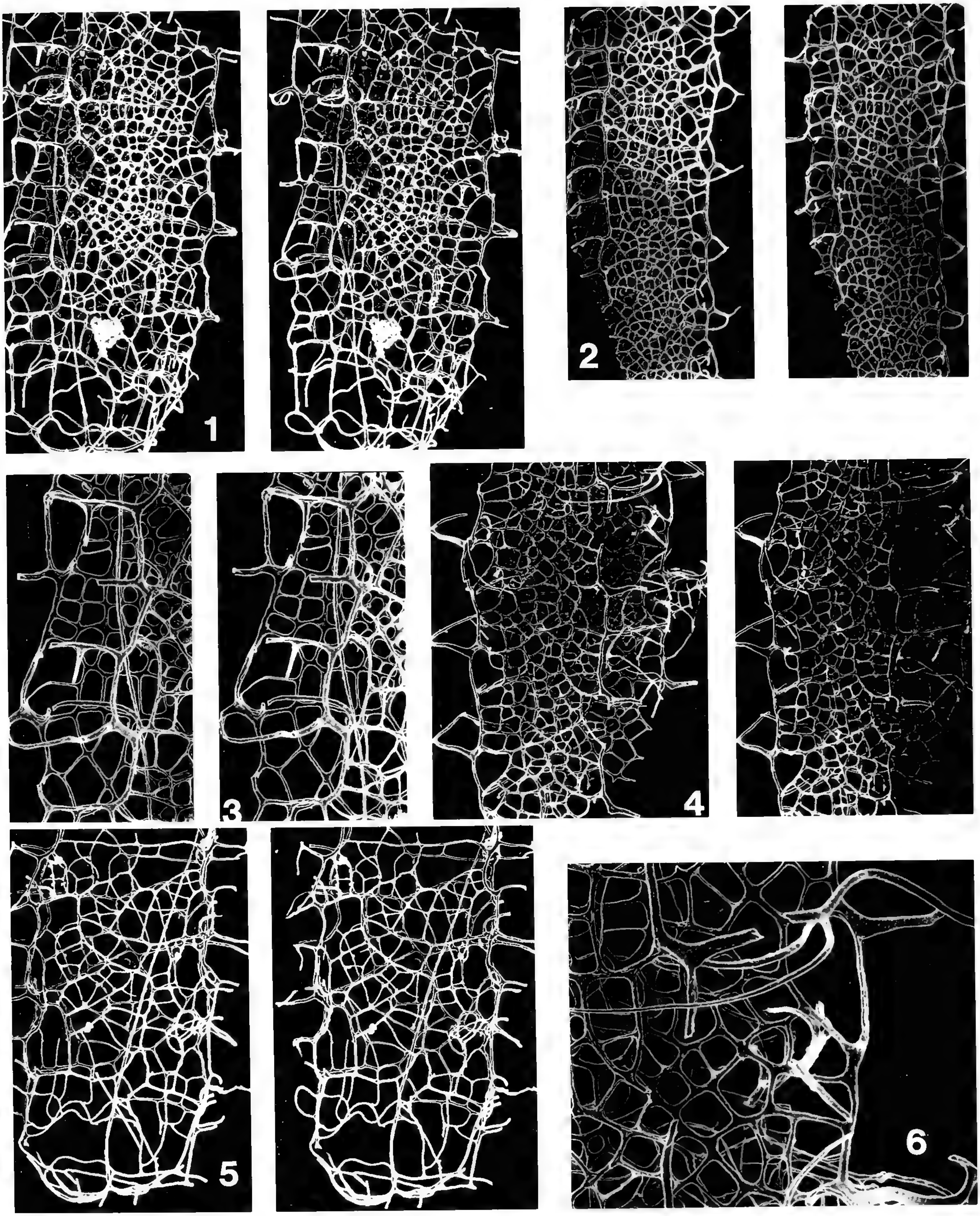
1. Stereopair of well preserved specimen with long virgula; locality 1, section SBC10E; GSC99161, ×22.
2. Stereopair of mid-region of rhabdosome; locality 1, section SBC3; GSC104059, ×18.
3. Stereopair enlargement of thecal wall of GSC99161, ×40.
4. Stereopair of mid-region of rhabdosome; locality 1, section SBC3; GSC104060, ×20.
5. Stereopair of immature specimen; locality 1, section SBC10E; GSC99159, ×25.
6. Enlargement of thecal list and spine of GSC104060, ×56.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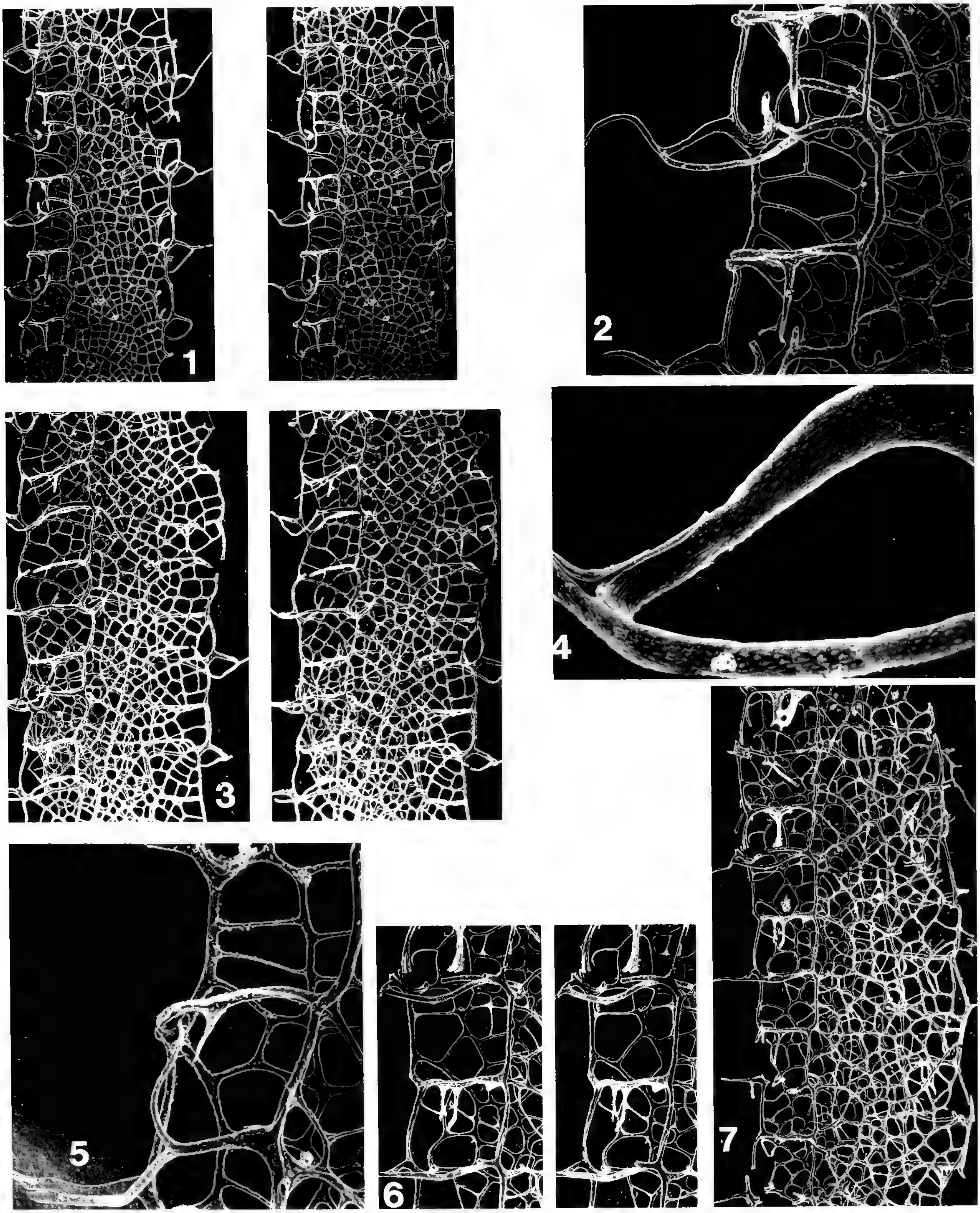

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1–7. ***Spinograptus nevadensis*** (Berry and Murphy) 23

1. Stereopair of mid-region with well preserved thecal walls and spines; locality 1, section SBC10E; GSC99162, ×18.
2. Enlargement of thecal wall and apertures of GSC99162, ×56.
3. Stereopair of mid-region; locality 1, section SBC3; GSC99160, ×20.
4. Enlargement of thecal "hood" and spine base of GSC99162, ×380.
5. Enlargement of thecal wall of GSC104059, ×80.
6. Stereopair of thecal walls of GSC104061, ×45.
7. Mid-region of rhabdosome; locality 1, section SBC10C; GSC104061, ×24.

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PREPARATION OF MANUSCRIPTS

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