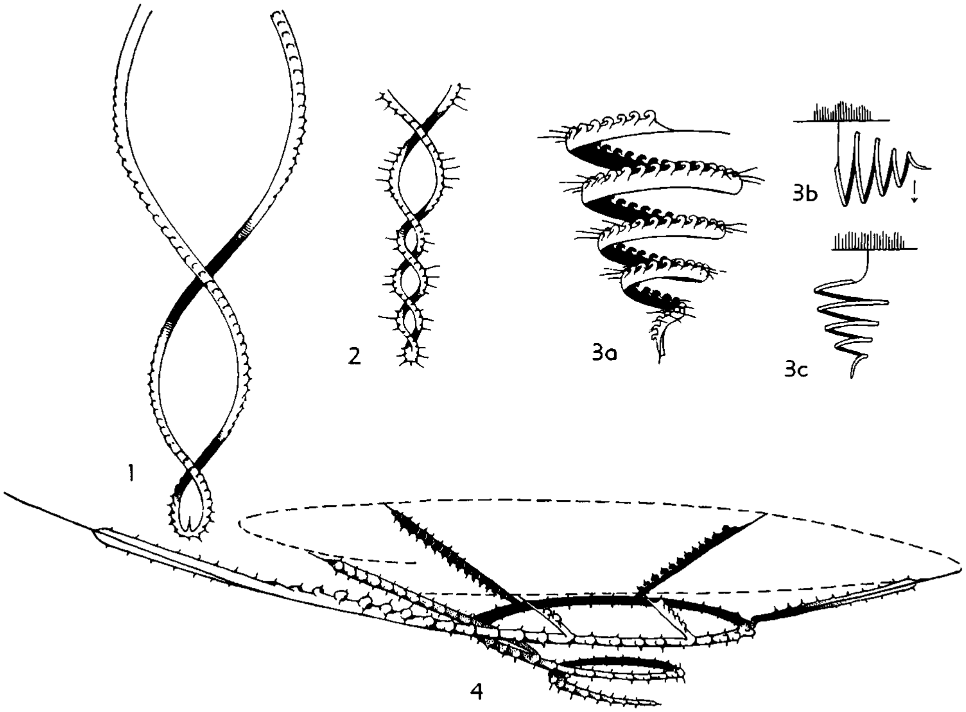

FIG. 72. Rhabdosome forms suggestive of gyratory motion (34).——*1. Dicellograptus caduceus,* ×2. ——*2. Dicranograptus furcatus bispiralis,* ×2.——*3. Monograptus turriculatus; 3a,* rhabdosome, ×3.5. ——*3b,c,* diagrams to show how attachment would distort nema *(3c)* so that growing rhabdosome could not attain regular helical form, unless oriented in defiance of gravity *(3b),* diagram.——*4.* Immature *Cyrtograptus* rhabdosome, based on *C. solaris,* ×3.

(Fig. 69,*1-4*); most adult examples show nothing centrally other than a tangle of slender fibers and it is unlikely that the synrhabdosome association constitutes primarily a buoyancy mechanism.

GEOGRAPHIC DISTRIBUTION

Since the distribution of the Graptoloidea during life was essentially dependent upon current drifting, the distribution of their fossil remains may be practically worldwide, almost coextensive with that of the rocks of a particular age. Nearly all families, the majority of genera, and some species are almost cosmopolitan; *Nemagraptus gracilis* and *Monograptus turriculatus* are examples of such species. It does not follow, however, that all graptolites are more or less universal in their occurrence and to judge by present records, many have a decidedly restricted distribution.

Partly, no doubt, this may be attributed to imperfect collecting and recording; but evidence of the existence of faunal provinces is found and on a much smaller scale, of geographical races, though the erratic distribution of some graptolites is not read-

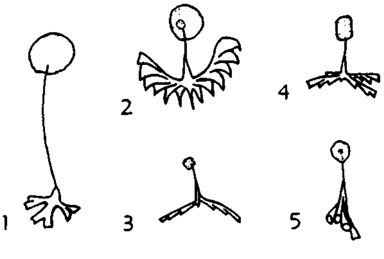

FIG. 73. Rhabdosome suspension; discs of attachment in immature rhabdosomes; all figures ×2 (201).——*1. Dictyonema flabelliforme.*——*2. Tetragraptus similis.*——*3. Adelograptus lapworthi.* ——*4. Staurograptus dichotomous.*——*5. Tetragraptus fruticosus.*

ily accounted for in any of these ways. The genus *Rastrites* remains virtually unknown in North America. *Pleurograptus,* again, is peculiarly localized; it occurs characteristically in Scotland but not in England and Wales, or indeed elsewhere in Europe, though it has been recorded from Australia (Victoria) and rather doubtfully from North America. On the other hand, *Pterograptus* is a somewhat rare genus with a wide distribution; species are known from North and South America, northwest Europe, China, and Australasia.

Clear evidence of the existence of faunal provinces among the Graptoloidea can be cited, though they remain to be more precisely defined, a process complicated by a mass of misidentifications among existing records. Two examples are here indicated broadly. First, the *Oncograptus-Cardiograptus* fauna, originally described from Victoria, Australia, and now recognized to some extent in North America, Texas, and China, does not reach eastern North America or Europe, apart from a few specimens of *Oncograptus* recorded from western Ireland, whereas the late pendent didymograptid fauna so characteristic of the Llanvirn of Europe and South America is unrecorded in the contemporaneous beds of Australia and New Zealand. Second, on a somewhat smaller scale, the Tremadoc *Anisograptus-Triograptus* fauna, originally described from eastern Canada and later recognized in Taimyr, Norway, and South America, contrasts with the contemporary *Clonograptus-Adelograptus* fauna of Sweden and Britain, now also known from the Sahara. The lower Tremadoc fauna of Australasia (and China) has a superficially different composition and perhaps even origin; considerable doubt attaches to Asiatic records of *Dictyonema flabelliforme* and probably to the records of *Clonograptus tenellus* from Australasia, while the reported New Zealand *Triograptus* is now known to be a misidentification.

The distribution of various distinctive species may provide clues to marine connections between various regions in the Early Paleozoic. Certain Australian species are now being recorded from northwestern Europe, and reference may be made to *Aulograptus* [formerly *Didymograptus*] *climacograptoides,* which was originally described from South America (where it occurs in Peru, Bolivia and Argentina) and which is now known from the English Lake District, southern Sweden, and Belgium. Again, distinctively Bohemian monograptid species are now being recognized in British Silurian assemblages.

At a low taxonomic level, the various subspecies of *Glyptograptus austrodentatus* and other species described from different countries suggest geographical variation, and most graptolithologists will agree that local differences are often detectable in a widely distributed species.

STRATIGRAPHIC DISTRIBUTION

The transition from Dendroidea to Graptoloidea involves the loss of bithecae and a consequent simplification of branch structure, but the process appears to have been a gradual one in several respects. It has probably occurred independently in more than one line of descent, and instances are known where bithecae are not uniformly present (i.e., they are present distally but absent proximally in *Kiaerograptus*). The relatively poor preservation of many of these early graptolites adds to uncertainty as to their nature; thus, it is not known whether early Arenig species of *Clonograptus* and *Bryograptus* possess bithecae. For these reasons, it is not yet possible to indicate the earliest graptoloid with any precision.

Several species of *Didymograptus* and some of *Tetragraptus* have been described from rocks of Tremadoc age in various parts of the world, but correctness of the graptoloid attribution of at least some of these records is quite doubtful.

Undoubtedly *Didymograptus* species occur in the basal Arenig associated in most areas with such multiramous forms as *Clonograptus* and *Bryograptus* which may or may not possess graptoloid branch structure. From such beginnings, the Graptoloidea quickly established their position as one of the most important components of marine fauna of the lower Paleozoic. On present records, they became extinct in the early Devonian (Siegenian or perhaps as late as Emsian).

The range of individual genera (Fig. 74) is usually short, few extending through more than part of a single geological period; that of individual species is variable, some being confined to a single zone, others extending through five or six zones. The zones themselves represent variable time spans. Radioactivity figures suggest that the Silurian Period endured some 40 million years, and in Britain this embraces some 20 graptolite zones; in Central and Eastern Europe, another eight or 10 have been claimed for the upper Ludlow. On this basis the duration of a single zone (or the length of life of a short-ranged species) would be somewhat less than two million years. The time value of other zones may be even shorter; in Australia HARRIS & THOMAS recognized 11 zones in the series La3 to Ya2, approximately equivalent to the English Arenig and presumably representing not more than 10 or 12 million years.

In most parts of the world, the shaly facies of the lower Paleozoic has now been zoned by means of graptolites, which are of exceptional value for long-range correlation; but while a general similarity in the succession obtains, local differences occur and it would be out of place here to attempt a world-wide correlation of graptolite zones. It is possible, however, to indicate a sequence of graptolite faunas capable of fairly general application. Faunal provinces are discernible in the earlier portion of the sequence, while the upper portion is more uniform and cosmopolitan. It should be emphasized that the terms employed are descriptive of general aspect and dominant composition of a fauna rather than definitive of its precise upper and lower limits. The full stratigraphical range of the families Dichograptidae and Diplograptidae, for example, is not coincident with the upper and lower boundaries of the faunas bearing their name.

Tabulations of the generally recognized British and Australian graptolite zones, representing the European and Pacific provinces in the Lower Ordovician, are given at the end of this section on "Stratigraphic Distribution."

ANISOGRAPTID FAUNA

The anisograptid fauna characterizes Tremadoc beds and their equivalents. Strictly it is not a graptoloid fauna at all, since it comprises various pelagic species of *Dictyonema* (such as *D. flabelliforme*) and their pendent and horizontal anisograptid descendants; the extent of any graptoloid (dichograptid) component is at present indefinite.

In northwestern Europe, North Africa, eastern North America and South America, *Dictyonema flabelliforme* and its subspecies are widespread, though in Quebec *D. canadense* and other species occur and *D. flabelliforme* has not yet been recorded. Probably no great disparity in age marks these species, since the associated anisograptid fauna is closely related to that succeeding the *D. flabelliforme* Zone of Norway and South America. The *Clonograptus-Adelograptus* fauna and the *Anisograptus-Triograptus* fauna, both of which succeed the *D. flabelliforme* Zone, if not mutually exclusive, dominate particular regions, the former northwestern Europe (except Norway) and North Africa, the latter eastern North America and South America. It is not yet decided whether the *Anisograptus-Triograptus* occurrence associated with *Clonograptus* in Texas is lower or upper Tremadoc.

Dictyonema flabelliforme (or varieties ascribed to it) have been described from China and Korea, but the determinations and hence the inferred horizons are questionable and some could even be Arenig species. In Australia, a staurograptid and two small siculate species *(D. scitulum* and *D. campanulatum)* presumably represent the lower Tremadoc fauna.

Upper Tremadoc graptolites are extremely rare. The best-known fauna is that described by MONSEN (1925) from the *Ceratopyge* Shale near Oslo, comprising *Kiaerograptus* and *Didymograptus?* with fragmentary *Clonograptus* and *Bryograptus;* and a similar fauna immediately underlies the *Ceratopyge* Limestone. The La2 fauna from Victoria and New Zealand is believed to be upper Tremadoc. The presence of any significant graptoloid element in even upper Tremadoc begins to appear unlikely.

DICHOGRAPTID FAUNA

The dichograptid fauna as now defined

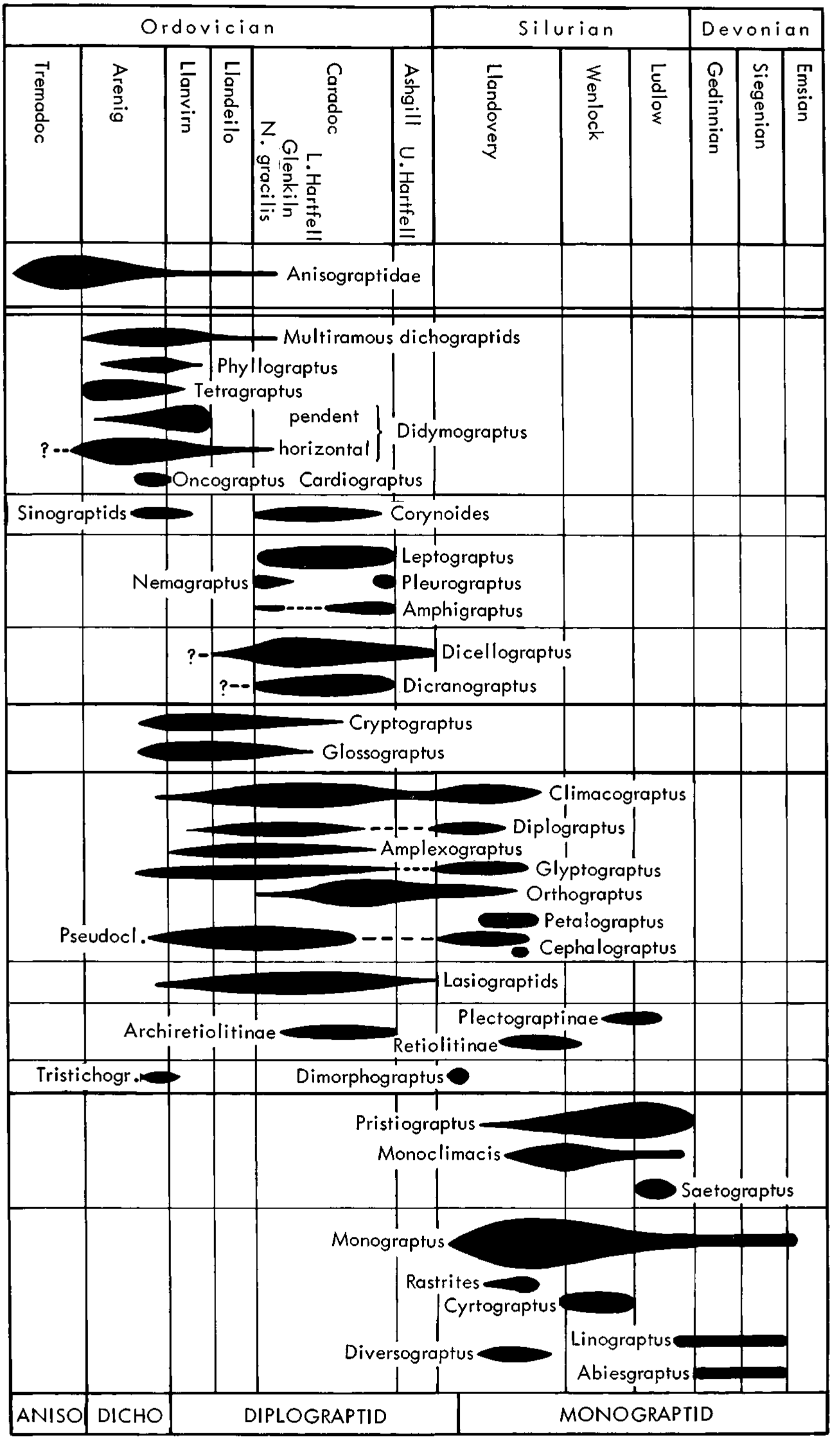

FIG. 74. Stratigraphic distribution of certain graptoloid genera. Number of species only approximately indicated; no attempt made to show relative importance of genera (Bulman, n). [Pseudocl.=*Pseudoclimacograptus;* Tristichogr.=*Tristichograptus.*]

characterizes Arenig beds and their equivalents and comprises a wide range of multiramous and pauciramous dichograptids.

In most countries, the base is marked by appearance of *Tetragraptus approximatus* associated with *Clonograptus* and with extensiform and pendent didymograptids and tetragraptids. Declined didymograptids and phyllograptids are well represented in the middle portion and tuning-fork didymograptids begin to be prominent in the upper portion, where also *Oncograptus, Cardiograptus,* and isograptids are distinctive, particularly in areas around the Pacific. Biserial graptolites (both monopleural and dipleural) make their appearance in the uppermost portion, but are not a numerically significant constituent of this fauna.

DIPLOGRAPTID FAUNA

Biserial graptolites became a distinctive element of the fauna by Llanvirn times and although in some areas they tended to be obscured by an extraordinary profusion of tuning-fork graptolites, it is at or just below this level that they underwent their major generic differentiation. They characterize the whole of the Ordovician graptolite fauna and are the only graptolites found in the basal part of the Silurian until the advent of *Monograptus*[1] and the dimorphograptids in the *Cystograptus vesiculosus* zone. The suggested subdivisions of this large time span are provisional, but are descriptive of general faunal characteristics of most areas. The boundary between the second and third subdivisions is indistinct, and zonal correlation at about this level (between the *Nemagraptus gracilis* and *Dicranograptus clingani* zones) is notoriously difficult.

GLYPTOGRAPTUS-AMPLEXOGRAPTUS SUBFAUNA, LLANVIRN AND LLANDEILO

The two genera named in the title are characteristic, but *Diplograptus, Hallograptus, Pseudoclimacograptus* and *Climacograptus* also occur, along with *Cryptograptus, Glossograptus,* and *Tristichograptus.* In addition to tuning-fork didymograptids and isograptids, late dichograptids include a number of multiramous genera, of which *Pterograptus* is particularly distinctive. The earliest *Dicellograptus* occurs in the *Glyptograptus teretiusculus* zone.

NEMAGRAPTUS-DICELLOGRAPTUS SUBFAUNA, BASAL CARADOC

The incoming of *Nemagraptus gracilis* produces an easily recognizable base to this subfauna, and *Leptograptus, Dicellograptus* and *Dicranograptus* rapidly assume prominence. Diplograptids are abundant. The last stragglers of the Dichograptidae (*Didymograptus superstes,* etc.) persisted into the basal levels.

ORTHOGRAPTUS-DICELLOGRAPTUS SUBFAUNA, CARADOC AND ASHGILL

Various species of *Orthograptus,* especially the *O. truncatus* and *O. calcaratus* groups, are the dominant diplograptids in most parts of the world, beginning at a level somewhat below the *Dicranograptus clingani* zone. *Leptograptus* and *Dicranograptus* disappear below the top of the subfauna, but *Dicellograptus* persists in association with *Orthograptus* and *Climacograptus* to the end of the Ordovician. The fauna of the upper portion, like that of the succeeding subfauna, has some of the characters of an impoverished fauna.

ORTHOGRAPTUS-CLIMACOGRAPTUS SUBFAUNA, BASAL SILURIAN

This subfauna is linked to those above and below, with both of which it has several species in common, but it is composed of biserial graptolites (dipleural); *Monograptus*[2] and the dimorphograptids have not yet appeared. Dwarfed forms of *Orthograptus* of the *O. truncatus* group persist from the underlying levels. Species referred to *Glyptograptus* and *Diplograptus* are present, though of a somewhat different aspect from the Ordovician forms and for this reason were not utilized in the subfaunal title. The most widespread species are *Climacograptus* commonly assigned to the *C. scalaris* group, and *Cephalograptus* [?=*Akidograptus*] *acuminatus* characterizes the upper portion.

MONOGRAPTID FAUNA

Like the diplograptid fauna, the monograptid fauna represents a large strati-

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[1] See p. V100.

[2] See footnote on p. V100.

graphic and time interval, from the incoming of *Monograptus* slightly above the base of the Silurian[1] to its extinction in Early Devonian times; the latest representatives seem at present to be *M. yukonensis, M. atops* (in Bohemia) or *M. thomasi* (in Australia), possibly Emsian in age. In terms of the graptolite succession, the Silurian-Devonian boundary is now taken to lie at the base of the *M. uniformis* zone.

The Llandovery succession begins with a subfauna of dominantly simple thecal type, though it is becoming evident that many apparently simple forms reveal unexpected apertural modifications when adequately preserved. Dimorphograptids occur in association with the monograptids but do not appear to antedate the earliest ones. Monograptids with triangulate thecae give a distinctive aspect to the middle part of the Llandovery, and hooked and lobate forms to the upper part. In addition to these typical monograptid rhabdosomes (=procladia of Urbanek), the diversograptid stage of astogenetic development is represented by *Diversograptus* as recorded from all three of these subfaunas.

The Wenlock is distinguished particularly by *Cyrtograptus,* with its conspicuous thecal metacladia, occurring in association with hooked monograptids.

The Ludlovian has yielded a diversity of monograptid forms about which is difficult to generalize. Forms with simple thecae are abundant, but others with quite extreme apertural modifications occur and include examples of lateral asymmetry (e.g., *Cucullograptus*), very rare among graptolites. The upper Ludlow fauna also includes species with modified apertures in addition to pristiograptids and it is at these high levels that greatest astogenetic complexity is reached in such forms as *Abiesgraptus.*

The Lower Devonian as presently known yields a sparse but widely distributed graptolite fauna which includes *Monograptus uniformis, M. hercynicus, M. thomasi,* and *M. yukonensis.* Most species possess hooked proximal thecae, passing distally into thecae with straight supragenicular walls and hoodlike structures overhanging the apertures. *Abiesgraptus* and *Neodiversograptus* occur in the lower part of this succession.

Almost to the last, therefore, the graptolites appear as an actively evolving group of organisms and no satisfactory explanation of their extinction has been suggested. Conditions obtaining in a local geosyncline may be quite irrelevant to the problem of graptolite extinction, especially if the main centers of evolution and distribution of these organisms were oceanic (e.g., Pacific). Biological as well as physical factors may be involved, acting through food supply or the appearance of a more efficient group of predators, but the cause of graptolite disappearance remains entirely speculative (Jaeger, 1959).

BRITISH AND AUSTRALIAN GRAPTOLITE ZONES

Tabulations of the graptolite zones thus far distinguished and generally recognized in Britain and Australia are introduced here. Graptolites are unrepresented in Devonian and upper Ludlow rocks of Britain, but occur elsewhere in Europe, mainly in Thuringia, Czechoslovakia and Poland. A standard zonal succession has not yet been agreed, but the following tentative scheme gives some indication of what is missing at the top of the sequence in Britain.

Devonian graptolites are represented in Australia by *Monograptus aequabilis* and *M. thomasi,* assigned to the Gedinnian (and perhaps early Siegenian) by Jaeger (1966). A large number of graptolites, including many well-known European species, attest the presence of lower Llandovery, Wenlock and lower Ludlow strata, but these have not yet been formally zoned.

Unpublished work by R. A. Cooper suggests that in New Zealand it may not be possible to distinguish all the finer subdivisions of the Bendigonian and Chewtonian.

PRINCIPLES OF CLASSIFICATION

At generic level, the Graptoloidea present a somewhat confused picture of taxa based on a variety of criteria. A century ago, the now obsolete catch-all genus *Graptolithus* began to be subdivided on

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[1] Since writing this, a *Monograptus* species has been discovered in the basal Silurian zone (Rickards & Hutt, 1970).

Graptolite Zones Distinguished in Britain and Other European Countries

SERIES OR STAGE	ZONE	
	DEVONIAN	
Siegenian	*Monograptus hercynicus*	
	Monograptus praehercynicus	
Gedinnian	*Monograptus uniformis*	
	SILURIAN	
Upper Ludlow	*Monograptus angustidens*	
	Pristiograptus transgrediens	
	Monograptus perneri	
	Monograptus bouceki	
	Saetograptus lochkovensis	
	Pristiograptus ultimus	
	Pristiograptus fecundus	
	Saetograptus fritschi linearis	
Lower Ludlow	*Saetograptus leintwardinensis*	
	Pristiograptus tumescens	
	Cucullograptus (Lobograptus) scanicus	
	Neodiversograptus nilssoni	
Wenlock	*Pristiograptus ludensis* (=*Monograptus vulgaris*)	
	Cyrtograptus lundgreni	
	Cyrtograptus ellesae	
	Cyrtograptus linnarssoni	
	Cyrtograptus rigidus	
	Monograptus riccartonensis	
	Cyrtograptus murchisoni	
	Cyrtograptus centrifugus	
Llandovery	*Monoclimacis crenulata*	
	Monoclimacis griestoniensis	
	Monograptus crispus	
	Monograptus turriculatus	
	Rastrites maximus	
	Monograptus sedgwicki	
	Monograptus convolutus	
	Monograptus gregarius	*Monograptus leptotheca*
		Diplograptus magnus
		Monograptus triangulatus
	Monograptus cyphus (lower part sometimes distinguished as *Monograptus acinaces*)	
	Cystograptus vesiculosus (=*Monograptus atavus*)	
	"Akidograptus" acuminatus	
	Glyptograptus persculptus	
	ORDOVICIAN	
Ashgill	*Dicellograptus anceps*	
	Dicellograptus complanatus	
Caradoc	*Pleurograptus linearis*	
	Dicranograptus clingani	
	Diplograptus multidens & *Climacograptus peltifer*	
	Nemagraptus gracilis	
Llandeilo	*Glyptograptus teretiusculus*	
Llanvirn	*Didymograptus murchisoni*	
	Didymograptus bifidus	
Arenig	*Didymograptus hirundo*	
	Didymogratus extensus	*Isograptus gibberulus*
		Didymograptus nitidus
	....	*Didymograptus deflexus*
Tremadoc	....	
	Clonograptus tenellus & *Bryograptus hunnebergensis*	
	Dictyonema flabelliforme	*Dictyonema flabelliforme flabelliforme*
		Dictyonema flabelliforme sociale

Graptolite Zones Distinguished in Australia

STAGE	ZONE
	ORDOVICIAN
Bolindian	*Dicellograptus complanatus*
	Pleurograptus linearis
Eastonian	*Dicranograptus hians*
	Climacograptus baragwanathi
Gisbornian	*Climacograptus peltifer* & *Diplograptus multidens*
	Nemagraptus gracilis
Darriwilian	*Glyptograptus teretiusculus*
	Diplograptus decoratus
	Glyptograptus intersitus
	Glyptograptus austrodentatus
Yapeenian	Ya 2 *Oncograptus* & *Cardiograptus*
	Ya 1 *Oncograptus*
Castlemainian	Ca 3 *Isograptus caduceus maximodivergens*
	Ca 2 *Isograptus caduceus victoriae*
	Ca 1 *Isograptus caduceus lunata*
Chewtonian	Ch 3 *Didymograptus balticus*
	Ch 2 *Didymograptus protobifidus*
	Ch 1 *Didymograptus protobifidus* & *Tetragraptus fruticosus*
Bendigonian	Be 4 *Tetragraptus fruticosus* (3-br)
	Be 3 *Tetragraptus fruticosus* (3-br and 4-br)
	Be 2 *Tetragraptus fruticosus* (4-br)
	Be 1 *Tetragraptus fruiticosus* & *Tetragraptus approximatus*
Lancefieldian	La 3 *Tetragraptus approximatus*
	La 2 *Bryograptus* & *Clonograptus*
	La 1 *Staurograptus* & *Dictyonema*

the basis of easily recognizable features of gross morphology such as distinctive general form *(Phyllograptus, Dicranograptus)*, number of branches *(Tetragraptus, Dichograptus, Monograptus)* or biseriality *(Diplograptus)*; occasionally some more minute feature, such as reticulate periderm *(Retiolites)* was utilized, but only rarely were thecal characters employed *(Rastrites, Climacograptus)*. At the other extreme are various recently described genera and subgenera *(Cucullograptus, Lobograptus)* defined on an accurate knowledge of the details of thecal form, and many of these at least approximate to phyletic entities. Between the extremes lies a whole range of genera based on somewhat more refined rhabdosomal characters, or on rather less exact and more contentious thecal characters.

Most of the characters which determine gross morphology of the rhabdosome seem to result from parallel evolution; often they represent the grades of biological improvement which constitute **anagenesis** (HUXLEY, 1958). In consequence, a high proportion of graptolite genera are polyphyletic. Thecal characters, which are largely used in specific diagnosis, are believed to represent **cladogenesis** and to provide a more reliable clue to genetic affinity; when such characters are used for generic diagnosis, they may define something approaching "natural genera."

A "natural classification" (i.e., a purely phyletic system) would classify products of cladogenesis (or genetic divergence) and ignore those of anagenesis (or grades of general biological improvement). Thus it would unite in a single taxon genetically related species of *Didymograptus, Tetragraptus*, and multiramous dichograptids (and ultimately of anisograptid dendroids as well as diplograptids and monograptids) while ignoring the existence of taxa named *Didymograptus, Tetragraptus*, and the like. It would trace a phyletic line using thecal similarity as its principal guide; but it would fail to recognize certain conspicuous features and stages, even though these have an obvious practical value. Any workably useful classification is a compromise and as concerns the Graptoloidea such compromise is determined by recognizing small, approximately phyletic units (genera) within larger grades of long-established "form genera."

However, the statement that thecal characters provide a reliable clue to genetic affinity requires qualification, for some evidence now shows that even "thecally based" genera are not necessarily monophyletic. The process of thecal differentiation within the grade represented by *Diplograptus (s. lat.)* appears to be essentially cladogenetic, not anagenetic, and the rapid diversification of the ancestral biserial forms with glyptograptid thecae results in the appearance of *Climacograptus, Diplograptus (s. str.), Amplexograptus,* and *Orthograptus.* But these genera seem also to include later gradations from one to another and it is possible that such transitions may occur in both directions. Thus the original transition from *Glyptograptus* to *Climacograptus* which occurs at the top of the Arenig may be followed by another in the lower Caradoc *(G. siccatus* to *C. brevis)* and yet another may be found of more uncertain direction in the Lower Silurian.

Ultimately, no doubt, such genera as *Climacograptus* will be subdivided into smaller and more "natural" units; already *Pseudoclimacograptus* has been discriminated, first as a subgenus and now as a genus divided into three subgenera. But the validity of such subdivision depends upon the accuracy of morphological diagnosis and any partitions based on full growth-line evidence of thecal structure and ontogeny are rare. All too often adequately detailed information is lacking and taxa defined without this information may be actually misleading. For this reason, many "technically valid' genera are not accepted here. It may also be noted that rare preservation of structural details may suggest desirable bases of classification which nevertheless cannot be applied to normally occurring and hence imperfectly preserved material. EISENACK's (1951) work on retiolitids illustrates this dilemma.

Finally, reference must be made to the taxonomic implications of penetrance in the introduction of new thecal types and the consequent occurrence of "bi-form" rhabdosomes combining different thecal types in the same colony (see also p. *V*66). These "penetrance intermediates" are of more importance than "expressivity intermediates" in the monograptids and it is regrettable that the detailed work now beginning along these lines no longer retains an undivided genus *Monograptus* as its *basis operandi.* Instead, a score or so of generic and subgeneric names are recognized, some founded on mere silhouette preservation and many so broadly conceived as to constitute form genera themselves. (See Addendum, p. *V*149.)

PHYLOGENY

The order Graptoloidea is divisible into four suborders, Didymograptina, Glossograptina, Diplograptina and Monograptina, which reflect three main events in graptoloid evolution, namely, origin of the Didymograptina from the order Dendroidea, development of scandent biserial rhabdosomes (monopleural and dipleural), and development of scandent uniserial rhabdosomes (Monograptina). As described below, the origin of the Graptoloidea results from a change which appears to be gradual and transitional forms occur. The other two changes are abrupt (mega-revolutionary) and no intermediates are recognized; they express major changes in rhabdosome construction resulting from the orientation and relationships of the earliest proximal thecae. The Didymograptina, Diplograptina, and Monograptina constitute a phyletic sequence, whereas the Glossograptina represent a relatively shortlived offshoot from the Didymograptina which died out without descendants.

DIDYMOGRAPTINA

DICHOGRAPTIDAE

The earliest of all graptoloid families is the Dichograptidae and its origin is synonymous with that of the Graptoloidea. It involves essentially the loss of bithecae and of sclerotized stolons (with consequent simplification of branch structure) and it follows upon the adoption of a pelagic mode of life. The change was gradual and the Anisograptidae is a family so completely transitional between the Graptoloidea and Dendroidea that it could be included in either, for the mode of life appears to have been graptoloid, whereas the branch structure remained characteristically dendroid. Bithecae have not yet been demonstrated in Arenigian species of *Clonograptus* and *Bryograptus,* though present in Tremadocian species of the same genera; but the inclusion of some forms with bithecae in a dendroid family (and, provisionally at least, in bitheca-bearing genera) involves no greater inconsistency than the converse. One effect of classing the Anisograptidae with the Dendroidea is to emphasize the polyphyletic origin of the Graptoloidea—and of the Dichograptidae; but this could only be avoided, if at all, by extending the scope of the Dichograptidae to include *Dictyonema flabelliforme (s. lat.).*

It was through their work on certain dichograptids that NICHOLSON & MARR (1895) first recognized the possibility that graptolite genera might be polyphyletic.[1] To these authors, the number of branches in a graptolite rhabdosome (though forming the basis of so many earlier generic definitions) was a feature of less importance than thecal characters, and using the criterion of thecal similarity and (to a less extent) angle of divergence, they recognized nine groups of *Didymograptus, Tetragraptus, Bryograptus,* and *Dichograptus* species as establishing the principle of stipe reduction. They stated: "It is comparatively easy to explain the more or less simultaneous existence of forms possessing the same number of stipes, but otherwise only distantly related, if we imagine them to be the result of variation of a number of different ancestral types along similar lines" (p. 537).

The principle of progressive stipe reduction thus propounded, with the generic series extended to become *Clonograptus-Loganograptus-Dichograptus-Tetragraptus - Didymograptus* (for horizontal forms), dominated discussions of dichograptid phylogeny for 40 years. Some difficulties were indicated by DIXON (1931) and it was more specifically challenged by HARRIS & THOMAS (1940a), who questioned the rigid application of this one criterion and advocated the exclusion of *Loganograptus* from any such series. It has been subsequently emphasized that no stratigraphic evidence supports strict chronological sequence of the genera involved in this series; indeed, species of *Tetragraptus* and *Didymograptus* appear to be the earliest true dichograptids. HARRIS & THOMAS indicated the probability that *Tetragraptus* and even *Didymograptus* also may have arisen from other multiramous ancestors (e.g., from *Schizograptus* or *Trochograptus,* by way of *Mimograptus*). And anisograptids may themselves achieve reduction to two stipes *(Kiaerograptus)* while still retaining typical dendroid branch structure. In effect, stipe reduction is now seen as a general feature of the evolution of the anisograptids as well as the dichograptids, and the phylogeny of the latter has assumed the character of a complicated network or plexus. The accompanying diagram (Fig. 75), doubtless inaccurate in detail, nevertheless gives some indication of possible lines of *Tetragraptus* and *Didymograptus* ancestry.

That reclined tetragraptids have given rise to the scandent quadriserial *Phyllograptus* can scarcely be doubted, though an appreciable time gap separates one possible morphological intermediate *Tetragraptus phyllograptoides* from the earliest species of *Phyllograptus.* Scandent biserial genera also exist which must be regarded as dichograptid. The relationship of *Oncograptus* and *Cardiograptus* to *Isograptus* is ambiguous; stratigraphical relations suggest analogy with the *Phyllograptus-Tetragraptus* series, but the only *Oncograptus* investigated in detail possesses a proximal end more "primitive" than any known isograptid. *Skiagraptus* is another biserial form which occupies a somewhat anomalous position, but which is here retained in the Dichograptidae.

No satisfactory subdivision of the large and varied family Dichograptidae on a formal subfamilial basis is yet possible and the arbitrary grouping into multiramous and pauciramous genera, further tentatively divided into arbitrary "sections," is here retained. Moreover, the recognition of such genera as *Pendeograptus* and *Ex-*

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[1] WIMAN (1895) seems independently to have postulated a polyphyletic origin for *Monograptus,* regarding some of the different thecal types as implying a distinct ancestry, but he gave no details.

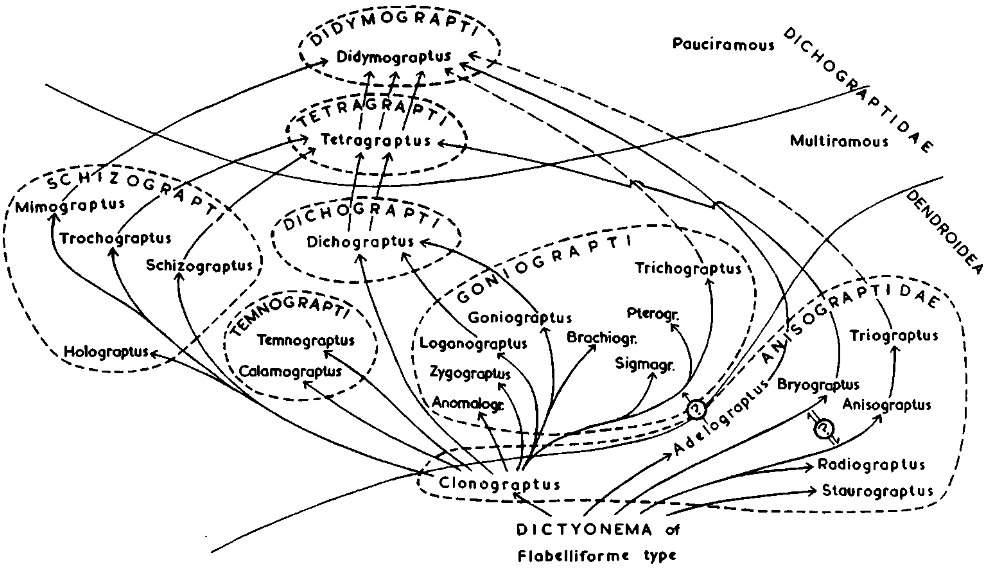

Fig. 75. Phylogeny of *Tetragraptus* and *Didymograptus* (tentative), with suggested grouping of the principal multiramous dichograptid genera and possible relations to the Anisograptidae (29).

tensograptus does not materially help to resolve the complicated phylogeny of *Tetragraptus* and *Didymograptus.* The unity of the genera comprising the Isograptidae of Harris is not yet convincingly demonstrated, but two compact families of highly specialized dichograptids have been recognized, the sinograptids and abrograptids.

SINOGRAPTIDAE AND ABROGRAPTIDAE

Characterized by progressive development of prothecal and metathecal folding, the Sinograptidae appear to represent a specialized offshoot from the Dichograptidae, though at what point is obscure, and some authorities assign the family an independent origin in the Anisograptidae. A stipe-reduction trend within the assemblage receives some support from the occurrence of the eight- and four-stiped *Pseudodichograptus* and *Allograptus* in the *Didymograptus hirundo* zone, while the thecally more extreme two-stiped genera *Tylograptus* and *Sinograptus* occur in the overlying *Amplexograptus confertus* zone of the Ningkuo Shale. *Nicholsonograptus* appears to represent the extreme of stipe reduction.

The highly specialized graptolites included in the Abrograptidae show a reduction of the periderm to a few sclerotized threads bearing apertural rings, but as in the retiolitid *Archiretiolites,* the sicula is normal. Their dichograptid origin is indicated by the presence of only a single crossing canal.

CORYNOIDIDAE

The affinities of the Corynoididae remain conjectural and some authorities assign it ordinal or subordinal status. Since the entire rhabdosome comprises not more than four individuals (including the sicula) it clearly represents arrested development. The prosicula appears to be devoid of the normal graptoloid longitudinal rods and it further resembles the dendroid prosicula in the apical position of the *th1* resorption foramen, but these features may occur in other (primitive) dichograptids. The second theca was believed (Bulman, 1947) to arise by resorption, but this was probably a misinterpretation of the delayed growth of *th2,* and Kozłowski (1953) has demonstrated that in *Corynites* the second theca (here the "microtheca") originates through a "primary notch." The mode of budding is thus probably normal and the alternating origin of the thecae is the equivalent of isograptid development. The extreme elongation of the metasicula and adnate thecae also recalls highly developed isograptids, for which reason the family is placed in its present position here; but a perceptible time gap sets off the last isograptids from the earliest *Corynoides* species. It is possible also that these forms represent or have arisen from giant larvae such as occur in modern plankton.

NEMAGRAPTIDAE AND DICRANOGRAPTIDAE

The leptograptid type of theca is foreshadowed in several species of *Didymograptus* and the superficial resemblance between *Leptograptus* and some slender *Dicellograptus* species has been considered to imply a phyletic relationship between these genera; but the presence of prothecal folds in several species of *Dicellograptus* is believed by other authorities to necessitate an independent origin from dichograptid or sinograptid stock (Jaanusson, 1965); but also Bulman, 1969). Lack of detailed information regarding the mode of development of the rhabdosome in *Leptograptus* is a source of uncertainty in discussions both of leptograptid ancestry and of *Leptograptus-Dicellograptus* relationships (see p. *V*76), for it is not known at what point the distinctive diplograptid (streptoblastic) development supersedes the dichograptid or isograptid type.

The view that *Dicranograptus* represents an intermediate phyletic stage between *Dicellograptus* and *Diplograptus* is no longer tenable and has been abandoned. Not only do various diplograptids long antedate the earliest known *Dicranograptus* (or *Dicellograptus*), but the distinctive dicranograptid theca is too specialized to be ancestral to that of any primitive diplograptid, and no progressive increase in length affects the biserial portion of the rhabdosome either in species time distribution, or in the range of a single *Dicranograptus* species. Rather do individual species give the impression of relatively stable semiscandent mutations, commonly ranging through several graptolite zones with negligible change. Rare examples of irregularity in rhabdosome construction have been figured by Ruedemann (1947) and have been named *Diceratograptus* by Mu (1963). The mode of development of all known species is decidedly diplograptid (streptoblastic) and the possibility of evolution *from* a diplograptid ancestor is perhaps not altogether fanciful.

The precise significance of the branched nemagraptids is also unknown. Branching, where it occurs, is always lateral and in some paired (e.g., *Amphigraptus, Syndyograptus*) in a manner somewhat suggestive of thecal cladia, while the centribrachiate rhabdosomes of *Leptograptus* similarly suggest sicular cladia production rather than normal proximal end branching. That the branched condition of *Pleurograptus* is in some way secondary and not primitive is rather suggested by its high stratigraphic position and even lower Caradocian branched nemagraptids are separated from any multiramous dichograptid by a time gap.

It is not considered probable that *Pseudozygograptus* Mu, Lee, & Geh represents a "leptograptid *Azygograptus*"; the dicalycal theca of a leptograptid, *th2*^{1}, is sufficient to prevent any simple derivation of the *Azygograptus* condition and the type of theca appears to be an inexact homeomorph.

GLOSSOGRAPTINA

In most areas of the world, the evolution of monopleural and dipleural biserial graptoloids is approximately contemporaneous, but their differences in structure and development are so great as to indicate a separate origin. That of the Glossograptina must lie in some unknown, presumably dichograptid, stock in which rhabdosome development was of a "primitive" type, with *th1*^{1} the dicalycal theca and a single crossing canal. In this respect, the isograptids are already too advanced to be ancestral (*cf.* Mu & Zhan, 1966), and though evidence is insufficient as to the mode of development of *Oncograptus* and *Cardiograptus,* the rhabdosomes of these genera are not monopleural.

The Glossograptidae and Cryptograptidae make their first appearance in association in so many regions that it is not yet possible to assign priority to either; but they must have diverged rapidly assuming the existence of a common ancestor (based on their monopleural rhabdosomes and closely comparable mode of development). *Paraglossograptus* was erected for glossograptids with a well-developed lacinia (though its morphology is imperfectly known) and *Lonchograptus* also is clearly a derivative of *Glossograptus.* The affinities of *Nanograptus,* however, are less certain; it is an uncommon genus which combines some of the characters of both *Glossograptus* and *Cryptograptus,* though for stratigraphical reasons it can scarcely be a primary intermediate between them. The lack of conspicuous spines gives its rhabdosome a cryptograptid appearance (extremely fine apertural spines are definitely present in *N. phylloides*); but the characters of the thecae more closely resemble those of the Glossograptidae in which family it is provisionally included.

The relative lack of diversification and comparatively short stratigraphical range of this suborder indicates that for some reason it was the less efficient version of the scandent biserial rhabdosome. The dicalycal *th*1^1 compels an almost static proximal end.

DIPLOGRAPTINA

The Diplograptina occupy a dominant position among Ordovician graptolites and persisted until the Late Silurian (early Ludlow). Like the Glossograptina, the suborder must have arisen from dichograptid stock, but with more "advanced" proximal end, for the dicalycal theca is *th*2^1 (or some later theca) and three or more crossing canals are present. The earliest representative is a *Glyptograptus* of latest *Didymograptus extensus* or *Didymograptus hirundo* Zone age, but diversification was rapid and by early Llanvirn times (*Didymograptus bifidus* Zone) the genera *Diplograptus, Amplexograptus, Climacograptus* and *Pseudoclimacograptus* were present, together with representatives of the Lasiograptidae.

DIPLOGRAPTIDAE

A streptoblastic developmental plan of diplograptids is common but can no longer be claimed to be universal among these early representatives and its significance is obscure. Running through the family is also a general tendency for progressive delay in the siting of the dicalycal theca, resulting in a progressively incomplete septum and ultimately an aseptate rhabdosome. This should be applied as a phyletic criterion only with caution. Similar changes seem to affect the Lasiograptidae and the Retiolitidae.

Most genera are of long standing and were based mainly on thecal characters, originally determined in flattened material. This was a consequence of the very stable rhabdosome form. More precise studies on three-dimensional material have led to the establishment of further genera and subgenera and have served to indicate the complexity of diplograptid phylogeny without as yet providing sufficient evidence to offer a solution to the problem. It is probable that most genera are polyphyletic and they appear not only to define the results of original diversification but to include later gradations from one genus to another. This is strongly suspected in the case of *Glyptograptus* and *Climacograptus,* where three possible transitions are already known (p. *V*103). It is also possible that Silurian representatives of *Glyptograptus* and *Diplograptus* are homeomorphs, rather than descendants of Ordovician species of these genera. On current interpretation, therefore, these older genera are essentially "form genera" and their relationships have been likened to a bundle of rods with *Glyptograptus* forming a central core and with transitional connections from one to another at various levels. For all these reasons the family is no longer divided into subfamilies as in the first edition of this *Treatise.*

Two genera, both at present monotypic, have each been assigned to separate families: the *Dicaulograptidae* and the *Peiragraptidae.* The former may be an aberrant lasiograptid, but both have disconcertingly dicranograptid features; on the assumption that these are due to homeomorphy, both are placed in the Diplograptina.

LASIOGRAPTIDAE

Derivation of the Lasiograptidae from diplograptid stock seems certain; JAANUSSON even reduced the assemblage to a subfamily of his Diplograptidae. The thecal type in *Lasiograptus* suggests simply a more extreme development of the general climacograptid type of theca, but the supragenicular wall in *Gymnograptus* and *Hallograptus* is exceedingly short and the infragenicular portion straight; the analogy with *Cryptograptus* (and its relation to *Glossograptus*) suggests the possibility of an independent origin from a straight orthograptid type in these genera. The whole group is retained here with the rank of a family.

RETIOLITIDAE

More detail has come to light in recent years concerning the Retiolitidae, but it is still impossible to recognize any phyletic grouping of genera and therefore they are retained in three arbitrary subfamilies reflecting an approximate increase in specialization. The Archiretiolitinae are the least modified, but represent a marked advance on any normal diplograptid. Almost the whole rhabdosome is reticular, but normal fusellar tissue persists in the sicula and to a varying degree in the initial parts of early thecae. Two genera have been described from fragmentary (?immature) proximal ends and two others are not known three-dimensionally; but the limited evidence of thecal characters and mode of development suggest that the subfamily comprises various stages in retiolitid specialization affecting several lines derived from more than one diplograptid ancestor.

The Retiolitinae are more specialized; no conclusive evidence indicates any continuous periderm except in the prosicula, and the recognizably diplograptid development of the Archiretiolitinae has been replaced by the ancora and corona stages (Fig. 59). Whether independently evolved or related to the preceding family is uncertain. The Plectograptinae include the latest and most highly modified genera of all, with the skeleton commonly reduced to little more than an open clathria.

DIMORPHOGRAPTIDAE

Regarded from the viewpoint of adult rhabdosomes, the dimorphograptids occupy a morphologically intermediate position between Diplograptidae and Monograptidae (and between Diplograptina and Monograptina), but as with the dicranograptids they were probably not phyletically intermediate. They do not represent an essential intermediate in the astogenetic changes involved; no time significance is seen in length of the uniserial portion of the rhabdosome; and stratigraphically the species are later than the earliest monograptids.[1] They are here included in the Diplograptina not only because they appear to represent diplograptids that have failed to become monograptid, but because the mode of development is more diplograptid in the downward direction of growth of the initial part of $th1^1$ in several forms and because of the lack of sinus and lacuna type of porus formation.

The disappearance of the dicalycal theca is not in itself sufficient to convert a diplograptid into a monograptid rhabdosome; *Peiragraptus* illustrates (Fig. 76,2) what results merely from this step in the process, and shows that the real problem is the reorientation (or elimination) of $th1^2$.

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[1] See p. V100.

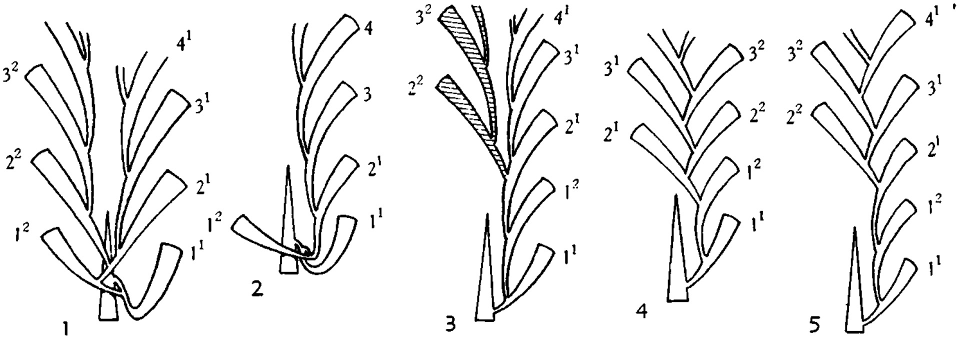

FIG. 76. Diagrams illustrating derivation of monograptid from diplograptid rhabdosome (Bulman, n).——*1.* Biserial rhabdosome with dicalycal $th2^1$.——*2.* *Peiragraptus,* a uniserial rhabdosome in which $th1^2$ retains its diplograptid orientation.——*3.* Hypothetical diplograptid with reoriented $th1^2$ and dicalycal $th2^1$; loss of $th2^2$ and descendant thecae (shaded) would convert to monograptid.——*4,5.* Possible dimorphograptid rhabdosomes with aseptate thecae.

Once this has been accomplished, the disappearance of the dicalycal theca, if it were *th2*^{1}, could result in the immediate production of a uniserial rhabdosome (Fig. 76,*3*) from a septate diplograptid. No such form as this has yet been recognized, possibly because it was extremely short-lived; most dimorphograptid species are aseptate (Fig. 76,*4,5*) or possess a partial septum, and from such forms the production of *Monograptus* would be a long and complicated process.

MONOGRAPTINA

Thecal elaboration affects the monograptids to an extent exceeding anything recognized among Ordovician graptolites. Unfortunately, preservation of early monograptids is generally very unsatisfactory and little detail is as yet available. Work in progress on the structure of many seemingly "simple" species, particularly of Elles & Wood's (1901-18) Group II, indicates unexpected thecal elaboration even at this level, and the possibility of polyphyletic origin for *Monograptus* cannot be excluded. At present the ancestry of such distinctive groups as the triangulate and hooked monograptids is quite unknown, and generic and subgeneric names for such groups are not here adopted. *Pristiograptus* and *Monoclimacis* are accepted in this edition, but these are long-ranging and may well prove to comprise unrelated species.

The long series of rhabdosomal changes, beginning with pendent or horizontal dichograptids, culminates little more than halfway through the geological history of the Graptoloidea in the scandent uniserial monograptids of the Silurian, and the development of cladia-bearing rhabdosomes represents the only further change possible. Reference has already been made (p. *V*88) to Urbanek's recognition of a series of astogenetic stages (monograptid to abiesgraptid) based on this cladia-production, which he compared with the developmental stages of other orders, especially the Diplograptina. Astogenetic stages in the Diplograptina have never been proposed as a basis for classification, but in the Monograptina they have been so used and to a large extent form the basis for the classification provisionally retained here. In this, the Monograptidae (without cladia) are separated from the Cyrtograptidae (with cladia) and the latter are subdivided into Cyrtograptinae (with thecal cladia only) and Linograptinae (with sicular cladia, with or without thecal cladia). We do not know to what cause cladia-production is a response and it may be that the same species may occur in more than one form. *"Monograptus" runcinatus* commonly appears to be a normal monograptid, but (as described by Strachan) it may develop a sicular cladium; the species then becomes recognizably diversograptid and would be assigned to a separate genus, here placed in a separate subfamily. *Neodiversograptus* doubtless provides comparable examples. Whether it is more reasonable to accept the diversograptid potentiality as the classificatory criterion or to accept the more common astogenetic condition, is clearly contentious, but the number of species involved seems at present to be small. Bipolar rhabdosomes lacking a sicula, which represent a regeneration process (p. *V*89) are not, of course, given any taxonomic rank.

SYSTEMATIC DESCRIPTIONS

Suborder DIDYMOGRAPTINA Lapworth, 1880, emend. Bulman, herein

[*nom. correct.* Jaanusson, 1960, p. 309, *ex* Didymograpta Lapworth, 1880, p. 192] [=Didymograpta+Dicellograpta Lapworth, 1880; Dichograptina+Leptograptina Obut, 1957; Didymograptina+Corynoidina *sensu* Jaanusson, 1960]

Uniserial, pendent to reclined, rarely biserial (dipleural) or quadriserial graptoloids without virgula; development platycalycal, ***thl***^{1}, ***thl***^{2} or ***th2***^{1} being the dicalycal theca. *Ord.*

Family DICHOGRAPTIDAE Lapworth, 1873

[Dichograptidae Lapworth, 1873, table 1 facing p. 555]

Rhabdosome bilaterally symmetrical, branching dichotomous or lateral, central disc present in some; pendent to scandent, usually declined or horizontal; stipes uniserial, rarely biserial or quadriserial; thecae typically simple, straight or with slight ventral curvature, denticulate, overlapping about one-half their length; development of dichograptid or isograptid type. *L.Ord.*

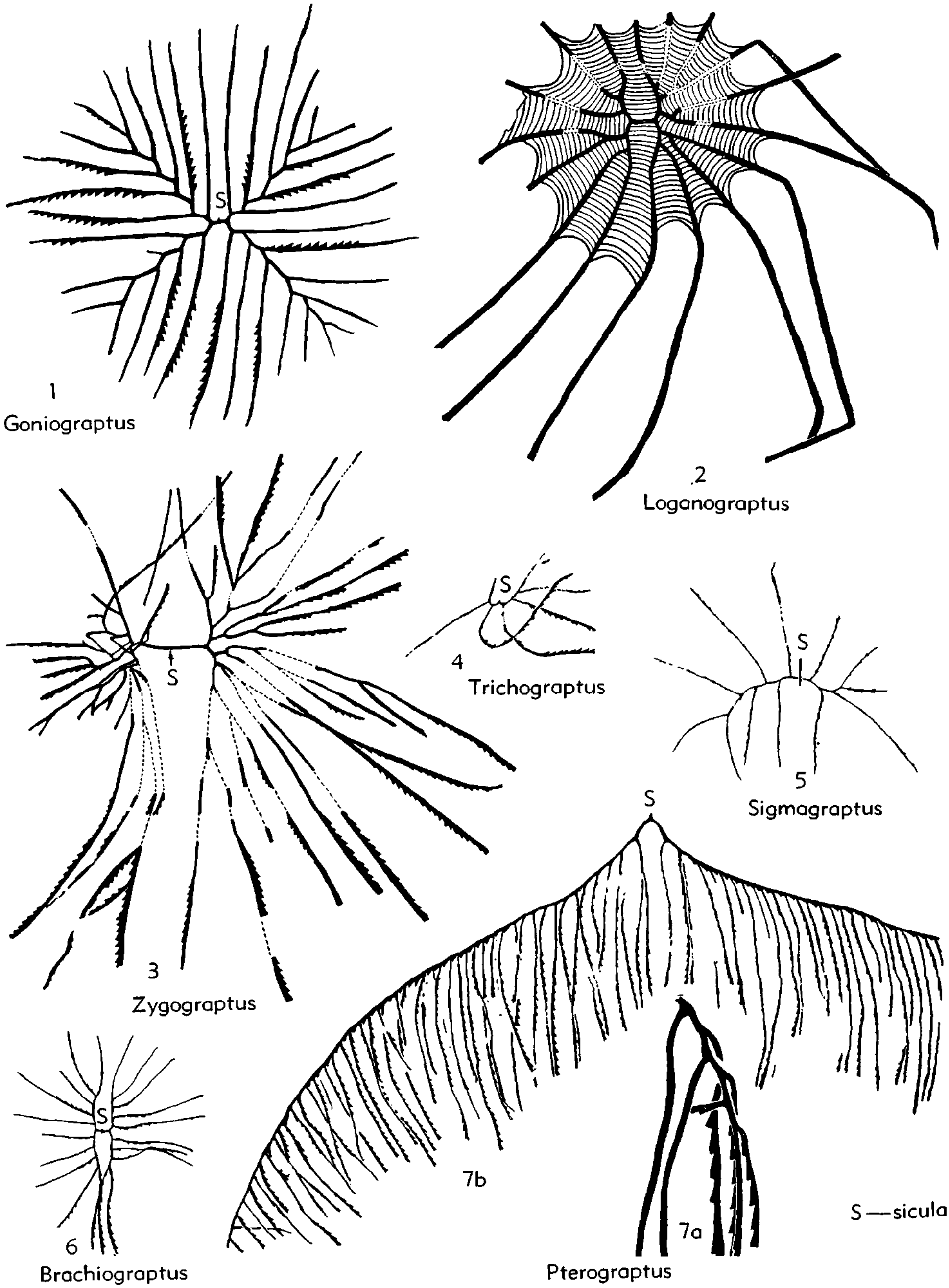

Fig. 77. Dichograptidae (Goniograpti) (p. *V*111-*V*112).

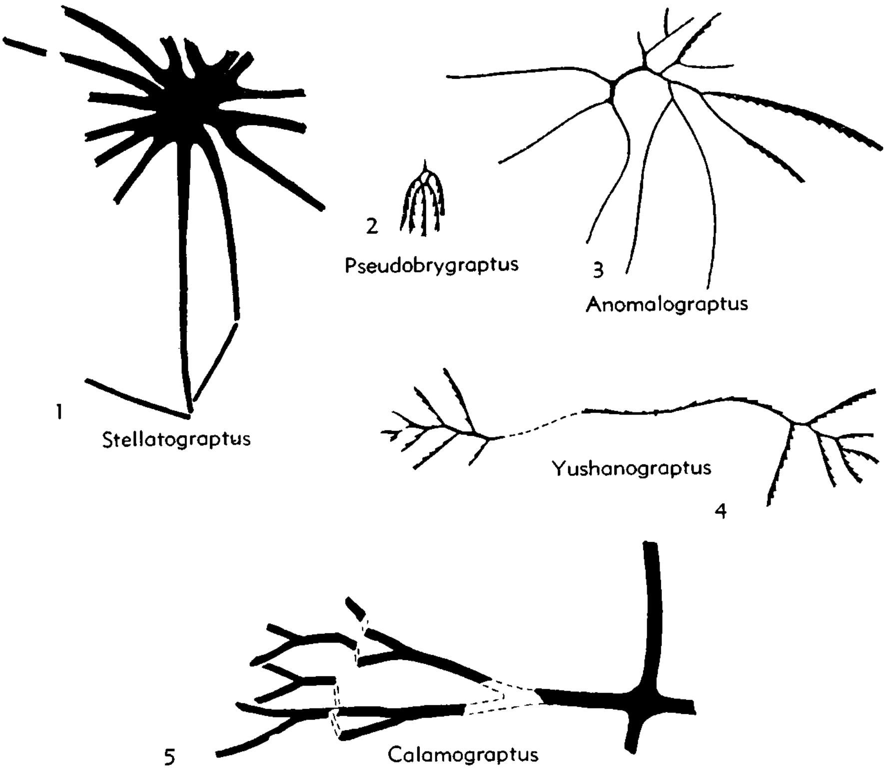

Fig. 78. Dichograptidae (Goniograpti) *(1-4);* (Temnograpti) *(5)* (p. *V*111-*V*114).

MULTIRAMOUS FORMS

Pendent to horizontal, rarely reclined; branching dichotomously to produce at least third-order branches (first-order branches constitute the "funicle" of Hall), or laterally from one or both sides of two or four main stipes. *L.Ord.*

Section GONIOGRAPTI

Based on didymograptid or tetragraptid foundation, with compact regular branching either dichotomous or lateral. *Ord.*

Goniograptus M'Coy, 1876; p. 130 [**Didymograpsus thureaui* M'Coy, 1876, p. 129; M]. With 4 zigzag main stipes, from angles of which undivided lateral stipes are produced with great regularity, so that form suggests regularly alternating dichotomy (Fig. 64,*3*) and in one subspecies dichotomous division occurs in some quadrants; thecae with low inclination and slight overlap. *L.Ord.,* N.Am.(Deepkill-?Normanskill)-N.Z.-Australia(Bendigon.-Castlemain.)-?NW. Eu.——Fig. 77,*1*. **G. thureaui* (M'Coy), Australia; ×1 (138).

Anomalograptus Clark, 1924, p. 63 [**A. reliquus;* OD]. Late aberrant clonograptid with asymmetrical and irregular dichotomies up to 6th order. *L.Ord. (Glyptograptus dentatus Z.),* Que.——Fig. 78,*3*. **A. reliquus;* ×1.5 (46).

Brachiograptus Harris & Keble, 1932, p. 43 [**B. etaformis;* M]. Small, composed of 4 main branches forming with funicle a letter H, from outer sides of which are produced close-set undivided lateral branches; thecae slender, with low inclination and slight overlap. *L.Ord.(Llanvirn),* N.Am.-S.Am.-Australia-?China.——Fig. 77,*6*. **B. etaformis,* Australia (Darriwil); ×1 (84).

Loganograptus Hall, 1868, p. 237 [**Graptolithus logani* Hall, 1858, p. 142; M]. Typically 16 to 8 branches, rarely exceeding 4th order, produced by proximally concentrated dichotomy; undivided terminal stipes mostly long and flexuous; central disc commonly present, enclosing proximal dichotomies; thecae moderately inclined with overlap of about one-half. *L.Ord.(low.Arenig-Llanvirn-?Normanskill),* NW. Eu.-N.Am.-Asia-Australia-N.Z.——Fig. 77,*2*. **L. logani* (Hall), Levis Sh., Que.; ×1 (77).

?**Oslograptus** Jaanusson, 1965, p. 427 [**O. peculiaris;* OD]. Similar in rhabdosome form to *Pseudobryograptus,* but with only second order branches; stipes with pronounced dorsal folds at level of thecal apertures; development ?isograptid. *L.Ord.(L. Didymograptus Sh.),* Eu.(Nor.).

Pseudobryograptus Mu, 1957, p. 421 [**P. parallelus;* OD]. Rhabdosome small, pendent; branching dichotomous, up to third order; thecae dichograptid. *L.Ord.(up.Arenig-low.Llanvirn),* China (Ningkuo Sh.)-Australia (Darriwil)-N. Am.-(Glenogle Sh.).——Fig. 78,*2*. **P. parallelus,* China; ×1.5 (149).

Pterograptus Holm, 1881, p. 74 [**P. elegans* (=*Graptolithus gracilis* Kjerulf, 1865, p. 4; *non* Hall, 1848), p. 274; M]. Pendent or declined, consisting of 2 primary stipes, each giving rise to undivided lateral branches alternately to right and left, forming a somewhat flabelliform rhabdosome; thecae denticulate, inclined at moderate angles. *L.Ord.(up.Arenig-Llanvirn),* NW. Eu.-S.Am.-Australia-China. ——Fig. 77,*7a*. **P. elegans,* U.*Didymograptus* Sh., S. Sweden; ×4 (Hadding, 1911).——Fig. 77,*7b*. *P. scanicus* Moberg, U.*Didymograptus* Sh., S. Sweden; ×1 (Hadding, 1911).

Sigmagraptus Ruedemann, 1904, p. 701 [**S. praecursor;* OD]. With 2 slender main branches from which slender undivided lateral branches originate alternately on both sides (genus is essentially a 2-stiped *Goniograptus*); thecae extremely slender, inclined at low angles and with slight overlap. *L.Ord.,* N.Am.(Deepkill)-Australia-N.Z. (Bendigo).——Fig. 77,*5*. **S. praecursor,* Deepkill, N.Y.; ×1 (201).

Stellatograptus Erdtmann, 1967, p. 343 [**S. stellatus;* M]. Like *Loganograptus* but with thick central web and tapering lateral alae to more distal branches. *L.Ord.(?up. Arenig, Levis Sh.),* N.Am.(Que.).——Fig. 78,*1*. **S. stellatus*; ×1.5 (61).

Triaenograptus T. S. Hall, 1914, p. 115 [**T. neglectus;* M] [=*Tridensigraptus* Zhao, 1964, p. 640 (type, *T. zhejiangensis*)]. Rhabdosome large, horizontal, composed of 4 main stipes, each with paired lateral branches some of which may bear paired (4th or higher order) branches. *L.Ord. (Isograptus* and *Didymograptus hirundo Z.)*; Australia(Victoria)-China.

Trichograptus Nicholson, 1876, p. 248 [**Dichograptus fragilis* Nicholson, 1869; OD]. With 2 slender primary stipes, straight or flexuous, originating at about 180 degrees from sicula, with slender undivided lateral branches regularly produced from one side only; thecae elongate with low inclination and very slight overlap. *L.Ord. (Arenig-Llanvirn),* NW. Eu.-S. Am.-Australia. ——Fig. 77,*4*. **T. fragilis* (Nicholson), Skiddaw Sl., N.Eng.; ×1 (59).

Yushanograptus Chen, Sun, & Han, 1964, p. 239 [**Y. separatus;* OD]. Rhabdosome of 2 long, declined stipes with goniograptid branching distally. *L.Ord.(up. Arenig, Ningkuo Sh.),* China. ——Fig. 78,*4*. **Y. separatus;* ×1 (44).

Zygograptus Harris & Thomas, 1941, p. 308 [**Graptolithus abnormis* Hall, 1857; OD]. With 2 long first-order stipes forming an exaggerated funicle, followed by repeated dichotomies at close intervals to 5th or higher order; thecae with moderate to low inclination and slight overlap.

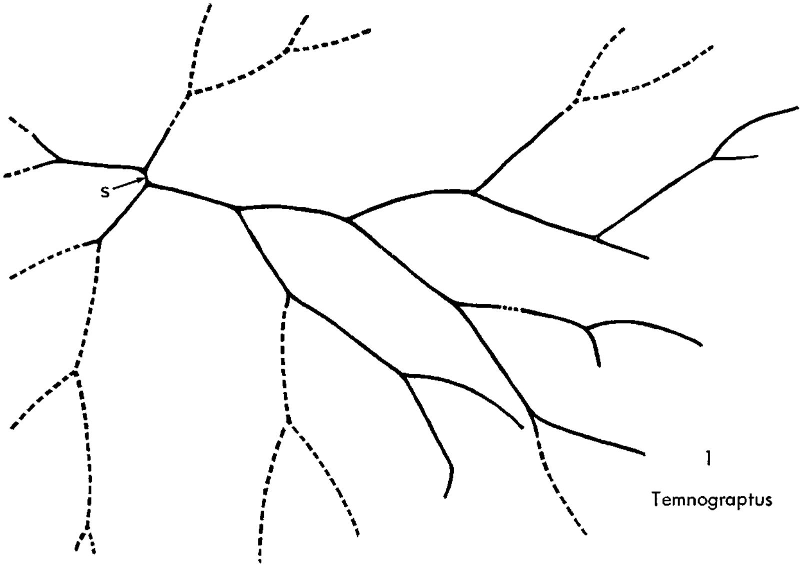

Fig. 79. Dichograptidae (Temnograpti) [*s,* sicula] (p. *V*113).

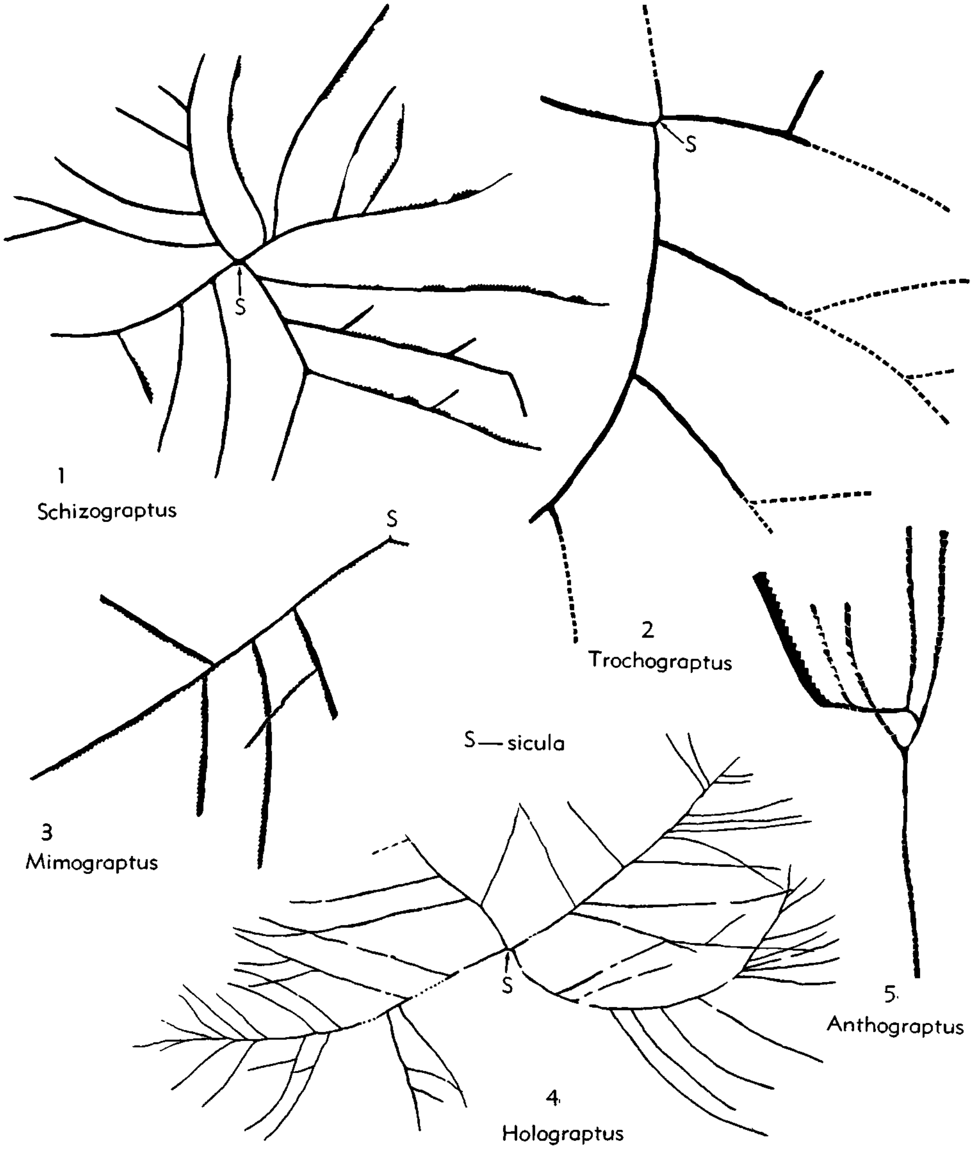

FIG. 80. Dichograptidae (Schizograpti) (p. *V*114).

L.Ord.(Arenig-?Llanvirn), Australia-N.Am.-?N.Z.——FIG. 77,*3*. **Z. abnormis* (HALL), Levis Sh., Que.; ×1 (88).

Section TEMNOGRAPTI

Widely and evenly spaced dichotomous branching based on a tetragraptid foundation; rhabdosome usually of large size. *L.Ord.*

Temnograptus NICHOLSON, 1876, p. 248 [**Dichograpsus multiplex* NICHOLSON, 1868, p. 129; OD]. Like *Clonograptus,* produced by regular dichotomous division but more consistently divergent, with very short funicle and long 2nd-order stipes, successive later orders being approximately equal in length to 2nd; thecae denticulate with moderate inclination and one-half to two-thirds overlap. *L.Ord.,* NW.Eu.*(Arenig)*-N.Am.*(?Athens).*——FIG. 79,*1*. **T. multiplex* (NICHOLSON), *Didymograptus* Sh., S.Sweden; ×0.7 [*s,* sicula] (241).

Calamograptus CLARK, 1924, p. 61 [**C. porrectus;* OD]. Like *Temnograptus* but with branches of

2nd order very long, higher orders slightly decreasing in length. *L.Ord.(Levis),* N.Am.(Que.).——FIG. 78,*5*. **C. porrectus;* ×0.5 (46).

Section SCHIZOGRAPTI

Usually of large size, based on either didymograptid or tetragraptid foundation, with laterally produced secondary branches. *L.Ord.*

Schizograptus NICHOLSON, 1876, p. 248 [**Dichograpsus reticulatus* NICHOLSON, 1868, p. 143; OD]. Rhabdosome based on 4 main stipes produced by dichotomous division from short funicle; lateral branches on one side only of main stipe; tertiary lateral branches rarely developed. *L.Ord. (Arenig),* NW.Eu.-N.Am.-Australia-N.Z.-?S.Am. ——FIG. 80,*1*. *S. rotans* TÖRNQUIST, *Didymograptus* Sh., S.Sweden; ×0.7 (241).

?**Anthograptus** TÖRNQUIST, 1904, p. 22 [**A. nidus;* M]. Proximal end unknown; ?2nd-order stipes of great length, at distal end with lateral branches and stipes of higher order produced by irregular dichotomy. *L.Ord.(L.Didymograptus Sh.),* S. Sweden.——FIG. 80,*5*. **A. nidus;* ×1 (241)

Holograptus HOLM, 1881, p. 45 [**H. expansus;* M] [=*Rouvilligraptus* BARROIS, 1893]. Like *Schizograptus* but lateral branches produced somewhat irregularly from both sides of 4 main stipes, particularly distally. *L.Ord.(Arenig),* NW. Eu.-Boh.——FIG. 80, *4*. *H. deani* ELLES & WOOD, Skiddaw Sl., N.Eng.; ×0.13 (59).

Mimograptus HARRIS & THOMAS, 1940, p. 197 [**M. mutabilis;* M]. Robust, consisting of 2 main stipes diverging from sicula at less than 180 degrees, bearing lateral branches at irregular intervals which in turn may bear tertiary branches; forms with few or no lateral branches also occur. *L.Ord.(Chewton.),* Australia.——FIG. 80,*3*. **M. mutabilis;* ×0.7 (87).

Trochograptus HOLM, 1881, p. 48 [**T. diffusus;* M]. Rhabdosome large, similar to *Schizograptus* but with more widely spaced lateral branches and tertiary branches common. *L.Ord.(Arenig),* NW.Eu.-N.Am.-Australia. —— FIG. 80,*2*. **T. diffusus,* L. *Didymograptus* Sh., Oslo; ×0.7 (89).

Section DICHOGRAPTI

With eight or fewer stipes, dichotomously dividing to third order only; first two orders generally short, equal in length, third order long and usually flexuous; thecae denticulate, inclined at moderate angles and with considerable overlap, less commonly with low inclination, slight overlap, and (rarely) long apertural spines. *L.Ord.*

Dichograptus SALTER, 1863, p. 139 [*nom. correct*

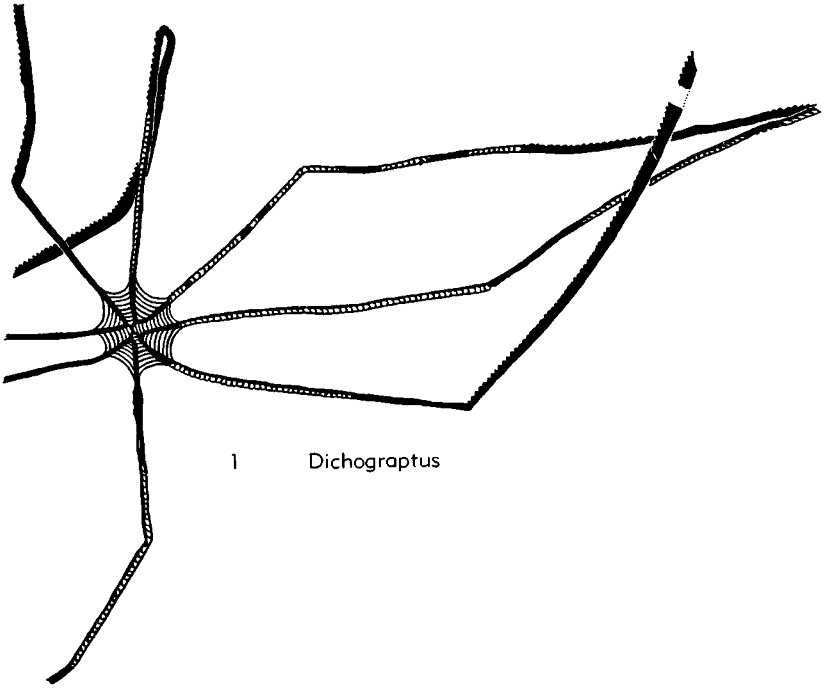

FIG. 81. Dichograptidae (Dichograpti) (p. V114-V115).

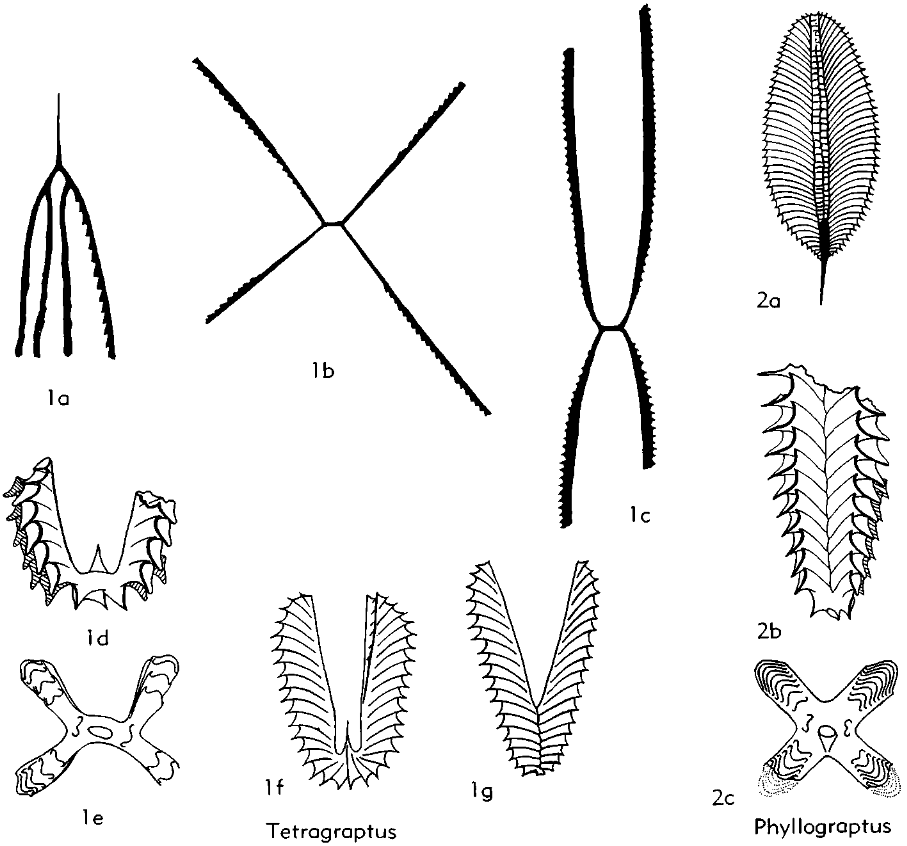

FIG. 82. Dichograptidae (Tetragrapti) (p. *V*115-*V*116).

HALL, 1865 (*pro Dichograpsus* SALTER, 1863), ICZN Opin. 650] [**Dichograpsus sedgwicki;* SD GURLEY, 1896, p. 64]. Characters of section; central disc in certain species. *L.Ord.(Arenig-Llanvirn),* almost world-wide.——FIG. 81,*1*. *D. octobrachiatus* (HALL), Levis Sh., Que.; ×0.5 (77).

PAUCIRAMOUS FORMS

Pendent, deflexed, declined, horizontal, reflexed, reclined or scandent, wholly or in part; branching dichotomous to first or second order only; thecae simple, rarely with sigmoidal curvature or elaborated apertural modifications. *L.Ord.-U.Ord.*

Section TETRAGRAPTI

Rhabdosome pendent to scandent, composed of four stipes of second order, rarely two stipes of second order and one of first order; theca simple, denticulate. *L.Ord.*

Tetragraptus SALTER, 1863, p. 140 [**Fucoides serra* BRONGNIART, 1828, p. 71 (=*Graptolithus bryonoides* HALL, 1858, p. 150); OD] [*nom. correct.* HALL, 1865 (*pro Tetragrapsus* SALTER, 1863), ICZN, Opin. 650] [=*Etagraptus* RUEDEMANN, 1904, p. 644 (type, *Tetragraptus (Etagraptus) lentus* RUEDEMANN, 1904, p. 666); *Eotetragraptus* BOUČEK & PŘIBYL, 1951, p. 7 (type, *Graptolithus quadribrachiatus* HALL, 1858, p. 125); *Pendeograptus* BOUČEK & PŘIBYL, 1951, p. 12 (type, *Tetragraptus pendens* ELLES, 1898, p. 491); *Paratetragraptus* OBUT, 1957, p. 33, 38 (type, *Tetragraptus approximatus* NICHOLSON, 1873, p. 136); *Ramulograptus* ROSS & BERRY, 1963, p. 84 (type, *R. surcularis*)]. Bilaterally symmetrical, pendent to reclined; central disc in some horizontal species; funicle usually short, commonly bearing one theca only; development dichograptid or isograptid. *L.Ord.(Arenig-Llanvirn),* worldwide. ——FIG. 82,*1a*. *T. fruticosus* (HALL), Levis Sh., Que.; ×1 (77).——FIG. 82,*1b*. *T. quadribrachiatus* (HALL), Levis Sh., Que.; ×1 (77).——FIG. 82,*1c*. *T. approximatus* NICHOLSON, *L.Didymograptus* Sh., S.Sweden; ×1 (241).——FIG. 82, *1d,e. T. bigsbyi* (Hall), *Orthoceras* Ls.(Ontikan), Öland, Sweden; *1d,e,* lat. and ventral views of specimens dissolved from limestone, ×4 (91).——Fig. 82,*1f,g. T. phyllograptoides* Linnarsson, L.*Didymograptus* Sh., S.Sweden; *1f,g,* ×2 (91).

Phyllograptus Hall, 1858, p. 137 [**P. typus;* OD]. Quadriserial, composed of 4 scandent 2nd-order stipes; nema unknown; thecae simple, slightly curved, with high inclination and large overlap; development where known isograptid. *L.Ord. (Arenig-Llanvirn),* worldwide.——Fig. 82,*2a.* **P. typus,* Levis Sh., Que.; ×1 (77).——Fig. 82,*2b,c. P. angustifolius* Hall, *Orthoceras* Ls.(Ontikan), Öland, Sweden; *2b,c,* lat. and ventral views of specimens dissolved from limestone, ×4 (91).

Tristichograptus Jackson & Bulman, 1970 [**Graptolithus ensiformis* Hall, 1859, p. 133; OD] [=*Trigonograpsus* Nicholson, 1869, p. 231 (type, *T. lanceolatus*); *Pseudotrigonograptus* Mu & Lee, 1958, p. 416 (type, *P. uniformis*)]. Rhabdosome scandent, triserial, without virgula, elongate fusiform in shape, triangular in cross section; thecae with slight ventral curvature; development elaborated on basis of dicalycal *th*1^2. In compressed examples, rhabdosome appears biserial and apertural margins produce an even line. *L.Ord.* (*up.Arenig,* almost worldwide; *Llanvirn,* Pacific province).——Fig. 98 (*see* p. *V*132). **T. ensiformis* (Hall), compressed specimen, Skiddaw Sl., N.Eng.; ×2 (59).

Section DIDYMOGRAPTI

Pendent to scandent, composed of not more than two stipes. *L.Ord.-U.Ord.*

Didymograptus M'Coy in Sedgwick & M'Coy, 1851, p. 9 [**Graptolithus murchisoni* Beck, in Murchison, 1839, p. 694; SD Miller, 1889] [*nom. correct.* Hall, 1865 (*pro Didymograpsus* M'Coy, 1851) ICZN Opin. 650] [=*Cladograpsus* Geinitz, 1852, p. 29 (type, *Graptolithus murchisoni* Beck, 1839, p. 694; SD Bulman, 1929, p. 169); *Expansograptus* Bouček & Přibyl, 1951, p. 13 (type, *Graptolithus extensus* Hall, 1858, p. 132); *Corymbograptus* Obut & Sobolevskaya, 1964, p. 27 (type, *Didymograpsus v-fractus* Salter, 1863, p. 137); *Cymatograptus* Jaanusson, 1965, p. 423 (type, *Didymograptus undulatus* Törnquist, 1901, p. 10)]. Pendent to reclined; development of dichograptid or isograptid type; thecae typically simple, straight or with slight ventral curvature. *L.Ord.-U.Ord.(Nemagraptus gracilis Zone),* worldwide.——Fig. 83,*1a. D. extensus* (Hall), L.Ord. (Levis Sh.), Que.; ×1 (77).——Fig. 83,*1b.* **D. murchisoni* (Beck), L.Ord.(Llanvirn), S.Wales; ×1 (59).——Fig. 83,*1c. D. nicholsoni* Lapworth, L.Ord.(Skiddaw Sl.), N.Eng.; ×1 (59).

Atopograptus Harris, 1926, p. 59 [**A. woodwardi;* OD]. Horizontal didymograptid with everted, reflexed thecal apertures; sicula unknown. *L.Ord. (Darriwil.),* Australia (Victoria)-China.——Fig. 83,*2.* **A. woodwardi;* ×5 (81).

Aulograptus Skevington, 1965, p. 25 [**Didymograptus cucullus* Bulman, 1932, p. 15; OD]. Pendent didymograptid with climacograptid thecae, with distally directed or slightly everted apertures; development isograptid. *L.Ord.(up. Arenig or low.Llanvirn),* NW.Eu.-S.Am.(Arg.-Peru)-?China.——Fig. 83,*3.* **A. cucullus* (Bulman), *Orthoceras* Ls. (Ontikan), Sweden(Öland); *3a,* proximal end; *3b,* diagram. long. sec. through thecae; ×10 (19).

Azygograptus Nicholson (*ex* Lapworth MS), 1875, p. 269 [**A. lapworthi;* OD] [=*Pseudazygograptus* Mu, Lee, & Geh, 1960, p. 37 (type, *Azygograptus incurvus* Ekström, 1937, p. 33)]. Asymmetrical, unilateral, composed of a single stipe which may be pendent to reclined. *L.Ord.-U.Ord.(Glenogle Sh.),* Eu.-China-N.Am.-S.Am.——Fig. 83,*4. A. suecicus* Moberg, L.Ord. (L. *Didymograptus* Sh.), S. Sweden; ×2 (144).

Cardiograptus Harris & Keble, 1916, p. 66 [**C. morsus;* M] [=*Paracardiograptus* Mu & Lee, 1958, p. 419 (type, *P. hsüi*)]. Biserial, elongate-ovate, emarginate distally, resembling an *Oncograptus* in which distal uniserial stipes have failed to develop. *L.Ord.(up.Yapeen.-Darriwil),* Australia-China-N.Am.——Fig. 83,*10.* **C. morsus,* Australia(Victoria); ×1 (234).

Isograptus Moberg, 1892, p. 345 [**Didymograptus gibberulus* Nicholson, 1875, p. 271 (?=*D. caduceus* Salter, 1853, p. 87); M]. Reclined; thecae elongate with high inclination and large overlap, especially proximally; development isograptid, 1st few thecae growing entirely downward. *L. Ord.(Arenig-L.Llandeilo),* NW.Eu.-N.Am.-S.Am.-Australia-Asia.——Fig. 83,*7.* **I. gibberulus* (Nicholson), L.*Didymograptus* Sh., S.Sweden; *7a,* rhabdosome, ×1 (144); *7b,* proximal end, ×5 (19).

Janograptus Tullberg, 1880, p. 314 [**J. laxatus;* M]. Resembling an extensiform *Didymograptus* but without apparent sicula, possibly representing pro- and pseudocladia. *L.Ord.(U.Didymograptus Sh.-L.Dicellograptus Sh.),* Sweden-Norway-S.Am.-China.——Fig. 83,*6.* **J. laxatus,* S.Sweden; ×2 (242).

Kinnegraptus Skoglund, 1961, p. 391 [**K. kinnekullensis;* OD]. Declined to horizontal didymograptids with 2 or more long, exceedingly slender stipes, thecae and sicula with prominent apertural processes; development dichograptid or isograptid. *L.Ord.(L. Didymograptus Sh.),* NW.Eu.——Fig. 83,*5.* **K. kinnekullensis,* Sweden; *5a,* immature rhabdosome, ×4; *5b,* proximal end with sicula, ×33; *5c,* apertural region of theca, ×33 (216).

Maeandrograptus Moberg, 1892, p. 344 [**M. schmalenseei;* M]. Reclined stipes of almost uniform width, composed of somewhat undulating elongate thecae with low inclination and large overlap; development of isograptid type, 1st theca of each stipe distally reclined. _L.Ord.(L.Didymograptus Sh.),_ S.Sweden.——Fig. 83,_8_. *_M. schmalenseei,_ S.Sweden; _8a,_ rhabdosome, ×2 (144); _8b,_ proximal end, ×5 (19).

Oncograptus T. S. Hall, 1914, p. 109 [*_O. upsilon;_ OD]. Initially scandent biserial, later diverging; thecae long, slender, with high inclination and considerable overlap; development dichograptid, $th1^1$ dicalycal, first thecae short, downwardly directed, increasing in length and changing direction distally. _L.Ord.(Yapeen.),_ Australia-N.Am.-S.Am.-W.Ire.-China-USSR(Taimyr). ——Fig. 83,_11_. *_O. upsilon,_ Australia; ×1 (234).

Parazygograptus Kozłowski, 1954, p. 129 [*_P. erraticus;_ OD]. Like _Azygograptus,_ but with single stipe based on $th1^2$ produced from initial bud, $th1^1$ without metathecal portion. _L.Ord._ (glacial boulders), Eu.(Pol.).——Fig. 50,_4_. *_P. erraticus;_ illustrating development of proximal end; ×35 (116). [Also p. 439 (Polish text).]

Skiagraptus Harris, 1933, p. 108 [*_Diplograptus gnomonicus_ Harris & Keble, 1916, pl. 1, fig. 5,6; OD]. Rhabdosome biserial; thecae short, proximal thecae growing entirely downward, later thecae horizontal and then distally directed; development pericalycal. _L.Ord.(Yapeen.),_ Australia-N.Am.——Fig. 83,_9_. *_S. gnomonicus_ (Harris & Keble), Australia; schematic, ×2 (after Harris, 1933).

Family SINOGRAPTIDAE Mu, 1957

[Sinograptidae Mu, 1957, p. 423]

Thecae with initial prothecal folds and typically with introverted apertural modi-

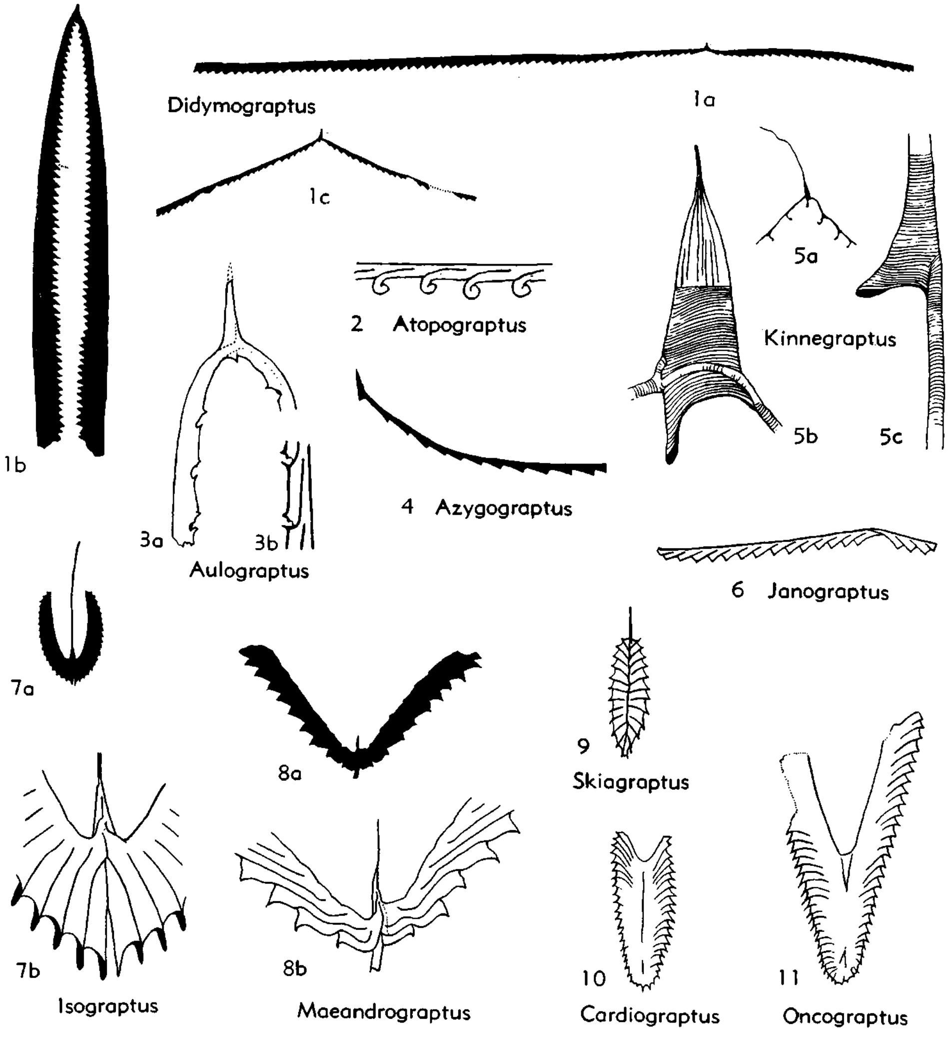

Fig. 83. Dichograptidae (Didymograpti) (p. *V*116-*V*117).

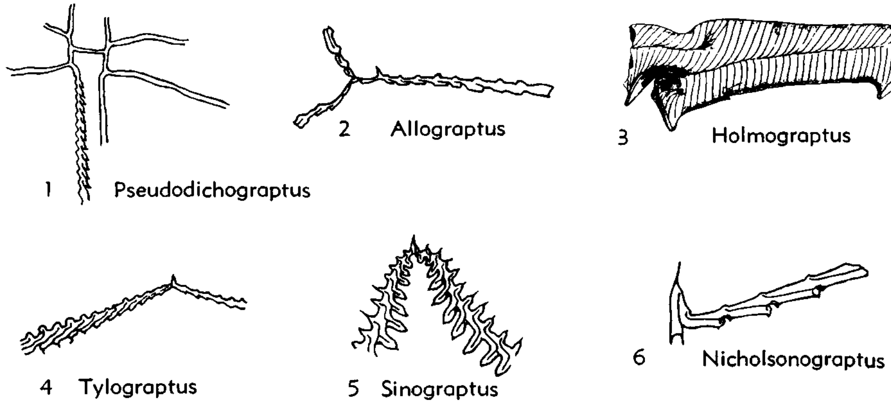

FIG. 84. Sinograptidae (p. *V*118).

fications; prothecal and metathecal nodes may bear spines; stipes typically showing pronounced increase in thecal overlap distally; development dichograptid. *L.Ord.(up.Arenig-low.Llanvirn).*

Sinograptus Mu, 1957, p. 434 [**S. typicalis;* OD]. Rhabdosome of 2 declined stipes; thecae with exaggerated prothecal and metathecal folds. *L. Ord.(low.Llanvirn),* China *(Ningkuo Sh.)*-Yukon *(Road River F.).*——FIG. 84,*5*. **S. typicalis, Amplexograptus confertus* Z., Changshan; ×3 (149).

Allograptus Mu, 1957, p. 423 [**A. mirus;* OD]. Rhabdosome of 4 or 3 horizontal stipes; thecae with prothecal folds and relatively unmodified apertures. *L.Ord.(up.Arenig),* China *(Ningkuo Sh.)*-Quebec *(Levis Sh.).*——FIG. 84,*2*. **A. mirus, Didymograptus hirundo* Z., Changshan; ×3 (149).

Holmograptus Kozłowski, 1954, p. 126 [**Didymograptus callotheca* Bulman, 1932, p. 16 (=?*D. lentus* Törnquist, 1911, p. 430); OD]. Rhabdosome of 2 declined stipes; thecae with prothecal folds accentuated by dorsal "notches" and introverted apertures with mesial spine and lateral lappets; an "apertural plate" on the succeeding metatheca further constricts the aperture. *L.Ord.(up.Arenig or low.Llanvirn),* NW.Eu.——FIG. 84,*3*. **H. callotheca* (Bulman), L. Ord. (glacial boulder), Pol.; ×35 (116). [Also p. 432 (Polish text).]

Nicholsonograptus Bouček & Přibyl, 1951, p. 14 [**Didymograpsus fasciculatus* Nicholson, 1869, p. 241; OD]. Rhabdosome of 1 reflexed stipe; thecae as in *Holmograptus*. *L.Ord.(low.Llanvirn),* NW.Eu.-China-S.Am.(Peru).——FIG. 84,*6*. **N. fasciculatus* (Nicholson), L.Ord. (*Didymograptus bifidus* Z.), N.Eng.; ×7.5 (Skevington, 1966).

Pseudodichograptus Chu, 1965, p. 102 [**P. confertus;* OD]. Rhabdosome dichotomously dividing to 3rd order; thecae with prothecal folds and incipient apertural modifications. *L.Ord.(up. Arenig),* China.——FIG. 84,*1*. **P. confertus, D. hirundo* Z., Chekiang; ×1.5 (45).

Tylograptus Mu, 1957, p. 428 [**T. regularis;* OD] [=*Pardidymograptus* Mu, Geh, & Yin, 1962, p. 73 (type, *P. acanthonotus*)]. Rhabdosome of 2 declined stipes, thecae with pronounced prothecal folding and weak to a strong apertural introversion; greatly increased thecal overlap distally. *L.Ord.(up.Arenig-low.Llanvirn),* China-Australia. ——FIG. 84,*4*. **T. regularis, Amplexograptus confertus* Z., Changshan; ×2.25 (149).

Family ABROGRAPTIDAE MU, 1958

[Abrograptidae Mu, 1958, p. 264)

Rhabdosome comprising two reclined stipes; sicula completely sclerotized, but stipe periderm reduced to one or two dorsal threads with complete or partial rings representing apertures; development dichograptid, with single crossing canal. *Ord. (?up.Arenig-Nemagraptus gracilis Z.)*

Abrograptus Mu, 1958, p. 264 [**A. formosus;* OD] [=*Parabrograptus* Mu & Qiao, 1962]. Stipes consisting of 2 dorsal threads united at intervals by apertural rings or half-rings. *Ord.,* China*(Glyptograptus teretiusculus* and *Nemagraptus gracilis Z.);* N.Am.(B.C.) *(Glenogle F.),* ——FIG. 85,*1*. **A. formosus;* diagram., ×5 (150).

Dinemagraptus Kozłowski, 1952, p. 87 [**D. warkae;* OD]. Stipes consisting of a single dorsal thread with complete apertural rings. *Ord.(?up. Arenig* to *Nemagraptus gracilis Z.),* NW.Eu.-China.——FIG. 85,*2*. **D. warkae,* diagram.; ×4 (115). [Also p. 292 (Polish text).]

?Jiangshanites Mu & Qiao, 1962, p. 7 [**J. ramo-*

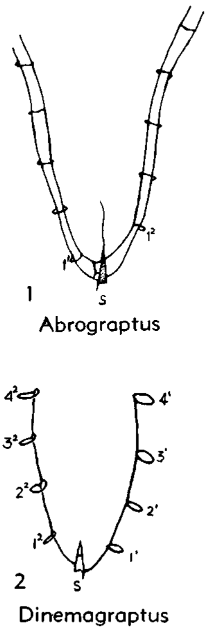

FIG. 85. Abrograptidae [*s*, sicula] (p. *V*118).

sus; OD]. A doubtful graptolite possibly representing a branched rhabdosome with comparable periderm reduction. *U.Ord.(Nemagraptus gracilis Z.),* China-N.Am.(B.C.) (156).

Family CORYNOIDIDAE Bulman, 1944

[Corynoididae BULMAN, 1944, p. 22] [*pro* Corynograptidae HOPKINSON & LAPWORTH, 1875, p. 633; Corynoideae RUEDEMANN, 1908, p. 233]

Rhabdosome consisting of a very long sicula, one or two pendent adnate thecae each bearing a broad, lamelliform apertural process, and one minute isolate theca; initial bud arises apically on prosicula; thecae alternating in origin. *U.Ord.*

Corynoides NICHOLSON, 1867, p. 108 [**C. calicularis;* M] [=*Corynograptus* HOPKINSON & LAPWORTH, 1875, p. 633]. Rhabdosome consisting of sicula with broad lamelliform virgella and 2 adnate thecae bearing broad apertural processes; where a 3rd theca occurs, it is small and isolate. *U.Ord.(Glenkiln* and *Hartfell Sh.),* NW.Eu.-N. Am.-Australia.——FIG. 86,*1*. **C. calicularis,* Ardwell Ser., S.Scot.; ×13 (23).

Corynites KOZŁOWSKI, 1956, p. 260 [**C. wyszogradensis;* OD]. Similiar to *Corynoides* but with only one adnate theca, the 2nd theca minute, coiled and distally directed; sicula curved and provided with elaborate apertural flanges. *U.Ord.* (glacial boulders), Eu.(Pol.).——FIG. 86,*2*. *C. divnoviensis* KOZŁOWSKI, Pol.; ×13 (117).——FIG. 39,*5*. **C. wyszogradensis;* illustrating apertural modifications of sicula, ×35 (117).

Family NEMAGRAPTIDAE Lapworth (ex Hopkinson MS), 1873

[Nemagraptidae LAPWORTH (*ex* HOPKINSON MS, 1873, p. 556)] [=Leptograptidae LAPWORTH, 1879, p. 27]

Uniserial, bilaterally symmetrical, with two slender flexuous stipes having a primary angle of divergence of about 180 degrees; branches (if present) lateral, rarely paired, simple or compound; thecae elongate, typically inclined at low angles and with well marked sigmoid curvature (leptograptid type); development of leptograptid type. *L.Ord.(Glyptograptus teretiusculus Z.), U.Ord.*

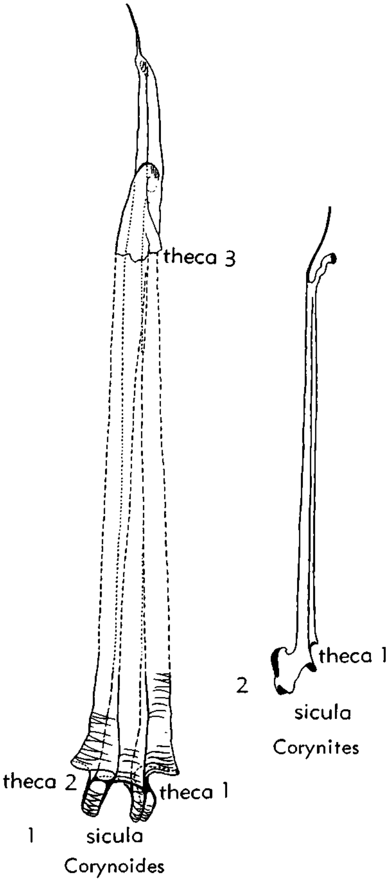

FIG. 86. Corynoididae (p. *V*119).

Nemagraptus EMMONS, 1855, p. 109 [*nom. correct.* HALL, 1859 (*pro Nemagrapsus* EMMONS, 1855), ICZN, Opin. 650] [**Graptolithus gracilis* HALL, 1848, p. 274 (=*Nemagrapsus elegans* EMMONS, 1855, p. 109; SD HALL, 1868, p. 211)] [=*Stephanograptus* GEINITZ, 1866, p. 124 (type, *G. gracilis* HALL, 1848); *Helicograpsus* NICHOLSON, 1868, p. 23 (type, *G. gracilis* HALL, 1848); *Geitonograptus* OBUT & ZUBTZOV, 1964, p. 320 (type, *G. suni*)]. Main stipes slender reclined or more usually curved to form letter S, with regularly produced lateral branches from convex side of each. *L.Ord.*

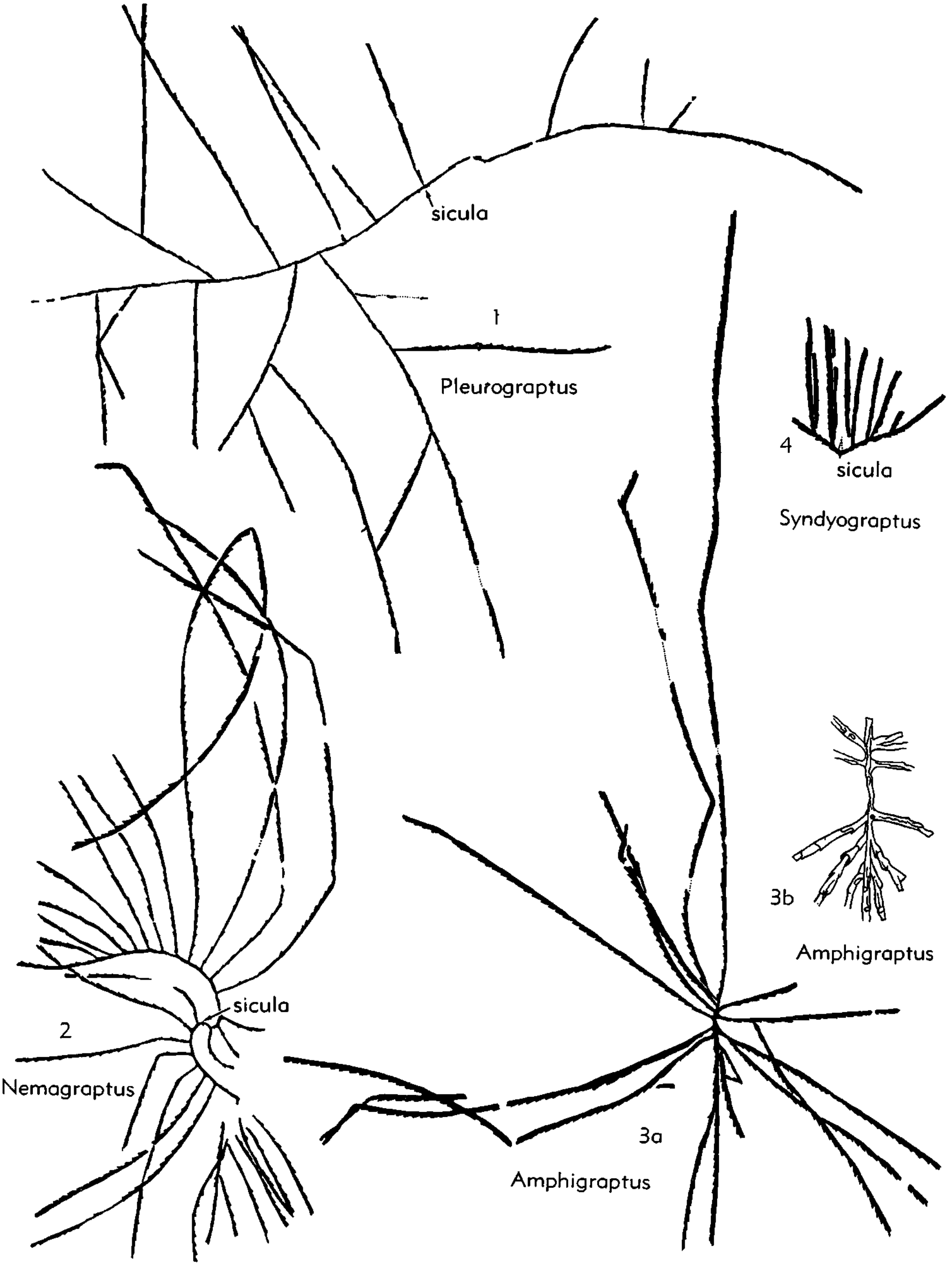

FIG. 87. Nemagraptidae (p. V120-V121).

(Glyptograptus teretiusculus Z.)-U.Ord.(Glenkiln-Normanskill), Eu.-N.Am.-S.Am.-Australia-Asia.——Fig. 87,*2*. **N. gracilis* (Hall), Glenkiln Sh., S.Scot.; ×1 (59).

Amphigraptus Lapworth, 1873, p. 559 [**Graptolithus divergens* Hall, 1859, p. 509; M] [=*Coenograptus* Hall, 1868, p. 179 (type, *Graptolithus divergens* Hall, 1859, p. 509; SD Miller, 1889, p. 668); *Clematograptus* Hopkinson, in Hopkinson & Lapworth, 1875, p. 652 (type, *Graptolithus multifasciatus* Hall, 1859, p. 508; SD Gurley, 1896, p. 93)]. Rhabdosome horizontal, composed of 2 straight main stipes with simple or compound, rigid lateral branches, typically produced in pairs. *U.Ord.(Normanskill-Hartfell),* Eu.-N.Am.-China.——Fig. 87,*3*. **A. divergens* (Hall), *3a,* rhabdosome from Hartfell Sh., S.Scot., ×1 (59); *3b,* proximal end of specimen from Normanskill, N.Y., ×3 (201).

Leptograptus Lapworth, 1873, p. 558 [**Graptolithus flaccidus* Hall, 1865, p. 143; M]. Biramous, stipes slender, flexuous, slightly reclined, without secondary branches except in centribrachiate mutations. *?L.Ord.(Glyptograptus teretiusculus Z.)-U. Ord.(Bala-Normanskill-Utica-M. Dicellograptus Sh.),* Eu.-N.Am.-Australia.——Fig. 88,*1b,d*. **L. flaccidus flaccidus* (Hall), Ord.(Hartfell Sh.), S.Scot.; *1b,* centribrachiate form, ×1 (59); *1d,* proximal end, ×8 (21).——Fig. 88,*1a*. *L. flaccidus macilentus* Elles & Wood, Ord.(Hartfell Sh.), S.Scot.; ×1 (59).——Fig. 88,*1c*. *L. flaccidus trentonensis* Ruedemann, Ord.(Utica), N.Y.; ×3 (201).

Pleurograptus Nicholson, 1867, p. 257 [*nom. correct.* Lapworth, 1873 (*pro Pleurograpsus* Nicholson, 1867), ICZN Opin. 650] [**Cladograpsus linearis* Carruthers, 1858, p. 467; OD] [=*Cladograpsus* Carruthers, 1858, p. 467, *non* Geinitz, 1852; *non* Emmons, 1855) (type, *C. linearis*)]. Main stipes somewhat flexuous, from one or both sides of which simple or compound branches are given off rather irregularly. *U.Ord. (Hartfell-Utica),* NW.Eu.-N.Am.-Australia-?China.——Fig. 87,*1*. **P. linearis* (Carruthers), Hartfell Sh., S.Scot.; ×1 (59).

Syndyograptus Ruedemann, 1908, p. 266 [**S. pecten;* OD] [=*Tangyagraptus* Mu, 1963, p. 377 (type, *T. typicus*)]. Like *Amphigraptus* but with reclined main stipes and paired erect branches. *U.Ord.,* N.Am.-China.——Fig. 87,*4*. **S. pecten,* Normanskill Sh., N.Y.; ×1 (201).

Family DICRANOGRAPTIDAE Lapworth, 1873

[Dicranograptidae Lapworth, 1873, table 1 facing p. 555]

Uniserial or uni-biserial, reclined or initially scandent, without branches; thecae with conspicuous sigmoid curvature, some species elaborated; development of diplograptid type. *L.Ord.(Glyptograptus teretiusculus Z.)-U.Ord.*

Dicranograptus Hall, 1865, p. 112 [**Graptolithus ramosus* Hall, 1848, p. 270; OD] [=*Cladograpsus* Emmons, 1855, p. 107 (type, *C. dissimilis;* SD Bulman, 1929, p. 173); *Diceratograptus* Mu, 1963, p. 377 (type, *D. mirus*)]. Proximally biserial, dividing distally to 2 uniserial reclined stipes. *L.Ord.-U.Ord.(Hartfell-Utica),* Eu.-N.Am.-S.Am.-Australia-Asia.——Fig. 89,*2a*. *D. ramosus longicaulis* Elles & Wood, Hartfell Sh., S.Scot.; ×1 (59).——Fig. 89,*2b*. *D. nicholsoni* Hopkinson, Balclatchie, S.Scot.; ×4 (23).

Dicellograptus Hopkinson, 1871, p. 20 [*nom. correct.* Lapworth, 1873 (*pro Dicellograpsus* Hopkinson), ICZN Opin. 650] [**Didymograpsus elegans* Carruthers, 1868, p. 129; SD Gurley, 1896, p. 70]. Rhabdosome of 2 reclined uniserial stipes, straight or curved. *L.Ord.-U.Ord.-(Glenkiln-Hartfell-Dicellograptus Sh.),* Eu.-N.Am.-S. Am.(Arg.)-Australia-Asia.——Fig. 89,*1a*. **D. elegans* (Carruthers), M.Ord.(Hartfell Sh.), S.

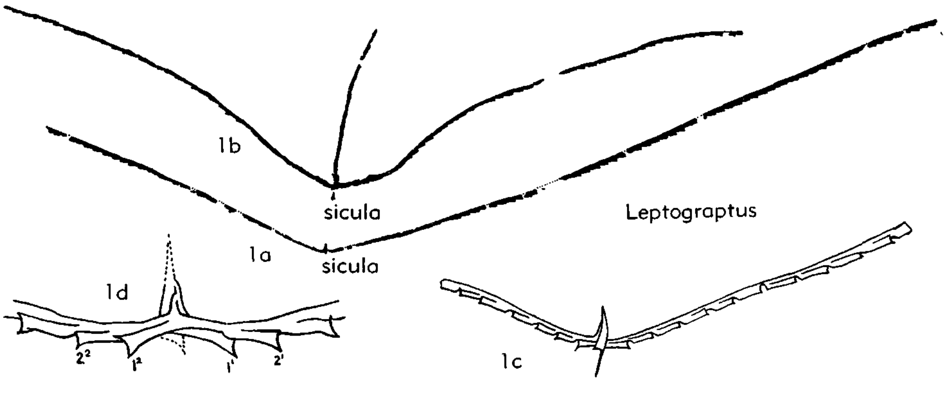

Fig. 88. Nemagraptidae (p. V121).

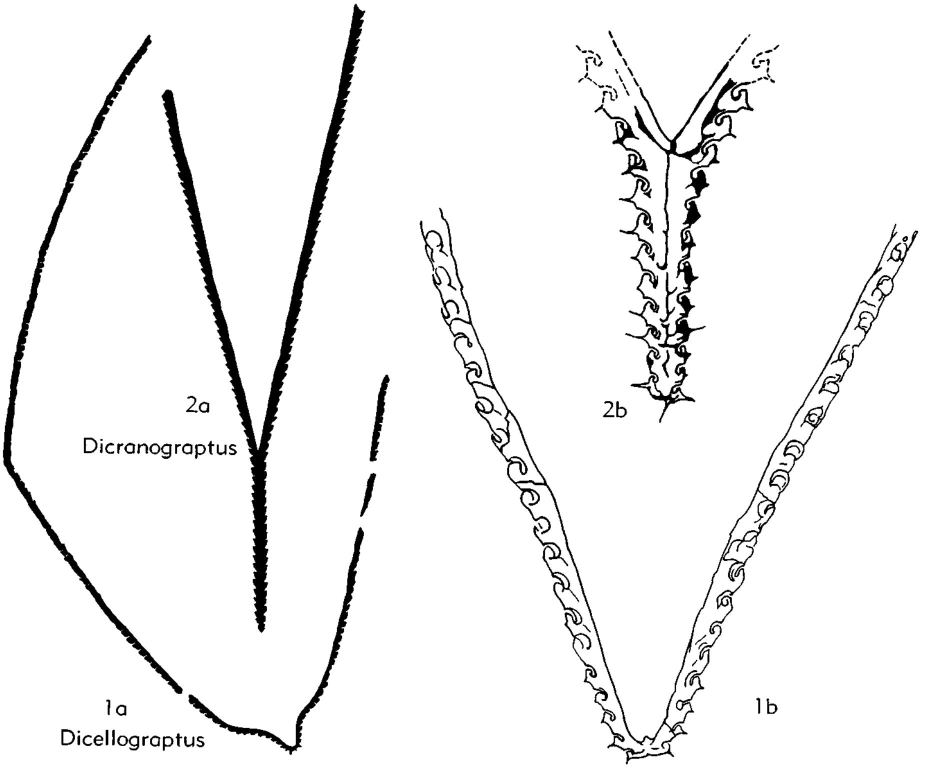

FIG. 89. Dicranograptidae (p. *V*121-*V*122).

Scot.; ×1 (59).——FIG. 89,*1b*. *D. morrisi*, M. Ord. (*Dicellograptus* Sh.), Sweden; ×4 (29).

Suborder GLOSSOGRAPTINA Jaanusson, 1960

[Glossograptina JAANUSSON, 1960, p. 319]

Biserial, monopleural, axonophorous graptoloids with pericalycal proximal end developed from dicalycal thl^1. *Ord.*

Family GLOSSOGRAPTIDAE Lapworth, 1873

[Glossograptidae LAPWORTH, 1873, table 1, facing p. 555]

Rhabdosome characteristically spined; thecae basically orthograptid but with apertural flanges in some species and commonly with secondary tissue at apertural margin. *Ord.*

Glossograptus EMMONS, 1855, p. 108 [*nom. correct.* HALL, 1865 (*pro Glossograpsus* EMMONS), ICZN Opin. 650] [**G. ciliatus;* SD LAPWORTH, 1873]. Rhabdosome with apertural, "dorsal" and lateral spines. *L.Ord.-U.Ord.*, almost worldwide.——FIG. 90,*1a,b*. *G. hinckṣi* (HOPKINSON); *1a,b*, biprofile and scalariform views; U.Ord.(Glenkiln Sh.), S. Scot., ×2 (59).——FIG. 90,*1c*. *G. holmi* BULMAN, Cow Head Gr., Newf., restor. of rhabdosome, ×4 (261). [*a.fl*, apertural flange; *as*, apertural spine; *ds*, "dorsal" spine; *il*, initial lacinia; *ls*, lateral spine; *s*, sicula; *v*, virgella.]

Lonchograptus TULLBERG, 1880, p. 313 [**L. ovatus;* M]. Like *Glossograptus* but with "dorsal" spines represented by a single pair of long, stout spines. *L.Ord.*, NW.Eu.——FIG. 90,*3*. **L. ovatus*, U. *Didymograptus* Sh., S.Sweden; *3a*, specimen showing thecal apertures; *3b*, outline of rhabdosome showing spines, ×2 (242).

Nanograptus HADDING, 1915, p. 328 [**N. lapworthi;* SD BULMAN, 1929, p. 179]. Rhabdosome minute; thecae denticulate or with very slender apertural spines; thl^1 and thl^2 opening downwards. *U.Ord.(Nemagraptus gracilis Z.)*, Eu.(S.Sweden-Scot.).——FIG. 90,*4*. **N. lapworthi*, L. *Dicellograptus* Sh., S.Sweden; *4a, rhabdosome*, ×5; *4b*, early growth stage, ×5 (71).

Paraglossograptus HSÜ (*ex* MU MS), 1959, p. 187 [**P. latus;* SD BERRY, 1966, p. 431]. Like *Glos-*

sograptus but with well-developed lacinia; *th*1^1 and *th*1^2 with outwardly directed apertural region. *L.Ord.(up.Arenig-low.Llanvirn),* China-?Australia-N.Am.——FIG. 90,*2*. *P. typicalis* MU, Shihuigon Sh., China; ×1.5 (151).

Family CRYPTOGRAPTIDAE Hadding, 1915, emend. Bulman, herein

[Cryptograptidae HADDING, 1915, p. 332]

Characters of genus. *L.Ord.-U.Ord.*

Cryptograptus LAPWORTH, 1880, p. 174 [**Diplograpsus tricornis* CARRUTHERS, 1859, p. 25; OD]. Rhabdosome parallel-sided, without spines other than basal spines (sicular, *th*1^1 and *th*^{2}); distal portions of *th*1^1 and *th*1^2 curved to open outwardly and distally; subsequent thecae inclined at a high angle, with geniculum distally and very short, vertical supragenicular wall, somewhat thickened ventrally; ringlike apertural lists. *L. Ord.-U.Ord.,* almost worldwide.——FIG. 90,*5*. **C. tricornis,* U.Ord.(Hartfell Sh.), S.Scot.; *5a,* complete rhabdosome, ×2 (59); *5b,* restoration of proximal part, ×10 (23).

Suborder DIPLOGRAPTINA Lapworth, 1880, emend. Bulman, herein

[=*nom. correct.* OBUT, 1957, p. 17 (*ex* Diplograpta LAPWORTH, 1880, p. 191)] [=Diplograptina JAANUSSON, 1960, p. 321, excl. Monograptidae]

Biserial, dipleural, axonophorous graptoloids with platycalycal proximal end developed from dicalycal *th*2^1 or later theca. *L. Ord.-U.Sil.*

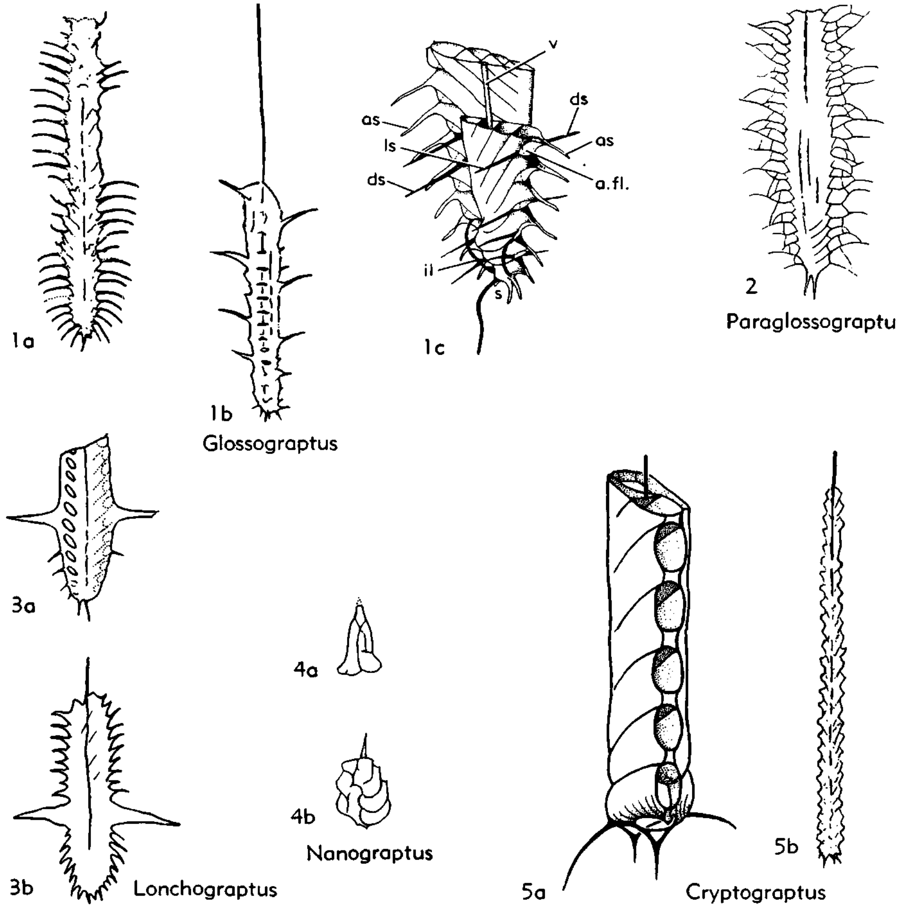

FIG. 90. Glossograptidae *(1-4);* Cryptograptidae *(5)* (p. V122-V123).

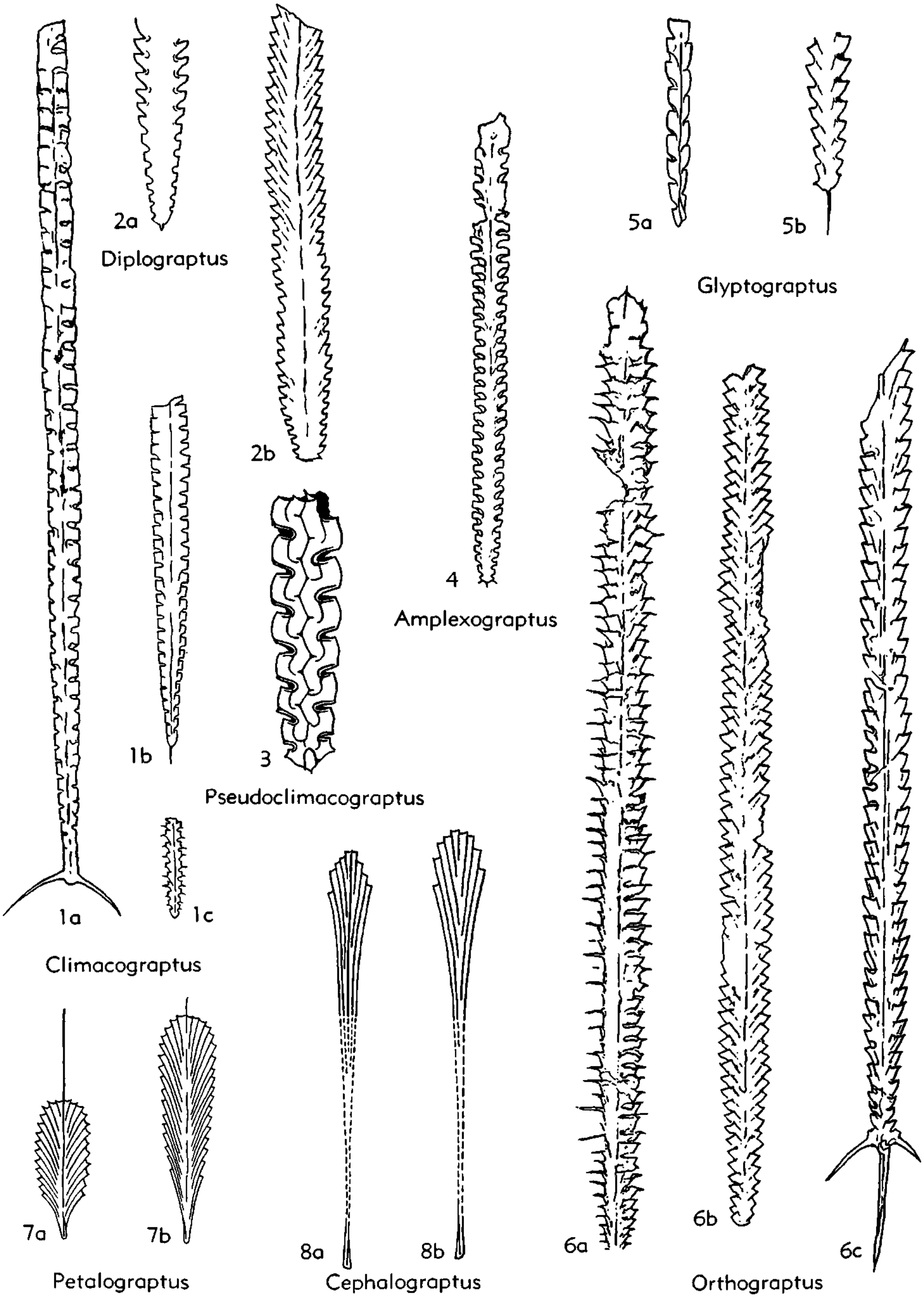

Fig. 91. Diplograptidae (p. *V*125-*V*126).

Family DIPLOGRAPTIDAE Lapworth, 1873

[Diplograptidae Lapworth, 1873, table 1 facing p. 555]

Rhabdosome biserial with or without median septum or with incomplete or partial septum; thecae straight (orthograptid) or with sigmoidal curvature (including glyptograptid) or with geniculum and variouslyinclined supragenicular wall; usually unspined or with apertural or mesial spines restricted to base of rhabdosome, which is oval, circular or tabular in cross section; periderm continuous, rarely attenuated or supported by lists; development streptoblastic or prosoblastic. *L.Ord.-L.Sil.*

Diplograptus M'Coy, 1850, p. 270 [*nom. correct.* Hall, 1865 (*pro Diplograpsis* M'Coy, 1850) ICZN, Opin. 650] [**Prionotus pristis* Hisinger, 1837, p. 114; SD Gurley, 1896, p. 78] [=*Mesograptus* Elles & Wood, 1907, p. 258 (type, *Graptolithus foliaceus* Murchison, 1839, p. 694)]. Basal thecae strongly sigmoidal with apertures in broad semicircular excavations (amplexograptid), becoming more gently sigmoid (glyptograptid) and almost straight (orthograptid) distally; periderm somewhat attenuated and with apertural lists proximally; cross section ovoid or nearly rectangular. *L.Ord.(Llanvirn)-L.Sil.*, almost worldwide.——Fig. 91,*2a*. **D. pristis* (Hisinger), U.Ord.(*Trinucleus* Sh.), Sweden; ×2. ——Fig. 91,*2b*. *D. foliaceus* (Murchison), L. Ord.(Meadowtown Ls.), Eng.; ×2 (Bulman, n).

Amplexograptus Elles & Wood, 1907, p. 258 [**Diplograptus perexcavatus* Lapworth, 1876, pl. 2, fig. 38; OD] [=*?Hedrograptus* Obut, 1949, p. 13 (type, *H. janischewskyi*); *Comograptus* Obut & Sobolevskaya in Obut, Sobolevskaya, & Merkureva, 1968, p. 60 (type, *C. comatus*)]. Rhabdosome ovoid or subrectangular in cross section, with a tendency to reduction in thickness of periderm; thecae strongly geniculate, apertural excavations deep and long, generally with selvage round infragenicular wall, sometimes developed into genicular flange and sometimes confluent with apertural selvage; supragenicular wall typically slightly inclined outwards, rarely parallel to axis of rhabdosome. *L.Ord.(Llanvirn)-U.Ord.*, almost worldwide; *L.Sil.*(USSR).——Fig. 91,*4*. **A. perexcavatus* (Lapworth), U.Ord.(Glenkiln Sh.), S. Scot.; ×2 (59).

Cephalograptus Hopkinson, 1869, p. 159 [*nom. correct.* Lapworth, 1873 (*pro Cephalograpsus* Hopkinson, 1869), ICZN, Opin. 650] [**Diplograpsus cometa* Geinitz, 1852, p. 26; OD]. An extreme development of *Petalograptus;* rhabdosome more or less triangular, with very elongate thecae and exposed sicula. *L.Sil.*, Eu.-Asia(China-Malaya)-USSR(Taimyr)-N.Am.(Arctic). ——Fig. 91,*8*. **C. cometa* (Geinitz), *Rastrites* Sh., Sweden; *8a*, obverse, *8b*, reverse; ×2 (239).

Climacograptus Hall, 1865, p. 111 [**Graptolithus bicornis* Hall, 1848, p. 268; OD] [=*Paraclimacograptus* Přibyl, 1947, p. 5 (type, *Climacograptus innotatus* Nicholson, 1869, p. 238)]. Rhabdosome nearly circular in cross section, scalariform views consequently common; thecae strongly geniculate, with deep apertural excavations, supragenicular wall straight, parallel to axis of rhabdosome. *L.Ord.-L.Sil.*, worldwide. ——Fig. 91,*1a*. **C. bicornis* (Hall), U.Ord. (Hartfell Sh.), S.Scot.; ×2 (59).——Fig. 91,*1b*. *C. rectangularis* (M'Coy), L.Sil.(Birkhill Sh.), S. Scot.; ×2 (59).——Fig. 91,*1c*. *C. innotatus* Nicholson, Birkhill Sh., S.Scot.; ×2 (59).

Cystograptus Hundt, 1942, p. 206, *emend.* Jones & Rickards, 1967, p. 181 [**Diplograpsus vesiculosus* Nicholson, 1869, p. 237 (=*Cystograptus speciosus* Hundt, 1942); SD Jones & Rickards, 1967, p. 181]. Rhabdosome rectangular in cross section, thecae with double sigmoid (ogee) curvature, apertures somewhat everted; point of origin of median septum variable; sicula typically elongate; vane structure commonly present distally on virgula. *L.Sil.*, Eu.(incl. USSR)-Asia(Malaya)-N. Am.(Arctic).——Fig. 92,*1*. *C. penna* (Hopkinson), *Monograptus acinaces* Z., central Wales; ×10 (110).

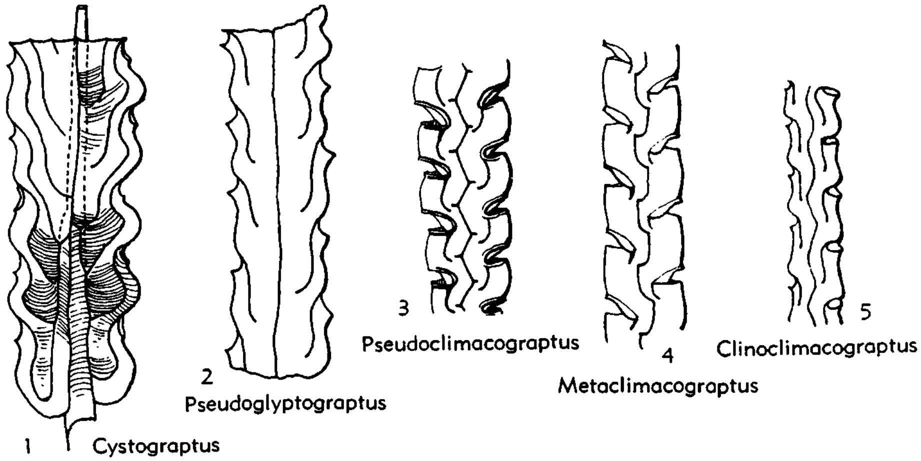

Fig. 92. Diplograptidae (p. *V*125-*V*126).

Glyptograptus Lapworth, 1873, table 1, facing p. 555 [**Diplograpsus tamariscus* Nicholson, 1868, p. 526; OD]. Thecae with gentle sigmoidal curvature (glyptograptid); supragenicular wall almost straight, sloping outwards, or rarely with gentle double curvature and everted apertures; apertural margin commonly undulate. *L.Ord.(up. Arenig)-L.Sil.*, worldwide.

G. (Glyptograptus). Thecae with gentle sigmoidal curvature, apertural margins commonly undulate. *L.Ord.-L.Sil.*, worldwide.——Fig. 91,*5a*. **G. (G.) tamariscus* (Nicholson), L.Sil.(Birkhill Sh.), S.Scot.; ×4 (59).——Fig. 91,*5b*. *G. (G.) dentatus* (Brongniart), L.Ord.(*Orthoceras* Ls.), Öland, Sweden; ×4 (19).

G. (Pseudoglyptograptus) Bulman & Rickards, 1968, p. 13 [**G. (P.) vas;* OD]. Supragenicular wall concavoconvex, with strongly everted aperture. *L.Sil.*, NW.Eu.——Fig. 92,*2*. **G. (P.) vas, Diplograptus magnus* Z., N.Eng.; ×10 (38).

Orthograptus Lapworth, 1873, table 1, facing p. 555 [**Graptolithus quadrimucronatus* Hall, 1865, p. 144; OD] [=*Glossograptus* Ruedemann, 1947, *partim* (*non* Emmons, 1855); *Rectograptus* Přibyl, 1949, p. 25 (type, *Diplograptus pristis* var. *truncatus* Lapworth, 1876, pl. 1, fig. 28); *Dittograptus* Obut & Sobolevskaya, in Obut, Sobolevskaya, & Merkureva, 1968, p. 69 (type, *D. fortuitus*)]. Thecae straight or with very slight sigmoidal curvature; paired apertural spines in one group, large basal spines not uncommon; rhabdosome rectangular or ovoid in cross section. *U.Sil.-L.Sil.*, worldwide.——Fig. 91,*6a*. **O. quadrimucronatus* (Hall), U.Ord. (Hartfell Sh.), S.Scot.; ×2 (59).——Fig. 91,*6b*. *O. truncatus* (Lapworth), U.Ord.(Hartfell Sh.), S.Scot.; ×2 (59).——Fig. 91,*6c*. *O. calcaratus* (Lapworth), U.Ord.(Hartfell Sh.), S.Scot.; ×2 (59).

Petalograptus Suess, 1851, p. 100 [*pro Diprion* Barrande, 1850, and *Petalolithus* Suess, 1851 (ICZN pend.)]. [**Prionotus folium* Hisinger, 1837, p. 114; SD Lapworth, 1873, table 1, facing p. 555]. Rhabdosome foliate, exaggeratedly rectangular in cross section; thecae long, straight or with gently ventral curvature, with large thecal overlap; thl^1 and thl^2 with pronounced upward direction of growth, leaving sicula largely exposed. *L.Sil.*, Eu.-Asia(USSR-China-Malaya)-Arctic Can.——Fig. 91,*7*. **P. folium* (Hisinger), *Rastrites* Sh., S.Sweden; *7a,b*, obverse and reverse views, ×2 (Tullberg, 1881).

Pseudoclimacograptus Přibyl, 1947, p. 5 [**Climacograptus scharenbergi* Lapworth, 1876, pl. 2, fig. 55; OD]. Like *Climacograptus* but with supragenicular walls convex, rarely nearly straight, or concavoconvex; median septum zigzag, angular and undulating in proximal region, sometimes becoming straighter distally; apertural excavations deep and short, often introverted. *L.Ord.(up.Arenig)-L.Sil.*, Eu.-Asia-N.Am.-?N.Afr.

P. (Pseudoclimacograptus). Supragenicular wall convex, apertural excavations short, deep and introverted; median septum mostly zigzag throughout. *L.Ord.* and basal *U.Ord.*, NW.Eu. (including USSR)-N.Am.-China.——Fig. 91,*3;* 92,*3*. **P. (P.) scharenbergi* (Lapworth), U.Ord. (Balclatchie beds), S. Scot.; 91,*3*, ×6 (23); 92,*3*, partly diagram.; ×10 (Bulman, n).

P. (Clinoclimacograptus) Bulman & Rickards, 1968, p. 8 [**P. (C.) retroversus;* OD]. Supragenicular wall convex proximally and concave distally; apertures strongly everted; median septum undulating proximally, straight distally. *L.Sil.*, NW.Eu.——Fig. 92,*5*. **P. (C.) retroversus*, Llandovery, Wales; partly diagram., ×10 (38).

P. (Metaclimacograptus) Bulman & Rickards, 1968, p. 3 [**Diplograpsus hughesi* Nicholson, 1869, p. 235; OD]. Supragenicular wall gently convex or almost straight; apertural excavations short, deep, introverted and partly covered by flanges from geniculum of succeeding theca; median septum angular to undulating. *L.Sil.*, NW.Eu., ?China-?Malaya-?N.Afr.——Fig. 92,*4*. *P. (M.) undulatus* (Törnquist), Llandovery, Wales; partly diagram., ×17 (38).

Family LASIOGRAPTIDAE Lapworth, 1879

[Lasiograptidae Lapworth, 1879, p. 188]

Rhabdosome usually somewhat flattened, cryptoseptate or with complete or incomplete median septum; thecae geniculate, with short inwardly-inclined supragenicular wall (lasiograptid or gymnograptid); periderm commonly attenuated; more or less well-developed clathria and conspicuous development of genicular (and ?thecal) spines sometimes associated with a lacinia; development streptoblastic or prosoblastic. *Ord.*

Lasiograptus Lapworth, 1873, p. 559 [**L. costatus;* OD] [=*Thysanograptus* Elles & Wood, 1908, p. 325 (type, *Diplograptus Harknessi* Nicholson, 1867, p. 262); *Prolasiograptus* Lee, 1963, p. 574 (type, *Lasiograptus retusus* Lapworth, 1880, p. 175)]. Thecae lasiograptid with somewhat inwardly-inclined supragenicular wall and inwardly-inclined (introverted) apertural margins, paired genicular spines associated with lacinia; clathria of apertural, pleural and weak parietal lists; development prosoblastic. *Ord.(up. Arenig-Caradoc)*, Eu.-N. Am.-S. Am.-Australia-China.——Fig. 93,*1a*. **L. costatus*, U.Ord. (*Climacograptus wilsoni* Z.), S.Scot.; ×2 (59).——Fig. 93,*1b*. *L. harknessi* (Nicholson), U.Ord. (Balclatchie beds), S.Scot.; somewhat schem.; ×15 (23).

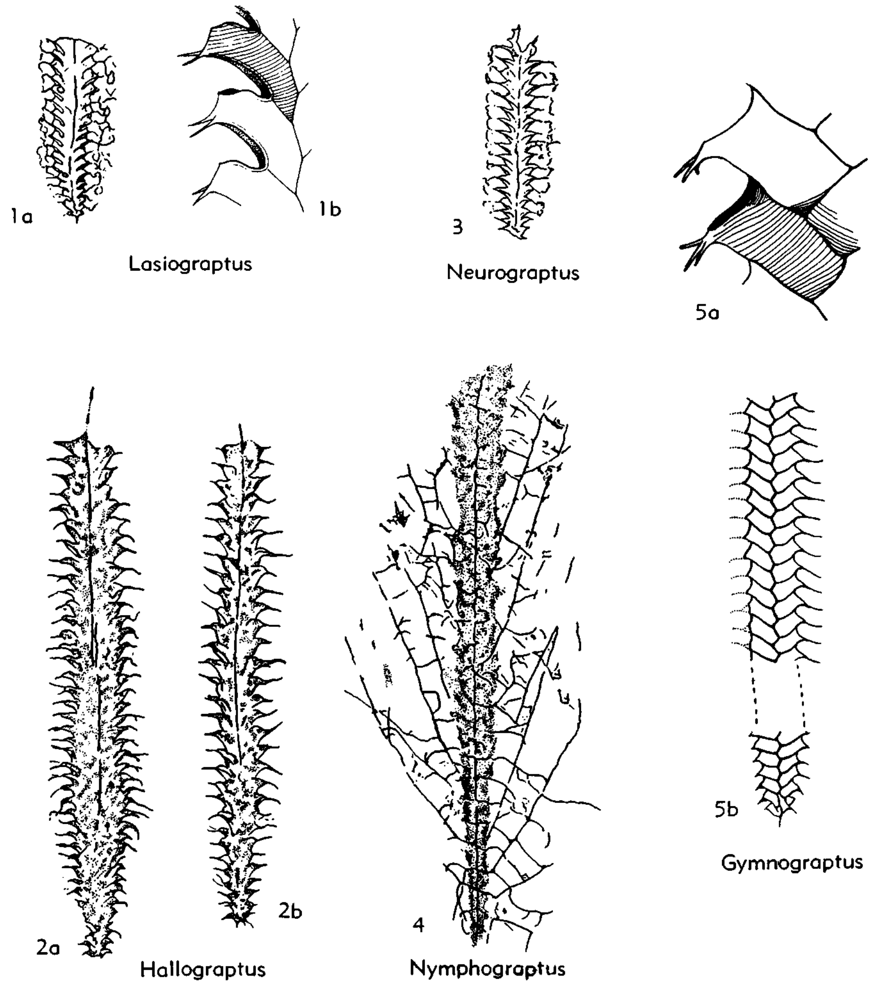

FIG. 93. Lasiograptidae (p. *V*126-*V*128).

Gymnograptus BULMAN (*ex* TULLBERG MS), 1953, p. 515 [**Diplograptus linnarssoni* MOBERG, 1896, p. 17; OD] [=?*Idiograptus* LAPWORTH, 1880, p. 169 (type, *I. aculeatus*)]. Rhabdosome somewhat flattened and more or less tabular in cross section; thecae gymnograptid, with very short supragenicular wall, everted (outwardly inclined) apertural margin accentuated by angular fuselli, and with paired genicular spines; median septum incomplete or cryptoseptate, with zigzag septal lists; development streptoblastic or prosoblastic. *L.Ord.-U.Ord.(Ogygiocaris Ser.* & *Ludibundus Ls.),* NW. Eu.-China.——FIG. 93,*5*. **G. linnarssoni* (MOBERG); *5a,* Pol.; enl. showing thecae with angular fuseli, glacial buolder, ×20; *5b, Ogygiocaris* Ser., Norway; ×3 (250).

Hallograptus LAPWORTH (*ex* CARRUTHERS MS), 1876, p. 7 [**Diplograpsus bimucronatus* NICHOLSON, 1869, p. 236; M]. Thecae lasiograptid, with extremely short supragenicular wall and single or paired genicular spines; clathria weakly developed, lacinia absent; septal processes (scopulae) visible in scalariform view. *Ord.(Arenig-low.Caradoc),* Eu.-N.Am.-Australia.——FIG. 93,*2a*. **H. bimucronatus* (NICHOLSON), U.Ord.(Glenkiln Sh.), S. Scot.; ×2 (59).——FIG. 93,*2b*. *H. mucronatus* (HALL), Glenkiln Sh., S.Scot.; ×2 (59).

Neurograptus ELLES & WOOD, 1908, p. 320 [=*Neurograptus* LAPWORTH, 1875, p. 641 *(nom. nud.)*] [**Lasiograptus margaritatus* LAPWORTH, 1876, pl. 2, fig. 60; SD BULMAN, 1929, p. 179]. Thecae as in *Hallograptus;* thecal spines breaking up distally into a highly developed lacinia; scopulate septal processes also well developed. *U.Ord.*, Eu.-N.Am.-Australia.——Fig. 93,*3*. **N. margaritatus* (Lapworth), Hartfell Sh., S.Scot.; ×2 (59).

Nymphograptus Elles & Wood (*ex* Lapworth MS), 1908, p. 320 [**N. velatus;* OD]. Thecae apparently as in *Hallograptus;* septal strands very strongly developed to form elaborate lacinia enveloping rhabdosome. *U.Ord.(Dicellograptus anceps Z.-Easton.),* Eu.-Australia.——Fig. 93,*4*. **N. velatus,* Hartfell Sh., S.Scot.; ×2 (59).

Family DICAULOGRAPTIDAE Bulman, n. fam.

Characters of genus. *L.Ord.*

Dicaulograptus Rickards & Bulman, 1965, p. 278 [**Lasiograptus hystrix* Bulman, 1932, p. 29; OD]. Rhabdosome minute; thecae 1^1 and 1^2 with isolate and introverted apertural region, mesial spine, and paired apertural spines; subsequent thecae almost dicranograptid, with angularly convex supragenicular wall bearing elongate mesial spine, apertures introverted, with flattened lateral processes fused with rhabdosome wall to leave rounded lateral foramina; long slender spines at the base of the pleural lists; development streptoblastic. *L.Ord.*, Eu.(Sweden).——Fig. 94,*1a-c*. **D. hystrix* (Bulman), Folkeslunda Ls. *(?Glyptograptus teretiusculus* Z.), Öland; *1a,* mature rhabdosome; ×6; *1b,* proximal end; ×14; *1c,* restoration showing thecal characters; ×14 (19).

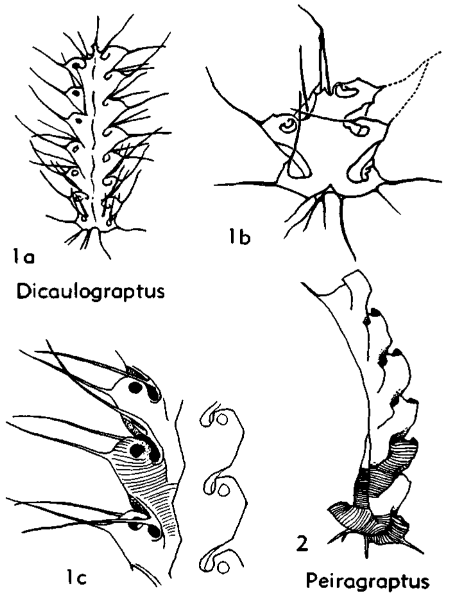

Fig. 94. Dicaulograptidae *(1);* Peiragraptidae *(2)* (p. *V*128).

Family PEIRAGRAPTIDAE Jaanusson, 1960

[*nom. transl.* Bulman, 1963, *ex* Peiragraptinae Jaanusson, 1960, p. 322]

Characters of genus. *U.Ord.*

Peiragraptus Strachan, 1954, p. 509 [**P. fallax;* OD]. Development of incomplete diplograptid type, with no dicalycal theca, $th2^1$ producing uniserial scandent stipe distal to $th1^1$, partially enclosing sicula; thecae geniculate, supragenicular wall almost parallel to axis, apertural margins with rounded lateral lappets. *U.Ord.*, N.Am. ——Fig. 94,*2*. **P. fallax,* U.Ord.(?Vaureal F.), Anticosti Is.; ×7.5 (226).

Family RETIOLITIDAE Lapworth, 1873

[Retiolitidae Lapworth, 1873, table 1 facing p. 555]

Rhabdosome scandent, biserial, dipleural; periderm reduced to meshwork composed of reticulum or clathria or both, lacinia present in some forms. Thecae markedly alternate. *U.Ord.-U.Sil.*

This undoubtedly is a polyphyletic assemblage which may for convenience be provisionally divided into the following groups.

Subfamily RETIOLITINAE Lapworth, 1873

[*nom. transl.* Bouček & Münch, 1952, p. 110 (*ex* Retiolitidae Lapworth, 1873)]

Well-developed reticulum supported on a distinct clathria, sicula unsclerotized or partially sclerotized (prosicula); development with partially developed ancora stage. *U. Ord.-M.Sil.*

Retiolites Barrande, 1850, p. 68 [*nom. conserv.* (ICZN Opin. 199)] [**Gladiolites geinitzianus* Barrande, 1850; M] [=*Gladiolites* Barrande, 1850, *nom. suppr.* ICZN Opin. 199; *Gladiograptus* Lapworth, 1875, p. 633 (type, *G. geinitzianus* Barrande, 1850); *Dimykterograptus* Haberfelner, 1936, p. 92 (type, *D. bončevi*); *Pseudoretiolites* Bouček & Münch, 1944, p. 22 (type, *Retiolites perlatus* Nicholson, 1868, p. 530)]. Reticulum on strongly developed clathria of parietal, pleural, apertural and aboral lists, with virgula rapidly incorporated on one side and dorsal list ("zigzag virgula") on other. *L.Sil.-M.Sil.*, almost worldwide.——Fig. 95,*5*. **R. geinitzianus* (Barrande), *5a,* rhabdosome from L.Sil., Boh., ×2 (13); *5b-d,* structural details of specimen from L.Sil., Dalarne, Sweden, ×12 (90).

Arachniograptus Ross & Berry, 1963, p. 159 [**A. laqueus;* M]. Like *Pseudoplegmatograptus,* but without lacinia. *U.Ord. (D. complanatus Z.),* N.Am.(Nev.).

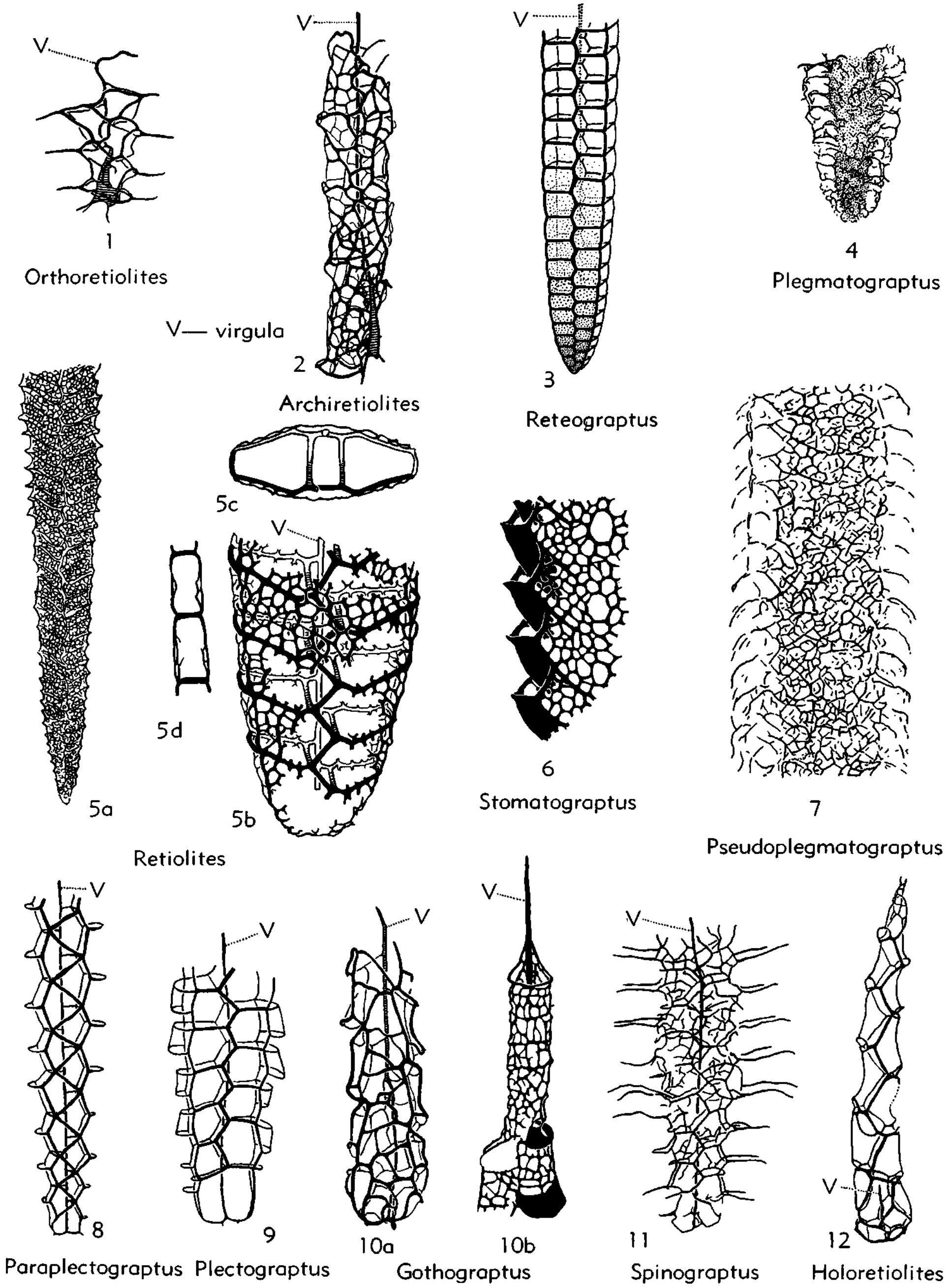

Fig. 95. Retiolitidae (Retiolitinae) *(5-7)*; (Archiretiolitinae) *(1-4)*; (Plectograptinae) *(8-12)* (p. V128-V131).

Pseudoplegmatograptus Přibyl, 1948, p. 22 [**Retiolites perlatus obesus* Lapworth, 1877, p. 137; OD]. Like *Retiolites* but with somewhat ill-defined clathria and well-developed lacinia. *L. Sil.*, Eu.-USSR(Kazakh.)-China.——Fig. 95,7. **P. obesus* (Lapworth), Gala, S.Scot.; ×4 (59).

Sinostomatograptus Huo Shih-Cheng, 1957, p. 521 [**S. mui;* OD]. Like *Stomatograptus,* but with lacinia. *L.Sil.-M.Sil.,* China.

Stomatograptus Tullberg, 1883, p. 42 [**S. törnquisti* (=*Retiolites grandis* Suess, 1851, p. 99); M]. Like *Retiolites* but with solid interthecal septa, less overlapping thecae, and median row of large pores in reticulum. *L.Sil.-M.Sil.,* Eu.(incl. USSR)-Australia-Canad. Arctic.——Fig. 95,*6*. **S. grandis* (Suess), L.Sil., Dalarne, Sweden, ×12 (26).

Subfamily ARCHIRETIOLITINAE Bulman, 1955

[Archiretiolitinae Bulman, 1955, p. 88]

Sicula and initial portions of one or more proximal thecae sclerotized; development basically diplograptid. *U.Ord.*

Archiretiolites Eisenack, 1935, p. 74 [**A. regimontanus;* M]. Sicula and initial bud sclerotized; reticulum well developed, with irregular ill-defined clathria; thecae with ventral margin approximately parallel to axis of rhabdosome; virgula internal, with sporadic rodlike attachments to reticulum. *U.Ord.,* NW.Eu.——Fig. 95,*2*. **A. regimontanus,* glacial boulder, NW. Ger.; ×48 (54).

Orthoretiolites Whittington, 1954, p. 614 [**O. hami;* OD]. Sicula, initial bud and proximal portion of $th1^2$ sclerotized; clathria with traces of attenuated periderm but without reticulum; thecae orthograptid; virgula incorporated in obverse wall, zigzag "virgula" in reverse wall. *U.Ord.,* N.Am.——Fig. 95,*1*. **O. hami,* Viola Ls. (*?Nemagraptus gracilis* Z.), Okla.; ×8 (259).

Phormograptus Whittington, 1955, p. 846 [**P. sooneri;* OD]. Similar to *Archiretiolites,* but with reticulum extending below sicular aperture, supported on virgella and apertural spines, and with more horizontal direction of growth of $th1^2$. *U.Ord.,* N.Am.——Fig. 96,*1*. **P. sooneri,* Viola Ls. (*?Nemagraptus gracilis* Z.), Okla.; ×30 (260).

Pipiograptus Whittington, 1955, p. 839 [**P. hesperus;* OD]. Sicula, much of $th1^1$ and $th1^2$ and the initial part of $th2^1$ sclerotized; later thecae coarsely reticulate, clathrium not clearly differentiated; thecal characters imperfectly known, but $th2^1$ with initial downward direction of growth. *U.Ord.,* N.Am.——Fig. 96,*2*. **P. hesperus,* Viola Ls. (*?Nemagraptus gracilis* Z.), Okla.; ×50 (260).

Plegmatograptus Elles & Wood, 1908, p. 340 [**P. nebula;* OD]. Reticulum with well-developed lacinia; ?membranous periderm and sclerotized sicula. Development unknown. *U.Ord.,* NW.Eu.-Australia-?N.Am.——Fig. 95,*4*. **P. nebula,* Hartfell Sh., S.Scot.; ×2 (59).

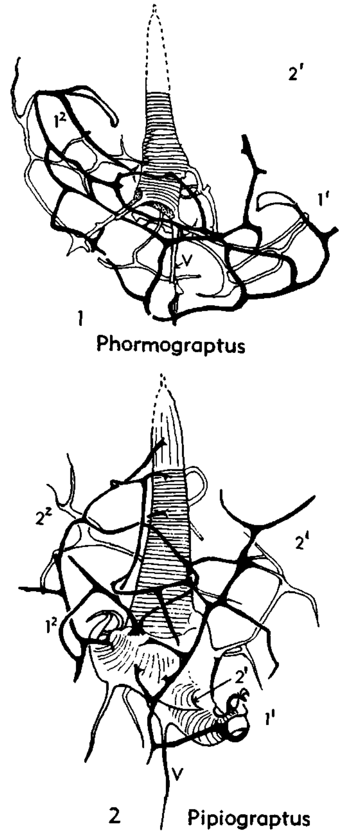

Fig. 96. Retiolitidae (Archiretiolitinae) [*V,* virgula] (p. *V*130).

Reteograptus Hall, 1859, p. 518 [**R. geinitzianus,* p. 518; OD] [=*Retiograptus* Hall, 1865, p. 115 (*nom. null.); Clathrograptus* Lapworth, 1873 (type, *C. cuneiformis)*]. Clathria only, supporting a membranous periderm at proximal end of rhabdosome; sicula ?sclerotized. *U.Ord.,* Eu.-N.Am.-China-?Australia. —— Fig. 95,*3*. **R. geinitzianus,* Normanskill, N.Y.; ×4 (201).

Subfamily PLECTOGRAPTINAE Bouček & Münch, 1952

[Plectograptinae Bouček & Münch, 1952, p. 110]

Clathria well developed, commonly without reticulum, lacinia absent; development with ancora stage; proximal end of rhabdosome usually somewhat inflated (corona), narrowing distally and in some genera terminating in a slender tubular "appendix." *?L.Sil., M.Sil.-U.Sil.*

Plectograptus Moberg & Törnquist, 1909, p. 18 [**Retiolites macilentus* Törnquist, 1887, p. 491; M]. Rhabdosome rectangular in cross section, composed of open, subhexagonal meshes (clathria) with subordinate reticulum, open distally, with central (free) virgula. *M.Sil.-U.Sil.*, Eu.——FIG. 95,*9*. **P. macilentus* (TÖRNQUIST), low.Ludlow, Boh.; proximal portion of rhabdosome, ×4 (13).

Gothograptus FRECH, 1897, p. 670 [**Retiolites nassa* HOLM, 1890, p. 25; OD]. More or less circular in cross section, thecal apertures connected by ventral instead of pleural lists, reticulum usually fairly well developed; rhabdosome tapering distally and terminating in tubular appendix; virgula central in the corona, later incorporated in lateral wall. *U.Sil.*, Eu.-USSR(Taimyr)-Arctic Can.——FIG. 95,*10b*. **G. nassa* (HOLM), Baltic; ×12 (264).——FIG. 95,*10a*. *G. intermedius* BOUČEK & MÜNCH, Baltic; ×12 (264).

Holoretiolites EISENACK, 1951, p. 153 [**Retiolites mancki* MÜNCH, 1931, p. 1; OD] [=*Balticograptus* BOUČEK & MÜNCH, 1952, p. 117 (type, *Holoretiolites erraticus* EISENACK, 1951, p. 136)]. Tapering rhabdosome with inflated corona, usually with distal appendix, composed of clathria only; thecae climacograptid, their apertures connected by ventral lists; virgula central, confined to proximal end (corona). *U.Sil.*, Eu.——FIG. 95,*12*. **H. mancki* (MÜNCH), Baltic; ×10 (Münch, 1929).

Paraplectograptus PŘIBYL (*ex* BOUČEK & MÜNCH MS), 1948, p. 21 [**Retiolites eiseli* MANCK, 1917, p. 338; OD]. More or less square in cross section, with virgula embedded in one wall and pleural lists arranged in zigzag line in other; reticulum subordinate or absent. *?L.Sil., M.Sil.*, Eu.-?Australia.——FIG. 95,*8*. **R. eiseli* (MANCK), M.Sil., Boh.; ×4 (13).

Spinograptus BOUČEK & MÜNCH, 1952, p. 130 [**Retiolites spinosus* WOOD, 1900, p. 485; OD]. Like *Plectograptus* but, with better-developed reticulum and paired apertural spines. *U.Sil.*, Eu.-Arctic Can.——FIG. 95,*11*. **S. spinosus* (WOOD), low.Ludlow, Boh.; ×4 (13).

Family DIMORPHOGRAPTIDAE Elles & Wood, 1908

[Dimorphograptidae ELLES & WOOD, 1908, p. 347]

Proximal portion of rhabdosome uniserial, with loss or re-orientation of *th*1^2 and generally lacking further thecae of the secondary series, becoming biserial distally; biserial portion usually with partial septum (or aseptate); development of modified diplograptid type, or with initially upward-growing *th*1^1 but apparently lacking monograptid sinus and lacuna stages. *L.Sil.*

Dimorphograptus LAPWORTH, 1876, p. 545 [**D. elongatus;* SD BASSLER, 1915, p. 441] [=*Bulmanograptus* PŘIBYL, 1948, p. 46 (type, *Dimorphograptus confertus* NICHOLSON, 1868, p. 526); *Agetograptus* OBUT & SOBOLEVSKAYA, in OBUT, SOBOLEVSKAYA, & MERKUREVA, 1968, p. 78 (type, *A. secundus*)]. Thecae orthograptid or glyptograptid, with a tendency in some species towards isolation of apertural region; uniserial portion of varying length; development with initial bud upwardly directed at origin. *L.Sil.*, Eu.-USSR-China-Malaya-Arctic Can.——FIG. 97,*2a*. *D. decussatus* ELLES & WOOD, Birkhill Sh., S.Scot.; ×2 (59).——FIG. 97,*2b*. **D. elongatus*, Birkhill Sh., S.Scot.; ×2 (59).

Akidograptus DAVIES, 1929, p. 9 [**A. ascensus;* OD]. Thecae climacograptid; proximal end obscure, without definite uniserial portion; initial bud downwardly directed at origin. *L.Sil.*, Eu.-China.——FIG. 97,*1*. **A. ascensus*, L.Birkhill Sh., S.Scot.; ×4.5 (47).

Rhaphidograptus BULMAN, 1936, p. 20 [**Climacograptus törnquisti* ELLES & WOOD, 1906, p. 190; OD] [=?*Metadimorphograptus* PŘIBYL, 1948, p. 46 (type, *Dimorphograptus extenuatus* ELLES & WOOD, 1908, p. 358)]. Thecae climacograptid; initial bud downwardly directed at origin. *L.Sil.*, Eu.-Malaya.——FIG. 97,*3a*. **R. toernquisti* (ELLES & WOOD), *Monograptus gregarius* Z.,

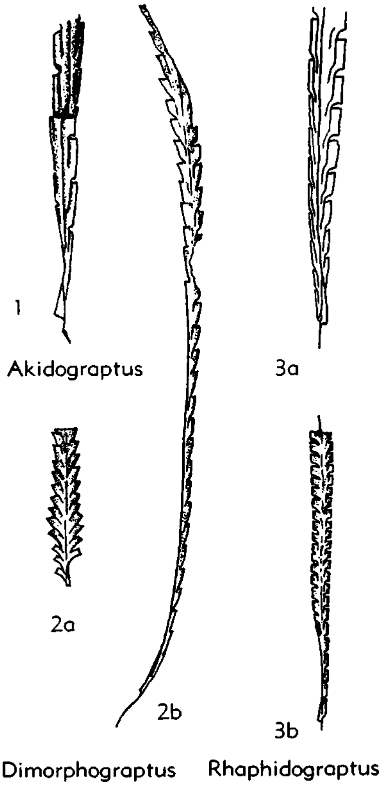

FIG. 97. Dimorphograptidae (p. *V*131-*V*132).

central Wales; ×3 (59).——Fig. 97,_3b_. _R. extenuatus_ (Elles & Wood), Birkhill Sh., S.Scot.; ×2 (59).

Fig. 98. Dichograptidae (Tetragrapti) (p. _V_116).

Suborder MONOGRAPTINA Lapworth, 1880

[_nom. correct._ Obut, 1957, p. 18 (_ex_ Monograpta Lapworth, 1880, p. 191)]

Scandent uniserial graptoloids; development monograptid, with sinus method of pore formation and initially upward direction of growth of _th1_. _L.Sil.-L.Dev._

Family MONOGRAPTIDAE Lapworth, 1873

[Monograptidae Lapworth, 1873, table 1 facing p. 555]

Scandent uniserial rhabdosomes without cladia. _L.Sil.-L.Dev._

Monograptus Geinitz, 1852, p. 32 [_pro Lomatoceras_ Bronn, 1835 (_etiam Monoprion_ Barrande, 1950) ICZN, Opin. 198, 1954] [*_Lomatoceras priodon_ Bronn, 1835, p. 56; SD Bassler, 1915, p. 822] [=_Pomatograptus_ Jaekel, 1889, p. 677 (obj.) (type, _Lomatoceras priodon_ (Bronn); SD Bulman, 1929, p. 180)] [The following names, mostly proposed as subgenera, are technically valid, but are here included as subjective synonyms mainly owing to lack of adequate information on structural details. Reasons for placing these names in synonymy are discussed in the Addendum, p. _V_149. _Campograptus_ Obut, 1949, p. 24 (*_Monograptus convolutus_ var. _communis_ Lapworth, 1876, p. 358; SD Obut, 1964, p. 328); _Coronograptus_ Obut & Sobolevskaya in Obut, Sobolevskaya, & Merkureva, 1968, p. 92 (*_M. gregarius_ Lapworth, 1876, p. 317; OD); _Demirastrites_ Eisel, 1912, p. 27 (*_Rastrites triangulatus_ Harkness, 1851, p. 59; SD Bulman, 1929, p. 175); _Globosograptus_ Přibyl (_ex_ Bouček & Přibyl MS), 1948, p. 37 (*_Monograptus wimani_ Bouček, 1932, p. 153; OD); _Lagarograptus_ Obut & Sobolevskaya, in Obut, Sobolevskaya, & Merkureva, 1968, p. 90 (*_L. inexpeditus;_ OD); _Mediograptus_ Přibyl (_ex_ Bouček & Přibyl MS), 1948, p. 39 (*_M. kolihai_ Bouček, 1931, p. 300; OD); _Oktavites_ Levina, 1928, p. 10 (*_Graptolithus spiralis_ Geinitz, 1842, p. 700; SD Obut, 1964, p. 328) (=_Obutograptus_ Mu, 1955, p. 10); _Pernerograptus_ Přibyl, 1941, p. 9 (*_Graptolithus argenteus_ Nicholson, 1867, p. 239; OD); _Pribylograptus_ Obut & Sobolevskaya, 1966, p. 33 (*_Monograptus incommodus_ Törnquist, 1899, p. 11; OD); _Spirograptus_ Gürich, 1908, p. 34 (*_Graptolithus turriculatus_ Barrande, 1850, p. 56; SD Bulman, 1929, p. 182) (=_Tyrsograptus_ Obut, 1949, p. 24); _Streptograptus_ Yin, 1937, p. 297 (*_Monograptus nodifer_ Törnquist, 1881, p. 436; OD); _Testograptus_ Přibyl, 1967, p. 49 (*_Graptolithus testis_ Barrande, 1850, p. 53; OD)]. Thecae and shape of rhabdosome variable, comprising all Monograptidae other than the genera recognized below. _L.Sil.(Cystograptus vesiculosus Z.)-L.Dev.(Monograptus hercynicus Z.),_ worldwide.——Fig. 99,_1a_. _M. cyphus_ Lapworth, L.Sil.(L. Birkhill Sh.), S.Scot.; ×2 (59).——Fig. 99,_1b_. *_M. priodon_ (Bronn), L.Sil. (Gala), S.Scot.; proximal and distal ends of long rhabdosome, ×2 (59).——Fig. 99,_1c_. _M. convolutus_ (Hisinger), L.Sil.(_Rastrites_ Sh.), S.Sweden; ×2 (240).——Fig. 99,_1d_. _M. discus_ Törnquist, L.Sil.(Tarannon), Wales; ×4 (59).——Fig. 99,_1e_. _M. turriculatus_ (Barrande), L.Sil., Bohemia; ×2 (2).

Cucullograptus Urbanek, 1954, p. 78 [*_C. pazdroi;_ OD]. Thecae long, with elongate straight protheca and short metatheca; aperture round to slitlike, with lateral (monofusellar) apertural lappets or lobes, forming complex auriculate structures in extreme forms, symmetrical or asymmetrical. _U.Sil.(low.Ludlow,_ chiefly _Lobograptus scanicus_ Z.), NW.Eu.-Australia(Victoria)-?N.Am.

C. (Cucullograptus). Aperture slitlike, with asymmetrical lateral lobes, left lobe larger, right lobe always smaller or atrophied (L. cucullograptids). _U.Sil.(low.Ludlow),_ between _Lobograptus scanicus_ and _Saetograptus leintwardinensis Z.),_ Eu. (Pol.-NW.Ger., boulders).——Fig. 100,_3_. _C. (C.) aversus rostratus, ?S. leintwardinensis_ Z.,

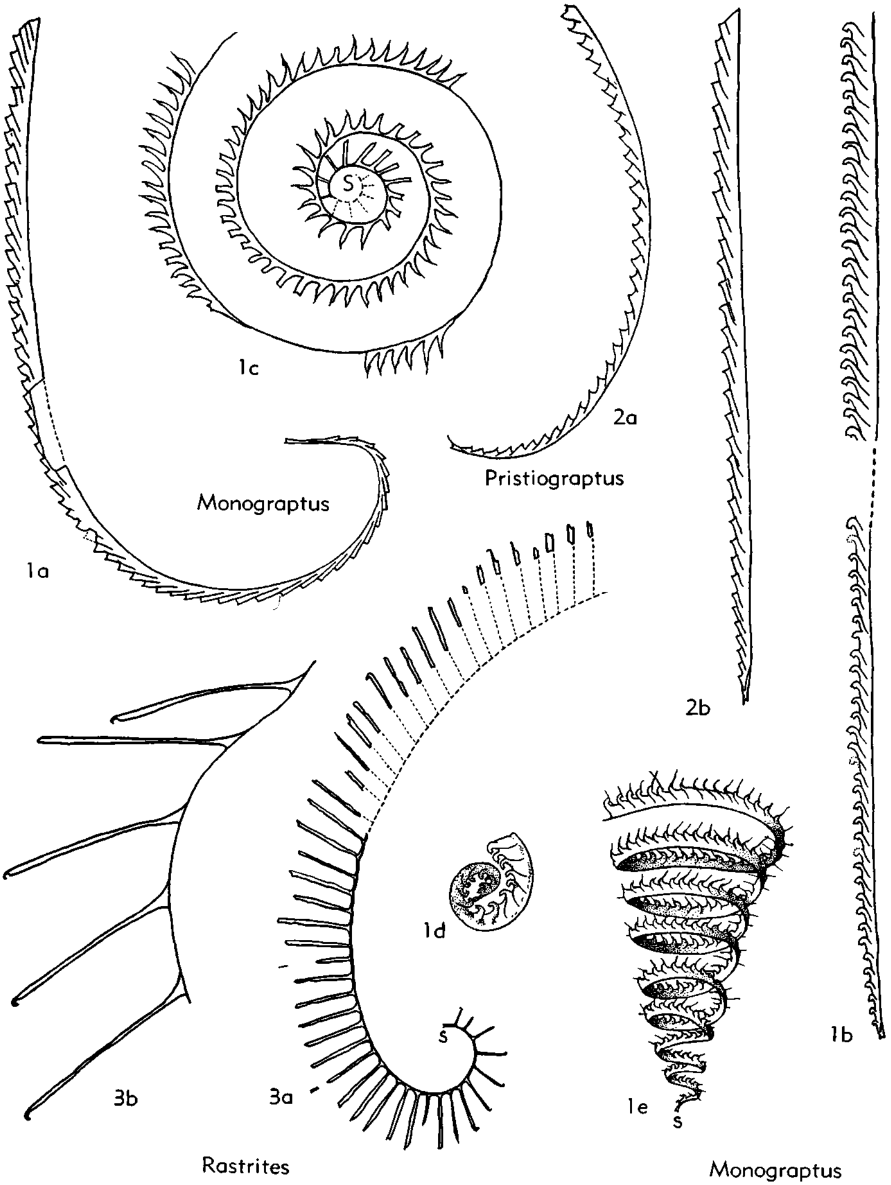

FIG. 99. Monograptidae [*S,* sicula] (p. *V*132, *V*134).

Pol.; *3a,* left side showing hypertrophied left lobe; *3b,* ventral view, ×35 (253).

C. (Lobograptus) URBANEK, 1958, p. 12 [**Monograptus scanicus* TULLBERG; OD]. Aperture rounded, with symmetrical, subsymmetrical or asymmetrical lateral lobes; where asymmetrical, the right lobe is larger (S and R cucullograptids). *U.Sil.(low.Ludlow, upper Neodiversograptus nilssoni* to *basal Saetograptus leintwardinensis Z.),* NW.Eu.-Australia(Victoria)-?N.Am.——FIG. 100,*1*. *C. (L.) simplex* URBANEK, *N. nilssoni* Z., Pol.; *1a,* right side; *1b,* ventral aspect; ×35 (253).——FIG. 100,*2*. *C. (L.) scanicus parascanicus* (KÜHNE); low.Ludlow boulder, Pol.; *2a,* right side;*2b,* left side, showing smaller left lobe; ×35 (253).

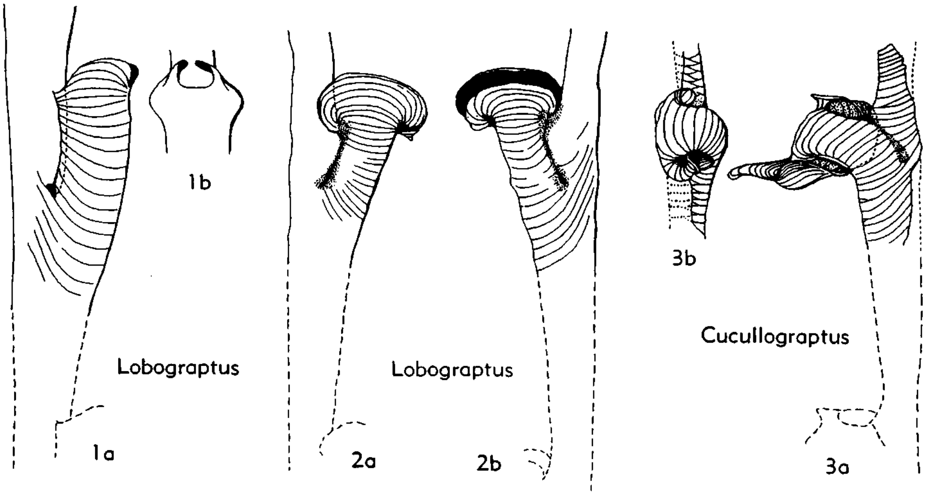

Fig. 100. Monograptidae (p. *V*132-*V*133).

Monoclimacis Frech, 1897, p. 621 [**Graptolithus vomerinus* Nicholson, 1872, p. 53; OD]. Thecae geniculate, with straight supragenicular wall approximately parallel to axis of rhabdosome; apertural margins somewhat everted; genicular flange of microfusellar tissue commonly present. *L.Sil.-U.Sil.,* almost worldwide.——Fig. 101,*1*. *M. micropoma* (Jaekel), low.Ludlow (glacial boulder), Pol.; proximal end, approx. ×20 (249).

Pristiograptus Jaekel, 1889, p. 667 [**P. frequens;* OD] [=*Bohemograptus* Přibyl, 1967, p. 134 (type, *Graptolithus bohemicus* Barrande, 1850, p. 40)]. Thecae simple, cylindrical, with straight or only slightly curved free ventral wall and without any distinctive apertural processes; rhabdosome straight or slightly curved ventrally. *L.Sil.-U.Sil.,* worldwide.——Fig. 99,*2a*. *P. bohemicus* (Barrande), low.Ludlow Sh., Wales; ×2 (59).——Fig. 99,*2b;* 101,*2*. *P. dubius* (Suess), low. Ludlow Sh., Eng.; 99,*2b,* ×2 (59); 101,*2,* proximal end, somewhat schematic; ×10 (247).

Rastrites Barrande, 1850, p. 64 [**R. peregrinus;* SD Hopkinson, 1869, p. 158] [=*Rastrograptus* Hopkinson & Lapworth, 1875, p. 633 (*pro Rastrites* Barrande); *Corymbites* Obut & Sobolevskaya, in Obut, Sobolevskaya, & Nikolaev, 1967, p. 132 (type, *C. sigmoidalis*); *Stavrites* Obut & Sobolevskaya, in Obut, Sobolevskaya, & Merkureva, 1968, p. 111 (type, *S. rossicus*)]. Rhabdosome dorsally curved; thecae straight, isolate and tubular, with retroflexed (hooked) aperture and lateral spines in some, arising widely spaced from a threadlike "common canal" at high angles. *L.Sil.(Monograptus gregarius-M. turriculatus Z.),* worldwide except S.Am. and ?N.Am.——Fig. 99,*3a*. *R. longispinus* (Perner), Birkhill Sh., S.Scot., ×2 (59).——Fig. 99,*3b*. *R. maximus* Carruthers, U.Birkhill Sh., S.Scot.; ×2 (59).

Saetograptus Přibyl, 1942, p. 11 [**Graptolithus chimaera* Barrande, 1850, p. 52; OD] [=*Colonograptus* Přibyl, 1942, p. 2 (type, *Graptolithus colonus* Barrande, 1850, p. 42)]. Thecae straight, cylindrical, with lateral apertural processes (lappets or spines) of monofusellar tissue on proximal thecae or throughout rhabdosome. *U.Sil.(low. Ludlow, Neodiversograptus nilssoni-Lobograptus scanicus Z.),* almost worldwide.——Fig. 101,*3a, 3c*. **S. chimaera* (Barrande), glacial boulder, Pol.; *3a,* proximal end showing long thecal spines, ×10; *3c,* almost complete rhabdosome; ×5 (249).——Fig. 101,*3b*. *S. colonus* (Barrande); proximal end, somewhat schematic; ×10 (Bulman, n).

Family CYRTOGRAPTIDAE Bouček, 1933

[Cyrtograptidae Bouček, 1933, p. 1]

Scandent uniserial rhabdosomes with thecal or sicular cladia or both. *L.Sil.-L. Dev.*

Subfamily CYRTOGRAPTINAE Bouček, 1933

[*nom. transl.* Yin, 1937, p. 296 (*ex* Cyrtograptidae Bouček, 1933, p. 1)]

Main stipe (procladium) generally spirally coiled, helicoidally at proximal end, with one or more thecal cladia, sometimes bearing second- or higher-order cladia; production of cladia typically regular. *M.Sil. (Wenlock).*

Cyrtograptus Carruthers, 1867, p. 540 [*nom. correct.* Lapworth, 1873 (*pro Cyrtograpsus* Carruthers, 1867), ICZN, Opin. 650, 1963] [**Cyrtograpsus murchisoni;* OD] [=?*Damosiograptus* Obut, 1950, p. 269 (type, *Cyrtograptus spiralis*

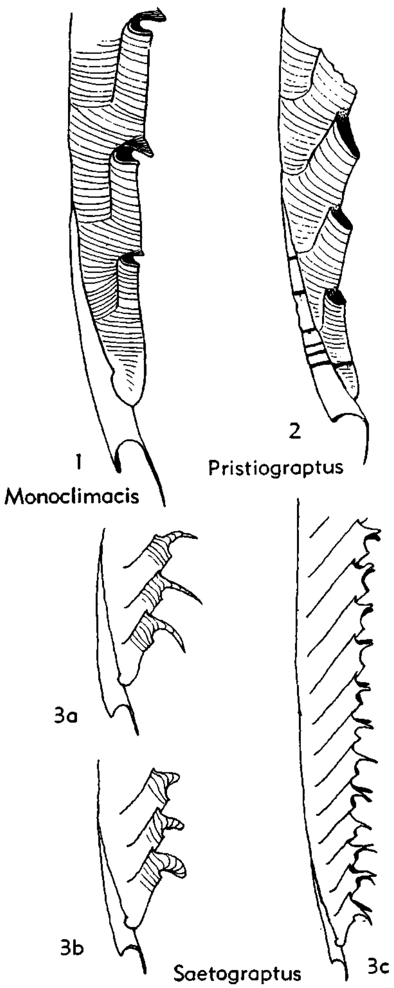

FIG. 101. Monograptidae (p.*V*134).

Averianow, 1931, p. 11); *Lapworthograptus* Bouček & Pribyl, 1952, p. 14 (type, *Cyrtograptus grayi* Lapworth, 1876, p. 545); *Uralograptus* Koregn, 1962, p. 136 (type, *U. insuetus*)]. Thecae biform, hooked, or triangulate proximally with retroflexed apertures, becoming simpler distally. *M.Sil.(Wenlock),* worldwide, except S.Am. ——Fig. 102,*1*. **C. murchisoni,* Czech.; ×2 (9).

Averianowograptus Obut, 1949, p. 29 [**Cyrtograptus magnificus* Averianow, 1931, p. 9; OD]. Like *Cyrtograptus,* but with multiple second-order cladia on 2nd thecal cladium. *M.Sil. (Wenlock),* USSR (C.Asia).——Fig. 103,*1*. **A. magnificus* (Averianow); ×0.5 (167).

Barrandeograptus Bouček, 1933, p. 62 [**Cyrtograptus pulchellus* Tullberg, 1883, p. 36; OD]. Stipes slender, thecae uniform, simple straight tubes without apertural modifications. *M.Sil. (Wenlock),* Eu.-?N.Am.——Fig. 102,*2*. **B. pulchellus* (Tullberg), S.Sweden; ×2 (243).

Subfamily LINOGRAPTINAE Obut, 1957

[*nom. transl.* Teller, 1962, p. 153 (*ex* Linograptidae Obut, 1957, p. 18)]

Rhabdosome comprising one or more sicular cladia, with or without thecal cladia. *L.Sil.-L.Dev.*

Linograptus Frech, 1897, p. 662 [**Dicranograptus posthumus* Richter, 1875, p. 267 (=*Linograptus nilssoni* Frech, 1897, p. 662) (*non Graptolithus nilssoni* Barrande, 1850, p. 51; *nec Monograptus nilssoni* Lapworth, 1876, p. 315); OD]. Rhabdosome composed of main stipe (procladium) with at least one and generally very numerous sicular cladia; virgella with virgellarium; thecae simple, without apertural processes. *U.Sil.(low. Ludlow, Neodiversograptus nilssoni Z.)-L.Dev. (Monograptus hercynicus Z.),* Eu.-N.Am.-?Australia(NewS.Wales).——Fig. 102, *4*. **L. posthumus* (Richter), low.Ludlow, Pol.(Silesia); ×3 (9). (Stages in development of the sicular cladia are shown in Fig. 67.)

Abiesgraptus Hundt, 1935, p. 3 [**A. multiramosus;* SD Bulman, 1938, p. 84] [=*Gangliograptus* Hundt, 1939 (type, *G. hoppeianus;* SD Müller, 1969)]. Rhabdosome complex, comprising procladium and 3 sicular cladia; procladium and central sicular cladium bear paired thecal cladia; thecae simple, without apertural modifications. *L.Dev.(Monograptus uniformis-M.hercynicus Z.),* C.Eu.-N.Afr.——Fig. 104,*1*. **A. multiramosus;* Ger.(Thuringia); ×0.7 (97).

Diversograptus Manck, 1923, p. 283 [**D. ramosus;* SD Bulman, 1929, p. 176]. Rhabdosome comprising one sicular cladium with or without thecal cladia; thecae hooked, with retroflexed apertures generally becoming simpler distally. *L.Sil.,* Eu.-Arctic Can.-?N.Am.——Fig. 102,*3a*. **D. ramosus,* Ger.(Thuringia); ×2 (140).——Fig. 102,*3b*. *D. runcinatus* (Lapworth), up. Llandov., S.Scot.; ×4 (225).

Neodiversograptus Urbanek, 1963, p. 149 [**Monograptus nilssoni* Lapworth, 1876, *sensu* Urbanek, 1954, p. 300]. Rhabdosome consisting of one (? or more) sicular cladia, without thecal cladia; thecae simple, without apertural modifications. *U.Sil.(low.Ludlow, N. nilssoni Z.),* NW.Eu-N. Am.-N.Afr.-Australia. (Details of production of sicular cladium in *Neodiversograptus beklemischevi* Urbanek are shown in Fig. 66.)

Sinodiversograptus Mu & Chen, 1962, p. 152 [**S. multibrachiatus;* OD]. Like *Diversograptus,* but with numerous more or less regularly developed thecal cladia. *L.Sil.(Monograptus turriculatus Z.),* China.——Fig. 103,*2*. **S. multibrachiatus; 2a,* ×2; *2b,* portion enlarged to illustrate cladia production (153).

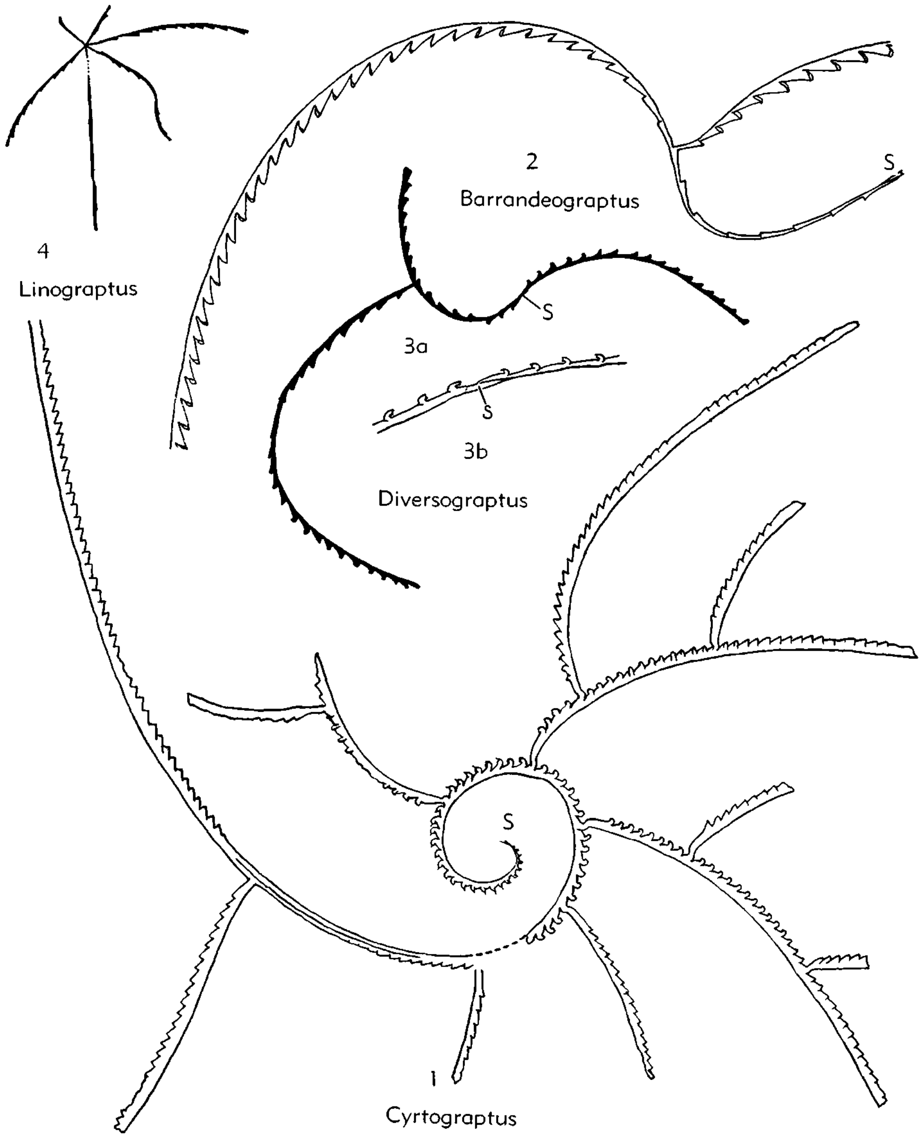

Fig. 102. Cyrtograptidae (Cyrtograptinae) *(1-2);* (Linograptinae) *(3-4)* [*S,* sicula] (p. *V*134-*V*135).

GRAPTOLITHINA INCERTAE SEDIS

Group GRAPTOBLASTI Kozłowski, 1949

[Graptoblasti Kozłowski, 1949, p. 206]

As originally described from the Tremadoc of Poland, the graptoblasts consist of small ovoid bodies, clearly attached by their lower surface, with an upper surface which exhibits a series of ridges closely resembling the fusellar segments of Graptolithina. One end shows a rounded protuberance, the umbilicus, with a circular

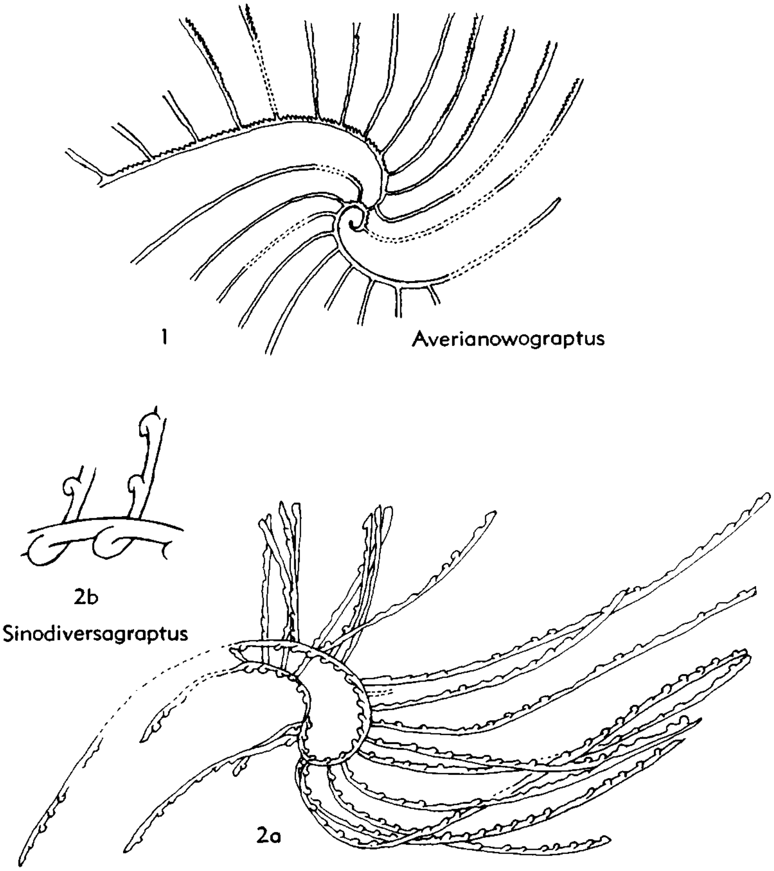

FIG. 103. Cyrtograptidae (Cyrtograptinae) *(1)*; (Linograptinae) *(2)* (p. *V*135).

opening called the cryptopyle; the other end terminates in a short spine called the filum. The vesicle itself may be undivided, or be divided into two chambers by an imperforate transverse partition, the larger of the two communicating with the exterior by the cryptopyle.

Later, KOZŁOWSKI (1962) described better-preserved material of *Graptoblastoides* from Llandeilo boulders which reveals the presence of a stolon, enclosed within a tubular stolotheca which passes into the base of the graptoblast vesicle. In the less well-preserved Tremadoc material, the filum doubtless represents a trace of the stolon, the stolotheca itself not being preserved. The upper wall in this later material is seen to be composed of two layers, a thin structureless external layer and a thick, opaque inner layer with fusellar structure. This material is intimately associated with various Crustoidea, a graptoblast occurring within the autothecal cavity of a crustoid completely filling the cavity, its walls adhering closely to those of the crustoid (see p. *V*51).

No crustoids have as yet been recorded from the Tremadoc and the relationships of the Graptoblasti remain problematic. *L.Ord.(Tremadoc-Llandeilo)*.

Graptoblastus KOZŁOWSKI, 1949, p. 210 [**G. planus*; OD]. Divided by transverse partition into anterior and posterior chambers. *L.Ord.(Tremadoc)*, Eu.(Pol.).——FIG. 105. **G. planus*; reconstr., ×40 (114).

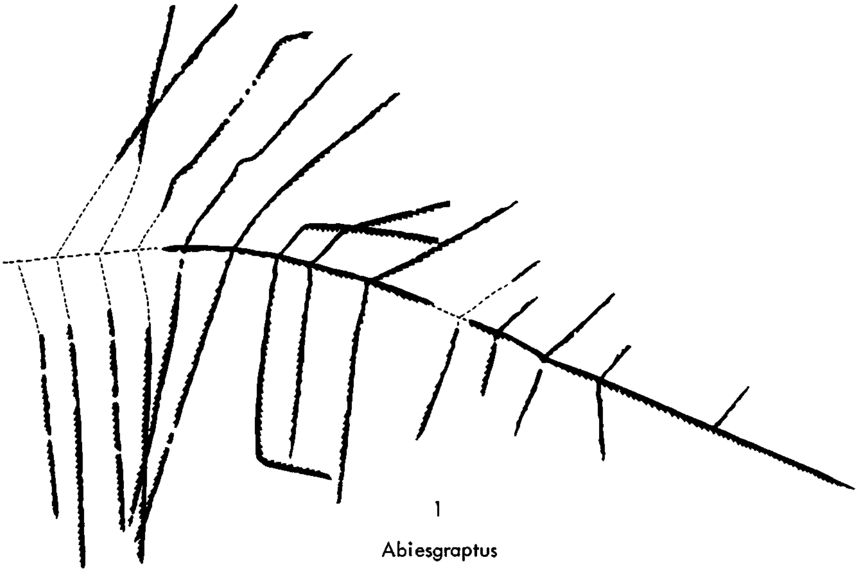

FIG. 104. Cyrtograptidae (Linograptinae) (p. V135).

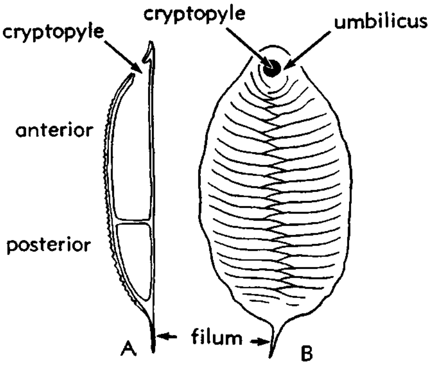

FIG. 105. Restoration of *Graptoblastus* in median section *(A)* showing anterior and posterior chambers; and in dorsal view *(B)* showing transverse ridges and median crest; approx. ×40 (114).

Graptoblastoides KOZŁOWSKI, 1949, p. 216 [**G. nowaki;* OD]. Without transverse partition. *L. Ord.(Tremadoc-Llandeilo),* Eu.(Pol.).

Group ACANTHASTIDA
Kozłowski, 1949

[Acanthastida KOZŁOWSKI, 1949, p. 217]

Small chitinous bodies with somewhat complicated structure which appear to represent secretion of sessile colonial organism of an unknown nature. Colony discoidal, 4 to 5 ~~mm. in~~ diameter, attached by flattened lower surface; upper surface convex, composed of central perforated area (reticulum) bearing a few large spines surrounded by a ring of long spines; these together with the subreticular cavity constitute the spinarium. Around the spinarium lies a peripheral region with an irregularly rugose or even spinose surface, called calotte (Fig. 106). A number of radially arranged chambers underlie the calotte and spinarium; these do not communicate with one another or with the exterior but their upper portion extends into adjacent trabeculae of the reticulum. *L.Ord.*

Acanthastus KOZŁOWSKI, 1949, p. 226 [**A. luniewskii;* OD]. *L.Ord.(Tremadoc),* Eu.(Pol.).——FIG. 106. **A. luniewskii;* reconstr., ×15 (114).

Group GRAPTOVERMIDA
Kozłowski, 1949

[Graptovermida KOZŁOWSKI, 1949, p. 204]

Small irregularly coiled chitinous tubes with fusellar structure. *L.Ord.*

Graptovermis KOZŁOWSKI, 1949, p. 206 [**G. spiralis;* OD]. Flexuous or irregularly coiled

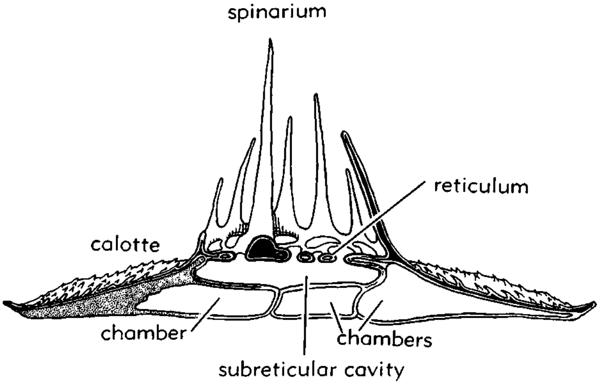

FIG. 106. Restoration of *Acanthastus,* in median section, approx. ×15 (114).

chitinous tubes with a diameter of 100 to 400 microns, attached by one surface; growth by addition of fusellar segments as in Graptolithina. *L.Ord.,* Eu.(*Tremadoc,* Pol.; *?up.Arenig,* Sweden).

UNRECOGNIZABLE GENERA

The following genera are not accepted as graptolites, represent unidentifiable preservational views (e.g., scalariform or subscalariform), or are too imperfectly known for description and taxonomic placement. [Most of HUNDT's genera were described in periodicals inaccessible outside Germany, but figures were published in HUNDT, 1953 and 1965.]

Birastrites GEINITZ, 1866, p. 125.
Buthograptus HALL, 1861, p. 18.
Cameragraptus HUNDT, 1951.
Cardograptus HUNDT, 1965.
Conograptus RUEDEMANN, 1947, p. 267.
Ctenograptus NICHOLSON, 1876, p. 248.
Cystoturriculograptus HUNDT, 1952.
Dawsonia NICHOLSON, 1873, p. 139 [*non* HARTT in DAWSON, 1868].
Demicystograptus HUNDT, 1942.
Dibranchiograptus HUNDT, 1949.
Didymograptoides HUNDT, 1951.
Eiseligraptus HUNDT, 1965.
Falcatograptus HUNDT, 1965.
Geminograptus HUNDT, 1951.
Labrumograptus HUNDT, 1952.
Limpidograptus KHALETSKAYA, 1962, p. 72.
Megalograptus MILLER, 1874, p. 343.
Mystiograptus HUNDT, 1965.
Nereitograptus HUNDT, 1951.
Nereograptus GEINITZ, 1852, p. 27.
Nodosograptus HUNDT, 1951.
Paradimorphograptus HUNDT, 1951.
Paragraptus HUNDT, 1965.
Phycograptus GURLEY, 1896, p. 89.
Planktograptus YAKOVLEV, 1933, p. 979.
Procrytograptus POULSEN, 1943, p. 302.
Protistograptus McLEARN, 1915, p. 55.
Protograptus MATTHEW, 1886, p. 31.
Protovirgularia M'COY, 1850, p. 272.
Spinosidiplograptus HUNDT, 1951.
Stelechograptus RUEDEMANN, 1947, p. 279.
Strophograptus RUEDEMANN, 1904, p. 716.
Thamnograptus HALL, 1859, p. 519.
Thecocystograptus HUNDT, 1947.
Thuringiagraptus HUNDT, 1935.
Trigonograpsus NICHOLSON, 1869, p. 231 [=*Trigonograptus* LAPWORTH, 1873, ICZN Opin. 650].
Triplograptus RICHTER, 1871, p. 251.
Triplograptus HUNDT, 1965.
Undograptus HUNDT, 1949.

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ADDENDUM

CLASSIFICATION OF THE GRAPTOLITE FAMILY MONOGRAPTIDAE LAPWORTH, 1873

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INTRODUCTION

In this second edition of Part V (Graptolithina) of the *Treatise on Invertebrate Paleontology,* the suborder Monograptina has been divided into two families, Monograptidae and Cyrtograptidae, and the latter further divided into the subfamilies Cyrtograptinae and Linograptinae. All forms which exhibit thecal or sicular cladia are there assigned to the Cyrtograptidae, and the distinction between the Linograptinae and the Cyrtograptinae rests respectively upon the presence or absence of sicular cladia. This is clearly no more than an arbitrary and provisional arrangement (a key rather than a classification), acceptable only until sufficient is known of monograptid phylogeny to attempt a more "natural" classification. On this basis, *Monograptus runcinatus* Lapworth is assigned to the genus *Diversograptus* (Linograptinae) although it is known in the diversograptid (bipolar) condition only by relatively few specimens; and in Britain, *Neodiversograptus nilssoni* (Lapworth, 1876, *sensu* Urbanek, 1954) has been recorded only recently in possession of sicular cladia. The number of such anomalies known is small, but if cladia production proves to be potentially possible in any monograptid, it is clear that this feature may cease to have much influence even on generic definitions. We do not at present know, for example, whether *Cyrtograptus* is monophyletic or whether the main lineages run through such "genera" rather than originate within them; but Urbanek (1963) has already suggested possible analogy between cladia production and the well-known developmental "stages" recognized in the Dichograptina [Didymograptina] and Diplograptina.

This note is not concerned with the issues raised above but with the attempted subdivision of *Monograptus* on the basis of thecal form and rhabdosome shape. A lengthy discussion of this is out of place in the Systematic Descriptions, but some reasoned justification is needed for the lack of recognition accorded to these genera therein and by most British and American workers. In other countries, this has been contrasted with the general recognition accorded to the genera of biserial graptolites.

Genera of the Didymograptina are based to a considerable extent on rhabdosome form. In the Diplograptina, the biserial rhabdosome is universal and genera were erected largely on thecal characters. This process began a century ago and the generic names, though they have not proved altogether satisfactory, have the sanction of long use. They are now themselves beginning to be subdivided on the basis of more subtle differences in thecal form.

The monograptids, with a comparable uniformity of rhabdosome plan, have a different history as regards taxonomy. LAPWORTH (1876) recognized a number of species groups, which he believed to be made up of closely allied species, but he erected no monograptid genera for them; and ELLES & WOOD (1901-18), after analyzing the biocharacters as then understood, modified these groups and their content, and elaborated them entirely in the manner of a key, but again refrained from designating any genera for them. This action carried the implication that further knowledge of the details of thecal structure was necessary before any satisfactory nomenclature could be achieved. A few generic names had already been proposed (*Monoclimacis* FRECH, 1897; *Pomatograptus* JAEKEL, 1889; *Pristiograptus* JAEKEL, 1889), but with the exception of *Rastrites* BARRANDE, 1850, these were not widely accepted; and in a presidential address on biological classification BATHER (1927) could write:

> . . . it would be worth while to experiment with the Graptolites, to see whether anything would really be gained by splitting up such a genus as *Monograptus*. So long as this name is retained, at least one is told the grade of structure. A few ideal schemes might be worked out on a clean slate, and provided they were all wiped out again before publication of the selected names, no harm would be done.

This expresses the conservative attitude toward subdivision of the genus *Monograptus* by most workers, especially in Britain, until well into this century; and although the devising of an "ideal scheme" would scarcely be regarded today as a profitable exercise, the hope remained that from the portmanteau genus *Monograptus* various soundly based genera could progressively be extracted as investigation of different species provided the opportunity.

However, elsewhere the temptation to name these monograptid species groups of ELLES & WOOD has latterly proved irresistible and nearly a score of technically valid genera have been proposed since 1940. The main objection to most such genera is that their erection was not accompanied by any addition to our imperfect knowledge of their morphology and phylogeny; their content is ill-defined and their application correspondingly uncertain. The sole purpose of a key is to aid the identification of species, and the bestowal of generic names on such categories or groups inevitably tends to burden the literature with names that are at best of doubtful value. The status of these and other genera is discussed below.

In conclusion, some reference should be made to the particular difficulty introduced by the prevalence of *biform* monograptids, where proximal and distal thecae of the same rhabdosome may differ to an extent scarcely paralleled in other graptolites. ELLES & WOOD concluded that the distal (mature) thecae "have always been considered to be the more characteristic and distinctive" and should take systematic precedence over the proximal thecae; but this is an oversimplification and even in the ELLES & WOOD "groups," the treatment of such species was by no means satisfactory. With the recognition that new characters can be introduced either proximally or distally, this taxonomic problem becomes more complex and the generic naming of the ELLES & WOOD "groups" becomes still more hazardous. This complexity has so far only been surmounted satisfactorily in URBANEK's *Lobograptus* and *Cucullograptus*, where the definition is supplemented by a convincing and comprehensive phylogeny; it has not yet been resolved in the so-called demirastritids, where several phylogenies have not yet been properly disentangled.

ACCEPTABLE GENERA

RASTRITES

Rastrites BARRANDE, 1850 (type, *R. peregrinus;* SD HOPKINSON, 1869). The distinctive appearance of *Rastrites* led to the erection of this genus as one of the first true graptolites to be distinguished from the now obsolete *Graptolithus.* Its relation to *Monograptus* was noted by LAPWORTH (1876) and it was reduced to subgeneric rank by ELLES & WOOD (1901-18) mainly with the object of emphasizing this relationship. It is now known from isolated material (HUTT, RICKARDS & SKEVINGTON, in press), and SUDBURY (1958) indicated the probable derivation of one (possibly two) species from triangulate monograptids. The genus is probably polyphyletic, but the number of species involved is relatively small and the lineages appear to be closely related.

The genus *Corymbites* OBUT & SOBOLEVSKAYA, 1967 (type, *C. sigmoidalis;* OD) appears to be a sigmoidally curved *Rastrites.* The taxonomic value of rhabdosomal curvature is discussed more fully below, under *Oktavites* (p. V152). *Stavrites* OBUT & SOBOLEVSKAYA, 1968 (**S. rossicus;* OD) appears to be a *Rastrites* in which both thecae and common canal are encased in some chloritic or other material; the pyritized thecal tubes and common canal can be seen centrally placed in several figures. No new structures were elucidated in the description and these genera are here regarded as junior synonyms of *Rastrites.*

MONOCLIMACIS

Monoclimacis FRECH, 1897 (type, *Graptolithus vomerinus* NICHOLSON, 1872; OD). The thecal structure of several species of *Monoclimacis,* including the type species, is now known from pyritized material, and the thecal hoods described by URBANEK (1958) in transparencies of the Ludlovian *M. micropoma* have now been recognized in pyritized Wenlock and Llandovery representatives (though it cannot yet be asserted that these too are composed of microfusellar tissue). The evolutionary roots of this genus are lost among the diverse lower Llandovery monograptids, but the thecal structure is reasonably well established over its long stratigraphic range and at present no indication is seen that the genus is other than monophyletic.

PRISTIOGRAPTUS

Pristiograptus JAEKEL, 1889 (type, *P. frequens;* OD). Certain species of *Pristiograptus,* though not the type species, are known in three-dimensional transparencies, and a large number of species are represented by pyritized material. The simple character of the thecae makes the interpretation even of flattened material relatively simple, though it would make any polyphyly the more difficult to detect. The genus represents a long-ranging and prolific stock (extending from lower Llandovery to upper Ludlow) and is the probable source of several genera recognized in the Ludlow, including some linograptids.

Most graptolite workers have been aware for some time of URBANEK's unpublished studies on the *Pristiograptus bohemicus* (BARRANDE) group of species, and it is regretable that PŘIBYL (1967) should at this stage have erected the genus *Bohemograptus,* with *P. bohemicus* as type species. The present definition of *Bohemograptus* differs in no significant respect from that covered by *Pristiograptus,* but presumably we can expect a redefinition by URBANEK in the near future; for the present the genus *Bohemograptus* is regarded as a junior synonym of *Pristiograptus.*

SAETOGRAPTUS

Saetograptus PŘIBYL, 1942 (type, *Graptolithus chimaera* BARRANDE; OD). The work of WALKER (1953) and URBANEK (1958) has placed *Saetograptus* on a satisfactory footing, though it depends for its recognition on structural detail not always visible in shale material. *Monograptus leintwardinensis* and similar species are probably to be included, but confirmation awaits the preparation of isolated rhabdosomes. The genus *Colonograptus* PŘIBYL, 1942 (**Graptolithus colonus* BARRANDE; OD), again elucidated by URBANEK (1958), differs only in the possession of more rounded lappets rather than spines of monofusellar tissue. Recently, isolated specimens of *M. varians* WOOD show that this species is intermediate between *Saetograptus* and *Colonograptus* (HUTT, 1969) and is in fact nearer to *Saetograptus,* as originally conceived, than to *Colonograptus,* where it was placed by PŘIBYL. The probable derivation of at least some species of *Saetograptus* appears to be through *Colono-*

graptus from a *Pristiograptus* of *P. ludensis* type. It is becoming clear that these genera were too narrowly conceived by Přibyl and that it is more realistic to regard *Colonograptus* as a junior synonym of *Saetograptus* rather than a subgenus.

CUCULLOGRAPTUS AND LOBOGRAPTUS

Cucullograptus Urbanek, 1954 (type, *C. pazdroi;* OD) and *Lobograptus* Urbanek, 1958 (type, *M. scanicus* Tullberg; OD). The two closely-related genera named *Cucullograptus* and *Lobograptus* are known from magnificent three-dimensional material and form the subject of one of the most reliable and detailed investigations into graptolite phylogeny (Urbanek, 1966). *Lobograptus* is represented by five divergent lineages, two of which culminate in species of *Cucullograptus.* We have preferred to regard *Lobograptus* Urbanek, 1958 as a subgenus of the terminal member (and senior taxon) *Cucullograptus* Urbanek, 1954, although recognizing that it was in every sense precisely defined.

GENERA OF DUBIOUS VALUE

GENERA BASED ON RHABDOSOME SHAPE

The synonymy of the principal genera concerned in this category—*Spirograptus* Gürich, 1908 (=*Tyrsograptus* Obut, 1949) (type, *Graptolithus turriculatus* Barrande; SD Bulman, 1929) and *Oktavites* Levina, 1928 (=*Obutograptus* Mu, 1955) (type, *Graptolithus spiralis* Geinitz; SD Obut, 1964) is complicated, but need not be elaborated here.

The use of rhabdosome shape together with thecal form is impossible to reconcile in a single classification. If thecal form be accepted as the ultimate basis of affinity (and hence classification), then rhabdosome shape must take second place, even if it can be shown to have any taxonomic value at all.

This inadequacy of rhabdosome shape is shown by the fact that *Monograptus communis,* one of the two groups of *"Spirograptus"* recognized by Přibyl in 1944, was made the type of a separate genus *Campograptus* by Obut in 1949 largely on thecal characters (Fig. 107,*A,B*). Still more significant, *M. exiguus* (Barrande), a species exhibiting pronounced *ventral* curvature of the rhabdosome and a fish-hook proximal end, is seen to possess thecae closely resembling those of the dorsally coiled *"Oktavites" spiralis* when isolated three-dimensional material is obtained (Hutt, Rickards & Skevington, in press).

The detailed morphology of not a single species normally included in the genus *Spirograptus* is known; even pyritized specimens of *Monograptus turriculatus* have failed to clarify the real nature of the spinose, hooked thecae and some specimens suggest the presence of more than two spines to each theca. In *Oktavites, M. spiralis* is the only species in which the thecal structure has yet been fully elucidated (Bulman, 1932; Sudbury, 1958). Such species as *"Spirograptus" tullbergi* (Bouček) could, on present evidence, be assigned to *Campograptus, Oktavites,* or *Spirograptus* (see also *Campograptus* below).

As and when full details become available, it may prove that certain groups of related species also have a tendency towards a particular rhabdosome shape, but exceptions (like *Monograptus exiguus*) appear inevitable.

Two other genera can be considered in this category because rhabdosome shape was given considerable emphasis in their diagnosis.

1) *Campograptus* Obut, 1949 (type, *Monograptus communis* Lapworth; SD Obut, 1964, p. 328) was defined as a dorsally curved monograptid with hooked thecae greatly expanded at their bases (Fig. 107,*A,B*). It was left to Bulman (1951) and Sudbury (1958) to illustrate the true characters of the thecae, and Sudbury attempted to assess the phyletic relationships of this and related species. Using Sudbury's work as a basis, it would be possible to define several "genera" more adequately. For example, it would be possible to reletter her figures 28 and 29 (p. 537, 539) showing *"Pernerograptus"* giving rise to *"Campograptus,"* restricted to the species *M. revolutus* and *M. communis* respectively. But what of the species *M. limatulus* Törnquist; and does the lineage *M. toernquisti* Sudbury-*M. pseudoplanus* Sud-

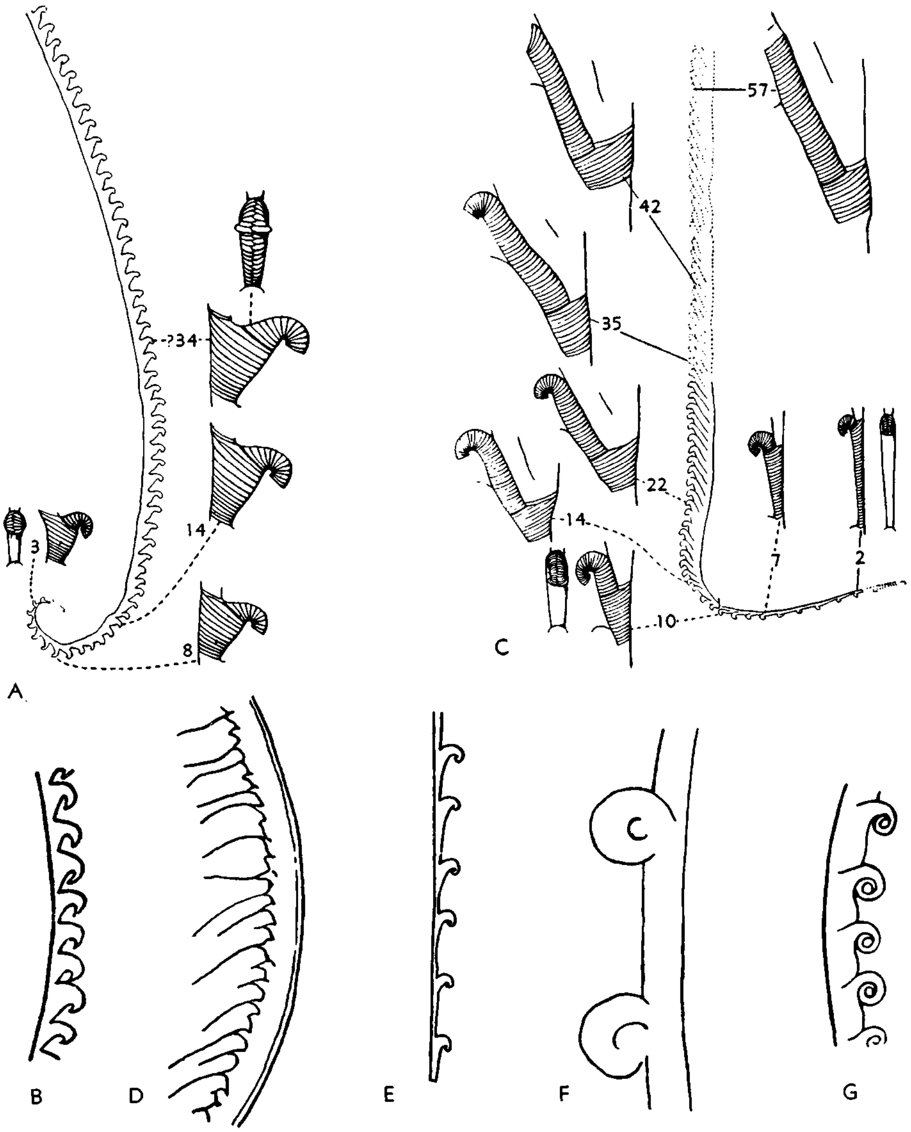

FIG. 107. Drawings of monograptids. (All figures at magnification given in original publications.)

A. Monograptus communis (LAPWORTH) (from Bulman, 1951).
B. "Campograptus" communis (LAPWORTH) (from Obut, 1949).
C. Monograptus argenteus (NICHOLSON) (from Bulman, 1951).
D. Monograptus ("Testograptus") testis (BARRANDE) (from Přibyl, 1967).
E. "Globosograptus" wimani (BOUČEK) (from Bouček, 1932, where it was described under the name *Monograptus wimani*).
F. Monograptus ("Mediograptus") kolihai BOUČEK (from Bouček & Přibyl, 1951).
G. Thecal form of *Streptograptus* YIN (from Bouček & Přibyl, 1942).

BURY-*M. planus* (BARRANDE) then require another new genus? Since new thecal types are being described in increasing numbers at this level, and the phyletic relationships appear to be complex, it is premature to propose new genera for every new variant discovered; but when the phylogenies are more completely assessed (in the manner of SUDBURY, 1958), the discrimination of useful genera containing several adequately known species may be possible.

2) *Testograptus* PŘIBYL, 1967 (type, *Graptolithus testis* BARRANDE; OD) is another genus based on general form of rhabdosome and silhouette preservation of thecae (Fig. 107,*D*); no new information was presented for the species concerned. The nature of the thecal hooks and spines in *Monograptus testis* has never been ascertained, though specimens in low relief from the Long Mountain (PALMER Coll., Trinity College, Dublin) (Fig. 108) suggest resemblance to *M. sedgwicki* (PORTLOCK). It seems probable that *M. testis* is more closely related to some of the hooked and spinous Wenlock representatives of the straighter *M. priodon*-type monograptids than to the curved, Llandovery *M. veles* (RICHTER) with which it was associated by PŘIBYL and which may well be closer to *M. turriculatus.*

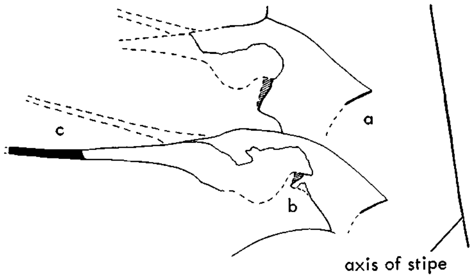

FIG. 108. *Monograptus testis* (BARRANDE), distal thecae of almost flattened specimen from the *Cyrtograptus lundgreni* Zone, Wenlock, of Long Mountain, Shropshire, ×15 (Palmer Collection no. 79 1" (i), Trinity College Dublin) [*a,* base of interthecal septum; *b,* ventral thecal wall somewhat crumpled; *c,* thecal spines (oblique shading indicates visible portions of thecal apertures)].

GENERA BASED MAINLY ON THECAL FORM

Coronograptus OBUT & SOBOLEVSKAYA, 1968 (type, *Monograptus gregarius* LAPWORTH, 1876; OD) is a name given to ELLES & WOOD's Group IA 1(a) *(M. gregarius, M. cyphus,* and *M. acinaces)* together with some new subspecies of *M. gregarius.* ELLES & WOOD's reluctance to name this group was justified by the recent discovery that JONES's specimens of *M. rheidolensis (=M. acinaces)* possess delicate ventral thecal processes of the kind described by HUTT (1968) in *M. tenuis.* Our examination of TÖRNQUIST's *M. acinaces* material confirm that *M. rheidolensis* and *M. acinaces* are conspecific, though TÖRNQUIST's Swedish material does not permit recognition of these delicate processes.

Recently isolated specimens of *Monograptus gregarius* show that the thecae possess a rounded geniculum and this structure deflects the apertural region of the preceding theca to give the appearance of an expanded aperture and, more important, to cause a distinct isolation of the apertural region in many specimens.

The use of *Coronograptus* to denote *Monograptus gregarius* and possibly *M. cyphus* serves little purpose and at best seems premature.

Demirastrites EISEL, 1912 (type, *Rastrites triangulatus* HARKNESS, 1851; SD BULMAN, 1929, p. 175). At first sight, there appears considerably more justification for the use of *Demirastrites* than most others in this category. SUDBURY's work (1958) has demonstrated that the type species is the precursor of one of the rastritids and she has made clear the nature of the thecal aperture characteristic of the distal portion of the rhabdosome. It would doubtless be possible to redefine *Demirastrites* so as to include precisely a small number of monograptid species similarly but less certainly related to other rastritids. Nevertheless, the phylogeny of the large group of triangulate monograptids is complex and involves more or less closely species which have been referred to *Demirastrites, Oktavites, Pernerograptus, Spirograptus,* and *Campograptus:* EISEL's six genosyntypes have already been referred by various authors to four of them. Thus the present use of any of these names would inevitably lead to repeated changes of nomenclature with increased knowledge of species morphology and phylogeny, which could only be a source of confusion to stratigraphers; and pending such further investigations we consider it preferable to retain all these species in *Monograptus.*

Globosograptus Bouček & Přibyl (in Přibyl, 1948) (type, *Monograptus wimani* Bouček, 1932; OD) was based on the silhouette appearance of a slender Llandovery species on which the thecae possess a long prothecal portion, no thecal overlap, and a seemingly enrolled metathecal portion (Fig. 107,*E*). The nature of this enrollment is indefinite in the type species or in any of the species originally assigned to the genus (1948); in *M. sartorius* Törnquist (included in the modified list of Bouček and Přibyl, 1951), it appears to comprise a sharply reflexed apertural region analogous to that figured by Bulman (1932) in *Monograptus* sp. Very little is known of the characters of the slender monograptids as a whole, but from work in progress in this country, it appears that their thecal form is quite variable and often indicates unsuspected links with more robust species. The genus has no precise significance and its application is quite impracticable.

In *Lagarograptus* Obut & Sobolevskaya, 1968 (type, *L. inexpeditus;* OD) the thecae are said to be hooked, but it is very difficult to determine the character of the hook from the half tone illustrations provided, the most conspicuous features in the figures being the long sicula and parallelism of the free ventral wall and dorsal wall of the stipe. Whether or not a geniculum is present and whether the hook is really in the nature of a genicular hood, as in *Monoclimacis,* is impossible to determine. On the published evidence, the erection of this genus can only be considered as highly speculative.

Mediograptus Bouček & Přibyl, in Přibyl, 1948 (type, *Monograptus kolihai* Bouček, 1931; OD). Like *Globosograptus,* the type species of *Mediograptus* is known in silhouette only, as a form with long cylindrical prothecae, no thecal overlap and vaguely "lobate" metathecae (Fig. 107,*F*). It is said to differ from *Streptograptus* and *Globosograptus* essentially by the "less coiled ends of the thecae," but the nature of the coiling is indeterminate and the figures are at best described as obscure.

In pyritized specimens of a British variety of *"Mediograptus" minimus* (Bouček & Přibyl, 1951), the dorsal wall of the metatheca consists of a reflexed shieldlike structure, transversely expanded toward its extremity, with dorsally directed winglike processes (Fig. 109,*1a-c*). To what extent this applies to other species, including the type species, is unknown; but *Monograptus antennularius* Meneghini, a species assigned to *"Streptograptus,"* has thecae identical with those of *"Mediograptus" minimus* (see also under *Streptograptus*) (Fig. 109,*2*).

Pernerograptus Přibyl, 1941 (type, *Graptolites argenteus* Nicholson, 1869; OD) is a name given to Elles & Wood's Group IB 1: monograpti in which the thecae are biform (proximally hooked and distally straight overlapping tubes) and the rhabdosome has a dorsal curvature. Přibyl chose *Monograptus argenteus* (Nicholson) as type, but made no additions to our knowledge of the group. Since then the thecae of *M. argenteus, M. revolutus,* and *M. difformis* have been more fully described by Bulman (1951) (e.g., Fig. 107,*C*) and those of *M. revolutus* with much greater refinement by Sudbury (1958). The value of this genus will become clearer when the structure of *M. limatulus* has been elucidated and when the relation of the group to *M. toernquisti* Sudbury and to *"Campograptus"* can be assessed.

Pribylograptus Obut & Sobolevskaya, 1966 (type, *Monograptus incommodus* Törnquist, 1899; OD) is a name bestowed in effect on Elles & Wood's Group II *(M. atavus, M. sandersoni, M. incommodus, M. tenuis* and *M. argutus),* and work by Rickards & Rushton (1968) has served to illustrate the composite nature of this group. *M. atavus* Jones and *M. tenuis* (Portlock) must be excluded and *M. leptotheca* Lapworth should certainly be included in it. A case could be made for the erection of a genus based on *M. incommodus, M. argutus* and *M. leptotheca,* but *Pribylograptus* was prematurely erected and much remains to be done on early Llandovery monograptids before such genera can be evaluated. The situation can only become confused by present use of the name, and it may be mentioned that Obut & Sobolevskaya (1968, pl. 16, fig. 8, pl. 17, fig. 1-5) have recently illustrated Russian specimens which they refer to *"Pribylograptus" incommodus* (Törnquist) which

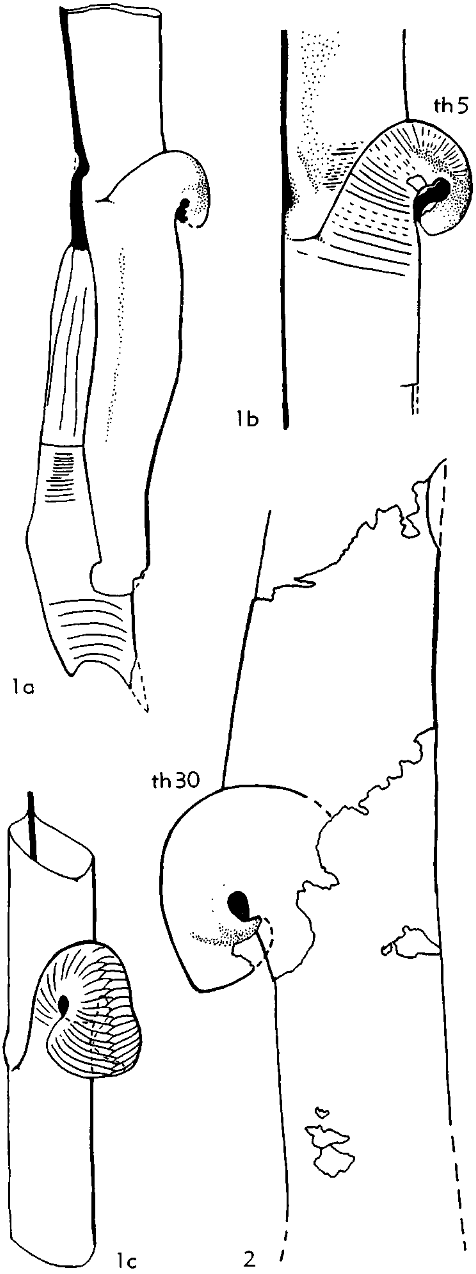

Fig. 109. Morphological features of monograptids. *1a-c. Monograptus minimus cautleyensis* Rickards, SM A62042, from the *Cyrtograptus centrifugus* Zone, Wenlock, of the Howgill Fells, Northern England; *a,* sicula and th^1; *b,* th^5 of same specimen as in *a; c,* reconstruction of thecal hook, subventral view; ×67.

2. *Monograptus antennularius* (Meneghini), Wenlock, Long Mountain, Shropshire (Palmer Collection no. 60d (i), Trinity College Dublin); thecal apertures, or visible parts thereof, in black, ×67.

are referable neither to Törnquist's species nor to Elles & Wood's concept of it.

Streptograptus Yin, 1937 (type, *Monograptus nodifer* Törnquist, 1881; OD). An examination of some of Törnquist's material of *M. nodifer,* together with other well-preserved Scandinavian specimens, shows that this species has thecal lobes quite unlike those depicted by Elles & Wood (1901-1918) or by Bouček & Přibyl (1942) (Fig. 107,*G*). The thecae possess a conspicuous bulbous flange near the aperture and this *M. nodifer* theca is unique, though a recently isolated species shows what may be a somewhat simplified version of it (Hutt, Rickards & Skevington, in press). The other species described under the emended *Streptograptus* by Bouček & Přibyl must be accommodated elsewhere and at present can only be referred to *Monograptus sensu lato;* the example of *M. exiguus* (p. V152), surely considered in the past as a typical streptograptid, is a timely warning against the premature subdivision of monograptids on imperfectly understood thecal structure.

INDETERMINATE GENERA

A number of "genera" erected by Hundt (1965) are generally agreed to represent indeterminate preservational views, probably of monograptids. They are *Falcatograptus, Mystiograptus, Nodosograptus,* and *Paragraptus.*

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