

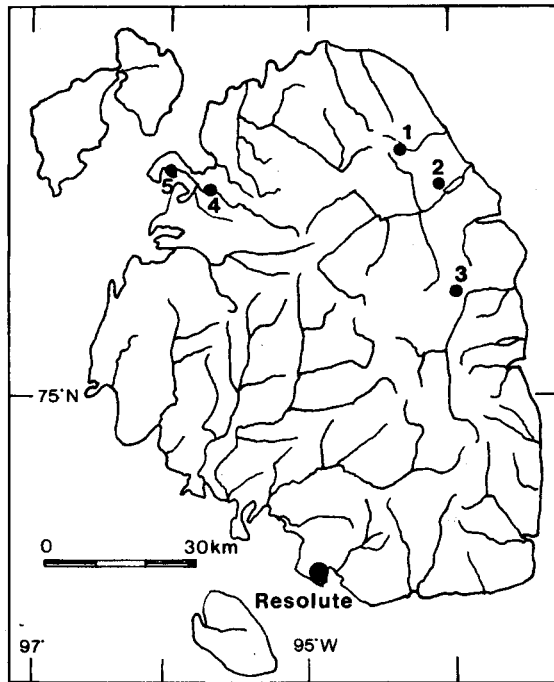
MORPHOLOGY AND PHYLOGENY
OF SOME EARLY SILURIAN 'DIPLOGRAPTID'
GENERA FROM CORNWALLIS ISLAND,
ARCTIC CANADA

by MICHAEL J. MELCHIN

ABSTRACT. A diverse assemblage of Llandovery (mainly Aeronian), biserial graptoloids has been recovered from the Cape Phillips Formation on Cornwallis Island, Arctic Canada. A study of the astogenetic patterns among these taxa can be used to define phylogenetically meaningful taxa at the generic and suprageneric level. Using previously defined astogenetic patterns, five families can be defined within the Diplogrptoidea: (1) Normalograptidae – Pattern H genera including *Normalograptus*, the root stock of the Monograptoidae; (2) Petalolithidae – Pattern I genera including *Petalolithus* and *Glyptograptus sensu stricto*; (3) Retiolitidae – Pattern R, the Silurian ancora-bearing retiolitids; (4) Dimorphograptidae – Pattern J, including the uni-biserial *Dimorphograptus* and the fully biserial *Akidograptus* and *Parakidograptus*; (5) Monograptidae – the uniserial, Pattern M. Of these five families, only the Normalograptidae occur in strata lower than highest Ashgill. *Normalograptus* – *Akidograptus* – *Dimorphograptus* – *Atavograptus* is suggested as a likely evolutionary sequence for the origin of the monograptids. This is consistent with the observed astogenetic patterns, requires few astogenetic modifications (apomorphies) at each step, and is not in conflict with the currently known stratigraphical ranges of these taxa.

IN the past several years, a number of attempts have been made by various authors to revise the generic and suprageneric classification of the graptoloids. Some of these involved only the use of traditional criteria of generic distinction, such as stipe number and orientation, and thecal morphology (the latter especially among the 'diplograptids' and 'monograptids'; see, for example, Rigby 1986). Fortey and Cooper (1986), Legrand (1987) and Mitchell (1987), however, employed a new approach to graptoloid classification, based primarily on the ontogeny of the sicula and early astogeny of the rhabdosome, combined with cladistic methodology to arrive at a classification that better reflects graptoloid phylogeny. Among the diplogrptoideans, which have been studied in detail by Mitchell (1987), this new approach has shown that thecal morphology is a highly 'plastic' feature that is easily duplicated in different lineages and, therefore, can only be applied to taxa above the specific level as a second-order criterion in relation to astogeny. The early growth stages and budding patterns appear to have been more conservative features of graptolite evolution and are, therefore, more reliable criteria for assignment of supraspecific taxa.

Mitchell (1987) recognized nine different proximal development types among the scandent, biserial graptolites that he designated the letters A to I. Of these, Patterns A to G are confined to the Ordovician. Pattern H forms occur in both Ordovician and Silurian strata, whereas Pattern I was considered to be restricted to the Silurian. Although able to distinguish between Pattern H and I astogenies, Mitchell's conclusions concerning Silurian diplogrptoideans were based on the very scanty published information about their development. Legrand (1987) recognized a single developmental pattern among Llandovery biserial graptolites, which he termed 'keroblastic'. It corresponds to Mitchell's patterns H and I. Legrand's paper, however, was not based on the study of any new, uncompressed material. Melchin and Mitchell (1991) recognized two new patterns, J and K. Pattern K was later described in detail (Stewart and Mitchell 1997) and is confined to



TEXT-FIG. 1. Map of Cornwallis Island showing sample locations. 1, Cape Manning (CM), 75° 26.8' N, 94° 20' W. 2, Eleanor Lake (EL), 75° 22.8' N, 94° 08' W. 3, Snowblind Creek (SC), 75° 11' N, 94° 02' W. 4, Rookery Creek (RC), 75° 22' N, 95° 46' W. 5, Marshall Peninsula (MP), 75° 24' N, 96° 00' W.

Ordovician taxa. Patterns H, I and J are the patterns recognized among Llandovery biserial and uniserial graptolites. Melchin and Mitchell (1991) also demonstrated the utility of this new phylogenetic classification in understanding the evolution and extinction patterns among Ashgill graptolites, as well as the biostratigraphical significance of the newly defined and revised genera. Loydell (1992) and Štorch and Serpagli (1993) used the new data on astogenetic patterns provided by Mitchell (1987) and Melchin and Mitchell (1991) to further revise the family-level classification of Silurian graptoloids. Koren' and Rickards (1996) utilized the classification proposed by Loydell (1992), with some modification, and recognized a number of new genera based on identification and clarification of a number of novel thecal and rhabdosomal features.

The purpose of this paper is to describe and illustrate the non-retiolitid, diplogrptoidean genera present in the Aeronian and early Telychian strata of the Cape Phillips Formation, and discuss their proximal development patterns and systematics in the context of the classifications of Fortey and Cooper (1986), Legrand (1987), Mitchell (1987), Melchin and Mitchell (1991), Loydell (1992), Štorch and Serpagli (1993) and Koren' and Rickards (1996).

MATERIAL

An abundant and diverse fauna of isolated, uncompressed diplogrptoideans occurs in the Aeronian portion of the Cape Phillips Formation. The Cape Phillips specimens permit an examination of the distribution of these growth patterns among some Silurian taxa, illustrate some of the variations within each pattern, and provide an indication of how the different patterns are manifest in both early growth stages and in mature rhabdosomes. These observations, in turn, elucidate the phylogeny of latest Ordovician and Silurian 'diplograptids' and 'monograptids'.

Most of the material used in this study has come from a reconnaissance sampling of a small stream section 10 km west of Cape Manning on north-eastern Cornwallis Island, N.W.T. (CM, locality 1; Text-fig. 1). Additional samples have come from Eleanor Lake (EL, locality 2),

Snowblind Creek (MSC, locality 3), Rookery Creek (RC, locality 4) and Marshall Peninsula (MP, locality 5), all on Cornwallis Island. Locality information for each figured specimen is given as the locality abbreviation, plus metres above the base of that locality. A study of the species-level taxonomy and morphology of the uncompressed graptolites from these collections, and from more recent detailed sampling of these and other sections, is now in progress.

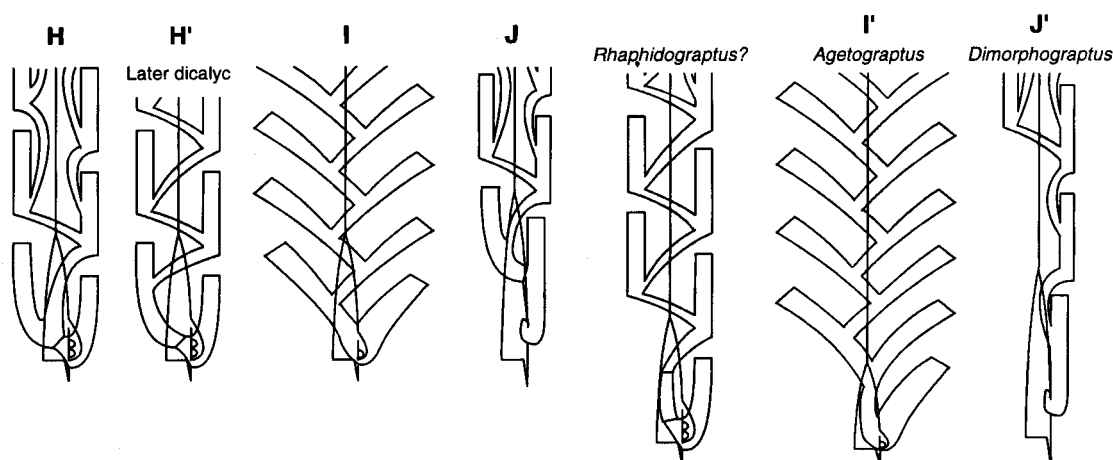
The descriptions of the proximal development patterns are based in part on those given by Mitchell (1987) and partly on observations made by light and scanning electron microscope on the present specimens. Text-figure 2 presents schematic illustrations of the basic proximal development patterns and their variations. Koren' and Rickards (1996) named each of these patterns after typical species and both the letter and species-name designations are given below.

ASTOGENETIC PATTERNS

Pattern H (normalis Pattern)

The sicula is commonly short and broad (e.g. Text-fig. 3A–B), usually 1 mm or less in Ordovician species, up to 1.7 mm in Silurian forms, although it is occasionally much longer (e.g. *Cystograptus*). Protheca 1¹ has a sinuous downward growth, growing toward the obverse side and then downward (Pl. 1, fig. 5). Two foramina open at its end: one opening downward for the th1¹ metatheca; one opening to the reverse side for the bud of protheca 1² (Pl. 1, fig. 5; Pl. 2, figs 10–11; Pl. 3, fig. 3). These foramina are separated by a list or rod (list A) which extends from the edge of the descending protheca to the sicula at its apertural rim. Metatheca 1¹ turns sharply upward just below the sicular aperture and partly encloses its protheca on the obverse side (Pl. 1, fig. 12) and the th1² foramen on the reverse side (Pl. 1, fig. 6). In many Pattern H species the reverse wall of metatheca 1¹ is free and not anchored against its protheca or the sicula during its growth except by another list (list B) which extends from the sicula to the free edge of the thecal wall (e.g. Pl. 2, fig. 10; Pl. 3, fig. 7). An interthecal septum forms at some later point and is generally not attached to the sicula. In some species, however (e.g. *Normalograptus nikolayevi* (= *Glyptograptus tamariscus nikolayevi* Obut, 1965)) this wall is anchored against the sicula by an interthecal septum that grows from the point of differentiation of protheca 1² (Pl. 1, fig. 8). List B forms the point of origin of this septum.

The point at which protheca 1² differentiates is somewhat variable but appears to be to some extent governed by the position of list B. In the Ordovician species described by Mitchell, the line of fusellar unconformity between th1¹ and th1² begins at the very base of th1¹ (at the sicular aperture) and curves to the right and upward, meeting list B, and extending upward to the base of th2¹ (see Mitchell 1987, text-fig. 3F–G). Theca 1² begins differentiation as a flange around its foramen at the base of protheca 1¹. In the Silurian species observed here, and, apparently in '*Climacograptus*' aff. *scalaris* of Barrass (1954) (= *Normalograptus scalaris ferganensis* (Obut, 1949)), the line of fusellar unconformity between the first two thecae extends at a variable angle downward and to the left from list B. In species of *Metaclimacograptus*, list B is 0.24 mm from the sicular aperture and the unconformity extends nearly straight downward from this point, giving an appearance very similar to that of the Ordovician species (Pl. 2, fig. 9; Text-fig. 4A). However, in many other species such as *Normalograptus nikolayevi*, *Pseudoglyptograptus barriei* Zalasiewicz and Tunnicliff, 1994 and those of *Neodiplograptus*, list B may be as much 0.4 mm above the sicular aperture and the line of unconformity extends downward and to the left at an angle of about 45° (Pl. 1, figs 7–8; Pl. 3, figs 7, 10; Text-fig. 4B). The result is that the point of differentiation of the two thecae is between 0.2 mm and 0.4 mm above the sicular aperture. The fusellae below this point are continuous with those of th1¹ extending in an arcuate path across part or all of the reverse side of the sicula. This results in an appearance similar to that seen in some Pattern I species. It must be stressed, however, that in all the Pattern H species, the initial bud of th1² emerges from the descending portion of th1¹ at the sicular aperture and it is only the manifestation of th1² in the form of a fusellar differentiation, by a sharp fusellar unconformity that is delayed in these species (contrast this with the Pattern I species described below).



TEXT-FIG. 2. Schematic diagram of astogenetic patterns found in Llandovery biserial and uni-biserial graptolites. The patterns that each represent a single genus with uniserial proximal ends are specifically identified.

The shift in position of the fusellar unconformity between $th1^1$ and $th1^2$ can be seen by comparing the latest Ordovician and earliest Silurian specimens of *Normalograptus angustus* (Perner, 1895) illustrated by Riva (1988). The latest Ordovician specimens (e.g. Riva 1988, fig. 3d) show the line of differentiation between $th1^1$ and $th1^2$ to be at a low angle to the rhabdosomal axis and to meet the sicula at its aperture as in the other Ordovician species illustrated by Mitchell (1987). The earliest Silurian specimens of *N. angustus* (e.g. Riva 1988, fig. 3t) show the line of differentiation of the first thecal pair to be at $c. 45^\circ$ to the rhabdosomal axis and to meet the sicula 0.25 mm above its aperture, as in many of the other Silurian species illustrated here.

From the point of differentiation of $th1^2$ (i.e. the position of list B) the growth of $th1^1$ always proceeds ahead of that of $th1^2$ (Pl. 1, fig. 8; Pl. 3, fig. 7; Text-figs 3A–B, 4A–B). The initial growth of $th1^2$ is diagonally upward and across the remainder of the reverse side of the sicula where it later turns upward.

Theca 2^1 begins to differentiate very early in most Pattern H species, often at, or just above the position of list B (Pl. 1, figs 3, 9; Pl. 2, fig. 1). In some species of *Neodiplograptus*, however, the budding of $th2^1$ is delayed until just below or at the aperture of $th1^1$ and its differentiation is like that of $th2^2$ and of all later thecae (Pl. 3, figs 8–9). This slightly modified pattern with only two primordial thecae is designated Pattern H'.

Pattern H graptolites have a relatively slender, rounded, asymmetrical proximal end and generally possess a small portion of the sicula exposed below $th1^2$. On the obverse side the sicula is commonly exposed to about the level of the $th1^1$ aperture where it is enclosed by $th1^2$ (Pl. 1, fig. 12; Pl. 2, fig. 2). Pattern H rhabdosomes usually have a complete median septum although in many Silurian species its formation is delayed until as late as the ninth thecal pair, a partial median septum being present before that point. Theca 2^1 is the earliest theca which may be dicalycal. The median septum may be straight or slightly undulose to angular. A probable exception is *Normalograptus? indivisus* (Davis, 1929) which appears to be entirely aseptate (Waern 1948). As Waern (p. 457) pointed out, however, and his excellent illustrations clearly show (especially pl. 27, fig. 6), the interthecal septa of the first three or four thecal pairs extend inward to the centre of the rhabdosome and those thecae are clearly alternate in origin. The interthecal septa of the following thecae run parallel to the outer walls and leave a significant central common canal. These more distal thecae give the distinct impression of having separated into two separately growing stipes at about the fourth thecal pair, despite the fact that no septum is present separating them.

Most Pattern H graptolites exhibit climacograptid to glyptograptid thecae, although pseudoclimacograptid to highly undulose thecae are also found in this group. Orthograptid thecae occur in the distal end of a few biform species such as *Neodiplograptus tcherskyi* subsp. nov. In addition, some of the latest Ashgill and earliest Llandovery 'orthograptids' reported from China and Kazakhstan may be Pattern H species (e.g. '*Orthograptus illustris* Koren' and Mikhailova, in Koren *et al.*, 1980, '*O. lonchoformis* Chen and Lin, 1978). Some genera have genicular thickenings or outgrowths (e.g. *Metaclimacograptus*, *Hirsutograptus* and *Talacastograptus*).

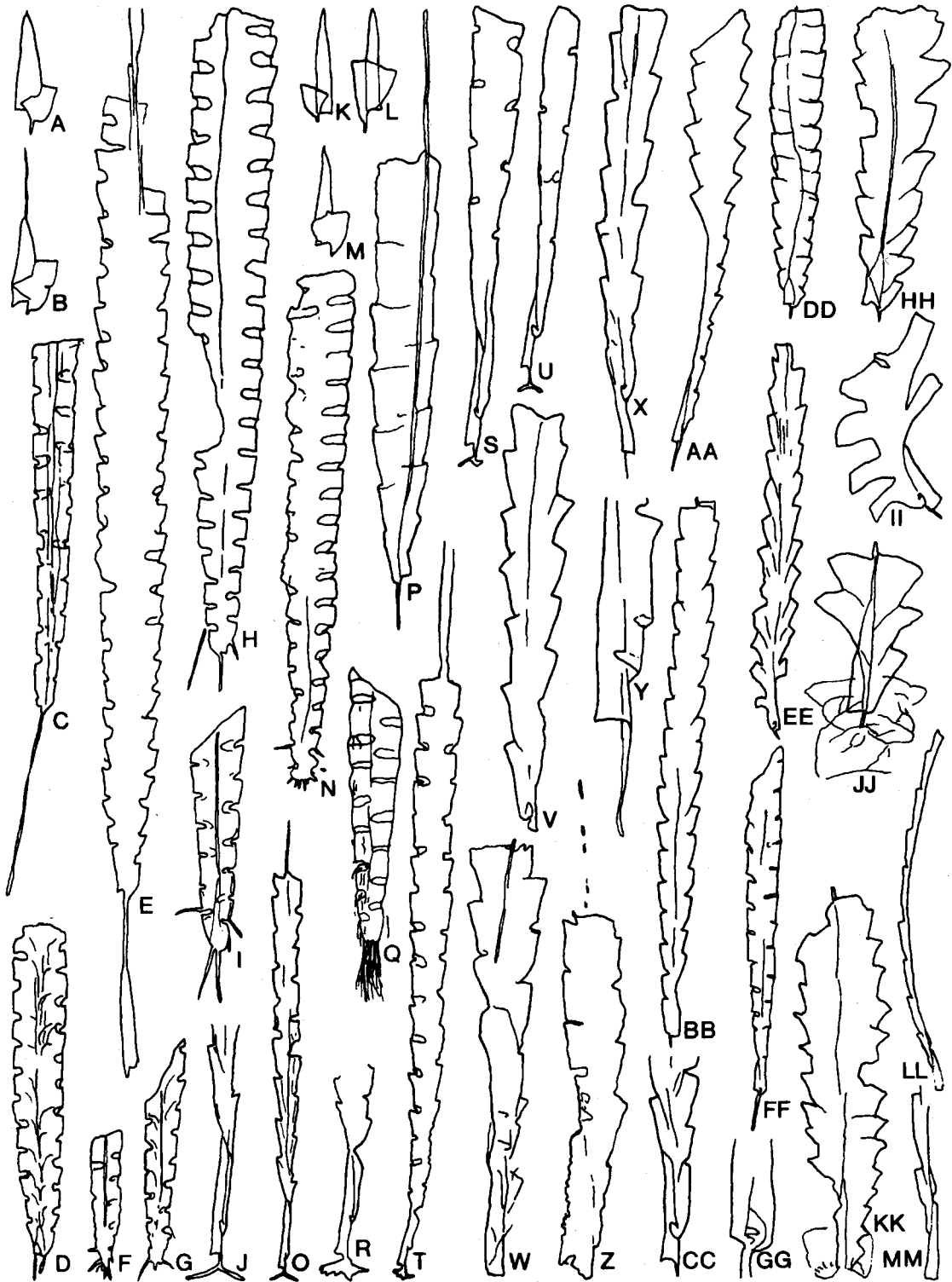
The proximal end is usually unornamented except for the virgella. The virgella can, in some species, achieve great length (e.g. *Normalograptus normalis* (Lapworth, 1877) (Text-fig. 3c) and *Neodiplograptus thuringiacus* (Kirste, 1919)). It may be distally thickened into a spatulate process (e.g. *Normalograptus wangjiawanensis* (Lin and Chen, 1984), Text-fig. 3E), branching at its base (e.g. *Normalograptus trifilis lubricus* (Chen and Lin, 1978)) or distally divided (e.g. *N. indivisus*, *N. radicans* (Chen and Lin, 1978)). *Hirsutograptus* is the only known Pattern H genus that commonly possesses spines on the sicular rim (Koren' and Rickards 1996). Species of this genus also possess a multiple-branching virgella and genicular spines on each theca. Several other normal Pattern H species, however, can occasionally be found with anomalous, spinose proximal ends. *Normalograptus serratus barbatus* (Elles and Wood, 1907) is the best known of these, although in the present collections spinose variants can also be found of *N. rectangularis* (M'Coy, 1850), *N. serus* (Obut and Sobolevskaya, 1968), *N. scalaris ferganensis* and *N. trifilis lubricus* (Text-fig. 3D, F-I).

Pattern I (tamariscus Pattern)

The sicula is commonly long in *Petalolithus* (1.4–3.2 mm) but is shorter in *Pseudorthograptus* and *Glyptograptus* (1.0–2.4 mm), very short (0.4 mm) in *Rivagraptus? bellulus?* (Törnquist, 1890) and *Rivagraptus? kayi* (Churkin and Carter, 1970), (Pl. 6, figs 12–13), and reduced to absent in the retiolitids. Theca 1¹ has a short descending segment and only a single foramen at its end, opening downward and sometimes obliquely to the reverse side (Pl. 4, figs 4, 12; Pl. 5, figs 3, 10; Pl. 6, fig. 7). The upward turn of th1¹ begins at or slightly below the sicular aperture and is sharp, with the obverse wall enclosing all or most of the descending portion (Pl. 4, fig. 12; Pl. 5, fig. 7). Occasional specimens can be seen where th1¹ turns upward above the sicular aperture (e.g. Hutt *et al.* 1970, pl. 1, fig. 10). Observations on the present material, however, suggest that this is the exception rather than the rule. The reverse wall of th1¹ grows upward and diagonally across the reverse side of the sicula. After this wall crosses the midline of the sicula, an interthecal septum appears differentiating the th1¹ metatheca from protheca 1² (Pl. 4, fig. 6; Pl. 5, fig. 7; Text-fig. 4C–D). The initial fusellae of th1² are conformable with those of th1¹ from which they emerge although they may be more condensed, interdigitate or curved at a different angle (Pl. 5, fig. 7; Pl. 6, fig. 8; Text-fig. 4C–D). The later growth of metatheca 1¹ and protheca 1² are more-or-less synchronous (Text-fig. 3K–M) and the growth of th1² is strongly upward. The differentiation of th1² is often quite late and it follows a pattern similar to that of all later thecae. Therefore, th1¹ is the only primordial theca and no crossing canal is present.

The proximal end is usually sharply pointed and a variable length of the sicula is exposed below th1². On the obverse side, all or a considerable portion of the sicula is usually exposed (Pl. 4, fig. 1; Pl. 5, figs 6, 8, 14), except in *Rivagraptus? bellulus?* and *R.? kayi* (Pl. 6, figs 6, 11–13). These species of *Rivagraptus?* differ from other petalolithids in having a very short sicula (0.4–0.5 mm long). The short, downward-growing portion of th1¹ near the sicular aperture, terminating in a single foramen, is a feature characteristic of Pattern I. Upward growth of th1¹ crosses both obverse and reverse side of the sicula at a high angle. The reverse wall almost completely obscures the sicula, leaving less than 0.1 mm exposed before turning upward and differentiating into theca 1². Only 0.1–0.2 mm of the sicula is exposed on the obverse side.

Pattern I rhabdosomes may be aseptate or have a narrow partial median septum on the obverse side (Pl. 4, fig. 2). In aseptate forms the virgula may be entirely free and central (Pl. 4, fig. 3; Pl. 5,



TEXT-FIG. 3. For caption see opposite.

fig. 12; Pl. 6, fig. 9), may be attached at the bases of the interthecal septa (Pl. 7, fig. 9) or it may be incorporated in the obverse wall (Pl. 5, figs 4, 6; Text-fig. 4c). However, it is important to note that none of the species known to possess Pattern I is fully septate or has a dicalycal theca. All show a single series of alternating thecae throughout the rhabdosome.

All of the known Pattern I species are Silurian with the exception of some reports of *Glyptograptus* and 'Orthograptus' from the *persculptus* Biozone (e.g. *Glyptograptus* ex gr. *G. tamariscus* from the *persculptus* Biozone of China (Li 1984); *Pseudorthograptus angustidens* from the *persculptus* Biozone of Arctic Canada (author's unpublished data)). Thecal forms ranging from climacograptid and pseudoglyptograptid to petalolithid are found in this group.

The sicular aperture possesses only a virgella, except in *Comograptus*, which has three or more spines emerging from the sicular rim normal to the sicular axis (Pl. 7, figs 7-8, 10-11). *Comograptus comatus* (Obut and Sobolevskaya, 1968) and *C.?* cf. *C.?* *tabukensis* also possess numerous spines on the proximal thecae (Text-fig. 3N, Q). The virgella may be greatly elongated (Pl. 6, figs 4, 10). The most elegant form of virgellar division is the ancora seen in the Retiolitidae and species of *Pseudorthograptus* and *Petalolithus*. Koren' and Rickards (1996) refer to this structure in non-retiolitid graptolites as a pseudoancora, distinguishing it from the ancora of the retiolitids (although they acknowledge that they may be homologous structures). However, the ultrastructural (e.g.

TEXT-FIG. 3. A-B, *Normalograptus* cf. *nikolayevi* (Obut, 1965); CM, 2-5 m. A, GSC104897; × 10. B, GSC104898; × 10. C, *Normalograptus normalis* (Lapworth, 1877); ROM45926; Troid Fiord, Ellesmere Island, NWT, 52.0 m (Melchin 1989); × 5. D, *Normalograptus scalaris ferganensis* (Obut, 1949); GSC104899; Troid Fiord, Ellesmere, Island, NWT, 61.0 m (Melchin 1989); note aberrant spine of sicular rim; × 5. E, *Normalograptus wangjiawanensis* (Lin and Chen, 1984); NI82790; × 5. F, *Normalograptus trifilis lubricus* (Chen and Lin, 1978); ROM45911; Truro Island, NWT, stream section, 52.0 m (Melchin *et al.* 1991); spinose variant; × 5. G, *Normalograptus serus* (Obut and Sobolevskaya, 1968); GSC104900; Truro Island, NWT, Stream Section, 62.0 m (Melchin *et al.* 1991); spinose variant; × 5. H-I, *Normalograptus rectangularis* (M'Coy, 1850); spinose variants; × 5. H, GSC104901; Huff Ridge, Ellesmere Island, NWT, 112.0-112.5 m (Melchin 1989). I, GSC104902; Troid Fiord, Ellesmere Island, NWT, 54.0 m (Melchin 1989). J, O, *Akidograptus gangjiawanensis* Ge; NI53998. J, enlargement of proximal end; × 10. O, × 5. K-M, *Glyptograptus tenuis* (Rickards, 1970); Troid Fiord, Ellesmere Island, NWT, 49.0 m (Melchin 1989); × 10. K, GSC104903. L, GSC104904. M, GSC104905. N, *Comograptus comatus* Obut and Sobolevskaya, 1968; GSC104906; Huff Ridge, Ellesmere Island, NWT, 118.5 m (Melchin 1989); × 5. P, *Glyptograptus tamariscus tamariscus* (Nicholson, 1868); GSC104907; Huff Ridge, Ellesmere Island, NWT, 118.5 m (Melchin 1989); × 10. Q, *Comograptus?* cf. *tabukensis* (Rickards and Koren', 1974); GSC104908; Troid Fiord, Ellesmere Island, NWT, 60.0 m (Melchin 1989); × 5. R, T, *Akidograptus parallelus* Li and Jiao; NI54215. R, enlargement of proximal end; × 10. T, × 5. S, U, *Akidograptus ascensus* Davies, 1929; Navan Borehole, Ireland, 759.6 m (Lenz and Vaughan 1994); × 10. S, TCD33912. U, TCD33913. V, *Parakidograptus acuminatus* (Nicholson, 1867); TCD33914; Navan Borehole, Ireland, 702.5 m (Lenz and Vaughan 1994); × 10. W, 'Akidograptus' *antiquus* Li and Ge, 1981; NI57678; very poorly preserved holotype specimen; × 10. X, *Parakidograptus primarius* Li; NI67279; × 10. Y, AA, *Dimorphograptus confertus swanstoni* Lapworth, 1876; GSC104909; Peel River, Yukon, 151.4 m (Lenz 1982). Y, enlargement of proximal end; × 10. AA, × 5. Z, *Dimorphograptus* cf. *minutus* (Chen and Lin, 1978); NI82806; × 10. BB-CC, *Dimorphograptus minutus* (Chen and Lin, 1978). BB, NI36082a; × 5. CC, GSC104909; Troid Fiord, Ellesmere Island, NWT, 56.5 m (Melchin 1989); enlargement of proximal end; × 10. DD, HH, *Agetograptus secundus* Obut and Sobolevskaya, 1968; Troid Fiord, Ellesmere Island, NWT, 61.0 m (Melchin 1989). DD, ROM45959; × 5. HH, GSC104910; × 10. EE, *Dimorphograptus decussatus partiliter* Elles and Wood, 1908; TCD33915; Navan Borehole, Ireland, 668.8 m (Lenz and Vaughan 1994); × 5. FF-GG, *Rhaphidograptus toernquisti* (Elles and Wood, 1906); TCD33916; Navan Borehole, Ireland, 666.0 m (Lenz and Vaughan 1994). FF, × 5. GG, enlargement showing sicular aperture and base of th¹; × 20. II, *Dimorphograptus decussatus decussatus* Elles and Wood, 1908; TCD33917; Navan Borehole, Ireland, 668.8 m (Lenz and Vaughan 1994); × 10. JJ-KK, *Pseudorthograptus? physophora alaskensis* (Churkin and Carter, 1970). JJ, GSC104911; Huff Ridge, Ellesmere Island, NWT, 112.5 m (Melchin 1989); × 10. KK, GSC104912; Troid Fiord, Ellesmere Island, NWT, 56.5 m (Melchin 1989); × 5. LL-MM, *Atavograptus primitivus* Li, 1983 (= *Pristiograptus antiquatus* Li, 1990); NI67315. LL, × 5. MM, enlargement of proximal end; × 10.

Bates and Kirk 1992) and phylogenetic evidence (Lenz and Melchin 1997) shows that these are, indeed, homologous structures, so there is no need for separate terms to distinguish them.

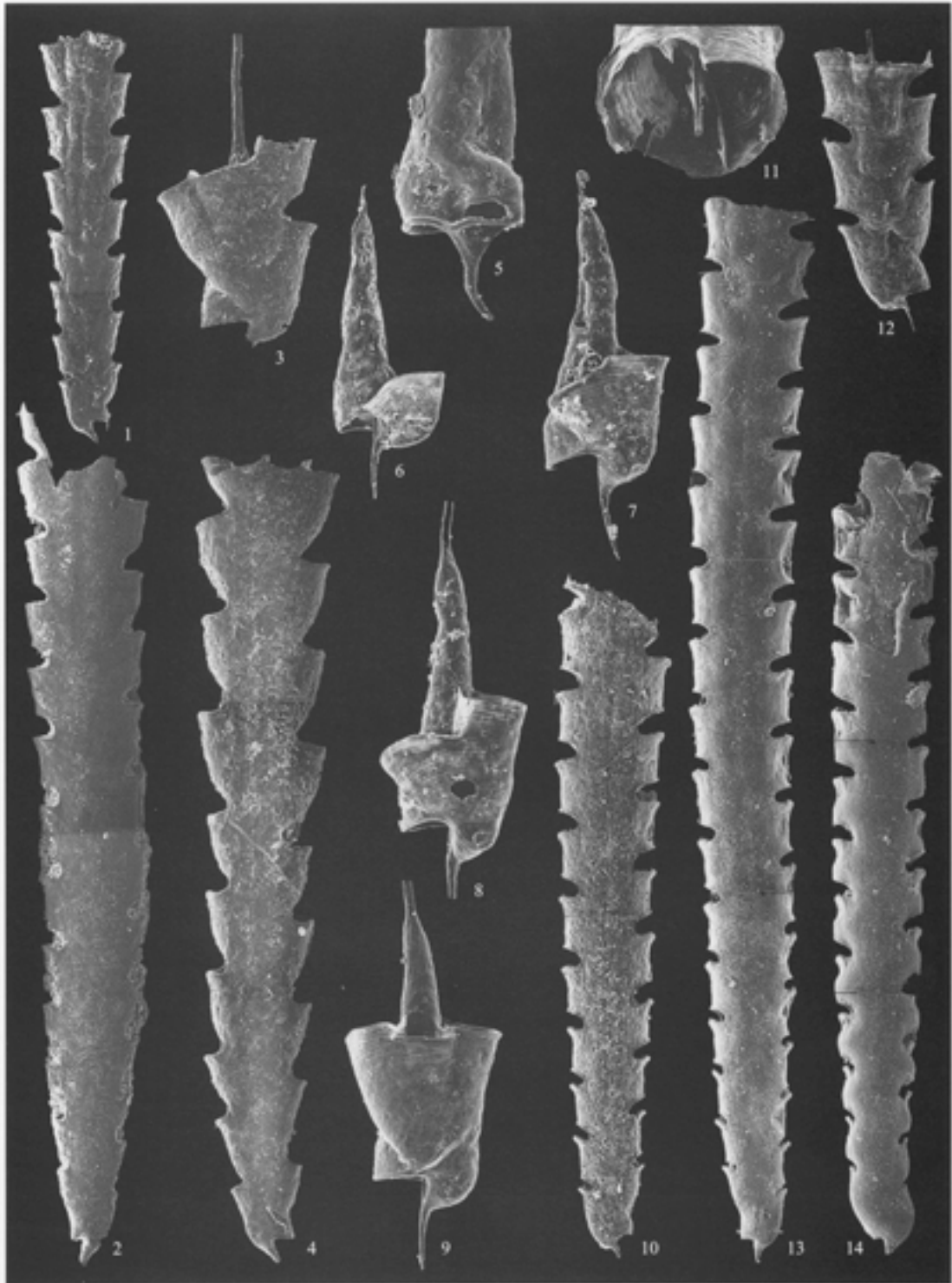
In *Pseudorthograptus* and *Petalolithus* the ancora ranges in form from a simple, four-pronged structure seen in such species as *Petalolithus ankyratus* (Mu, Li, Ge, Chen, Ni, Lin and Mu, 1974) (type 1 ancora of Bates and Kirk 1984 – see Pl. 4, fig. 5), to four prongs with a terminal loop and subsidiary loops and an internal spiral (type 3) as occurs in *Pseudorthograptus inopinatus* (Bouček, 1943) (Pl. 4, figs 7–8) and four prongs with long double spiral lists extending outward from the origin (type 2). The last is probably the type seen in *Pseudorthograptus obuti* (Rickards and Koren', 1974, figs 7–9; Koren' and Rickards 1996, text-fig. 15) and *Pseudorthograptus? physophora alaskensis* (Churkin and Carter, 1970) (Text-fig. 3JJ), and is also seen in *Pseudoretiolites* cf. *decurtatus* (Lenz and Melchin 1987a, pl. 1, figs 5, 8). Compressed specimens of *P. obuti* and *D. physophora* show that the more complex ancora types can enclose a considerable portion of the proximal end of the rhabdosome and may bear a sheet of continuous periderm between the ancora lists (Text-fig. 3KK; Rickards and Koren' 1974, pl. 1, fig. A; Koren' and Rickards 1996, text-figs 15J, 18C, 19A, D–E).

Pattern J (ascensus Pattern)

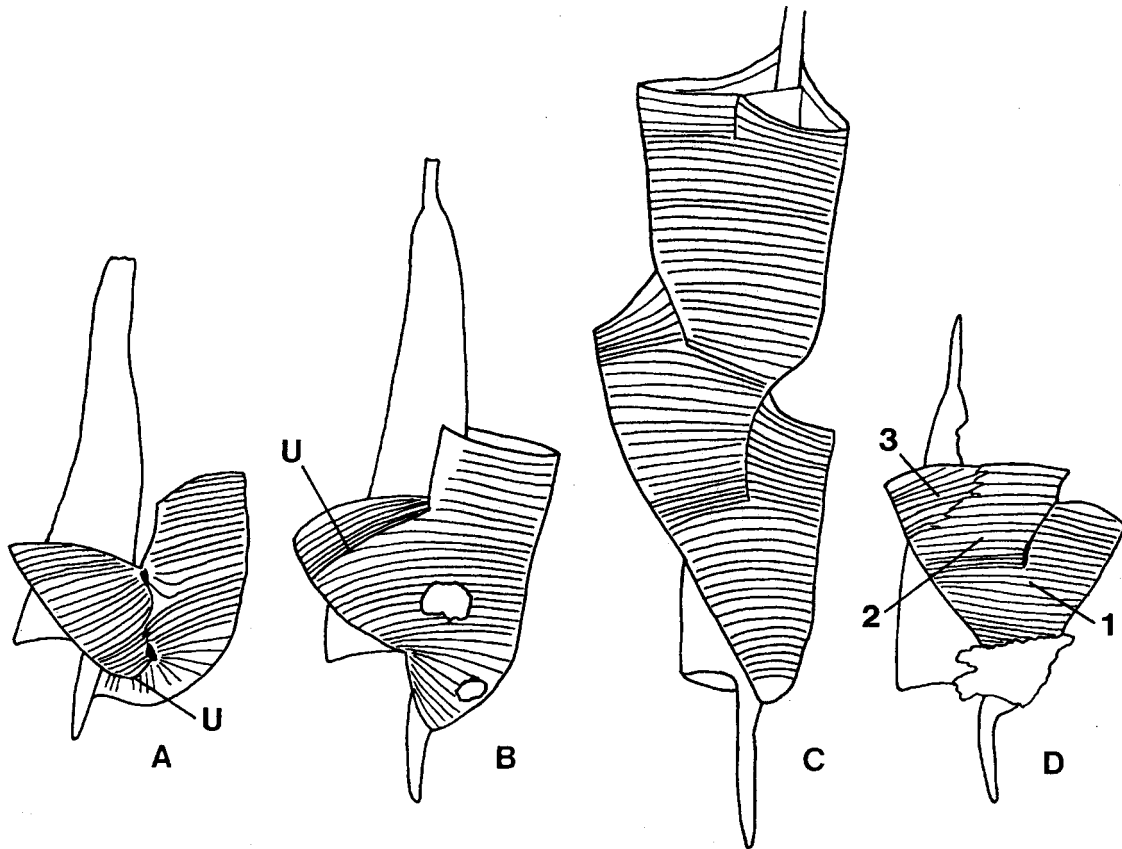
Although Mitchell recognized only nine distinct proximal growth patterns, an examination of the available literature and well-preserved, compressed dimorphograptids from Yukon, Arctic Canada and Ireland suggests that the proximal development of *Dimorphograptus (sensu stricto)*, *Akidograptus* and *Parakidograptus* shows significant differences from Pattern H or I. This has been designated Pattern J by Melchin and Mitchell (1991) (Text-fig. 2). Davies (1929) and Stein (1965) have illustrated well-preserved, early growth stages of *Akidograptus* that show a long sicula and a $th1^1$ with an exceedingly short downward-growing portion that does not reach the sicular aperture, followed by a long, straight upward growth. The reverse wall of $th1^1$ does not grow obliquely across the sicula at the beginning of the upward growth as in Pattern I species but grows straight upward for about half of the thecal length before the $th1^2$ bud begins to diverge. Well-preserved, uncompressed specimens of *Akidograptus* examined by Williams (1983) as well as the material studied by Li and Ge (1981) suggest that the metatheca 1^2 is not reduced, as suggested by Bulman (1970) and others, but that the growth series is of normal diplograptid type. Examination of well-preserved compressed specimens of several species of *Akidograptus* and *Parakidograptus* from China and Ireland shows that they all appear to share this early growth pattern (Text-fig. 3I, O, R–V, X).

EXPLANATION OF PLATE I

- Figs 1–3. *Normalograptus medius brevicaudatus* (Churkin and Carter, 1970). 1, GSC104816; CM, 2–5 m; $\times 12$. 2, GSC104817; CM, 2–5 m; $\times 12$. 3, GSC104818; CM, 0–2 m; $\times 40$.
- Figs 4–9. *Normalograptus nikolayevi* (Obut, 1965); CM, 0–2 m. 4, GSC104819; $\times 20$. 5, GSC104820; apertural half of sicula with descending portion of $th1^1$; note sinuous downward path and presence of two foramina, one opening downward for metatheca 1^1 , the other opening across the reverse side of the sicula for protheca 1^2 ; note also the list (list A) separating the foramina; $\times 100$. 6, GSC104821; sicula and early growth of metatheca 1^1 ; $\times 40$. 7, GSC104822; sicula and growth of metatheca 1^1 to point of differentiation of protheca 1^2 ; $\times 40$. 8, GSC104823; sicula and metatheca 1^1 with early growth of protheca 1^2 ; note complete dorsal wall of metatheca 1^1 against reverse side of sicula and fusellar unconformity at base of $th1^2$; $\times 40$. 9, GSC104824; completion of metathecae 1^2 and early growth of protheca 2^1 ; $\times 40$.
- Figs 10–14. *Pseudoglyptograptus barriei* Zalasiewicz and Tunnicliff, 1994; note the increasing degree of external thecal curvature and apertural lip development with increasing rhabdosomal maturity, fig. 14 being the most mature specimen; note also the more nearly climacograptid appearance of the more distal thecae. 10, GSC104825; CM, 5–7 m; $\times 12$. 11, GSC104826; CM, 5–7 m; distal end view showing complete median septum by $th2^2$; $\times 40$. 12, same as fig. 11, immature rhabdosome displaying nearly climacograptid thecae with only very weak apertural lip development; $\times 20$. 13, GSC104827; CM, 5–7 m; $\times 12$. 14, GSC104828; SC, 140 m; $\times 12$.



MELCHIN, *Normalograptus*, *Pseudoglyptograptus*



TEXT-FIG. 4. Drawings of early growth stage specimens showing fusellar growth patterns of the origin of the early thecae. Note that the Pattern H taxa (A–B) show a fusellar unconformity (U) at the point of origin of $th1^2$, whereas the Pattern I forms (C–D) show conformable fusellae at this point; all $\times 60$. A, *Metaclimacograptus orientalis* (Obut and Sobolevskaya, 1966); GSC104912; CM, 0–2 m. B, *Normalograptus nikolayevi* (Obut, 1965); GSC104823; CM, 0–2 m; note delayed position of $th1^2$ fusellar unconformity relative to that in *M. orientalis*. C, *Glyptograptus tamariscus tamariscus* (Nicholson, 1868); GSC104914; CM, 5–7 m. D, *Agetograptus spiniferus*, Obut and Sobolevskaya, 1968; GSC104915; CM, 5–7 m; fusellar pattern indicative of Pattern I', showing (1) first theca, (2), reversal of direction of growth of second thecae and (3) origin of the third theca.

Dimorphograptus shares two important features of the proximal development with *Akidograptus*: the downward growth of $th1^1$ is reduced and it does not reach the sicular aperture (the specimen identified as *Dimorphograptus* illustrated by Bulman 1970, fig. 61, is considered here to be a specimen of *Agetograptus* – see discussion below); the reverse wall of the upward-growing portion of $th1$ grows straight up, rather than diagonally crossing the reverse side of the sicula (Text-fig. 3Y, AA–CC, EE, II). This is, therefore, named Pattern J' and is considered a modification of Pattern J (Text-fig. 2).

The generic diagnosis of *Dimorphograptus* (Elles and Wood 1908; Bulman 1970) states that the growth of $th1$ is upward from its origin, although no evidence has been presented, based on well-preserved, early growth stages, to show that this is actually the case. Well-preserved, compressed, mature rhabdosomes of *Dimorphograptus confertus swanstoni* Lapworth, 1876 from the collections of Lenz (1982) from Yukon, Canada (Text-fig. 3Y), immature and mature specimens of *D. decussatus decussatus* Elles and Wood, 1908 and *D. decussatus partiliter* Elles and Wood, 1908 from the

collections of Lenz and Vaughan (1994) from the subsurface of Ireland (Text-fig. 3EE, II), and *D. minutus* (Chen and Lin, 1978) from China and the present collections (Text-fig. 3CC) shows what appears to be a very short, downward-growing portion pressed through the base of th1. This has been overgrown subsequently by cortical tissue obscuring the rounded appearance of the base of this theca. A drawing of an early growth stage of *Dimorphograptus* cf. *longissimus* (Kurck, 1882) illustrated by Elles and Wood (1908, text-fig. 232a) also shows what appears to be a short downward-growing portion and a distinctly rounded base to th1. More well-preserved specimens of other species of *Dimorphograptus* will have to be examined in detail to determine if they do, indeed, lack a downward growth portion or if it is merely obscured by later cortical material.

The question of number of primordial thecae among the Pattern J genera cannot be satisfactorily answered until isolated material becomes available. Mitchell (1987) has argued that the fact that the second theca in *Dimorphograptus* is redirected means that it is no longer primordial. In *Akidograptus*, the late derivation of the 1² from the upward-growing portion of th1¹ suggests that it, too, is no longer primordial. The insertion of the median septum between th2¹ and th2² indicates that th2¹ is the dicalycal theca rather than th1² as suggested by Li and Ge (1981), Štorch (1983a) and Li (1990).

Pattern J rhabdosomes show a wide range of thecal forms, especially in the uniserial portions of *Dimorphograptus*, including monoclinal or isolate thecae not found in other biserial graptolites. *Akidograptines* have a complete median septum as do all of the dimorphograptids observed by the author, in the biserial portion of the rhabdosome.

Ancora-like structures have been observed on species of *Akidograptus* and *Parakidograptus* but it is not clear if these are homologous with those of the Petalolithidae and the Retiolitidae or if they are independently derived, branching virgellae. Their less regular appearance, the variable distance between the sicular aperture and the first bifurcation and between the first and second bifurcations, and the fact that these structures grow outward and downward (e.g. Text-fig. 3J, o, R-U; Štorch 1983a, fig. 1B, H-I), but not upward toward the sicula, suggests that they may not be homologous. Furthermore, the akidograptines are confined to the highest Ashgill and lowest Llandovery *persculptus* and *acuminatus* biozones whereas ancora-bearing petalograptines are not known from strata lower than high in the *vesiculosus* Zone. Štorch (1983a, fig. 1E) also illustrates a specimen of *Parakidograptus acuminatus* that appears to show complex spines emerging from around the sicular aperture.

Although both patterns I and J show a short, downward-growing th1¹ and delayed differentiation of th1² (th2 in *Dimorphograptus*) there are several important features that distinguish them and suggest that they may be independently derived from Pattern H. In Pattern J species the first theca turns upward before reaching the sicular aperture and both the obverse and reverse walls grow straight upward for a significant distance before budding the second theca. In addition, all known Pattern I species are aseptate, lacking a dicalycal theca, whereas Pattern J species are fully septate.

Other 'dimorphograptid' patterns

There are several uni-biserial graptolite taxa that have been placed in the Dimorphograptidae but do not share many of the astogenetic features noted above.

Agetograptus. The genus *Agetograptus* Obut and Sobolevskaya, 1968 was erected to encompass several species with one uniserial theca. These species differ from other dimorphograptines in that the sicula is very short and not exposed for much of its length and that th1¹ is also very short. They pointed out very strong overall similarities with *Orthograptus bellulus* (designated by Koren' and Rickards (1996) the type species of *Rivagraptus*). Observations on the present specimens of *Agetograptus* have borne out the suggestions of the distinctness of this genus. As in *Rhaphidograptus* (and unlike *Dimorphograptus sensu stricto*), th1¹ grows down to or slightly below the sicular aperture and its upward growth is diagonally across the obverse and reverse face of the sicula (Pl. 7, fig. 2; Text-figs 3DD, HH, 4D). Unlike *Rhaphidograptus*, it is aseptate. Furthermore, the

downward-growing portion of $th1^1$ terminates in a single foramen (Pl. 7, fig. 5). These features clearly ally this genus with Pattern I species, particularly *Rivagraptus*, and this astogenetic pattern is named I' (Text-fig. 2).

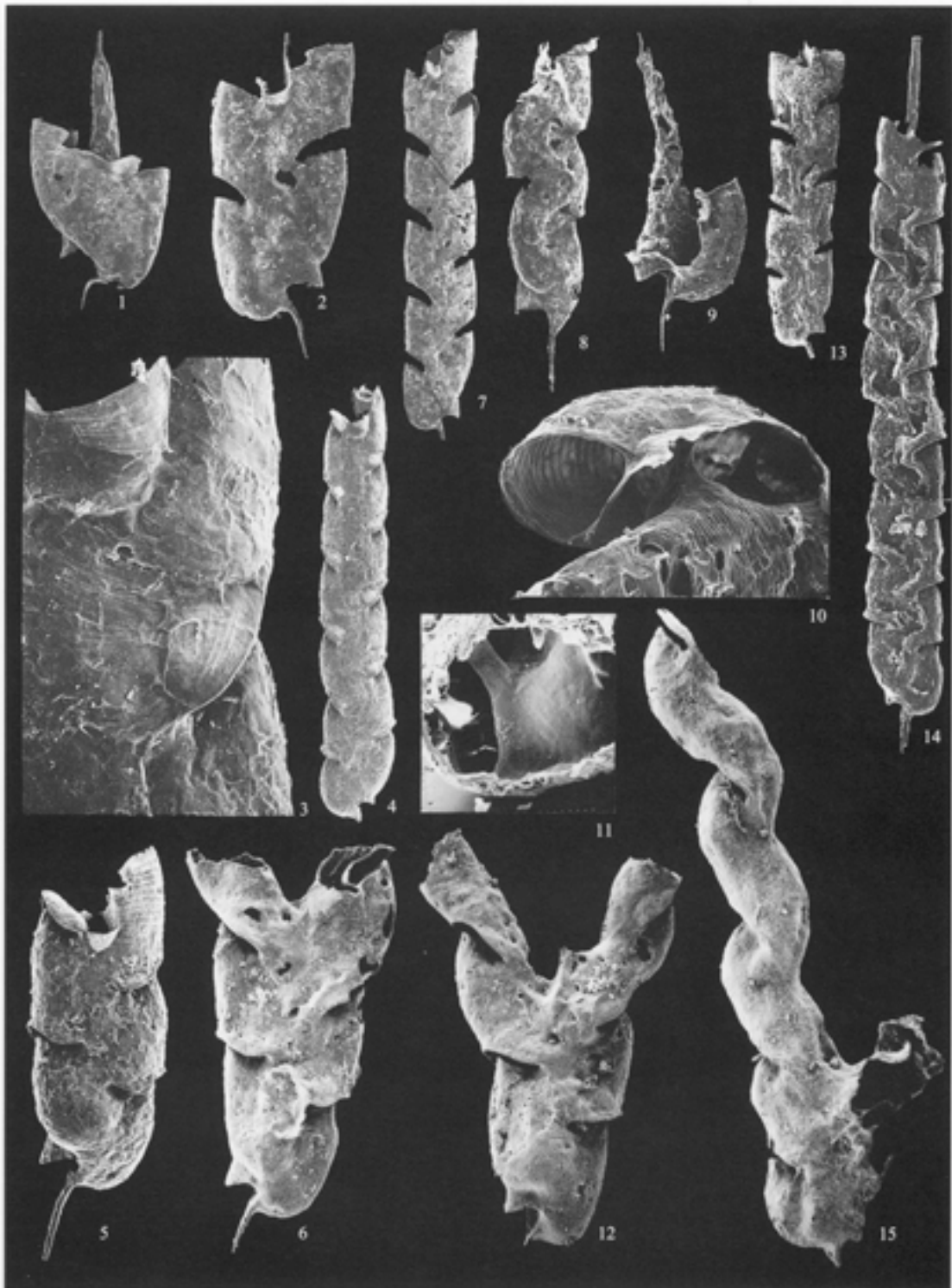
Loydell (1991) and Koren' and Rickards (1996) also recognized the distinctness of *Agetograptus* from *Dimorphograptus*. They suggested, however, that the appearance of a uniserial first theca was achieved by an elongation of theca 1^2 beyond the aperture of $th2^1$ with all subsequent series 2 thecae having their apertures above those of the succeeding thecae of the first series. *Agetograptus*, however, is aseptate and its thecae are alternate in origin throughout the length of the rhabdosome (Pl. 7, fig. 6). The geometry of a budding pattern as described by Loydell (1991) and Koren' and Rickards (1996) would, therefore, require that all subsequent series 2 thecae be significantly longer than their series 1 counterparts in order to keep the apertural levels evenly spaced, which is not seen in the present specimens. Therefore, the species of this genus must possess a truly uniserial theca 1.

An early growth stage specimen (Text-fig. 4D) shows a series of slightly condensed fusellae at the point of insertion of the dorsal wall of the first theca (i.e. the first interthecal septum) indicating the origin of the second theca. After another several fusellae are added to the second theca another divergence of fusellae occurs marked by lateral interdigitation and a change in angle. This appears to mark the differentiation of the third theca. In between the latter and $th1^1$ the fusellae continue, uncondensed and undistorted, suggesting that it is $th2^1$ that has emerged from $th1^1$. The uniserial condition appears to have been achieved by a redirection of the second theca over the top of the first rather than away from it and the resultant reversal of all subsequent thecae. A similar growth pattern has been described by Bulman (1970, p. V79, fig. 61) based on the illustration of a specimen of *Agetograptus* (identified as *Dimorphograptus* sp.) also from the Cape Phillips Formation, although Bulman did not recognize the short, downward growing portion of $th1^1$, which is completely obscured by that theca's upward growth (a number of specimens conspecific with the specimen illustrated by Bulman have been recovered from Cape Phillips Formation concretions that do show the short, downward-growing segment of $th1$). It is possible that in these specimens the uniserial appearance of the first theca is achieved through suppression, rather than redirection of the second metatheca, although the continuity of width and direction of fusellae seen in these specimens (not evident in Bulman's illustration) suggest that it is redirected rather than suppressed.

Rhaphidograptus. The proximal development of *Rhaphidograptus toernquisti*, has been illustrated by Hutt *et al.* (1970) and several well-preserved, compressed specimens from Bornholm and from

EXPLANATION OF PLATE 2

- Figs 1–2, 7. *Metaclimacograptus orientalis* (Obut and Sobolevskaya, 1966); CM, 0–2 m. 1, GSC104829; immature specimen showing early growth of $th2^1$; $\times 40$. 2, GSC104830; note incipient growth of $th3^1$; ventral wall proceeds slightly ahead of lateral walls; $\times 40$. 7, GSC104831; $\times 20$.
- Figs 3–5, 9–10. *Metaclimacograptus minimus* (Paškevičius, 1976); RC, 55–0 m. 3, GSC104832; aperture of $th5^2$; note the unconformable overgrowth of the lateral walls over the hood; $\times 120$. 4, same as fig. 3; $\times 20$. 5, GSC104833; note the ventral wall of $th3^2$ which forms an umbrella-hood over $th2^2$ aperture well in advance of the lateral thecal walls; $\times 40$. 4, $\times 20$. 9, GSC104834; broken early growth stage; $\times 40$. 10, same as fig. 9, oblique distal view showing base of interthecal septum, list B (centre) and silhouette of list A (right); $\times 120$.
- Figs 6, 11–12, 15. *Neodicellograptus siluricus* (Mu, Li, Ge, Chen, Ni, Lin and Mu, 1974); CM, 13–5 m. 6, GSC104835; $\times 40$. 11, GSC104836; oblique distal view of proximal end broken open showing internal view of descending protheca 1^1 with list A separating $th1^1$ and $th1^2$ foramina; $\times 125$. 12, GSC104837; $\times 40$. 15, GSC104838; $\times 30$.
- Fig. 8. *Metaclimacograptus sculptus* (Chen and Lin, 1978); GSC104839; CM, 5–7 m; $\times 20$.
- Figs 13–14. *Metaclimacograptus undulatus* (Kurck, 1882); SC, 140 m. 13, GSC104840; note less pronounced hood development than on more mature specimen in fig. 14; $\times 20$. 14, GSC104841; note angular median septum and somewhat more pronounced hoods proximally than distally; $\times 20$.

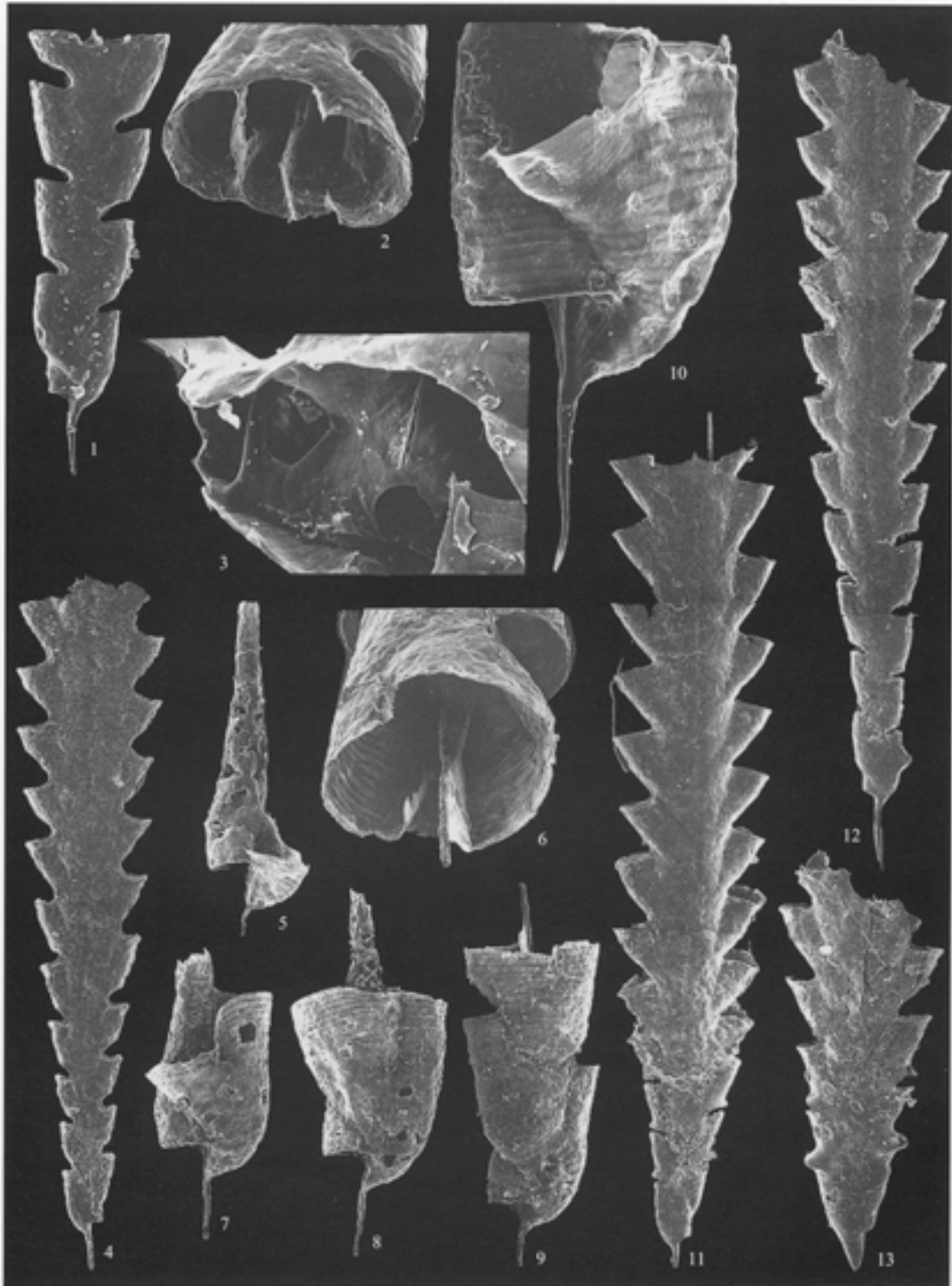


MELCHIN, *Metaclimacograptus*, *Neodicellograptus*

the subsurface of Ireland have been examined by the author. It differs from other dimorphograptids in the following respects: $th1^1$ grows down to or below the sicular aperture before turning upward; the base of $th1^1$ appears to show the rims of two foramina separated by a thickened list at the end of protheca 1^1 , pressed through the metatheca 1^1 that has grown over it (Text-fig. 3GG); the reverse wall of metatheca 1^1 shows some tendency to grow diagonally across the reverse and obverse face of the sicula as it grows upward (although this occurs at a low angle and may be within the range of variation of true dimorphograptid growth); and, the uniserial portion, as described by Hutt *et al.* (1970), is formed by growth of protheca 1^2 but suppression of the metatheca. Koren' and Rickards (1996) re-examined the evidence for suppression of $th1^2$ but were unable to substantiate that this was the mode production of the uniserial $th1$, suggesting that the other alternative was an unusually elongate $th1^2$. Although the same problems may apply for this proposed mode of development as suggested for *Agetograptus* above, the presence of dicalycal $th2^1$ make this suggestion at least possible for *Rhaphidograptus*. In either case, it is unlikely that this is the mode of formation of the uniserial portion in true dimorphograptids, which usually have more than one uniserial theca and whose lateral thecal walls do not cross the midline of the sicula or enclose the virgula in the uniserial portion. Rather, their uniserial portion is most probably formed by late differentiation and redirection of growth of the early thecae. If the uniserial portion of *Rhaphidograptus* is generated by suppression or elongation of metatheca 1^2 then it is most likely to have been derived independently of the true dimorphograptids, because the metatheca of the second theca is redirected rather than suppressed or elongated in Pattern J'. Furthermore, since $th1^1$ grows down to the sicular aperture in *Rhaphidograptus* the development of that genus from a true dimorphograptid ancestor would require a reversal of the trend toward upward growth above the sicular aperture seen in earlier dimorphograptids. On the other hand, derivation of *Rhaphidograptus* directly from a Pattern H ancestor would have required only suppression or elongation of metatheca 1^2 without any other major modifications. In fact, the proximal development of *R. toernquisti* bears a strong resemblance to that of *Neodiplograptus* with a delayed differentiation of $th1^2$ as well as a delayed $th2^1$ (Hutt *et al.* 1970, pl. 1, fig. 22). Although the delay of the first unconformity is slightly later than any observed here, the fusellar unconformity is more pronounced than is seen in Pattern I species and the rhabdosome shows other features that indicate associations with the other Pattern H species, especially a complete median septum distally and the presence of small genicular hoods, none of which has yet been found on any Pattern I species. The most compelling piece of evidence in favour of a Pattern H development in *Rhaphidograptus*, however, would be confirmation, in isolated specimens, of the presence of two terminal foramina on protheca 1^1 , as apparently seen pressed

EXPLANATION OF PLATE 3

- Figs 1–3, 10, 12. *Neodiplograptus tcherskyi tcherskyi* (Obut and Sobolevskaya, 1967). 1, GSC104842; CM, 0–2 m; $\times 20$. 2, same as fig. 1; distal end view showing partial median septum at fourth thecal pair; $\times 40$. 3, GSC104843; CM, 0–2 m; oblique internal view of proximal end broken open showing descending protheca 1^1 with list A and $th1^1$ and $th1^2$ foramina; $\times 135$. 10, GSC104844; CM, 5–7 m; proximal end of early growth specimen showing fusellae of $th1^1$, unconformity and closely packed fusellae at base of protheca 1^2 , and formation of list B; $\times 120$. 12, GSC104845; CM, 2–5 m; mature specimen with small, aberrant ridge on $th1^1$; $\times 12$.
- Figs 4–9, 13. *Neodiplograptus sinuatus sinuatus* (Nicholson, 1869). 4, GSC104846; CM, 2–5 m; $\times 12$. 5, GSC104847; RC, 55.0 m; sicula and early growth of $th1^1$; $\times 40$. 6, GSC104848; RC, 55.0 m; distal end view showing formation of partial median septum below apex of sicula; $\times 80$. 7, GSC104849; RC, 55.0 m; growth of metatheca 1^1 and protheca 1^2 ; $\times 40$. 8, GSC104850; RC, 55.0 m early growth stage with first thecal pair, note late differentiation of $th2^1$; $\times 40$. 9, GSC104851; RC, 55.0 m; immature rhabdosome showing growth of second thecal pair; $\times 40$. 13, GSC104852; CM, 5–7 m; gerontic specimen showing aberrant hood growth over proximal thecae; $\times 20$.
- Fig. 11. *Neodiplograptus tcherskyi* subsp. nov.; GSC104853; CM, 2–5 m; $\times 12$.



MELCHIN, *Neodiplograptus*

through here, a feature that clearly differentiates Pattern H from either I or J, in which the differentiation of the second theca occurs on the upward-growing portion of the first theca.

'*Dimorphograptus physophora physophora* (Nicholson, 1868) and '*D. physophora alaskensis* Churkin and Carter, 1970 appear to resemble species of *Pseudorthograptus* such as *P. obuti* (Rickards and Koren', 1974) in all respects of rhabdosomal and thecal form as well as possessing a large ancora (apparently type 2; Text-fig. 3JJ–KK) that suspends a continuous membrane. Unlike other species of *Dimorphograptus*, th1 grows down to the sicula aperture (Text-fig. 3JJ). Although no other astogenetic details can be discerned from the presently available material, this species has most probably developed directly from *Pseudorthograptus*, either by redirection or suppression of metatheca 1². Koren' and Rickards (1996) have also recognized the distinctness of '*D. physophora* ssp. from *Dimorphograptus* and their close relationship with *Pseudorthograptus* and assigned this species to the subgenus *Pseudorthograptus (Dimorphograptoides)*. *Dimorphograptoides* is here raised to the genus level because it is as distinctive in its rhabdosomal form from *Pseudorthograptus* as *Agetograptus* is from *Rivagraptus*.

It may be, therefore, that the 'dimorphograptid condition' of a uniserial proximal end may have been achieved in four different lineages (possibly more) as suggested by Rickards *et al.* (1977) and Li (1987), rather than one as suggested by Mitchell (1987). To derive the later occurring *Agetograptus*, *Rhaphidograptus* and *Pseudorthograptus? physophora* from *Dimorphograptus* would have required a reversal of the trends that resulted in the Pattern J proximal end as described above, and this seems highly unlikely. Confirmation of this hypothesis will require the study of isolated specimens of *Rhaphidograptus*, *Dimorphograptus sensu stricto* and *Dimorphograptoides*.

Pattern M (ceryx Pattern)

The astogeny of the uniserial monograptids, Pattern M, has been fully described by Walker (1953), Bulman (1970) and reviewed by Mitchell (1987). The unique astogeny of some of the earliest monograptids has been described by Lukasik and Melchin (1994, 1997).

Pattern R (new)

The lack of complete sclerotization in most retiolitids makes recognition of the astogenetic patterns difficult, although Lenz (1994) has described specimens of *Agastograptus robustus* Obut and Zaslavskaya, 1983 with fully sclerotized thecae and sicula. These specimens demonstrate that the thecal astogeny is essentially identical to Pattern I. However, the most distinguishing feature of all of the Silurian retiolitids is that they possess an ancora that is incorporated into the framework of the first thecal pair, and this is designated as Pattern R. This differentiates this group from any of the Ordovician 'archiretiolitids' (Mitchell 1987; Bates and Kirk 1991) or any of the ancora-bearing petalolithids.

EXPLANATION OF PLATE 4

- Figs 1–2, 4. *Petalolithus ankyratus* (Mu, Li, Ge, Chen, Ni, Lin and Mu, 1974); CM, 5–7 m. 1, GSC104854; × 20. 2, same as fig. 1, oblique distal view, virgula and partial median septum; × 160. 4, GSC104855; sicula and early growth of th1¹; × 25.
- Figs 3, 9–10. *Parapetalolithus* sp.; SC, 320 m. 3, GSC104862; distal end view; note lack of virgula, indicating that it was free and central; × 20. 9, GSC104861; immature rhabdosome; × 40. 10, same as fig. 3; × 20.
- Fig. 5. *Petalolithus intermedius* (Bouček and Příbyl, 1941a)?; GSC104856; RC, 55–0 m; sicula with descending portion of protheca 1¹, showing single terminal foramen; × 40.
- Figs 6–8, 11–12. *Pseudorthograptus inopinatus* (Bouček, 1943); CM, 2–5 m. 6, GSC1048857; immature specimen showing growth of first thecal pair; × 40. 7, GSC104858; sicula with ancora and early growth of th1¹; × 40. 8, GSC104859; immature rhabdosome; × 40. 11, GSC104860, distal fragment; × 20. 12, same as fig. 7; distal view of descending protheca 1¹ and single, terminal foramen; × 160.



MELCHIN, *Petalolithus*, *Pseudorthograptus*, *Parapetalolithus*

SYSTEMATIC PALAEONTOLOGY

Figured specimens in Plates 1–7 and Text-figure 4 are housed at the Geological Survey of Canada (GSC). Specimens illustrated in Text-figures 3 and 6 are housed at the GSC, the Royal Ontario Museum (ROM), the Nanjing Institute of Geology and Palaeontology (NIGP) and Trinity College, Dublin (TCD). Locality information for each figured specimen from Cornwallis Island is given as a locality abbreviation (see Text fig. 1), plus metres above the base of that locality section, or depth within in the borehole. Locality information for illustrated flattened specimens (Text-figs 3, 6) from other localities are given in captions, together with reference to the paper where the localities are described in detail. Locality details are not available for the Chinese specimens.

Order GRAPTOLOIDEA Lapworth, 1875

Suborder VIRGELLINA Fortey and Cooper, 1986

Superfamily DIPLOGRAPTOIDEA Lapworth, 1880, emend.

Remarks. Mitchell (1987) proposed that all Virgellina, with the exception of the stem group Phyllograptidae, be grouped into the superfamily Diplogrptoidea, and included all the Pattern H and I taxa, as well as the Silurian retiolitids and the uniserial monograptids, in the family Monograptidae. Aside from the aesthetic arguments against these family-level assignments (e.g. there are biserial Monograptidae), this has also posed practical problems for further subdivisions within the Monograptidae, and Loydell (1992) and Storch and Serpagli (1993) made a convincing case for making family-level subdivisions among Silurian graptoloids.

Despite the strong cladistic argument provided by Mitchell (1987) for inclusion of the uniserial 'monograptids' within the same clade as the Silurian biserial forms, Loydell (1992) and Koren' and Rickards (1996) retained a separate superfamily Monogrptoidea for the uniserial forms. Loydell cited the profound change in astogenetic pattern between the 'diplograptids' and 'monograptids' as the main reason for keeping the monograptids in a distinct superfamily. These changes, as described by Mitchell (1987), involved modifications in both sicular (e.g. the primary porus) and early thecal ontogeny. However, subsequently, Lukasik and Melchin (1994, 1997) demonstrated that the earliest monograptids differ only slightly from their biserial and uni-biserial ancestors in early astogeny, and that the significant changes in sicular ontogeny leading to development of the primary porus occurred during later monograptid evolution. On the other hand, Koren' and

EXPLANATION OF PLATE 5

- Figs 1–5. *Glyptograptus tamariscus tamariscus* (Nicholson, 1868). 1, GSC104863; CM, 2–5 m; mature rhabdosome with proximal end broken open; $\times 20$. 2, GSC104864; CM, 2–5 m; mature, partly compressed rhabdosome; $\times 20$. 3, same as fig. 1, aperture of sicula and short descending protheca 1¹ with single terminal foramen; $\times 160$. 4, GSC104865; CM, 5–7 m; distal end view showing laterally embedded virgula; note strong distal curvature of fusellae of obverse wall where they meet the virgula; $\times 60$. 5, same as fig. 4; distal fragment with long virgula; $\times 20$.
- Figs 6, 9. *Glyptograptus tamariscus acutus* Packham, 1962; RC, 55.0 m. 6, GSC104866; note complete exposure of sicula and curvature of fusellae on obverse wall at virgula; $\times 40$. 9, GSC104867; immature rhabdosome; $\times 40$.
- Figs 7–8, 11–12, 14. *Glyptograptus cf. fastigatus* Haberfelner, 1931; MP (loose). 7, GSC104868; proximal half of early growth stage showing fusellar differentiation of protheca 1² and metatheca 1¹; $\times 80$. 8, GSC104869; immature specimen in obverse view showing enclosure of sicula; $\times 40$. 11, same as fig. 8; distal end view; $\times 80$. 12, GSC104870; same as fig. 14; distal end view, showing free, central virgula; $\times 80$. 14, GSC104871; immature specimen; $\times 40$.
- Figs 10, 13. *Glyptograptus elegans* subsp. nov.; MP (loose). 10, GSC104872; early growth stage specimen showing aperture of sicula and descending portion of protheca 1¹; note single foramen; $\times 120$. 13, GSC104873; immature rhabdosome; $\times 40$.



MELCHIN, *Glyptograptus*

Rickards (1996) cited biostratigraphical and nomenclatural practicality as the main reasons for complete separation of the monograptoids from the diplograptoids. Whereas the practical need to distinguish several families with the Silurian graptoloids, including a distinct, fully uniserial Monograptidae, is clear, the necessity for distinction of the 'monograptids' at the superfamily level is not, particularly in relation to the subdivision of the rest of the Graptoloidea. Although Loydell (1992) and Koren' and Rickards (1996) employed the phylogenetic classification of Fortey and Cooper (1986) and Mitchell (1987) at the level of suborder, they departed from the cladistically derived classification at the level of superfamily and below, resulting in a classification hierarchy of Silurian graptoloids that is inconsistent with that of the rest of the Graptoloidea. Further changes in superfamily-level classification of the graptoloids should await a more comprehensive phylogenetic restudy of both the Ordovician and Silurian clades, in light of all of the new data that have come to light since 1987. For this paper, all of the Silurian graptoloid taxa are included within the Diplograptoloidea, as proposed by Mitchell (1987), but are subdivided into several families as described below.

Fortey and Cooper (1986) published the name Glyptograptidae (citing Mitchell, then in press, as the author although Mitchell did not, in his 1987 paper use this taxon at the family level) to encompass the Pattern B, H and I genera. This name was based on Mitchell's (1987) work which suggested that *Glyptograptus* was a Pattern H genus. Accordingly, a subfamily, namely Glyptograptinae, was erected to encompass the Pattern H species. Recognizing that the type species of *Glyptograptus*, *G. tamariscus* (Nicholson, 1868), exhibits a Pattern I proximal structure, Melchin and Mitchell (1991) placed the Pattern H-bearing species with climacograptid to glyptograptid thecae within *Normalograptus* Legrand, 1987. Mitchell placed the Pattern I species with the 'retiolitids' in the Retiolitinae.

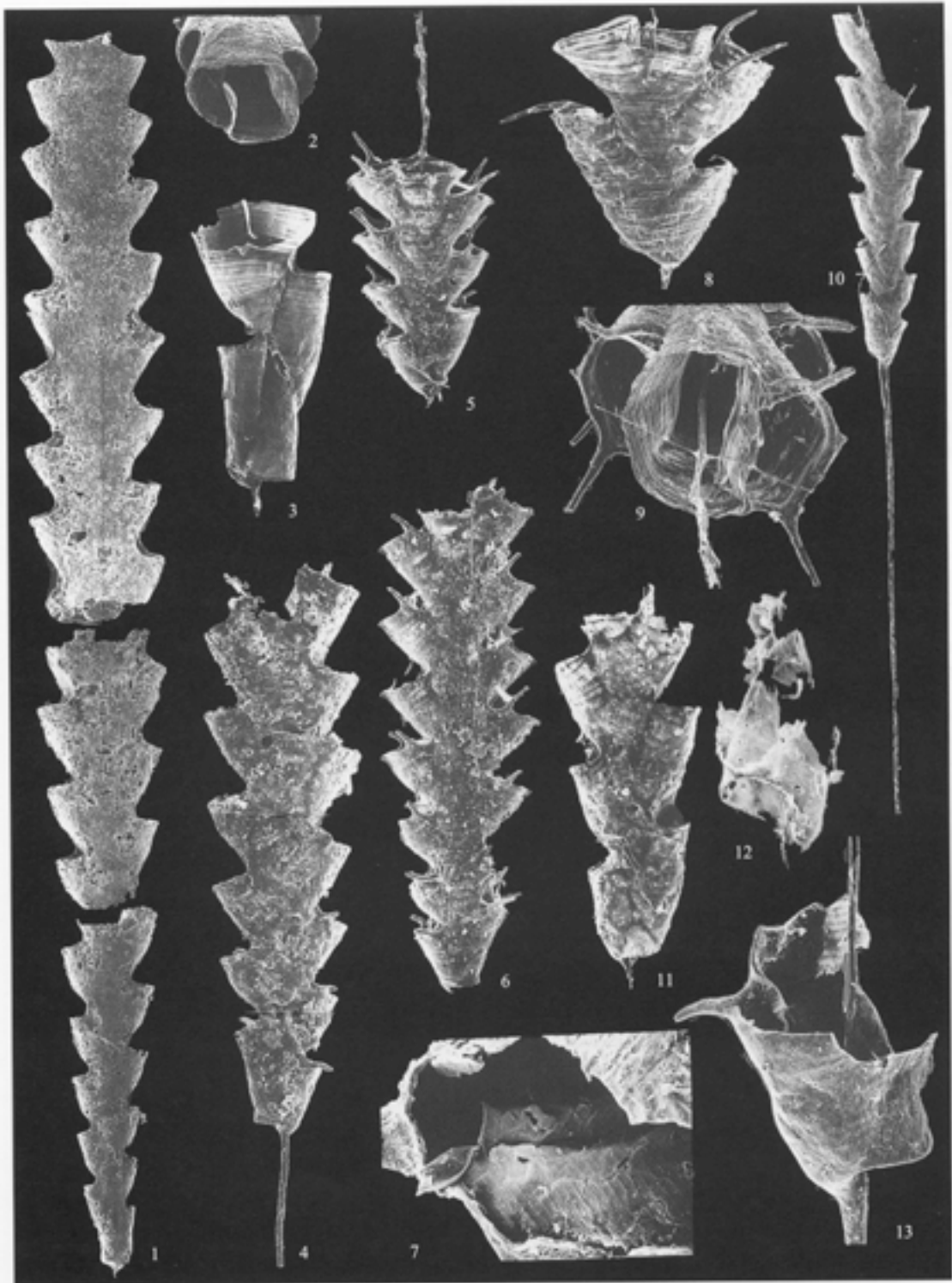
Loydell (1991) employed the subfamilies Glyptograptinae, Retiolitinae, and Monograptinae, all within the family Glyptograptidae. Loydell (1992) raised the three subfamilies to the level of family: Glyptograptidae, Retiolitidae, and Monograptidae, the latter being assigned to the superfamily Monograptoloidea, as noted above. Loydell (1992) included all Pattern H and continuous-periderm Pattern I taxa within the Glyptograptidae, although Petalolithidae (originally erected as the subfamily Petalograptinae Bulman, 1955) is the family-group name that has priority for this taxon, since it includes *Petalolithus* (the senior synonym of *Petalograptus* (see Loydell 1992)).

Storch and Serpagli (1993) also recognized the need for more family-level taxa and distinguished four families among Silurian graptoloids: Normalograptidae (Pattern H taxa), Retiolitidae (Pattern I taxa, with subfamilies Petalograptinae and Retiolitinae), Dimorphograptidae (Pattern J taxa, with subfamilies Akidograptinae and Dimorphograptinae), and Monograptidae (uniserial taxa). They did not explicitly assign these families to any higher-level taxa.

Koren' and Rickards (1996) noted that the differences between the astogenetic patterns of Silurian diplograptoids are small compared with those of Ordovician taxa. As a result, they

EXPLANATION OF PLATE 6

- Figs 1–3. *Glyptograptus elegans* subsp. nov. 1, GSC104874; SC, 260 m; mature rhabdosome that broke into three fragments; $\times 20$. 2, same as fig. 1; distal end view of the proximal fragment; note lack of virgula, indicating that it was free and central; $\times 40$. 3, GSC104875; MP (loose); $\times 40$.
- Figs 4–9, 13. *Rivagraptus? bellulus?* (Törnquist, 1890). 4, GSC104876; CM, 2–5 m; note decreasing degree of spine development distally; $\times 20$. 5, GSC104877; CM, 5–7 m; obverse view; note rapid enclosure of sicula; $\times 20$. 6, GSC104878; CM, 5–7 m; $\times 20$. 7, GSC104879; CM, 2–5 m; view inside broken proximal end showing very sort descending protheca ¹ with single terminal foramen; $\times 160$. 8, GSC104880; CM, 5–7 m; immature rhabdosome; $\times 40$. 9, same as fig. 13; distal end view showing interthecal septa and free, central virgula; $\times 40$. 13, GSC104881; CM, 2–5 m; broken proximal fragment showing very short sicula; $\times 60$.
- Figs 10–12. *Rivagraptus? kayi* (Churkin and Carter, 1970); CM, 5–7 m. 5, GSC104882; $\times 12$. 11, GSC104883; broken proximal end of immature specimen, showing very short sicula; $\times 60$. 12, GSC104884; obverse view showing rapid enclosure of sicula; $\times 30$.



MELCHIN, *Glyptograptus*, *Rivagraptus*?

followed Loydell (1992) and included most of the Pattern H (*normalis* Pattern) and Pattern I (*tamariscus* Pattern) genera within the Glyptograptidae. Of the Pattern H and I genera, only *Metaclimacograptus* was removed from the Glyptograptidae and assigned to its own family, Metaclimacograptidae, citing 'spectacular morphological changes' that had taken place within this lineage. Whereas the thecal and rhabdosomal style are, indeed, distinctive for *Metaclimacograptus*, they seem to be no less differentiated from their *Normalograptus* roots than, for example, *Petalolithus*, *Cephalograptus*, *Pseudorthograptus* or *Agetograptus*, which show significant changes in both thecal and developmental style from *Normalograptus*. Although it is true that the range of variability in astogenetic patterns is not as great in Silurian taxa as in Ordovician forms (Koren' and Rickards 1996), the fact remains that, based on present evidence, the Pattern I development appears to have arisen only once, in which case all of the taxa bearing this pattern represent a monophyletic group. Therefore, it provides a consistent means of establishing the phylogenetic relationships among the Silurian biserial genera and grouping them at the family level in a way that is consistent with the classification of other diplograptoids.

A cladogram illustrating the proposed relationships between the Silurian graptoloid families is shown in Text-figure 5, including the synapomorphies that characterize each branching event. Although it is based to a large extent on text-figures 13A and 16 of Mitchell (1987) it incorporates the observations and modifications discussed above and in the following descriptions. Table 1 summarizes the classification employed.

Family NORMALOGRAPTIDAE Štorch and Serpagli, 1993

Diagnosis. Pattern H (*normalis*) primordial astogeny. Thecae glyptograptid, climacograptid, pseudoclimacograptid or sinuous. Median septum complete distally, and straight or undulose. Stipes rarely diverge distally.

Genera included. *Normalograptus* Legrand, 1987, *Clinoclimacograptus* Bulman and Rickards, 1968, *Cystograptus* Hundt, 1942, *Hirstuograptus* Koren' and Rickards, 1996, *Metaclimacograptus* Bulman and Rickards, 1968, *Neodicellograptus* Mu and Wang, 1977, *Neodiplograptus* Legrand, 1987, '*Neodiplograptus*' ex gr. '*N. modestus*', *Persculptograptus* Koren' and Rickards, 1996, *Pseudoglyptograptus* Bulman and Rickards, 1968, *Rhaphidograptus* Bulman, 1936, *Talacastograptus* Cuerda, Rickards and Cingolani, 1988 and possibly *Paraclimacograptus* Přibyl, 1947.

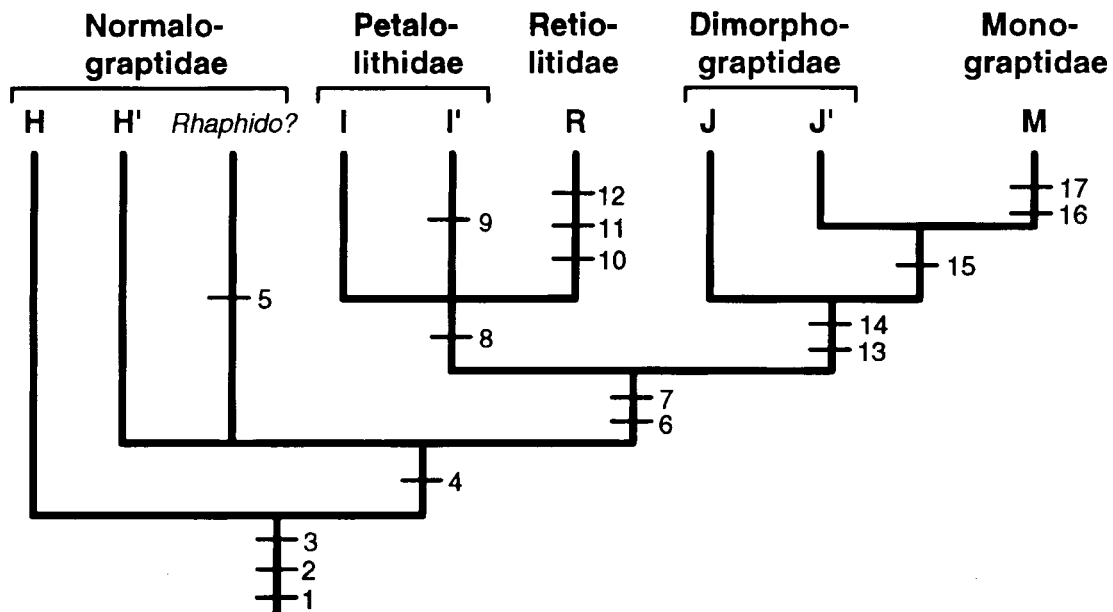
Remarks. Although the details of proximal development of *Normalograptus normalis* (the type species of *Normalograptus*) are not known from uncompressed, isolated specimens, the very close

EXPLANATION OF PLATE 7

- Figs 1–3, 5–6. *Agetograptus spiniferus* Obut and Sobolevskaya, 1968. 1, GSC104885; CM, 2–5 m; × 12. 2, GSC104886; CM, 2–5 m; × 20. 3, GSC104887; CM, 2–5 m; obverse view showing enclosure of sicula; × 20. 5, GSC104888; CM, 2–5 m; view inside of proximal end of broken specimen showing very short descending protheca 1^1 with single terminal foramen; × 120. 6, GSC104889; SC, 140 m; distal fragment showing internal arrangement of intertheal septa; × 12.
- Fig. 4. *Agetograptus? hubeiensis* (Ni, 1978); GSC104890; RC, 80–105 m; reverse view of immature rhabdosome; × 40.
- Figs 7–13. *Comograptus gorbiachinensis* Obut and Sennikov, 1980; CM, 0–2 m. 7, GSC104891; mature rhabdosome; × 20. 8, GSC104892; immature rhabdosome; × 20. 9, GSC104893; distal end view showing virgula attached to base of intertheal septum; × 60. 10, GSC104894; proximal end view of immature specimen showing three sicular apertural spines and virgella; × 80. 11, GSC104895; immature rhabdosome showing differentiation of $th2^1$; × 40. 12, same as fig. 10; sicula and $th1^1$ to point of differentiation of $th1^2$; × 40. 12, GSC104896; sicula and early growth of $th1^1$; note short descending protheca 1^1 and that spines on either side of virgella are not yet formed; × 40.



MELCHIN, *Agetograptus*, *Agetograptus?*, *Comograptus*



TEXT-FIG. 5. Cladogram illustrating proposed relationships within the Silurian Diplograptidae. Terminal branches are identified according to astogenetic pattern, except for *Rhaphido?*, which represents the possible astogeny for *Rhaphidograptus toernquisti* (Elles and Wood, 1906). Numbered synapomorphies are as follows: (1) origin of $th1^2$ delayed until downward end of protheca 1^1 ; (2) $th1^2$ begins growth upward and outward, unconformably on $th1^1$; (3) protheca 1^1 partly enclosed by metatheca 1^1 ; (4) delay in differentiation of $th2^1$ – no longer primordial; (5) metatheca 1^2 suppressed giving a uniserial appearance to $th1^1$; (6) short descending protheca 1^1 with only one terminal foramen – $th1^2$ no longer primordial; (7) potential for ancora production; (8) loss of dicalycal theca and complete median septum; (9) $th1^2$ reoriented to grow over $th1^1$ giving a uniserial proximal end; (10) reduction or complete desclerotization of the sicula; (11) reduction of thecal periderm to thecal framework and reticulum; (12) integration of ancora with framework of first thecal pair; (13) downward growth of protheca 1^1 reduced leaving sicula exposed for its full circumference near its aperture; (14) reverse wall of first theca grows straight upward for much of its length before budding second theca; (15) reorientation of one or more thecae above $th1$ producing a uniserial proximal end; (16) $th1$ grows outward and upward from its origin (may no longer be primordial); (17) rhabdosome uniserial throughout its length.

similarities in both thecal and rhabdosomal morphology with other, better known species of *Normalograptus* (e.g. *N. aff. N. scalaris*, Barrass 1954, here assigned to *N. scalaris ferganensis*; *N. medius brevicaudatus*, this study) strongly suggests that their proximal development pattern is also the same.

Based on presently available information, it is not possible to determine whether species of the genus *Paraclimacograptus* possess a Pattern H or I astogeny. If they have Pattern I development, this genus should be included within the Petalolithidae. Mitchell (1987) and Štorch and Serpagli (1993) suggested a Pattern H astogeny. However, the uncompressed specimen of *P. innotatus innotatus* illustrated by Crowther (1981) has only a partial median septum at the fourth thecal pair (Crowther, pers. comm. 1986), and a complete median septum is not visible distally in any of the compressed specimens studied by the author (e.g. Text-fig. 6A). The relatively acicular proximal end is within the range of variation of both Pattern H and I forms.

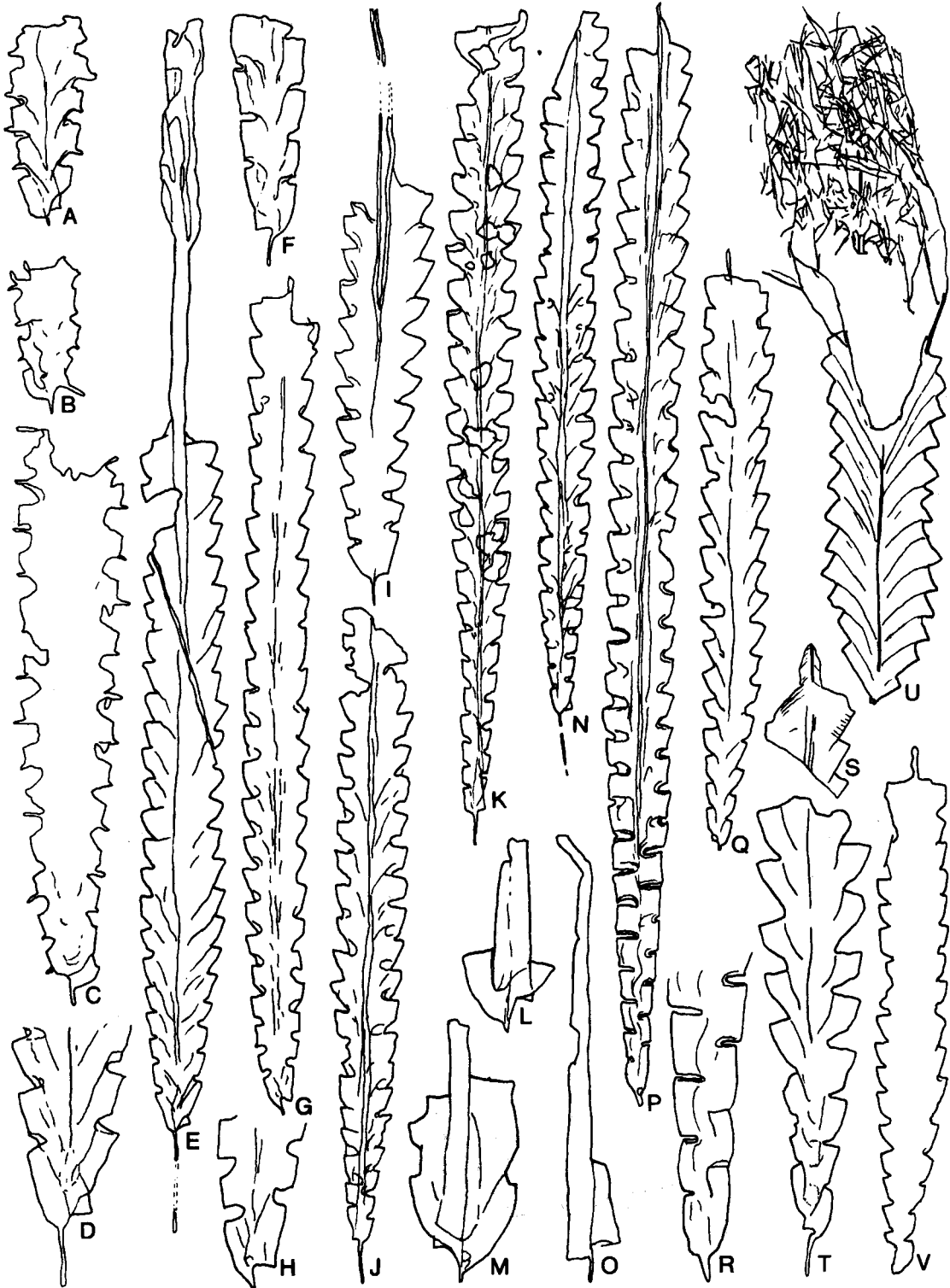
Riva (1988) illustrated a topotype specimen of *P. innotatus innotatus* that shows what appears to be an antivirgellar spine. Accordingly, he grouped several other mid Ashgill species with genicular hoods and antivirgellar spines within *Paraclimacograptus*. Judging from other topotype material as well as the numerous other observations of this species from around the world, including the uncompressed specimen illustrated by Crowther (1981), all of which lack any proximal spines

TABLE 1. Proposed classification for the Silurian Diplogrptoidea.

Order GRAPTOLOIDEA
 Suborder VIRGELLINA Fortey and Cooper, 1986
 Superfamily DIPLOGRAPTOIDEA Lapworth, 1873 (*sensu* Mitchell, 1987)
 Family NORMALOGRAPTIDAE Štorch and Serpagli, 1993: Pattern H
 Genus NORMALOGRAPTUS Legrand, 1987
 Genus PSEUDOLYPTOGRAPTUS Bulman and Rickards, 1968
 Genus METACLIMACOGRAPTUS Bulman and Rickards, 1968
 Genus CLINOCLIMACOGRAPTUS Bulman and Rickards, 1968
 Genus TALACASTOGRAPTUS Cuerda, Rickards and Cingolani, 1988
 Genus HIRSUTOGRAPTUS Koren' and Rickards, 1996
 Genus NEODICELLOGRAPTUS Mu and Wang, 1977
 Genus NEODIPLOGRAPTUS Legrand, 1987
 'Neodiplograptus' modestus Lapworth species group
 Genus CYSTOGRAPTUS Hundt, 1942
 ?Genus RHAPHIDOGRAPTUS Bulman, 1936
 Family PETALOLITHIDAE Bulman, 1955 (emend.): Pattern I
 Genus PETALOLITHUS Suess, 1851
 Genus PARAPETALOLITHUS Koren' and Rickards, 1996
 Genus CEPHALOGRAPTUS Hopkinson, 1869
 Genus SUDBURIGRAPTUS Koren' and Rickards, 1996
 Genus PSEUDORTHOGRAPTUS Legrand, 1987
 Genus DIMORPHOGRAPTOIDES Koren' and Rickards, 1996
 Genus RIVAGRAPTUS Koren' and Rickards, 1996
 Genus AGETOGRAPTUS Obut and Sobolevskaya, 1968
 Genus GLYPTOGRAPTUS Lapworth, 1873
 Genus COMOGRAPTUS Obut and Sobolevskaya, 1968
 ?Genus PARACLIMACOGRAPTUS Pířbyl, 1947
 ?Genus VICTOROGRAPTUS Koren' and Rickards, 1996
 ?Genus CORBOGRAPTUS Koren' and Rickards, 1996
 Family RETIOLITIDAE Lapworth, 1873: Pattern R
 Subfamily RETIOLITINAE Lapworth, 1873
 Subfamily PLECTOGRAPTINAE Bouček and Münch, 1952
 Family DIMORPHOGRAPTIDAE Elles and Wood, 1908: Pattern J
 Subfamily AKIDOGRAPTINAE Li and Ge, 1981
 Genus AKIDOGRAPTUS Davies, 1929
 Genus PARAKIDOGRAPTUS Li and Ge, 1981
 Subfamily DIMORPHOGRAPTINAE Elles and Wood, 1908
 Genus DIMORPHOGRAPTUS Lapworth, 1876
 Family MONOGRAPTIDAE Lapworth, 1873: all scandent, uniserial forms.

except the virgella, this one specimen that appears to possess an antivirgellar spine is either an artefact of preservation or an anomalous specimen. Spinose variants have been reported among other Pattern H species (e.g. *Normalograptus serratus barbatus*, *N. medius* (Elles and Wood 1906, p. 189), *N. rectangularis* and *N. scalaris ferganensis* from the study material; Text-fig. 3E, H-I). As noted above, species of *Hirsutograptus* possess spines on the sicular margin but their variable number and distribution suggests that these are not homologous with the true antivirgellar spines seen in patterns F, G and K (Mitchell 1987; Melchin and Mitchell 1991).

Among the other species grouped by Riva (1988) in *Paraclimacograptus* are '*P.* *decepiens* Riva, 1988 and '*P.* *manitoulinensis* (Caley, 1936). Specimens of '*P.* *manitoulinensis* from the type locality on Manitoulin Island, Ontario have been examined by the author and these clearly possess a Pattern G primordial astogeny (Text-fig. 6B-C) and, as a result, are more closely allied with *Amplexograptus* (*sensu* Mitchell 1987) than with *Paraclimacograptus*. The specimens of '*P.*



TEXT-FIG. 6 For caption see opposite.

decipiens illustrated by Riva (1988, fig. 2o–s) have been examined by the author; they possess a Pattern K (Melchin and Mitchell 1991) astogeny.

The taxon originally described as *Climacograptus innotatus nevadensis* Carter, 1972 was considered by Riva (1988) to be more closely allied with *Climacograptus tubuliferus* Lapworth than with *Paraclimacograptus* and was questionably placed as a distinct species in the genus *Normalograptus* by Riva and Ketner (1989). As noted below, *C. tubuliferus* and *C. nevadensis* are here regarded as more probably belonging to the genus *Climacograptus sensu* Mitchell (1987) or *Ensigraptus* Riva, in Riva and Ketner, 1989.

Genus NORMALOGRAPTUS Legrand, 1987, emend.

Type species. *Normalograptus normalis* Lapworth, 1877.

Diagnosis. Pattern H species with (usually) unornamented climacograptid to glyptograptid thecae. Proximal end relatively narrow, rounded and asymmetrical with strongly alternating thecae. Median septum straight and complete, with th² or some later theca dicalyca.

Species included. Among the species assigned to this genus typical forms include *Normalograptus normalis* (Lapworth, 1877) (Text-fig. 3D), *N. medius brevicaudatus* (Churkin and Carter, 1970) (Pl. 1, figs 1–3), *N. brevis* (Elles and Wood, 1906) (see e.g. Finney 1986), *N. extraordinarius* (Sobolevskaya, 1974) (see e.g. Williams 1983), *N. trifilis lubricus* (Chen and Lin, 1978), *N. euglyphus* (Lapworth) (see e.g. Finney 1986), and *N. nikolayevi* (Obut, 1965) (Pl. 1, figs 4–9).

Remarks. As noted by Melchin and Mitchell (1991) there seems to be a morphological continuum between species with climacograptid thecae and those with glyptograptid thecae within both the Ordovician and Silurian lineages of this subfamily. This especially seems to be true in the Ordovician–Silurian boundary species of the *N. ojsuensis*–*N. extraordinarius* group. Until much more information is available concerning the boundary-interval species and many of the older Early Llandovery Pattern H species with glyptograptid thecae, it seems prudent to include both here within an expanded *Normalograptus*.

Melchin and Mitchell (1991) also assigned to *Normalograptus* several species previously assigned to *Diplograptus*, in particular the '*D.* *modestus*' group. They argued that these species were distinct

TEXT-FIG. 6. A, *Paraclimacograptus innotatus innotatus* (Nicholson, 1869); GSC104916; Huff Ridge, Ellesmere Island, NWT, 112.5 m (Melchin 1989); × 10. B–C, *Amplexograptus manitoulinensis* (Caley, 1936); type locality, Manitoulin Island (Caley 1936); × 10. B, GSC104917. C, GSC104918. D–E, '*Neodiplograptus*' *modestus modestus* (Lapworth, 1876); ROM45921; Troid Fiord, Ellesmere Island, NWT, 52.0 m (Melchin 1989). D, enlargement of proximal end; × 10. E, × 5. F, K, *Neodiplograptus?* *elongatus* (Churkin and Carter, 1970); Twilight Creek, Bathurst Island, NWT, 13.5 m (Melchin 1989). F, GSC104919; × 10. K, ROM45941; × 5. G–I, '*Glyptograptus bohemicus*' Marek, 1955 (= *Normalograptus* cf. *N. ojsuensis* (Koren' and Mikhaylova, in Koren' et al., 1980)). G, GSC104815, Truro Island, NWT, borehole, 42.8 m (Melchin et al. 1991); × 5. H, same specimen as G, enlargement of proximal end; × 10. I, NI82229, × 5. J, N, *Neodiplograptus?* cf. *elongatus* (Churkin and Carter, 1970); Troid Fiord, Ellesmere Island, NWT, 63.0 m (Melchin 1989); × 5. J, GSC104920. N, GSC104921. L–M, O, *Cystograptus vesiculosus* (Nicholson, 1868); Navan Borehole, Ireland, 620.5 m (Lenz and Vaughan 1994); early growth stages; × 10. L, TCD33918. M, TCD33919. O, TCD33920. P, R–S, *Neodiplograptus?* sp. nov.; Twilight Creek, Bathurst Island, NWT, 13.5 m (Melchin 1989). P, ROM45942. R, GSC104922; enlargement of proximal end; × 10. S, GSC104923; distal end; × 5. Q, T, *Neodiplograptus sinuatus sinuatus* (Nicholson, 1869). Q, NI35904a; × 5. T, NI35909a; × 10. U, *Dischodograptus mirabilis* (Mu, Li, Ge, Chen, Ni, Lin and Mu, 1974); NI21427; × 5. V, '*Glyptograptus persculptus-sinuatus* transient' (*sensu* Chen and Lin 1978); NI35911a; × 5.

at a generic level from true *Neodiplograptus* Legrand, 1987, the type species of which is *N. magnus* Lapworth, 1990, but difficult to separate from other *Normalograptus* species. Further work by the author (unpublished data) with some latest Ordovician and Early Silurian taxa with bifurcate thecae has shown, however, that these are relatively distinct from *Normalograptus*. Accordingly, species of the 'D.' *magnus* group are here assigned to *Neodiplograptus*, whilst those of the 'D.' *modestus* group are tentatively assigned to '*Neodiplograptus*' as discussed below.

Riva (1988, *in* Riva and Ketner 1989) considered *Climacograptus tubuliferus* and some allied species to belong to *Normalograptus*. Several partial relief specimens illustrated by Williams and Bruton (1983, fig. 15A, N), however, clearly show that $th1^2$ has an initial downward direction in its growth, a feature not seen in Pattern H taxa. The specimen illustrated by Riva (1988, fig. 2j) shows a particularly wide descending protheca 1^1 . This morphology is typical of Pattern D species of *Climacograptus* (*sensu* Mitchell 1987), especially *C. caudatus*, a species designated as the type species of *Ensigraptus* by Riva (*in* Riva and Ketner 1989). From these illustrations, and from material acquired by Mitchell (*pers. comm.*, 1992) it seems most likely that *C. tubuliferus* and its allies such as *C. putillus* (Hall, 1865) and *C. nevadensis* Carter, 1972 are not species of *Normalograptus*, but rather species of *Climacograptus* (e.g. Mitchell 1987) or *Ensigraptus*. All of the above species show a more rounded profile in the proximal end and less exposure of the sicula below $th1^1$ than is typical of *Normalograptus*.

Genus PSEUDOGLYPTOGRAPTUS Bulman and Rickards, 1968, emend.

Type species. Glyptograptus (Pseudoglyptograptus) vas Bulman and Rickards, 1968.

Emended diagnosis. Pattern H species similar to *Normalograptus* but with gently sigmoidal thecae, apertural margins commonly undulate.

Species included. Pseudoglyptograptus vas Bulman and Rickards, 1968, *P. cf. vas* (Melchin 1989), *P. barriei* Zalasiewicz and Tunnicliff, 1994 (= *P. n. sp.* Melchin 1989; *P. spp.* 1, 2 Rickards 1972; and *P. sp.* Bjerreskov 1981) (Pl. 1, figs 10–14) and possibly *P. rigidus* Chen and Lin, 1978.

Remarks. Examination of the Canadian Arctic material has added several insights to the understanding of this genus. First, the fact that it possesses a Pattern H rather than Pattern I astogeny (Koren' and Rickards 1996) allies it with *Normalograptus* rather than *Glyptograptus*, the latter being a Pattern I genus.

Second, the strong affinities of this genus with *Normalograptus* are seen in the immature specimens of *Pseudoglyptograptus barriei*, which show almost climacograptid thecae (Pl. 1, figs 10, 12). With increasing maturity of the rhabdosome the degree of sinuosity of the thecal profile and degree of development of the apertural lip increases, giving a more typical pseudoglyptograptid profile (Pl. 1, figs 13–14). This range of variation in the thecal form, also illustrated by Zalasiewicz and Tunnicliff (1994), as well as the wide range of dimensions seen in *Pseudoglyptograptus barriei*, indicates that *Pseudoglyptograptus spp.* 1, 2 of Rickards (1972) and *P. sp.* of Bjerreskov (1981) are all within the range of variation of this single species.

Third, two species previously assigned to *Pseudoglyptograptus*, *P. rhyaderensis* Rickards and Koren', 1974 and possibly *P. tabukensis* Rickards and Koren', 1974 are here assigned to *Comograptus* based on the presence of numerous spines on the sicular rim, as well as an extensively exposed sicula and the complete lack of a median septum, both indicating a Pattern I astogeny (see discussion of the genus *Comograptus* below).

Genus METACLIMACOGRAPTUS Bulman and Rickards, 1968, emend.

Type species. Diplograptus hughesi Nicholson, 1869.

Emended diagnosis. Biserial rhabdosome, circular to ovate in cross section. Thecae strongly geniculate with convex to straight supragenicular walls, introverted to straight apertures and deep, short excavations. Geniculum marked by a hood or, less commonly, a thickening which may partly obscure the thecal apertures. Median septum complete, beginning between the second pair of thecae and showing distinct, rounded or angular undulations. Pattern H proximal development type. Proximal end profile is rounded with sicula exposed only slightly below $th1^2$ and for about half its length on the obverse side. Proximal ornamentation, other than a short virgella, is lacking.

Species included. Among the species included are *Metaclimacograptus hughesi* (Nicholson, 1869) (e.g. Bulman and Rickards 1968), *M. fidus* Koren' and Mikhailova, in Koren' *et al.*, 1980, *M. minimus* (Paškevičius, 1976) (Pl. 2, figs 3–5, 9–10), *M. orientalis* (Obut and Sobolevskaya, 1966) (Pl. 2, figs 1–2, 7; Text-fig. 4A), *M. pictus* Koren' and Mikhailova, in Koren' *et al.*, 1980, *M. sculptus* (Chen and Lin, 1978) (Pl. 2, fig. 8) and *M. undulatus* (Kurck, 1882) (Pl. 2, figs 13–14).

Remarks. The characteristic sinuous median septum and convex supragenicular walls are features shared by both the Ordovician and Silurian 'pseudoclimacograptids' and have long been considered evidence for their close relationship. The proximal development types, however, are distinctly different. The early growth stages of *Metaclimacograptus* very closely resemble those of other Silurian normalograptids and are much simpler than those of *Pseudoclimacograptus scharenbergi* (Lapworth, 1876b) as illustrated by Bulman (1947) and Mitchell (1987). As a result, the Silurian forms are considered as a separate genus, having arisen from a separate stock, probably among the earliest Silurian normalograptids such as *N. angustus* or *N. mirnyensis* (Obut and Sobolevskaya, 1967).

Metaclimacograptus orientalis was assigned by Rickards *et al.* (1977) to *P.* (*Pseudoclimacograptus*) since it lacks genicular hoods. However, their illustration (fig. 3b) shows a slight thickening of the genicular rim and this can be clearly seen in the present material (Pl. 2, figs 2, 7). In addition, the present specimens clearly show that the proximal development is of the same type as the more typical *M. undulatus*.

Based on the above considerations, *Metaclimacograptus* is raised to the genus level as suggested by Paškevičius (1976), Mitchell (1987), Loydell (1991) and Koren' and Rickards (1996). In compressed material, the Silurian species can be reasonably distinguished from their Ordovician counterparts in that the former lack any proximal ornamentation other than a virgella and the sicula is always at least slightly exposed below $th1^2$. Based on this, several new species of 'Pseudoclimacograptus' described by Chen and Lin (1978), including *P. sculptus*, can be reassigned to *Metaclimacograptus*.

The present collections have also yielded an abundance of '*Lithuanograptus*' *minimus* Paškevičius, 1976 and a detailed comparison can be made between this species and the uncompressed specimens of the similar *Metaclimacograptus undulatus*. The only appreciable differences occur in the development of the genicular hood. In *M. undulatus* the hood of theca $x+1$ is first formed only as the flat infragenicular wall of theca $x+1$, with a thickened rim, which grows well in advance of the fusellae of the lateral walls of theca $x+1$ (Pl. 2, fig. 14). The overhanging hood is later grown by the accretion of material onto the thickened rim. In '*L.*' *minimus* the infragenicular wall of theca $x+1$ grows at once as a concave upward surface, its edges overhanging the aperture of theca x (Pl. 2, figs 4–5). It also grows in advance of the fusellae of the lateral walls, apparently by about the same amount as in *M. undulatus*. The hood is later unconformably overgrown by the lateral thecal walls (Pl. 2, fig. 3) but it appeared as an overhanging structure from its inception. The main distinction between these 'genera' then is only a matter of timing and degree of hood development, but the basic hood-forming structure (the infragenicular wall) and the timing of its development are the same. From a practical point of view, the distinction of these genera relies on knowledge of the details of hood development, information rarely available in compressed specimens and often not even discernible from uncompressed material. It is doubtful that these two genera could be distinguished in any but the most well-preserved, uncompressed specimens unless the specimens

could first be assigned to a species known to belong to one or the other genus. I consider that these criteria do not merit distinction of a separate genus, and that *Lithuanograptus* is a junior synonym of *Metaclimacograptus*, a conclusion drawn also by Loydell (1992, p. 55).

Talacastograptus Cuerda, Rickards and Cingolani, 1988 may represent an extreme development of the metaclimacograptid thecal form, with rounded supragenicular walls, introverted thecae, and very pronounced genicular hoods, that impart a hooked appearance to the thecae when fully developed. The gently undulose median septum also points to metaclimacograptid affinities.

Genus NEODICELLOGRAPTUS Mu and Wang, 1977, emend.

Type species. *Neodicellograptus dicranograptoides* Mu and Wang, 1977.

Emended diagnosis. Pattern H species with distally diverging stipes. Thecae 'pseudoclimacograptid' with introverted apertures and undulose dorsal stipe walls.

Species included. *Neodicellograptus dicranograptoides* Mu and Wang, 1977 (e.g. Chen and Lin 1978), *N. siluricus* Mu, Li, Ge, Chen, Ni, Lin and Mu, 1974 (Pl. 2, figs 6, 11–12, 15) and *N. superstes* Chen and Lin, 1978.

Remarks. This genus, placed in Dicranograptidae by Mu and Wang (1977) and Chen and Lin (1978), was considered by Melchin and Mitchell (1991) to possess a Pattern H astogeny, based on well-preserved, flattened specimens (Melchin and Mitchell 1991, fig. 7A–C). Uncompressed specimens (Pl. 2, figs 6, 11–12, 15) clearly show that *N. siluricus* does, indeed, possess a Pattern H astogeny rather than the Pattern A' seen among the Dicranograptidae (Mitchell 1987). This genus appears to have arisen by secondary distal stipe divergence of a Pattern H diplograptid. *Metaclimacograptus* is the most likely ancestor based on the similarities in both astogenetic pattern and thecal form.

The apex of the sicula is exposed in some specimens, but is enveloped within the first thecal series in most specimens (Pl. 2, fig. 12), rarely the second in others. The nema is usually free but short.

A case could be made for the inclusion of *Neodicellograptus* species in *Metaclimacograptus* since the thecal form is the same. Rare examples of some otherwise normal biserial species show distal stipe divergence (e.g. *Normalograptus normalis*, Williams 1983, text-fig. 3b; *Normalograptus* cf. *ojsuensis* (Koren' and Mikhailova) (Text-fig. 6i). In these cases, however, the virgula divides and follows the dorsal walls of both stipes. *Neodicellograptus* differs from *Metaclimacograptus* not only in that both stipes grow out of contact with the virgula, but also in that the dorsal walls of the stipes are undulose across their width rather than being straight in the centre where they contact the virgula and undulose along the lateral margins.

Of the four species previously assigned to this genus, three (*N. dicranograptoides*, *N. siluricus* and *N. superstes*) appear to differ only slightly in thecal form, dimensions and in the timing and angle of stipe divergence. The present collections of compressed and uncompressed specimens, however, show a considerable range of variation in timing and angle of stipe divergence. In some specimens the stipes diverge at the base of the second thecal pair (Pl. 2, figs 12, 15; Melchin and Mitchell 1991, fig. 7A) whereas in others this takes place at the third (Pl. 2, fig. 6; Melchin and Mitchell 1991, fig. 7C) or fourth thecal pair (Melchin and Mitchell 1991, fig. 7B). This evidence suggests that these three species may be synonymous. The other species, *Neodicellograptus* sp. (Chen and Lin 1978), possesses a much more blunt proximal end with mesial spines on all of the thecae. It is Ordovician in age and appears to be a true dicranograptid.

Genus NEODIPLOGRAPTUS Legrand, 1987, emend.

Type species. *Diplograptus magnus* H. Lapworth, 1900.

Emended diagnosis. Modified Pattern H species, most with only two primordial thecae, a delayed $th2^1$, and weakly to strongly biform thecae. Proximal thecae normally climacograptid, less commonly glyptograptid or possibly pseudoclimacograptid, with an abrupt geniculum, parallel supragenicular walls and relatively close spacing. Proximal end relatively narrow and widens rather abruptly as thecae become more gently sigmoidal to almost straight distally. Partial median septum in the proximal end becomes complete at or slightly beyond the point of thecal change, between the fourth and ninth thecal pair, except in a few possible 'ancestral' forms where the median septum is complete from the second thecal pair.

Species included. *Neodiplograptus magnus* (H. Lapworth, 1900) (see e.g. Rickards *et al.* 1977), *Neodiplograptus tcherskyi tcherskyi* (Obut and Sobolevskaya, 1967) (Pl. 3, figs 1–3, 10, 12), *Neodiplograptus tcherskyi* subsp. nov. (Pl. 3, fig. 11) and *Neodiplograptus sinuatus sinuatus* (Nicholson, 1869) (Pl. 3, figs 4–9) have been observed in the present material to share the attributes noted above. The following taxa appear to have similar thecal and rhabdosomal characteristics and are, therefore, included in this group: *Neodiplograptus tcherskyi sectilis* (Chen and Lin, 1978); *N. tcherskyi variatus* (Chen, 1984); *N. thuringiacus* (Kirste, 1919) (see e.g. Bjerreskov 1975); *N. mucroterminatus* (Churkin and Carter, 1970); and *Neodiplograptus sinuatus crateriformis* (Rickards, 1970). *Neodiplograptus? elongatus* (Churkin and Carter, 1970) (Text-fig. 6K), *N.? cf. elongatus* (Melchin 1989; Text-fig. 6J, N) and *N.? sp. nov.* (Melchin 1989; Text-fig. 6P, R–S) may also be assigned to this group.

Remarks. Among Pattern H graptolites, there are at least two distinct groups of species with biform to polyform thecae (Štorch 1983b). There are those with a robust, rapidly widening proximal end and generally 'amplexograptid' thecae proximally, which will hereafter be referred to as 'Neodiplograptus' (e.g. 'Neodiplograptus' *modestus* and its allies). The second group defined by Štorch possesses a more tapering proximal end with 'climacograptid' thecae, including '*D.*' *elongatus* and '*D.*' *thuringiacus*, here assigned to *Neodiplograptus*. Štorch considered that '*D.*' *tcherskyi* and possibly '*D.*' *magnus* belong to the '*N.*' *modestus* group, although examination of the illustrations of '*D.*' *magnus* of Elles and Wood (1907) and Rickards *et al.* (1977) and those of '*D.*' *tcherskyi* in Obut and Sobolevskaya (1967) and in the present collections suggests that these two taxa are much more similar to *N. thuringiacus* than to '*N.*' *modestus*. Štorch showed that these two species groups represented two different, independent lineages and, as discussed below, they may have arisen from two or more separate *Normalograptus* ancestors.

Two of the taxa assigned to *Neodiplograptus* that have been found in uncompressed form here are *N. tcherskyi tcherskyi* and *N. tcherskyi* subsp. nov. These differ from normal Pattern H species in that theca 2^1 is derived from near the aperture of $th1^2$ in a manner like that of all subsequent thecae and is, therefore, not a primordial theca as defined by Mitchell (1987). In addition, the fusellae of $th1^2$ are differentiated rather late from $th1^1$, although $th1^2$ still emerges from the foramen in protheca 1^1 as in all other Pattern H species. The result is a very slender first thecal pair. Other characteristic features of these two taxa that are shared with other *N. tcherskyi* subspecies, *N. thuringiacus*, *N. mucroterminatus* and *N. magnus* are the relatively strongly tapered proximal end, the fact that the change in thecal form is abrupt and coincides with a change in rate of widening and with the insertion of the complete median septum (the septum is partial in the proximal end). Whether or not these other named species share the delayed $th2^1$ is not known. This suite of features is not shared with other Pattern H 'Neodiplograptus' species such as '*N.*' *modestus*.

'*Glyptograptus*' *sinuatus sinuatus* has also been found in uncompressed form in the present collections and shares all of the above noted features, including the delayed differentiation of $th2^1$. The only way in which this species differs from *N. tcherskyi* is that the proximal thecae are not sharply geniculate but change from strongly sigmoidal to very weakly sigmoidal (see also Hutt 1974, pl. 4, figs 1–4, 10; Loydell 1991, pl. 1, fig. 2). This species, therefore, is included in *Neodiplograptus*.

A problem arises when attempting to assess the relationship between *Neodiplograptus* and *Normalograptus*, and the systematic position of *Neodiplograptus? elongatus*, which does not exhibit all of the above features. It does not show an abrupt change in either thecal form or rate of widening. It does, however, show a rather slender, tapering proximal end and climacograptid proximal thecae (Text-fig. 6K). Several compressed specimens assigned to *Neodiplograptus? cf.*

elongatus were found in the present collections that appear to be transitional between *N.?* *elongatus* and *N. thuringiacus* in that there are fewer climacograptid thecae, the thecae change more abruptly and the rhabdosome widens more rapidly (Text-fig. 6J, N). It is possible, that *N.?* *elongatus* and *N.?* cf. *elongatus* represent the transition from *Normalograptus* to *Neodiplograptus*. The first step in this transition would be distal introduction of weakly sigmoidal thecae on to a long, gently tapering rhabdosome with climacograptid thecae, such as that of *Normalograptus rectangularis* or *N. normalis*. The next step would be accelerating and increasing the abruptness of the thecal change and the rate of widening. Delaying the insertion of the median septum allows the proximal end to become more slender relative to the distal regions. The delay of the origin of th₂¹ allows the first thecal pair to be even more compact.

A third species closely related to *N.?* *elongatus* found in the Canadian Arctic is *Neodiplograptus?* sp. nov. (Text-fig. 6P, R-S). This new species is similar to *N.?* *elongatus* in rhabdosomal form and dimensions, but the first five thecae are pseudoclimacograptid with convex supragenicular walls, slightly introverted apertures and a wavy median septum. The following five thecae are climacograptid and thereafter they change gradually through glyptograptid to fully orthograptid distally. This species appears to be unique in that four different thecal morphologies are represented in a single rhabdosome and it illustrates the intergradational and transitional nature of these various thecal styles.

Whereas *Neodiplograptus?* *elongatus* represents one line along which *Neodiplograptus* may have arisen directly from *Normalograptus*, another possible ancestral line is the '*Glyptograptus?* *persculptus-sinuatus*' transient forms described by Chen and Lin (1978) (Text-fig. 6v). If these forms are indeed transitional between these two taxa as suggested by Chen and Lin, and if '*G.?* *sinuatus*' does indeed belong in *Neodiplograptus* as suggested here, then this may represent the line of origin for this species group. In fact, some of the specimen assigned by Chen and Lin to *N. sinuatus* are preserved in partial relief and appear to show an early origin for th₂¹ (Text-fig. 6Q, T), so there may be some variability in this feature within this species. *Neodiplograptus sinuatus* appears to be the earliest reported member of this genus.

A third possibility is that some or all of the *Neodiplograptus* species arose directly from species such as '*N.?* *modestus*', by acquiring a narrower, more tapering proximal end and delaying the origin of th₂¹. Only further work on well-preserved Early Llandovery material will allow resolution of these problems.

Genus 'NEODIPLOGRAPTUS' Legrand, 1987

Diagnosis. Pattern H species with biform thecae that widen rapidly from a relatively blunt proximal end. Proximal thecae normally amplexograptid, less commonly climacograptid, becoming glyptograptid to orthograptid distally. Median septum complete, normally inserting at or slightly beyond the second thecal pair. Rhabdosome usually broad, sometimes foliate in profile.

Species included. Among the species included are '*Neodiplograptus?* *modestus* (Lapworth, 1876b) (Text-fig. 6D-E), '*N.?* *africanus* (Legrand, 1970), '*N.?* *diminutus* (Elles and Wood, 1907), '*N.?* *fezzanensis* (Desio, 1940) (see e.g. Štorch 1983b), '*N.?* *lanceolatus* Štorch and Serpagli, 1993, '*N.?* *parajanus* (Štorch, 1983b), and possibly '*N.?* *merzlyaslovi* (Obut and Sobolevskaya, 1968) and '*N.?* *orientalis* (Ye, 1978).

Remarks. Species of '*Neodiplograptus?*' tend to have a proximal end that is relatively blunt in comparison with other normalograptids, although the sicula is still exposed below th₁². Usually, the maximum width is achieved rapidly, the proximal thecae are amplexograptid rather than climacograptid (i.e. with inclined supragenicular walls), and the change in thecal form is gradual, in some species almost imperceptible, to gently sigmoidal or straight distally, and does not coincide with a change in rate of widening as it does in *Neodiplograptus*. The complete median septum is commonly evident, even in completely flattened specimens, and appears to arise at or near the second thecal pair in species where it can be seen.

The proximal end appears to possess a normal Pattern H development, $th2^1$ originates at the base of $th1^2$ (Text-fig. 6D) as in *Normalograptus* species, as opposed to the delayed origin of $th2^1$ seen in many species of *Neodiplograptus*.

All these features taken together suggest that this group may, indeed, be distinct at the generic level from *Neodiplograptus*, although the range of variation within each group and the lines of distinction between them are still unclear. The origin of '*Neodiplograptus*' was clearly from a *Normalograptus* ancestor, such as *N. normalis*, within the latest Ashgill.

Genus CYSTOGRAPTUS Hundt, 1942

Type species, Diplograptus vesiculosus Nicholson, 1868.

Species included. Cystograptus vesiculosus (Nicholson) (Text-fig. 6L-M, O), *C. penna* (Hopkinson, 1869) (see Jones and Rickards 1967) and possibly *C.? ancestralis* Storch, 1985.

Remarks. This genus has yet to be found in Arctic Canada but well-preserved, compressed specimens of *C. vesiculosus* from Ireland examined by the author (Text-fig. 6L-M, O) show that, despite the very long sicula and downward-growing portion of $th1^1$, the latter still terminates in two foramina, and $th1^2$ grows across the reverse side of the sicular and upward as in all other Pattern H species.

Storch (1985) has suggested a likely origin for *Cystograptus*. The oldest species, *C.? ancestralis*, from the *ascensus* and *acuminatus* biozones, possesses a relatively short sicular (2.5–3.0 mm long) and less strongly sinuous thecae than *C. vesiculosus* or *C. penna*, and most arose from a *Persculptograptus* or *Neodiplograptus* species with sinuous thecae (e.g. *Persculptograptus persculptus* or '*Neodiplograptus*' ex gr. '*N. modestus*').

Family PETALOLITHIDAE Bulman, 1955, emend.

Emended diagnosis. Biserial graptolites with Pattern I primordial astogeny and continuous thecal periderm. Thecae commonly glyptograptid to petalolithid, less commonly climacograptid or (possibly) pseudoglyptograptid. Proximal end commonly acicular or slender and rounded. Rhabdosome aseptate or with a partial median septum (obverse side); no dicalycal theca is present. Ancora may be present but is not integrated with the proximal thecal framework.

Genera included. Petalolithus Suess, 1851, *Agetograptus* Obut and Sobolevskaya, 1968, *Cephalograptus* Hopkinson, 1869, *Comograptus* Obut and Sobolevskaya, 1968, *Dimorphograptoides* Koren' and Rickards, 1996, *Dischidograptus* Ni, 1978, *Dittograptus* Obut and Sobolevskaya, 1968, *Glyptograptus* Lapworth, 1873, *Parapetalolithus* Koren' and Rickards, 1996, *Pseudorthograptus* Legrand, 1987, *Rivagraptus* Koren' and Rickards, 1996, *Sudburigraptus* Koren' and Rickards, 1996 and possibly *Paraclimacograptus* Přibyl, 1947, *Victorograptus* Koren' and Rickards, 1996 and *Corbograptus* Koren' and Rickards, 1996.

Remarks. Description of the Pattern I development type and comparisons with other subfamilies are discussed in preceding sections. Some unique modifications of the petalograptine rhabdosome, however, should be pointed out here. Unlike most of the Silurian Diplograptoidae, which possess an unornamented proximal end (apart from the virgella and its modifications), *Comograptus* is characterized by spines on the sicular rim. These spines are not considered homologous with the antivirgellar spines of the Pattern F and G forms (within the Orthograptidae; see Mitchell 1987) but are secondarily derived within this group.

Another apparent anomaly within this subfamily is *Dischidograptus* Ni, 1978 (type species, *D. mirabilis* (Mu, Li, Ge, Chen, Ni, Lin and Mu, 1974)) in which the stipes give the appearance of

diverging at the distal end. Close examination of the type specimens of *D. mirabilis*, however (Text-fig. 6U), shows that stipe divergence does not take place, but that the distalmost thecae arose alternately, but are long and slender and no periderm is preserved between the last two thecae. The virgula appears to split in two and then distally ramify into numerous fine strands. Ni (1978) considered that *Petalolithus ovatus scopaeularis* Schauer, 1971 (a junior synonym of *P. regius* (Hundt, 1957); see Loydell 1992, pp. 51–52) also belongs in this genus as it shows a similar distal 'divergence' of stipes and virgula.

Koren' and Rickards (1996) described an array of styles of virgellar and thecal apertural modification seen in petalolithid genera. They also erected a number of new genera within this group, based on groups of taxa that share these features.

One aspect of the rhabdosomal structure that has received very little attention from the point of view of its possible phylogenetic significance in Silurian diplograptoids is the position of the virgula and presence or absence of a partial or complete median septum. This aspect of the internal structure can often be deduced from well-preserved, flattened and pyritized specimens. As noted previously, all the Pattern H species studied to date are fully septate distally, and therefore possess a dicalycal theca that divides the rhabdosome into two, separately growing series of thecae, whereas all the Pattern I species are either aseptate or partly septate and the thecae originate by alternate budding of a single growth series throughout the rhabdosome. However, within the Pattern I forms the position and mode (or lack) of attachment of the virgula is variable and these features may have significance at the specific and generic level.

The possible inclusion of *Paraclimacograptus* in this family is discussed in the remarks for the Normalograptidae, above. The possible astogenetic development patterns for the genera *Victorograptus* and *Corbograptus* are discussed by Koren' and Rickards (1996).

Genus PETALOLITHUS Suess, 1851

Type species. *Prionotus folium* Hisinger, 1837.

Diagnosis (after Koren' and Rickards 1996). Pattern I species with ventrally concave proximal thecae and concave to straight distal thecae, disposed at moderate to high angles to the rhabdosome producing a foliate profile. Apertures usually everted. Rhabdosome ovate to tabular in cross section. Proximal end bears an ancora.

Species included. Among the species included are *Petalolithus folium* (Hisinger, 1837) (see e.g. Lenz 1982), *P. ankyratus* Mu, Li, Ge, Chen, Ni, Lin and Mu, 1974 (Pl. 4, figs 1–2, 5), *P. intermedius* (Bouček and Příbyl, 1941a) (e.g. Lenz 1982), *P. minor* (Elles, 1897), *P. ovatus* (Barrande, 1850) (see e.g. Bouček and Příbyl 1941b).

Remarks. Loydell (1992) established that the name *Petalolithus* has priority over *Petalograptus*. The definition of this genus was expanded by Mitchell to include Silurian species of *Orthograptus* (assigned by Legrand 1987 to *Pseudorthograptus*) with the Pattern I proximal end. The line of distinction between the Silurian 'orthograptids' and 'petalograptids' had been rather ill-defined in the past, with some *Petalolithus* species (e.g. *P. tenuis* (Barrande, 1850)) having straight thecae and a rhabdosome which is not particularly foliate and some *Orthograptus* species (e.g. *O. mutabilis*) with a relatively protracted proximal end and strongly upward-growing early thecae. In addition, Loydell (1992) noted that the presence or absence of an ancora may be of phylogenetic significance among these species. Koren' and Rickards (1996) restricted the definition of this genus to include only those species with ventrally curved thecae (at least proximally) and an ancora. Their analysis of the evolutionary relationships among these species indicates that they do, indeed, represent a monophyletic group. The limited data available suggest that these taxa also share a partial median septum (Pl. 4, fig. 2).

Genus PARAPETALOLITHUS Koren' and Rickards, 1996

Type species. *Parapetalolithus dignus* Koren' and Rickards, 1996.

Diagnosis (after Koren' and Rickards 1996). Pattern I species with straight ('orthograptid') thecae, with everted, unornamented apertures. Proximal thecae are protracted and strongly upward-growing. Proximal end bears only a simple, undivided virgella.

Species included. Typical species include *Parapetalolithus dignus* Koren' and Rickards, 1996, *P. kurcki* (Rickards, 1970), *P. palmeus* (Barrande, 1850) and *P. sp.* (Pl. 4, figs 3, 9–10).

Remarks. Koren' and Rickards (1996) erected this genus to include those taxa previously included in *Petalolithus* that lack an ancora, and typically possess straight rather than conspicuously ventrally curved proximal thecae and a less foliate rhabdosome. They also suggested a distinct evolutionary origin for these taxa, from *Sudburigraptus* Koren' and Rickards, 1996, rather than *Pseudorthograptus*. The differences between *Sudburigraptus* and *Parapetalolithus* are subtle, the former possessing a less protracted proximal end, and species of the latter being generally larger and more robust (Koren' and Rickards 1996). *P. sp.* is aseptate with a free, central virgula (Pl. 4, fig. 3), but the internal structure of other species of this genus is unknown.

Genus PSEUDORTHOGRAPTUS Legrand, 1987

Type species. *Diplograptus insectiformis* Nicholson, 1869.

Diagnosis (after Koren' and Rickards 1996). Pattern I species with straight ('orthograptid') thecae, with spinose apertures. Proximal end bears an ancora that may be very large and supports a continuous membrane.

Species included. Typical species include: *Pseudorthograptus insectiformis* (Nicholson, 1869), *P. inopinatus* (Bouček, 1943) (Pl. 4, figs 6–8, 11–12), *P. mutabilis* (Elles and Wood, 1907), and *P. obuti* (Rickards and Koren', 1974).

Remarks. Koren' and Rickards (1996) restricted the definition of this genus to include only those taxa with spinose apertures and an ancora. It may be also noted that *P. inopinatus* is aseptate, and this condition may characterize the genus and serve to distinguish it further from *Petalolithus*, at least some species of which possess a thin, partial median septum.

Genus SUDBURIGRAPTUS Koren' and Rickards, 1996

Type species. *Orthograptus eberleini* Churkin and Carter, 1970.

Remarks. Koren' and Rickards, 1996 erected this genus to include species with Pattern H or I development, unornamented orthograptid thecae and an unornamented, relatively unprotracted proximal end. The type species, *S. eberleini*, appears to be aseptate (Churkin and Carter 1970, pl. 3, fig. 2) and most probably possesses a Pattern I astogeny, although the internal and astogenetic details of none of the taxa assignable to this genus (Koren' and Rickards 1996) are known for certain. Assuming that the Pattern I astogeny arose only once in the latest Ashgill or earliest

Llandovery (see Llandovery graptoloid phylogeny below) then a genus encompassing both Pattern H and I 'orthograptids' would probably include two independently evolving groups of species, although further taxonomic revisions of these forms must await analysis of new, better preserved material.

Genus RIVAGRAPTUS Koren' and Rickards, 1996

Type species. Diplograptus bellulus Törnquist, 1890.

Remarks. Koren' and Rickards (1996) erected this genus, with *Rivagraptus bellulus* as its type species. However, their description of *R. bellulus* indicates the presence of a sicula at least 1 mm long and a full median septum distally, whereas the specimens described by Bjerreskov (1975) are aseptate and show a much shorter sicula. The present specimens match well with those of Bjerreskov in all respects, accounting for the differences in width that would accompany compression. The author has not had the opportunity to examine the original material of Törnquist (1890), so the question of the real nature of the proximal and internal structure of this species must await re-examination of the type specimens. If the present specimens match Törnquist's material (i.e. if *R. bellulus* is aseptate with an exceptionally short sicula), then the generic diagnosis should be revised to reflect this unique development and structure, and the scope of the genus revised to encompass those species that share those features (e.g. *Rivagraptus? kayi* (Churkin and Carter, 1970)). Those other species assigned by Koren' and Rickards (1996) to this genus (e.g. *R. cyperoides* (Törnquist, 1897) and some new species erected by Koren' and Rickards) that possess a much longer sicula, should be assigned to another genus (e.g. *Sudburigraptus*).

The species that are here questionably assigned to this genus show the key Pattern I characteristics: only one primordial theca and normal differentiation of all subsequent thecae; and a short, downward-growing portion of th_1^1 with a single terminal foramen at the sicular aperture (Pl. 7, fig. 7). They have, however, acquired a proximal appearance quite unlike other petalolithids with their extremely short, obscured sicula and blunt proximal end (Pl. 7, figs 4–6, 8, 11–13). Even in compressed form, the short, obscured sicula and blunt, rounded proximal end are evident (e.g. Törnquist 1890, pl. 1, figs 27, 29) differentiating species of this genus from other Llandovery genera.

Genus GLYPTOGRAPTUS Lapworth, 1873, emend.

Type species. Diplograptus tamariscus Nicholson, 1868.

Emended diagnosis. Pattern I species with glyptograptid to climacograptid thecae. Proximal end rather slender, unornamented and tapering. Rhabdosome circular to ovate in cross section, aseptate, virgula central and free or attached to bases of interthecal septa, or lateral and embedded in obverse wall.

Species included. *Glyptograptus tamariscus* (Nicholson) (Pl. 5, figs 1–6, 9) (except *G. tamariscus magnus* Churkin and Carter, 1970), *Glyptograptus alternis* (Packham, 1962), *G. elegans* Packham, 1962 (Pl. 5, figs 10, 13; Pl. 6, figs 1–3), *G. enodis* Packham, 1962, *G. tamariscoides* (Packham, 1962).

Remarks. There has long been difficulty in distinguishing species of *Glyptograptus* from *Climacograptus* in Llandovery collections and arbitrary criteria have been variously employed (e.g. Packham 1962). This has resulted in what many authors have considered a phylogenetically unrealistic classification, even from the point of view of thecal morphology and rhabdosomal form alone (Rickards *et al.* 1977). Mitchell (1987) suggested that all the Llandovery glyptograptids and

climacograptids possess the same proximal development pattern (Pattern H) and he decided to include both within an expanded *Glyptograptus* until further information was available to distinguish more phylogenetically consistent subgroups. The present material has clearly shown, however, that some of the Llandovery glyptograptids are of the Pattern I type, including *G. tamariscus*, the type species, whilst others (e.g. *G. nikolayevi*) possess the Pattern H proximal growth form and are here grouped with the Pattern H climacograptids in the genus *Normalograptus* (Melchin and Mitchell 1991). Likewise, some Pattern I species such as '*Climacograptus*' *tamariscoides* and '*C.*' *alternis* possess climacograptid thecae and, despite the fact that they were considered by Packham (1962) to have evolved directly from the *Glyptograptus tamariscus* group, they were still placed in the genus *Climacograptus* on the basis of their thecal morphology. These forms clearly possess the same astogenetic pattern and rhabdosomal structure as *Glyptograptus sensu stricto* and are, therefore, placed in that genus. Koren' and Rickards (1996) generally used the concept of *Glyptograptus* of Melchin and Mitchell (1991), that includes only Pattern I taxa, although several of the species that they assigned to this genus are septate with a rather blunt proximal end (resulting from early derivation of th1²) and are most probably Pattern H species assignable to *Normalograptus* (e.g. *G. bulbosus* Koren' and Rickards, 1996, *G. incertus* Elles and Wood, 1907, *G. cf. serratus* Elles and Wood, 1907 and *G. tamariscus nikolayevi* Obut, 1965 (= *Normalograptus nikolayevi*; Pl. 1, figs 4–9).

Genus COMOGRAPTUS Obut and Sobolevskaya, 1968, emend.

Type species. *Comograptus comatus* Obut and Sobolevskaya, 1968.

Emended diagnosis. Pattern I species with at least three spines (often many) projecting outward from the sicular rim. Thecae climacograptid to pseudoglyptograptid, possibly glyptograptid, and may bear mesial and/or genicular spines, especially proximally. Rhabdosome aseptate with central virgula.

Species included. *Comograptus comatus* Obut and Sobolevskaya, 1968 (Text-fig. 3N), *C. gorbiachinensis* Obut and Sennikov, 1980 (Pl. 7, figs 7–13), *Comograptus rhayaderensis* (Rickards and Koren', 1974) and possibly '*Pseudoglyptograptus*' *tabukensis* Rickards and Koren', 1974 (cf. Text-fig. 3Q).

Remarks. This genus remains largely unchanged from the definition of Obut and Sobolevskaya (1968), except that it has been found here to include only Pattern I species (probably not *Normalograptus? serratus barbatus* which appears to be a spinose variant of an otherwise normal Pattern H species). The proximal development, as seen clearly in present isolated specimens of *C. gorbiachinensis* and *C. comatus*, is typical of the petalolithids and this type of proximal end can also be seen in the uncompressed specimen of '*Pseudoglyptograptus*' *rhayaderensis* illustrated by Rickards and Koren' (1974, fig. 17). The long sicula exposed for a considerable length on the obverse side and the absence of a median septum, even on the obverse side, are characteristic of Pattern I species. The presence of spines on the sicular rim is also indicative of this genus.

'*Pseudoglyptograptus*' *tabukensis* is less well preserved but also shows the sicular spines and in other ways is similar to *C. rhayaderensis*. It is, therefore, included questionably in *Comograptus*.

Koren' and Rickards (1996) recognized that the type species bears a Pattern I astogeny, but restricted the definition of the genus to include only those taxa bearing spines on the sicula and proximal thecae. This definition excludes those taxa listed above that do not bear thecal spines, including *C. gorbiachinensis*, which was assigned to this genus by Obut and Sennikov (1980). Observations on the present material suggest that the degree of thecal spine development varies between as well as within species depending on the growth stage, whereas the spines on the sicular rim formed at the time of completion of growth of the metasicula, and combined with the Pattern

I astogeny and thecal form, provide a more reliable guide for phylogenetic grouping of these taxa. It appears that *C. comatus* represents the extreme end-member of this group of Pattern I species with varying degrees of proximal spinosity.

Genus AGETOGRAPTUS Obut and Sobolevskaya, 1968, emend.

Type species. *Agetograptus secundus* Obut and Sobolevskaya, 1968.

Emended diagnosis. Pattern I species in which a dimorphograptid appearance has been achieved either by redirection of $th1^2$ above $th1^1$ or suppression of the $th1^2$ metatheca, and all the following thecae are in a normal biserial pattern. Thecae orthograptid to glyptograptid, possibly climacograptid and may bear apertural spines. Sicala relatively short, often with a long virgella. Rhabdosome aseptate.

Species included. *Agetograptus secundus* Obut and Sobolevskaya, 1968 (Text-fig. 3DD, HH), *A. primus* Obut and Sobolevskaya, 1968, *A. spiniferus* Obut and Sobolevskaya, 1968 (Pl. 7, figs 1–3, 5–6), *A. tenuilongissimus* Obut and Sobolevskaya, 1968, and *A. zintchenkoae* Obut and Sobolevskaya, 1968. In addition, *Dimorphograptus anhuiensis* Li, 1987, *D. brevis* Li, 1987, and *D. hubeiensis* Ni, 1978 (Pl. 7, fig. 4) may be referable to this genus.

Remarks. Obut and Sobolevskaya (1968) recognized that the difference between *Agetograptus* species and *Dimorphograptus* was the short sicala, not fully exposed below $th1^1$ and the short first theca, and recognized the similarities with other Pattern I species such as *Rivagraptus bellulus* (see remarks of *Rivagraptus* above). The distinctness of *Agetograptus* was also recognized by Loydell (1991) and Koren' and Rickards (1996). The genus is expanded here to include all *Rivagraptus*- to *Glyptograptus*-like Pattern I species with relatively short sicalae in which there is a uniserial portion consisting of only one theca.

Many of the 'dimorphograptid' species described from China in which the uniserial portion consists of only one theca are questionably included in this genus, such as *A.?* *hubeiensis* and *A.?* cf. *A.?* *sichuanensis* (Ye, 1978), which have been found in the present collections and *A.?* *anhuiensis* and *A.?* *brevis*, both illustrated by Li (1987). Although Li (1987) suggested diverse origins for several of these species, his conclusions were based on thecal form and overall rhabdosomal profile. More information is necessary regarding the details of the proximal end and internal structure before the mono- or polyphyletic origin of this genus can be determined.

Family RETIOLITIDAE Lapworth, 1873, emend.

Emended diagnosis. Sicala reduced to absent. Thecae represented by thecal framework and/or reticulum that may show some development of continuous periderm. Ancora always present and incorporated in framework of first thecal pair.

Remarks. This family comprises the groups assigned to the Retiolitinae and the Plectograptinae, which include, as far as presently known, all the Silurian 'retiolitids'. The Ordovician forms (the 'archiretiolitids') previously included in the Retiolitidae (*sensu* Bulman 1970), and the order Retiolitida of Obut and Zaslavskaya (1986), have a different proximal development pattern not involving an incora and have been included by Mitchell (1987) within the Orthograptidae (see also Bates 1990).

Mitchell (1987) discussed some of the profound differences between the normal diplograptid periderm and the retiolitid thecal framework and reticulum, but chose to include both within the same

subfamily (Retiolitinae). However, recent work on the skeletal architecture of many retiolitid genera by Bates and Kirk (1978, 1984, 1992), Crowther (1981), Obut and Zaslavskaya (1986), Lenz and Melchin (1987a, 1987b) and Lenz (1993, 1994) as well as many observations made by myself on both retiolitids and ancora-bearing petalolithids shows that several profound differences exist both in the early growth stages and distal architecture between these two groups. The first is the partial to total desclerotization of the sicula, considered by Fortey and Cooper (1986) and Mitchell (1987) to be the most phylogenetically conservative feature of the graptolite rhabdosome. Although some specimens of *Pseudoretiolites* preserve a portion of the metasicula, no retiolitids have yet been found in which a resorption foramen or initial bud of $th1^1$ is preserved, except for the unusually sclerotized specimens of *Agastograptus* described by Lenz (1994), which show the foramen but not the downward growing portion of $th1^1$. A second feature is the integration of the ancora with the basic thecal framework of the first thecal pair, which contrasts sharply with any of the known ancora-bearing petalolithids in which the ancora is not involved in the construction of the first thecae. In addition, Bates and Kirk (1992) have pointed out some ultrastructural differences between petalolithid and retiolitid ancorae. The third (and most obvious) distinction is the total apparent replacement of preservable, primary thecal periderm with the open mesh of the thecal framework and/or reticulum. Lenz (1994) has shown that, even within Late Wenlock plectograptines, the sicular and thecal astogeny is identical to that of the petalograptines (Pattern I), and that the thecal framework and reticulum are almost entirely external to the thecae themselves. Therefore, Bates' (1990) suggestion that since the key attributes of the retiolitids arise early in astogeny, this group ought to be given subordinal status, is not supported by Lenz's observation regarding retiolitid thecal astogeny.

Lenz and Melchin (1997) have completed a phylogenetic analysis of the Silurian retiolitids and, from the point of view of their overall classification, came to two major conclusions. The first is the fact that all share the several derived characteristics (e.g. synapomorphies 10–12 on Text-fig. 5), as described above, which suggests that they represent a monophyletic clade. Ultrastructural studies on the nature of the ancora (Bates and Kirk 1992) suggest that, although this structure may have some ultrastructural differences among the Llandovery biserial graptolites, the ultrastructure is consistent within the retiolitids. The second major conclusion of Lenz and Melchin (1997) was that the Retiolitidae can be divided into two main subclades. The first includes those genera traditionally included within the Retiolitinae: e.g. *Pseudoplegrammograptus*, Přibyl, 1948a *Retiolites* Barrande, 1850 and *Stomatograptus* Tullberg, 1883 (*Pseudoretiolites* Bouček and Münch, 1944 was identified as the stem-group for both subclades). The second includes those genera assigned to the Plectograptinae (*sensu* Lenz 1993) as well as *Rotaretiolites* Bates and Kirk, 1992 and a new taxon that shares attributes of *Rotaretiolites* and *Paraplectograptus*, which may belong to the genus *Eorograptus* Sennikov, 1984.

Family DIMORPHOGRAPTIDAE Elles and Wood, 1908, emend.

Emended diagnosis. Pattern J graptolites which may be uni-biserial or fully biserial. Sicula long (usually 1.7–2.0 mm), fully exposed on its dorsal side. Downward growing portion of $th1^1$ strongly reduced and does not reach down to sicular aperture, leaving a portion of sicula exposed for its full circumference. Obverse and reverse walls of $th1^1$ both growth straight upward for all or much of their length. Rhabdosome fully or partly septate. Thecae commonly orthograptid to climacograptid but may be isolate or slightly hooked, especially in uniserial portions.

Genera included. *Dimorphograptus* Lapworth (= *Bulmanograptus* Přibyl, 1948b, *Metadimorphograptus* Přibyl, 1948b), *Akidograptus* Davies, 1929 and *Parakidograptus* Li and Ge, 1981.

Remarks. The descriptions of the Pattern J astogeny, and the distinction of the 'true' dimorphograptids from *Rhaphidograptus* Bulman, 1936 and *Agetograptus*, are discussed above in

the description of proximal development patterns and below in the discussion of their recognition in non-isolated graptolites.

Several authors have recognized that *Akidograptus* and *Parakidograptus* do not possess a uniserial first theca (e.g. Williams 1983; Li and Ge 1981) and this led them to include these genera within Diplograptidae rather than Dimorphograptidae. Despite the fact that they have a fully biserial rhabdosome, the early astogeny (Pattern J), particularly the early upward growth of th¹, is more like that of the dimorphograptids (Pattern J') than the other diplograptid groups and they are, therefore, included within Dimorphograptidae here (see cladogram, Text-fig. 5).

Storch and Serpagli (1993) recognized the distinction between the uniserial and the uni-biserial genera within this family at the subfamily level and that distinction is recognized here. Koren' and Rickards (1996) distinguished Akidograptidae and Dimorphograptidae as separate families. The classification of Storch and Serpagli (1993) is preferred for these taxa because it recognizes the strong astogenetic similarities and close phylogenetic relationship between these two groups.

Subfamily AKIDOGRAPTINAE Li and Ge, 1981, emend.

Emended diagnosis. Pattern J graptolites which are fully uniserial. Thecae climacograptid to orthograptid. Proximal end protracted, often bearing an 'ancora'. Dicalycal theca 2¹, fully septate rhabdosome.

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

Genus AKIDOGRAPTUS Davies, 1929

Type species. *Akidograptus ascensus* Davies, 1929.

Diagnosis. Biserial rhabdosome with protracted proximal end and early upward growth of first two thecae (Pattern J). Thecae strongly geniculate (climacograptid).

Species included. *Akidograptus ascensus* Davies, 1929, *A. anhuiensis* Ge, *A. cultus* Mikhailova, *A. gangjiawuensis* Ge, *A. giganteus* Yang, *A. macilentus* Chen and Lin, 1978, *A. parallelus* Li and Jiao, *A. priscus* Hsü and *A. shannanensis* Yu *et al.*

Remarks. No attempt has been made here to assess the status of the various species assigned to this genus with respect to synonymy. It is clear, however, that considerably more variability exists within both this genus and *Parakidograptus* in China than in other parts of the world.

Akidograptus antiquus Li and Ge, 1981 is the only reported member of this family from *persculptus* Zone strata. The holotype, and apparently only known specimen of this species, has been examined by the author (Text-fig. 3w) and is too poorly preserved to be confidently assigned to this genus. Both *Akidograptus* and *Parakidograptus*, therefore, appear to be confined to the *persculptus*, *acuminatus* and basal *vesiculosus* biozones.

Genus PARAKIDOGRAPTUS Li and Ge, 1981

Type species. *Diplograptus acuminatus* Nicholson, 1867.

Diagnosis. Rhabdosome with protracted proximal development (Pattern J). Thecae straight to weakly geniculate.

Species included. *Parakidograptus acuminatus* (Nicholson, 1867), *P. aculeatus* Yu *et al.*, *P. xixiangensis* Yu *et al.*, *P. angustitubis* Li, *P. helixiensis* Li, *P. huloensis* Li and *P. primarius* Li.

Remarks. Distinction of this genus from *Parakidograptus* is made on the basis of thecal form. *Akidograptus* possesses strongly geniculate thecae whereas *Parakidograptus* weakly geniculate to, more commonly, straight (orthograptid) thecae.

Subfamily DIMORPHOGRAPTINAE Elles and Wood, 1908, emend.

Emended diagnosis. Pattern J species with a uni-biserial rhabdosome (Pattern J'). Uniserial portion consisting of one or several thecae, apparently achieved by redirection of theca(e) following th1. Thecae orthograptid to climacograptid, although they may be isolate or slightly hooked, especially in the uniserial portion. Biserial portion appears to be fully septate.

Genus included. *Dimorphograptus* Lapworth, 1876 (= *Bulmanograptus* Přibyl, 1948b and *Metadimorphograptus* Přibyl, 1948b).

Genus DIMORPHOGRAPTUS Lapworth, 1876, emend.

Type species. *Dimorphograptus elongatus* Lapworth, 1876.

Emended diagnosis. Pattern J species with a uni-biserial rhabdosome (Pattern J'). Uniserial portion, consisting of one or several thecae, apparently achieved by redirection of theca(e) following th1. Thecae orthograptid to climacograptid although they may be isolate or slightly hooked, especially in the uniserial portion. Biserial portion appears to be fully septate.

Species included. Typical species include *Dimorphograptus elongatus* Lapworth, 1876, *D. confertus* Nicholson, 1868, *D. decussatus* Elles and Wood, 1908, *D. erectus* Elles and Wood, 1908, and *D. extenuatus* (Elles and Wood, 1908).

Remarks. This genus, as employed here, includes all Pattern J species with a uniserial proximal portion. Other genera have been introduced to subdivide this group according to thecal shape (e.g. *Bulmanograptus*, *Metadimorphograptus*), but many authors have not accepted them because their morphological or phylogenetic basis was considered questionable. A great deal more work needs to be done, especially to define the details of thecal form of some of the dimorphograptids, which appear to be rather complex in many species.

Family MONOGRAPTIDAE Lapworth, 1873

Diagnosis. Scandent, uniserial rhabdosomes with Pattern M astogeny.

Remarks. The various cladia-bearing genera of the Monograptidae are not considered by many workers to be a monophyletic group (Rickards *et al.* 1977) and as many as four or more separately derived lineages may be involved. For this reason, the cyrtograptids are not separated at the subfamily level here until more is known about the relationships within and between the various cladia-bearing groups.

Bulman (1970) and Fortey and Cooper (1986), as well as many other authors, have considered that the origin of th1 from a sinus rather than via a resorption foramen was a distinctive and universal feature among the monograptids. Mitchell (1987) cautioned that this feature had not been observed in any of the earliest monograptids but hypothesized that its appearance was coincident

with the achievement of the early upward growth of th1 and the uniserial rhabdosome. Isolated, compressed specimens of several Early and Mid Llandovery monograptids clearly show that th1 emerges from a resorption foramen (Lukasik and Melchin 1994, 1997). It can also be seen that th1 grows outward, then upward, with no downward growth component. Lukasik and Melchin (1997) designated this primitive monograptid pattern, with a resorption porus as Pattern M_r, and the more advanced development with a primary porus as Pattern M_p. The timing or mode of origin of Pattern M_p from M_r is currently unknown.

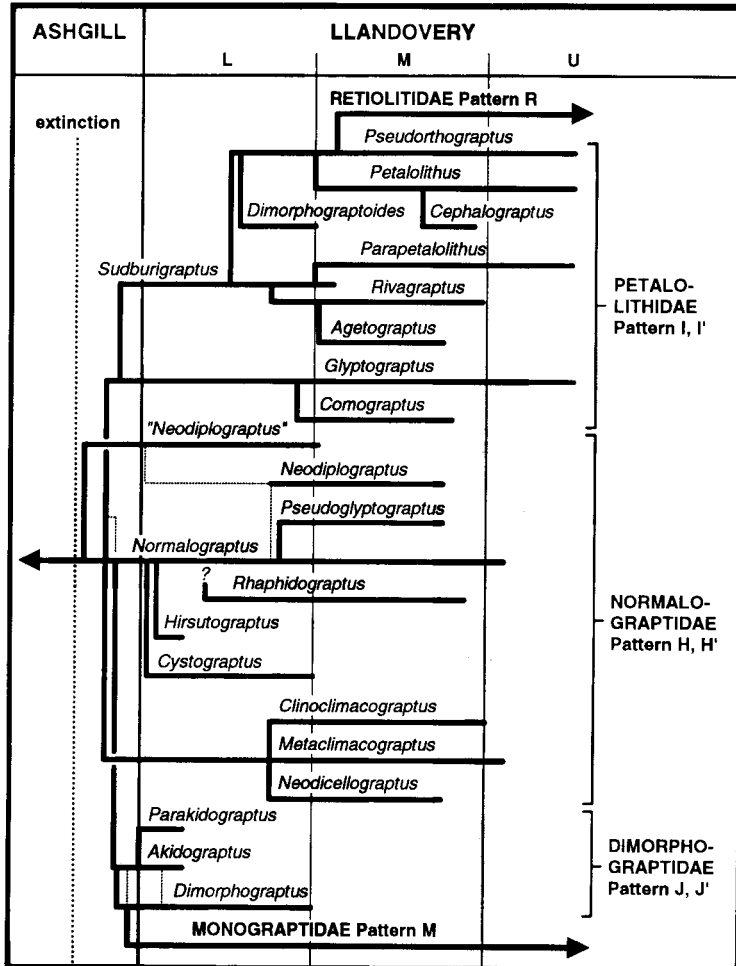
LLANDOVERY GRAPTOLOID PHYLOGENY

As a result of the late Ordovician extinction event, only one of the then extant graptoloid families, Normalograptidae, survived from the end of the *pacificus* Zone into the Early Llandovery (Melchin and Mitchell 1991). The only graptoloid species known to cross the extinction boundary (i.e. the *pacificus*-*extraordinarius* zonal boundary) are *Normalograptus normalis*, *N. angustus*, *N. ojsuensis* Koren' and Mikhaylova, in Koren' *et al.*, 1980 and *N. extraordinarius*. '*Diplograptus bohemicus*' Marek, 1955 has been reported from several localities in China, occurring with both pre-extinction and post-extinction faunas (Mu 1988; Melchin *et al.* 1991). However, Storch and Loydell (1996) have demonstrated that *Diplograptus bohemicus* is a junior synonym of *Persculptograptus persculptus* (Elles and Wood, 1907). Most of the Chinese specimens previously assigned to *D. bohemicus* are not *P. persculptus*, however, and are here assigned tentatively to *Normalograptus cf. ojsuensis*.

The only *Akidograptus* species reported from pre-*persculptus* Zone strata is *A. antiquus* Li and Ge, 1981 from the *typicus* Zone (= middle *pacificus* Zone) in China. As noted above, the holotype (and apparently only specimen) of this species (Text-fig. 3w) is too poorly preserved to be confidently assigned to this genus. The earliest reliable report of *Akidograptus* is that of *A. parallelus* from the lowermost *persculptus* Zone of Shaanxi, China (Yu *et al.* 1988), where it predates the first occurrence of *A. ascensus* or *Parakidograptus acuminatus*. None of the pre-*extraordinarius* Zone taxa that have been previously assigned to *Paraclimacograptus* or as subspecies of *P. innotatus* are considered here to belong to that genus.

It thus appears, from both the currently available biostratigraphical evidence and, more importantly, from the astogenetic evidence (Text-fig. 5), that the Normalograptidae were ancestral to all of the Silurian graptoloids. Text-figure 7 depicts a suggested phylogeny for the Llandovery biserial graptolites.

The origin of the first species of *Glyptograptus* (the earliest species with a Pattern I astogeny) from a Pattern H-bearing *Normalograptus* species primarily involved a delay in the budding of th1² from th1¹. In addition, the style of budding of th1² is as in all subsequent thecae, suggesting that only th1¹ is primordial. Among *Normalograptus* species, th1² emerged from the foramen at the downward end of protheca 1¹. In *Glyptograptus tamariscus* and related species, th1² appears to have emerged from the upward-growing portion of th1¹ and developed without a pronounced fusellar unconformity as in all later thecae. Based on the present evidence, this transition appears to have been accompanied by a loss of the dicalyca theca, thereby producing an aseptate (or partly septate) rhabdosome. The majority of species previously assigned to *Glyptograptus* from the *extraordinarius* Zone (= upper '*bohemicus*' Zone) have broad proximal ends, are fully septate, and, therefore, are assigned here to *Normalograptus* (e.g. '*G.* *elegantulus* Mu and Ni, 1983, '*G.* *asthenus* Mu and Ni, 1983, '*G.* *daedalus* Mu and Ni, 1983). *Glyptograptus praetamariscus* Li, 1984, from the uppermost '*bohemicus*' Zone of Jingxian, Anhui, China, strongly resembles *G. tamariscus* in its rhabdosomal form and may be an example of one of the earliest of the Petalolithidae. Species of what appear to be *Glyptograptus sensu stricto* are better documented from the *persculptus* Zone, including several reports of *G. tamariscus* (e.g. Li 1984). *Sudburigraptus? angustifolius* (Chen and Lin, 1978), which also appears to be a Pattern I species, is found in the *persculptus* Zone in Arctic Canada (author's unpublished data). Derivation of other petalolithid genera from *Glyptograptus* involves only changes in thecal form or proximal and thecal ornamentation. Koren' and Rickards (1996) discussed the evolutionary relationships among those taxa here included in Petalolithidae, and most of their conclusions



TEXT-FIG. 7. Proposed phylogeny for the Llandovery Diplogrptoidea and approximate generic ranges. Dashed lines indicate possible alternative line of origin. Genera of uncertain family affinities (e.g. *Paraclimacograptus*, *Victorograptus* and *Corbograptus*) are not shown.

are consistent with the data presented here. However, they regarded the evolutionary origin of *Pseudorthograptus* as unknown, and raised the possibility that *Sudburigraptus* was derived from an Ordovician species of *Rectograptus*. They noted that this would involve a loss of the proximal spines typical of *Rectograptus* but it would also require a reorganization of the early growth patterns of the first three thecae, from the Pattern G astogeny (Mitchell 1987). On the other hand, the early species of *Glyptograptus* and *Sudburigraptus* have the same astogenetic development and differ only slightly in thecal form, and it is proposed that the latter genus was derived from the former. From *Sudburigraptus*, the derivation of *Pseudorthograptus*, *Parapetalolithus* and *Rivagraptus* requires only minor changes in degree of protraction of the (still Pattern I) proximal end and, in some cases, the addition of apertural spines (*Pseudorthograptus* and *Rivagraptus*) and/or an ancora (*Pseudorthograptus* and *Petalolithus*).

The close morphological similarity between the ancorae seen in some species of *Pseudorthograptus* (e.g. *P. inopinatus* and *P. obtus*) and those of the Retiolitinae strongly suggests that the earliest retiolitid (*Pseudretiolites*) evolved from either a *Pseudorthograptus* or possibly *Petalolithus* ancestor.

This suggestion has been questioned by Bates (1990), based on some observed ultrastructural differences in the ancorae. It is supported, however, by the thecal form of the fully sclerotized retiolitid described by Lenz (1994).

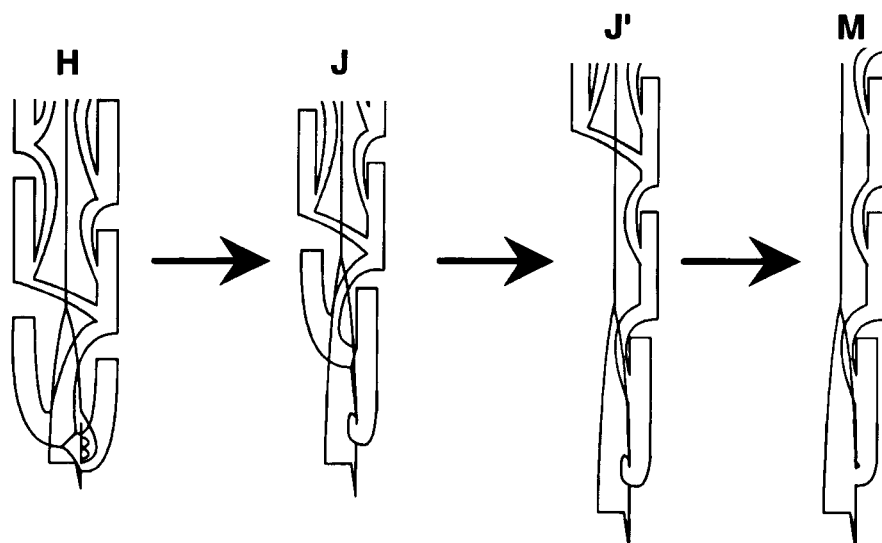
As in the Petalolithidae, the evolution of different genera within the Normalograptidae involves only modification in thecal form, or, in the case of *Hirsutograptus*, addition of proximal and thecal spines (Koren' and Rickards 1996). The origins of *Neodicellograptus* and *Cystograptus* are discussed in the remarks for those genera. *Rhaphidograptus* is discussed in the section on proximal development patterns.

The oldest reliable record of the Dimorphograptidae is *Akidograptus parallelus* from the base of the *persculptus* Zone in China (Yu *et al.* 1988). Li and Ge (1981) and Li (1990) have discussed the origin of the akidograptines from an ancestor that would here be placed within the Normalograptidae (e.g. *Normalograptus*). This involves the development of a longer sicula, the emergence of $th1^1$ from a point on the metasicula farther from the aperture, the early upward growth of $th1^1$, and the delayed budding of $th1^2$ (see also discussion of Pattern J astogeny). The delayed budding of $th1^2$ is an apomorphic feature shared with the Petalolithidae (Pattern I). The presence of a complete median septum and dicalycal $th2^1$, however, is a plesiomorphic feature retained from the Normalograptidae (Pattern H), not observed in any known Pattern I species. Although the possibility exists that the earliest species of *Akidograptus* and *Glyptograptus* achieved the delayed (non-primordial) $th1^2$ independently, a more parsimonious solution is that Pattern J was derived from an unknown, septate Pattern I ancestor within the *persculptus* Zone. In this case, the petalolithid ancora and the ancora-like structures seen in some akidograptines may be homologous. In either case, both groups share ancestry among the latest Ordovician normalograptids. More work on isolated material from this critical stratigraphical interval is required to clarify these relationships.

Since Rickards and Hutt (1970) discovered *Atavograptus ceryx* in the *persculptus* Biozone it has been widely considered that *Atavograptus*, the earliest monograptid genus, evolved directly from a septate species of '*Glyptograptus*' (here assigned to *Normalograptus*). The akidograptines and *Dimorphograptus* were cited by Rickards (1988) as an example of 'echoic evolution' because their uniserial proximal end (not present in *Akidograptus* or *Parakidograptus*) was considered a later 'pale echo' of the uniserial stipe of *Atavograptus* (Rickards 1988, p. 223).

Bulman (1970) noted that the elimination of $th1^2$ from the astogenetic sequence has been a difficulty in understanding the origin of the monograptids. This question has been discussed by Mitchell (1987) and Li (1990), both of whom suggested an ancestor for *Atavograptus* among the akidograptines (or possibly the Petalolithidae). In fact, the transition from a Pattern H ancestor to a monograptid (Pattern M) rhabdosome requires three separate astogenetic changes to occur: the immediate outward-upward growth of the first theca; the redirection of the second theca so that it is no longer alternate; and the loss of the second thecal series distally (loss of the dicalycal theca). All these changes also involve a transition from two or three primordial thecae as seen in Pattern H to one or none in Pattern M_r.

Li (1990) has correctly noted that the early upward growth of $th1^1$ among the akidograptines is more similar to monograptid astogeny and that a derivation of *Atavograptus* from among the akidograptines requires less drastic astogenetic reorganization than from a *Normalograptus* ancestor. Li also noted strong similarities in thecal form between several akidograptine and earliest monograptid species. He considered, however, that four of the reported earliest monograptids (*Atavograptus ceryx*, *A. primitivus* (Li, 1983), '*Pristiograptus antiquatus* Li, 1990 and '*Monograptus?*' sp. Bjerreskov 1975) were derived from four separate akidograptid ancestors with similar thecal forms, thus implying a polyphyletic origin for the Monograptidae. (Based on its strongly climacograptid thecal form and relatively great width in comparison with other earliest monograptids it seems likely that the single fragment assigned to *Monograptus?* sp. reported by Bjerreskov (1975, text-fig. 17f) is a distal fragment of a single stipe of a *Normalograptus* species such as *N. normalis*. As noted above and by a number of previous workers (e.g. Mu and Ni 1983; Williams 1983) single stipes of such species can grow to considerable lengths either as a result of



TEXT-FIG. 8. Schematic diagram of astogenetic pattern in the evolutionary origin of *Atavograptus* from a normalograptid ancestor. Note that the Pattern J species may have been derived from Pattern H through an intermediate, septate Pattern I species. See text for explanation.

stipe divergence or termination of growth of one stipe.) *Atavograptus primitivus* and '*Pristiograptus antiquatus*' have been shown to be synonymous (Lukasik and Melchin 1994), and this species (Text-fig. 3LL-MM) differs only slightly in thecal form from *A. ceryx*. Based on presently available data, there is no evidence to support a polyphyletic origin for the Monograptidae.

In the transition from Pattern H to Pattern J, possibly with a septate Pattern I intermediate step, the early upward growth of $th1^1$ was achieved, and $th2^1$ and probably $th1^2$ are no longer primordial.

The transition from Pattern J to J' involves only redirection of the second theca (and usually one or more subsequent thecae) above $th1$. Thus, two of the conditions necessary for the transition from a normalograptid ancestor to *Atavograptus* were achieved in *Dimorphograptus*. The only changes necessary to evolve from *Dimorphograptus* to *Atavograptus* are the loss of the short downward-growing portion of $th1$ and the loss of the second thecal series distally. From the information currently available, it is not clear if the second thecal series in the *Dimorphograptus* species is produced directly from a dicalycal theca or if any of the thecae in the biserial portion of the rhabdosome are alternate in origin. If the second thecal series arose directly from a dicalycal theca then suppression of the dicalycal theca results in a fully uniserial rhabdosome.

Since Rickards and Hutt (1970) described *Atavograptus ceryx*, the principal objection to a dimorphograptid ancestor for *Atavograptus* has been that the earliest known species of *Dimorphograptus* occurs almost two zones later than the origin of *Atavograptus*: in the *atavus* Zone for the former and upper *persculptus* Zone for the latter (Rickards *et al.* 1977). However, Li (1987) lists three *Dimorphograptus* species from the *acuminatus* Zone. Lin and Chen (1984) have reported '*Rhaphidograptus minutus*' (here assigned as *Dimorphograptus?* cf. *minutus*) from the middle of the *persculptus* Biozone, below the first occurrence of *Akidograptus ascensus* or *Parakidograptus acuminatus*. Their illustrated specimen has been examined by the author and although it is rather poorly preserved (Text-fig. 3Z), it may be a true *Dimorphograptus*, although the sicula is much wider than is typical of this species in higher samples or of coeval akidograptines. It is too poorly preserved to see if it possesses an initial downward growing portion of $th1$. Its occurrence in *persculptus* Zone strata, however, is significant because it demonstrates the possible presence of this genus in strata coeval with or slightly earlier than the first *Atavograptus*.

A suggested evolutionary sequence for the origin of *Atavograptus* is as follows (Text-fig. 8).

1. A Pattern H ancestor (e.g. *Normalograptus*) gave rise to Pattern J (e.g. *Akidograptus*) by early upward growth of th1¹, the late derivation of th1² from the upward-growing portion of th1¹, and general protraction of the proximal end (this may have involved a septate Pattern I intermediate step as discussed above);
2. Pattern J' (*Dimorphograptus*) developed from Pattern J by redirection of the second theca above th1 and the second thecal series arises by some later dicalycal theca;
3. Pattern M (*Atavograptus*) arose from Pattern J' by loss of the downward growth of th1 and loss of the second thecal series distally. The sinus and lacuna stage development of the th1 porus apparently developed at some later stage in monograptid evolution.

By comparison with the suggestions of Rickards and Hutt (1970), that *Atavograptus* be derived directly from a Pattern H ancestor, or Li (1990), that it be derived from *Parakidograptus* and *Akidograptus* along several different individual lineages, this phylogenetic sequence is the most parsimonious. It involves the fewest number of synapomorphies at each step and the fewest number of parallelisms in the astogenetic development. Furthermore, with the discovery of *Dimorphograptus?* cf. *minutus* in the *persculptus* Biozone in China, this sequence may no longer be in conflict with the known stratigraphical ranges of the taxa involved. If *Dimorphograptus?* cf. *minutus* is not a true dimorphograptine and that genus does not arise until the overlying zone, then it may be that *Atavograptus* was derived directly from *Akidograptus* as suggested by Li (1990), and the uniserial proximal end of *Dimorphograptus* must have arisen independently from that of *Atavograptus*, also from an akidograptine ancestor.

RECOGNIZING SUPRASPECIFIC TAXA IN NON-ISOLATED GRAPTOLITES

Mitchell (1987) recognized that his new classification scheme, based on early astogeny, would be difficult to work with in the short term until more well preserved material was studied in detail and more species could be definitely assigned within this new scheme. He pointed out that, although the study of isolated material was necessary to define the proximal growth patterns, it is not essential to place a species within the classification once established. Another important point he noted was that, even if a species cannot be assigned with certainty to a genus within the new system, it does not diminish its utility. The species is the prime entity in biostratigraphical studies and this new classification scheme will not affect the stability of the species, only supraspecific taxa. In fact, the application of this new classification greatly enhances the usefulness of the generic and higher taxa since many have a much more limited range than the previously defined, thecal form-genera.

In his tables 1 and 2, Mitchell (1987) listed the species that could definitely be placed within his new classification and pointed out some diagnostic features, recognizable in well-preserved, non-isolated specimens, that could be used to distinguish the astogenetic patterns. I emphasize some of those points here, particularly with respect to Llandovery faunas, and add some new points of distinction between the Silurian genera based on the present findings.

Melchin and Mitchell (1991) have re-examined graptolite generic distributions in the Ashgill and Lower Llandovery. They have outlined criteria for distinction of the lower Ashgill, 'pre-extinction' faunas dominated by Pattern D-G and K genera, from the uppermost Ashgill-lowermost Llandovery, 'post-extinction' faunas dominated by Pattern H-J and M genera. They have also demonstrated the great utility of this new generic classification in revealing the precise level and the magnitude of the late Ordovician extinction event.

Distinction between Pattern H, I and J species can be a more difficult matter since it was discovered as part of this work (Melchin and Mitchell 1991) that *Glyptograptus sensu stricto* (including a few species with climacograptid thecae) have a Pattern I proximal development. However, even these Pattern I species tend to have a more pointed proximal end and the early growth of th1² is usually slightly delayed and more strongly upward than outward in comparison with a Pattern H proximal development. In specimens preserved in partial relief, a change in surface topography can often be seen at the origins of th1² and th2¹ in Pattern H species but is not seen in

Pattern I. If the primordial origin of $th2^1$ can be established (this can often be seen in compressed or partial relief specimens – e.g. Text-fig. 6D, H) then the species is Pattern H, although not all Pattern H species show this. In the early growth stages, Pattern H species show $th1^1$ growing ahead of $th1^2$ (Text-fig. 3A–B), whereas in Pattern I the two grow synchronously (Text-fig. 3K–M). In addition, in some rare cases, the two foramina at the base of protheca 1^1 in Pattern H species and the list separating them can be seen pressed through the periderm of methatheca 1^1 in flattened specimens (Text-figs 3GG, 7M).

In most compressed specimens, however, the proximal details are not clear enough for positive assignment. The principal criterion employed here, and one which is applicable to reasonably well-preserved, flattened specimens, is the presence or absence of a median septum. As noted above, as far as can be determined from the present material and by comparison with previous reports, there are no known Pattern I species with a complete median septum, although some possess a small partial median septum (always on the obverse side). Partly septate Pattern I species are mostly, if not exclusively, *Petalolithus* species with the typical petalolithid rhabdosomal form. Pattern H species, on the other hand, appear usually to have a complete median septum, although in many species it appears only distally. It is on this basis that I have separated *Glyptograptus* from *Normalograptus* in compressed specimens where proximal details are unclear. This method of distinction is one which can be employed on a variety of preservational types including uncompressed specimens embedded in rock (especially internal moulds) or in compressed specimens where the septum can be seen pressed through (Text-figs 3C, 6J, N, P). In specimens where the distal end is complete, the median septum can sometimes be seen projecting beyond the distal thecae (Text-fig. 6P, s). If, at the distal end, one stipe grows beyond the other, then a median septum must be present (Pl. 5, fig. 9; Text-figs 3E, 6G), because in the aseptate Pattern I species the two rows of thecae must grow synchronously. In those Pattern I species in which the virgula is embedded in the obverse wall, such as *Glyptograptus tamariscus* ssp., the position of the virgula will be close to the edge of those compressed specimen preserved in subscleriform view (Text-fig. 3P) and the fuselli on the distal end may be seen to extend out on onto the virgula. In those species where the virgula is central and unattached, the virgula may be seen to 'wander' laterally along the length of the rhabdosome (Text-fig. 3DD). It must be admitted that still only a relatively small proportion of the Llandovery biserial fauna has been studied in enough detail and further work, especially with Ashgill and Early Llandovery species, may reveal fully septate petalolithids or aseptate normalograptids. The distinction based on internal structure, however, seems reasonable if one assumes that rhabdosomal architecture is, at least to some extent, a product of early astogeny.

Distinction of Pattern J species from patterns H and I in non-isolated specimens is accomplished in most cases by recognition of a fully exposed sicula below $th1^1$. In addition, there are, as yet, no known Pattern H or I species with more than one uniserial theca, whereas most *Dimorphograptus* species have at least two uniserial thecae. It is important to note that in many *Dimorphograptus* species, the space between the downward end of $th1$ and the sicular aperture is often overgrown with later cortical deposits, although the original downward position can often be seen 'pressed-through' in compressed specimens (Text-fig. 3Y). Although in a few Pattern I species $th1^1$ does not grow down to the sicula, this does not occur, to my knowledge, in any *Agetograptus* or *Rhaphidograptus* species. The growth of the reverse wall of metatheca 1^1 straight upward can easily be seen in well preserved akidograptines, even when compressed (Text-fig. 3J, O, R–S, U, X). On the other hand, its growth across the reverse face of the sicula is difficult to see in slender species tentatively assigned to *Agetograptus* such as *A.?* *hubeiensis* (Ni, 1978), although it can clearly be seen in uncompressed examples (Pl. 7, fig. 4). Distinction between *Rhaphidograptus* and some slender *Agetograptus?* species is more difficult unless the fuselli can be seen over the first three thecae. For compressed material, the presence or absence of a median septum, or genicular hoods must be employed for their distinction.

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