EVOLUTION AND PHYLOGENETIC CLASSIFICATION OF THE DIPLOGRAPTACEA

by CHARLES E. MITCHELL

ABSTRACT. The complex astogenetic patterns produced by the specialized, first few thecae (primordial thecae) of graptoloid rhabdosomes were conserved during evolution and provide a reliable guide to 'propinquity of descent' among diplograptids. Using this principle one can redefine their taxonomy, establish phylogenetically meaningful higher taxa, and obtain an improved understanding of diplograptacean phylogeny. The Diplograptacea comprises four major subclades. 1. Orthograptidae: archaic orthograptids (species of the 'Glyptograptus teretiusculus' species group), Orthograptus and Amplocragnostus, together with archiretiolidids, lasiograptids, and ' Climacograptus 'typicalis 'G.' lorrainensis' species groups, 2. Dicranograptidae: dicranograptids plus nemagraptids; 3. Diplograptidae: pseudoclancragnostids and Climacograptus s.s., together with Diplograptus s.s. and offshoots; 4. Monograptidae: 'G.' dentatus' and descendants including Undulograptus paradoxus, G. euglypheus, 'C.' normals, and all the Silurian diplograptids including the universal monograptines. The first three families dominated Ordovician faunas. Taxa with complex proximal end structures were succeeded during the Llandoil and Caradoc by taxa with simpler astogenies. Following extinction of the dominant Ordovician taxa, monograptids (sensu lato) underwent explosive evolution in the Llandovery. New generic group taxa: Archiclimacograptus, Arnheimograptus, Diplocragnostus, Eoglyptograptus, Geniculograptus, Hustedograptus, Oelandograptus, Pseudamplexograptus, and Urbaneanograptus. New family group taxa: Eoglyptograptinae and Orthograptidae.

The first-formed few thecae of graptoloid colonies exhibit specialized ontogenies. These specialized features are largely prothecal in origin and are associated with the formation of the primary stipes. Elles (1922), and later Bulman (especially 1933a and 1936), grouped graptoloid astogenies into a series of 'developmental types' distinguished from one another by budding pattern, direction of thecal growth, and position of the dicalycal theca in the budding sequence. These general developmental types were defined following the recognition that graptoloid astogeny displayed a limited range of basic patterns and that individual patterns characterized large segments of the Graptolidea.

The early astogeny of members of the Suborder Diplograptina Bulman, 1970 is especially complex. Each of the first several thecae exhibit unique features and ontogenetic patterns that are orchestrated to establish the foundation of the rhabdosome. This complex orchestration is, in turn, repeated with great precision among all members of a given species—a regularity not unlike that of the metathecal morphoclines exhibited by monograptids (Bulman 1968, p. 1353; Urbanek 1973). Despite these seemingly useful features, graptoloid (and particularly diplograptinid) astogeny has been largely ignored in both systematic and phylogenetic studies of these organisms. Astogenetic pattern has been seen as simply another of the many features of graptoloid colonies that underwent extensive parallel change (Bulman 1933a, p. 2) and so bears no consistent relationship to taxonomy: '[The Diplograptus type of development ... exhibits considerable modifications which occur indiscriminately in the various genera and sub-genera [of the Diplograptidae]. ...]' (1933a, p. 3). This treatment of astogeny has remained the standard approach, e.g. Urbanek's (1959, p. 326) discussion of Gymnograptus astogeny and Rickards et al.'s (1977, p. 23) discussion of the appearance of the monograptid condition.

Cooper and Fortey (1982, 1983), Kearsley (1982, 1985), and Mitchell (1981, 1986) have argued for a different interpretation of astogenetic similarity. We have each independently concluded that graptoloid astogeny shows a striking parallelism with von Baer's Law, i.e. that primordial

astogenetic features were not altered with great ease or frequency but rather were highly conserved during the evolution of graptoloid colonial design. The features of early astogenetic stages and the sicula were more refractory to change than were later stages in astogeny. In most cases, detailed structural and developmental similarities in early astogeny among graptoloids are homologies. Accordingly, these can and should be used to determine evolutionary relationships among graptolites and to establish a phylogenetic classification. I have presented a theoretical basis for this view, together with detailed supporting evidence, elsewhere (1986; see also Gould 1977 for a discussion of von Baer’s law).

There are now sufficient data available on the astogeny of the Diplograptina to permit an accurate survey of the range of their developmental patterns. I believe that the distribution of these data across the group is also sufficient to trace the outlines of the phylogenetic history of this complex and interesting group and to begin the reorganization of the traditional diplograptinid form taxa into more meaningful units.

DIPLOGRAPTINID ASTOGENETIC PATTERNS

Primitively, the Diplograptina exhibit an early astogenetic pattern in which each of the first four thecae have specialized ontogenies. For convenience, we may refer to these specialized, first few thecae of graptolite colonies as primordial thecae (adapting somewhat a term employed early in the study of graptolites: see Holm 1895), and to that part of astogeny that encompasses the growth of these thecae as the primordial astogeny. Among primitive diplograptinids th₂¹ is dicalycal and th₁² to th₂² include crossing canals. This is essentially the definition of the Diplograptus developmental type of Elles (1922). Bulman (1936) subdivided this pattern into a number of ‘stages’ (again seen solely as grades of organization) as part of his study of graptoloid orthogenesis. While retaining the general definition for the Diplograptus developmental type, with its emphasis on three crossing canals, Bulman (1963a, 1970) later abandoned these ‘stages’ and simply recognized two grades of organization among the range of diplograptinid developmental patterns: 1, the primitive streptoblastic condition in which th₁² is S-shaped and initially grows upwards from its origin; and 2, the derived prosoblastic condition in which th₁² is J-shaped and the initial upward growth is lost. This simple structural distinction does indeed appear to have been crossed repeatedly during the evolu-

![Text-Fig. 1. Thecal diagrams of the diplograptid astogenetic Patterns A–I (letter designations are those used to refer to these patterns throughout the text).](image-url)
tion of the Diplograptina. Consequently, I do not place any great emphasis on it in the definition of the diplograptinid primordial astogenetic patterns, except to note that the streptoblastic condition is restricted to the more primitive members of the group (i.e., those with astogenetic Patterns A, B, and C, see discussion of these patterns below). I believe these astogenetic patterns have strict phylogenetic significance.

The Diplograptina and the Dicranographtidae (including Leptograptus; see Finney 1985) are characterized by the unique left-handed origin of th1² from th1¹. Fuselli from the obverse side of

**Table 1.** Generic assignments of Ordovician ‘diplograptid’ species with known primordial astogeny (*= type species).

| Pattern B | EGLOLYTICNOPTUS gen. nov.: Glyptograptus cernus Jaanusson, G. dentatus (Brongniart)*, Pseudoclimacograptus jaroelvi Bouček. UNDULOGRAPTUS Bouček, 1973: Climacograptus paradoxus Bouček* |
| Pattern E | CLIMACOGRAPTUS (DIPLOCANTHOGRAPTUS) subgen. nov.: C. dorotheus Riva, C. longispinus T. S. Hall, C. spiniferus Ruedemann*, C. venustus Hsu |
TEXT-FIG. 2. Camera lucida drawings of species exhibiting Pattern A and Pattern C primordial astogenies. All are reverse views unless noted otherwise.

th₁ swing around the theca and form a hood over the foramen in the reverse side of th₁² (see, for instance, text-figs. 2e, 6b, 9i, j). The foramen of th₁² is completed, as is the contribution of th₁¹ to the hood of th₁², when the next fusellus passes around th₁² to meet with the reverse wall of th₁² or the sicula, rather than continuing around the leading edge of the hood (e.g. text-figs. 2e and 9a, d). Following the completion of the hood of th₁², the crossing canal of th₁² begins to grow downward, across the reverse side of the sicula. I employ the term 'crossing canal' to refer only to the sicula-crossing, tubular prothecae of primordial thecae. Diploraptinid structures force this restriction of the term because species with a comparatively simple primordial astogeny and a delayed dicalycal theca (such as *Amplexograptus bekkeri*, in which th₁³ is dicalycal) could be said to have four or five crossing canals, several of which differ in no significant structural way from later thecae. Hence, the term 'crossing canal' retains greater meaning if restricted in its application to the prothecae of the specialized early thecae that cross the sicula.

Beyond its initial origin the growth of th₁² includes several major variants among the Diploraptina and, together with the ontogenetic variations exhibited by the crossing canals of th₂¹ and th₂², these variants define nine basic primordial astogenetic patterns. The exact position of the dicalycal theca contributes very little to the distinctiveness of the patterns, however. In almost any given pattern, some species possess a delayed dicalycal theca. However, the level of the dicalycal theca's *earliest occurrence* within each astogenetic pattern is of significance. Consequently, I do not use Cooper and Forsey's (1983, p. 171) two diploraptinid 'developmental types', which they recognized on the basis of the position of the dicalycal theca.

The nine diploraptinid primordial astogenetic patterns are illustrated diagrammatically in text-fig. 1 and have been designated 'A'-'I', roughly in stratigraphic order of first appearance, elsewhere (Mitchell 1986). I have chosen not to name them after seemingly typical species or genera. None of these patterns are invariant. To name them after a particular taxon promotes a stereotypic and,

---

**B-D, J, Oelandograptus (gen. nov.) astrostomatus oelandicus** (Bulman in Skevington 1965) exhibiting Pattern A primordial astogeny; Holm Limestone, Kunda Stage (Humberanian Substage, D. hirundo Zone), Hålludden, Öland. a, c, Cn 59811 (from horizon - 120D), obverse and reverse views; note quasi-symmetrical disposition of primordial thecae, × 20. d, Cn 59892 (Holm Collection), showing streptoblastic crossing canal of th₁² and left-handed origin of th₂¹, × 20. j, Cn 59891 (Holm Collection), note visible th₂³ descending crossing canal and undulating median septum formed by successive prothecae, × 9.

**H, R, Dicranograptus nicholsoni longibasis** Ruedemann and Decker, Viola Springs Formation (0.3 m above base of section D; Alberstadt 1973), Rocklandian Stage (upper C. bicornis Zone), Arbuckle Mtns., Oklahoma. h, MCZ 9461/1, young growth stage equivalent to δ; note dorsal notch, lateral lappets, and paired notches adjacent to virgella, × 14. r, MCZ 9461/2, obverse view showing dicroanograpic sicula and prominent nema, × 9.

**I, N, O, Pseudoclinothecagrapta (Archiclinocergraptus subgen. nov.) angulatus sebenderis** Jaanusson exhibiting Pattern C primordial astogeny; Holm Collection, Folkeslund Limestone, Lasnamägi Stage ('G. teretiusculus Zone'). i, Cn 59885, Gärderlösa, Öland, specimen showing streptoblastic th₁¹ with origin of th₁² from its right side (specimen damaged subsequent to sketching), × 20. n, q, Cn 59803, Sjöstorp, Öland, obverse and reverse views, × 20.

**L, M, Hustedoragraptus (gen. nov.) teretiusculus sensu** Jaanusson, 1960, Cn 59886, Folkeslund Limestone, Lasnamägi Stage ('H. teretiusculus Zone'), Sjöstorp, Öland (Holm Collection), obverse and reverse views; note paired lappets on dorsal margin of sicula, prominent crossing canal of th₂¹, and dicalycal th₂², × 20.

**O, P, Pseudoplexypropagrus (gen. nov.) distichus** (Eichwald), exhibiting Pattern C primordial astogeny; Folkeslund Limestone, Lasnamägi Stage ('G. teretiusculus Zone'), Lerkaka, Öland (Holm Collection). o, Cn 59222, showing formation of th₂¹, th₂² and foramen from which th₁³ arises. p, Cn 59921, note right-handed origin of th₁² from th₁¹, both × 20.

Abbreviations: an, ancora; av, antivirgellar spines; cc, crossing canal; dt, dicalycal theca; fl, upward growing flange; fo, foramen; la, lappets; ls, list scar; m, mesial spine; ms, median septum; s, sicula; p, protheca; pr, prothecal rods; v, virgella. Repositories: BMNH, British Museum (Natural History), London; MCZ, Museum of Comparative Zoology, Harvard University; Cn, Naturhistoriska Riksmuseet, Stockholm; SM, Sedgwick Museum, Cambridge University; Ö and Vg, Paleontological Institute, Uppsala University; USNM, United States National Museum, Smithsonian Institution, Washington.
at times, seriously distorted view of the astogenetic patterns. Finally, these patterns do not apply to the Silurian retiolitids (although most of the archiretiolitids are encompassed by the scheme). Table 1 indicates the astogenetic pattern of more than eighty diplograptinid species known in relief or from isolated preparations, and for which I have been able to obtain data. The stratigraphic range of the genera exhibiting these patterns is indicated in text-fig. 17.

**Pattern A** (text-fig. 2A–H, J–M, R)

The sicula is straight. Its aperture is commonly plain except for a prominent virgella. In a few species the aperture is elaborated in the form of a pair of antivirgellar lappets or antivirgellar spines. The crossing canal of th1² is usually streptoblastic. Th1² gives rise to the crossing canal of th2¹ from its left side by bifurcation of a broad hood formed early in the ontogeny of th1² (text-fig. 2B, H). The crossing canal of th2¹ also grows downward, toward the virgella and along the reverse wall of th1¹. An isolated fusellar flange forms near the sicular aperture in advance of the approaching crossing canal of th2¹, and grows upwards. They fuse and form a symmetrical pair of foramina from which the metatheca of th2¹ arises on the biological left side, and of th2² on the right (text-fig. 2A). From this point, both thecae grow upward and surround the crossing canal of th2¹, which remains visible for a large part of its length. There are, thus, four primordial thecae and three crossing canals (th1²–th2²). Either th2¹ or some later theca may be dicalydal.

In obverse view, both th1¹ and th1² diverge widely from the sicula, forming a blunt to broadly rounded proximal end that is usually sub-symmetrical. Th2¹ and th2² enclose the sicula together with subsequent thecae. In species exhibiting a Pattern A astogeny, the median septum may be undulating to straight, and their post-primordial thecae range in shape from glyptograptid to orthograptid. Species exhibiting Pattern A include the earliest known diplograptinids. This developmental pattern is also found throughout the Dicranograptoidea, as noted by Bulman (1970, pp. V76–V78).

**Pattern B** (text-fig. 3A–E, I, J)

The sicula is straight to slightly deflected. The sicular aperture bears only a short stout virgella. Th1² may be prosoblastic or streptoblastic. The crossing canal of th1² grows downward obliquely across the sicula and away from th1¹. The third theca arises from th1² on its left side, as in Pattern A. Th2¹ grows downward at first and then turns upward before giving rise to th2². Th2² arises by a pattern of differentiation like that of distal thecae. The dicalydal theca may be th2¹ or later. The median septum may be undulating to straight. There are three primordial thecae and two crossing canals (th1² and th1¹). The proximal end is asymmetric with the first two thecal apertures at markedly different levels. In obverse view the sicula is exposed only to the level of the aperture of th1¹ or th1². Thecal shapes among species exhibiting Pattern B range from glyptograptid to climacograptid. This pattern is relatively poorly known: only the primordial astogeny of Glyptograpthus dentatus (Brongniart) and Undulograpthus paradoxus (Bouček) (= Climacograpthus pauperatus Bulman) are known in any detail (Bulman 1963a).

**Pattern C** (text-figs. 2I, N–Q, 4A–O)

The sicula is straight and generally slender. With rare exceptions (e.g. Diculograpthus hystrix (Bulman), text-fig. 4), the sicular aperture bears only a virgella. The growth of th1²–th2² is like that seen in Pattern A, except that the crossing canal of th2¹ arises from the right side of th1². Th2¹ (or rarely, th2²) is dicalydal. Among a large number of early species, th3¹ originates from a foramen in the metatheca of th2¹ (text-figs. 2O, Q, 4E). This feature commonly produces what appears to be a continuous arch connecting th2² and th3¹ (see text-fig. 4I). Because the crossing canal of th2¹ must swing out and away from the sicula a considerable distance to grow around th1², it is commonly exposed as a diamond-shaped patch in the central region of the rhabdosome above the th2²–th3¹ arch. This feature is exhibited clearly by Pseudoclaimacograpthus olivieri Bouček and P. angulatus (Bulman 1953, text-figs. 1b and 2b, respectively, but note that the origin of th2¹ in his text-figs. 1c
TEXT-FIG. 3. Camera lucida drawings of species exhibiting Pattern B and Pattern H primordial astogenies. See text-fig. 2 for explanation of abbreviations and specimen repositories.

A–E, Undulograptus paradoxus (Bouček), Seby Limestone, Lushnamägi Stage (D. murchisoni Zone), Seby, Öland. A, B, OI unnumbered, reverse and obverse views of early growth stage showing streptoblastic th1 and delayed origin of th2', × 32. C, D, OI 983, obverse and reverse views; note budding sequence with diacylcal th2'; × 16. E, OI unnumbered, reverse view; note paired th1' and th2', × 20.

F–H, K, L, Glyptograptus brevis (Elles and Wood), ‘Climacograptus’ band; Balclachie beds, Caradoc Series (’D.’ multidens Zone), Laggan Burn, Ayrshire, Scotland. F, MCZ 9462/1, oblique reverse view showing list that links free reverse wall of th1 with sicula, × 32. G, MCZ 9462/2, reverse view; note origin of th2', × 26. H, MCZ 9462/3, obverse view; note origin of th2' by simple distal differentiation, × 32. K, L, MCZ 9462/4, reverse and obverse views; specimen partly flattened distally to present sub-scalariform view, × 15.

I, J, Eoglyptograptus (gen. nov.) densatus (Brongniart) sensu Bulman, 1963a, Holen Limestone, Kunda Stage (D. bifidus Zone), + 0 + 15D, Hagudden, Öland. I, OI 9937, note shape of proximal end and cuspsate thecal apertures, × 10. J, OI 1228, early th2' stage; see text and Skevington (1965) for further discussion, × 34.
TEXT-FIG. 4. Camera lucida drawings of species exhibiting Pattern C primordial astogeny. See text-fig. 2 for explanation of abbreviations and specimen repositories.

A-F, *Pseudoclanculograptus* (Archiclanulograptus subgen. nov.) *eurystoma* Jaanusson, Folkeslunda Limestone, Lasnamägi Stage ('G.' *teretiusculus* Zone?), Gärdsösa, Öland. A-D, Cn 59921, oblique right-lateral, reverse, oblique reverse, and left-lateral views, respectively, showing construction of right-handed crossing canal of th2^1^ and its origin from th1^2^, \( \times 27 \). E, F, Cn 59922, oblique reverse and reverse views; note final hood-like form of crossing canal of th2^3^ and origin of th2^2^ and th3^1^, \( \times 27 \).

G-I, *Prolasiograptus* *haphas* (Jaanusson), Folkeslunda Limestone, Lasnamägi Stage ('G.' *teretiusculus* Zone?), Gärdsösa, Öland. G-H, Cn 59925, obverse and reverse views; note exposed patch of crossing canal of th2^1^ in
and 2c is shown, incorrectly, as left-handed). This morphology appears to be distinctive of species with Pattern C primordial astogeny.

Species exhibiting Pattern C commonly possess a zigzag median septum, but it may become straight (or nearly so) after the first few thecae, as in 'C.' distichus (Eichelwald) (Bulman 1932, pl. 4, figs. 24 and 25) or 'A.' munimentus Berry (1964, pl. 14, text-figs. 1–4). The proximal end of rhabdosomes exhibiting Pattern C is evenly rounded to blunt and generally broad. In obverse view the sicula is exposed only to the level of the aperture of th\(^1\) or th\(^2\). Sharply geniculate thecae predominate in this species group.

**Pattern D** (text-figs. 5, 6, 7A–C)

The sicula in this group is rather broad for its length, and its axis is usually strongly deflected toward the dorsal side of the sicula. The aperture bears only a virgella. The metascula commonly exhibits a series of dense, raised bands comprising two or three condensed fuselli (text-fig. 6c, n). The prosicula is usually absent and is replaced by one or two stout rods that merge with the virgula. Th\(^1\) is small and possesses a tightly upturned metatheca that grows closely adpressed to its protheca. Th\(^1\) is prosoblastic and bifurcates shortly after crossing th\(^1\), giving rise to th\(^2\) from its right side, as in Pattern C (text-fig. 5C–E). The crossing canals of both th\(^1\) and th\(^2\) grow across the sicula in a nearly horizontal direction. The crossing canal of th\(^2\) ceases growth near the sicular axis and exhibits a hood-like form. The flange, that in Patterns A and C had grown upward from near the sicular aperture, to fuse with the approaching edge of the crossing canal of th\(^2\), appears in Pattern D on the dorso-lateral side of the crossing canal of th\(^1\) (text-figs. 5m and 5c). As the flange grows upward it is linked to the hood of th\(^2\) by a list (text-figs. 5i, 6l, 7b). This event marks the differentiation of the protheca of th\(^2\) and th\(^2\). There are four primordial thecae and two crossing canals (th\(^1\) and th\(^2\)). Th\(^2\) or some later theca is dicalycal. The median septum may be zigzagged, may become straight distally, or may be straight throughout (as in C. bicornis) among species known to possess this astogenetic pattern. The proximal end of these species is narrow and evenly rounded. In obverse view the sicula is exposed only to the level of the aperture of th\(^1\) or th\(^2\).

**Pattern E** (text-fig. 7d–l)

The sicula is like that described for Pattern D. The long virgella is angled across the sicular aperture. The metatheca of th\(^1\) is tightly upturned and adpressed against its protheca. The hood over the foramen of th\(^2\) is completed enclosed by the metatheca of th\(^1\). The crossing canal of th\(^1\) originates as an isolated flange located on th\(^1\) below the foramen of th\(^2\) (text-fig. 7h, i). From this origin, it grows upward diagonally across the sicula with no downward component of growth. Th\(^2\) grows from th\(^2\) above a prominent growth-line unconformity by a pattern of differentiation like that seen in the budding of distal thecae (text-fig. 7h, k). Accordingly, there are two primordial thecae and one crossing canal (th\(^1\)).

Rhabdosomes of species with this astogenetic pattern may be septate, with a straight median septum and th\(^2\) or some later theca dicalycal, or they may be aseptate. The proximal end is narrow.
TEXT-FIG. 5. Camera lucida drawings illustrating Pattern D primordial astogeny in Climacograptus (Climacograptus) sp. cf. C. (C.) candatus Lapworth; Viola Springs Formation (101 m above base of section H; Alberstadt 1973), Maysvillian Stage ('C.? pygmaeus' Zone), Arbuckle Mtns., Oklahoma. All illustrations are reverse views unless noted otherwise. See text-fig. 2 for explanation of abbreviations and specimen repositories.

A, c, MCZ 9463/1, obverse and reverse views; note prosoblastic form of th1². n, MCZ 9463/2. p, MCZ 9463/3; note list linking crossing canal of th1² with sicula and marking differentiation of right-handed th2¹. r, f, MCZ 9463/4, reverse and left-lateral view of later stage in growth of crossing canal of th2¹. g, j, MCZ 9463/5, reverse and left-lateral views of early th2² stage; list links upward-growing flange of prolisteca of th2¹ with hood-like crossing canal. h, i, MCZ 9463/6, reverse and oblique left-lateral views. k, l, MCZ 9463/7,
and unevenly rounded to somewhat rectangular. The markedly offset sicula lies almost entirely to the right of the plane of symmetry in obverse view and is exposed to the level of the aperture of th1 (text-fig. 7L). Post-primordial thecae are sharply geniculate, climacograptid thecae with nearly vertical suprageneric walls.

**Pattern F** (text-fig. 8)
The sicula is slender and bears a prominent pair of antivirgellar spines in addition to the usual virgella. The metatheca of th1 is tightly recurved and grows upward along its protheca. Th1 is prosoblastic and the hood which covers the foramen of th1 is generally short and largely or entirely enclosed by th1 (text-fig. 8D, I, M). The crossing canal of th1 arises as an isolated flange on th1 below the foramen (text-fig. 8E, J), as in Pattern E. It subsequently grows diagonally upward across the sicula. Near the mid-line of the sicula, this upward-growing flange bifurcates to produce both the metatheca of th1 and the protheca of th2 (text-fig. 8I, N). Th2 arises by a pattern of differentiation that is like that of all subsequent thecae (text-fig. 8I). There are three primordial thecae and one crossing canal (th1).

Pattern F rhabdosomes are aseptate. The proximal end is strongly asymmetrical and generally quite narrow compared to the distal width of the colony. In obverse view the sicula is exposed for a large part of its length, nearly to the level of the aperture of th2. Post-primordial thecae range from climacograptid with prominent genicular flanges to glyptograptid or nearly orthograptid.

**Pattern G** (text-figs. 9 and 10)
The sicula is long and slender with a virgella and a pair of antivirgellar spines on the sicula aperture. Th1 gives rise to a prosoblastic th1. The crossing canal of th1 grows diagonally downward across the sicula in the form of a hood that is free on its ventral (proximal-ward) side (text-figs. 9A and 10A). It fuses with an upward-growing, wedge-shaped flange that arises partly on the sicula and partly on th1 near the sicula aperture. The hood of th1 continues to grow downward but now as a complete tube (text-figs. 9D and 10C, E). The edge of the open ventral margin of the earlier hood of th1 bears a thickened rim and, together with one edge of the upward-growing flange, forms a foramen from which th2 develops (text-fig. 9B). Thus, th1 and th2 form a somewhat asymmetrical pair with a smooth arch connecting their prothecae across the reverse side of the sicula. The protheca of th1 expands rapidly, growing upward along the dorsal wall of the crossing canal of th1 (text-fig. 9E, F). Th2 differentiates from the protheca of th1 above a growth line un conformity, in a fashion like that by which all subsequent thecae arise (text-figs. 9G and 10B). There are three primordial thecae and one crossing canal (th1).

The first several thecal pairs alternate, and the dicalyceal theca may be th3 or, more commonly, some later theca. Many species exhibiting Pattern G are aseptate. Septate species have a straight median septum. The proximal end is tapered bluntly and markedly asymmetric. On the obverse side of the colony the sicula is visible for most of its length, up to a level near the aperture of th2, as in Pattern F. Post-primordial thecae range from orthograptid to amplexograptid or lasiograptid in shape.
TEXT-FIG. 6. Camera lucida drawings of species exhibiting Pattern D primordial astogeny. All illustrations are reverse views unless noted otherwise. See text-fig. 2 for explanation of abbreviations and specimen repositories.

Pattern H (text-figs. 3f–h, k, l, n, 11, 12k–o)

The sicula is commonly relatively short and broad (about 1 mm or less in length among many Ordovician representatives), but varies greatly (e.g. *Cystograptus penna*). The sicular aperture bears only a virgella. However, the dorsal margin is often prolonged and somewhat incurvate. The metathec of th1 is generally sharply upturned, as in Patterns E and F, and may partially enclose its protetheca on the obverse side. It also encloses the foramen and small hood of th1 on its reverse side. In many species with this pattern (but not *Climacograptus kuckersianus* Wiman), the reverse wall of the metathec of th1 is free and is not anchored against either the sicula or the protetheca of th1 (text-fig. 3r). The crossing canal of th2 begins as an isolated flange located on th1 near the sicular aperture. As it grows diagonally upward, across the sicula, its ventral edge grows along the edge of the reverse wall of th1. Early in the growth of the protetheca of th2, th2 begins to differentiate—a process marked by the interfering of wedge-shaped fuselli in the region adjacent to th1 (text-figs. 11h, i and 12x). Th2 differentiates in a fashion like that of later thecae (text-figs. 3m, 11m, 12k). There are three primordial thecae and one crossing canal (th1). Rhabdosomes are usually septate with the dicaly whole theca at the primitive location (th2) or later. The majority of Pattern H species exhibit a straight median septum, but among some Silurian species (e.g. *Clinoclimacograptus retroversus* and *Metaclimacograptus undulatus*) the median septum is undulate to zigzagged.

The proximal end is quite narrow and sharply rounded or fusiform and strongly asymmetrical. In obverse view, th2 partly encloses the sicula, which is exposed only up to the level of the aperture of th1 or, at most, nearly up to the level of the aperture of th1 (text-figs. 3h, l, and 11i, l). Among Ordovician Pattern H species, post-primordial thecae are restricted to glyptographtid and climacographtid in shape. The rhabdosomes tend to be narrow and parallel sided with little distal widening. However, Silurian species encompass a broad range of diplograptinid thecal shapes and colony forms.

Pattern I (text-fig. 12a–j)

The long sicula bears only a virgella projecting from its simple aperture. Th1 arises relatively close to the sicular aperture and has an exceptionally short descending segment. The foramen of th1 in the right lateral wall of the protetheca of th1 bears only a minute hood, or no hood at all. Th1 turns upward very sharply, and grows upward with its left lateral wall partly or completely enclosing its descending protetheca in obverse aspect (text-fig. 12c, h). As th1 grows, its right lateral wall begins to sweep out on to the metascula and to enclose the latter's reverse side (text-fig. 12a, b, d). After this wall crosses the sicula's mid-line and the theca approaches its mature length, an interthecal septum appears that divides the right lateral wall into a metathec of th1 and a protetheca of th1 (text-fig. 12a, d). A growth line unconformity may also mark the separation of the protetheca of th1.

of th1, h, i, MCZ 9464/7, obverse and reverse views; dicaly whole th2 arises by simple differentiation from distal portion of protetheca of th2.

1–r. *Climacograptus* (*Climacograptus*) *bicorns* (Hall), Viola Springs Formation (0–3 m above base of section D; Alberstadt 1973), Rocklandian Stage (upper *C. bicorns* Zone), Arbuckle Mts., Oklahoma. i, MCZ 9465/1, showing paired prosiccular rods, raised fusellar ridges on metascula, and origin of th2 near aperture of hood-like crossing canal of th2 (cf. text-figs. 6l and 7a). k, MCZ 9465/2, l, MCZ 9465/4, proximal end of rhabdosome with portion of reverse side broken away, revealing hood-like crossing canal of th2 and list that linked crossing canal with reverse wall of protetheca of th2 (cf. text-figs. 5r and 6o). m, n, MCZ 9465/5, ventral and reverse views of immature metascula, showing dorsal deflection and concave ventral side; note regularly spaced fusellar rings and paired prosiccular rods. o, MCZ 9465/3. p, MCZ 9465/6, early growth stage showing prosoblastic th1.

All x 35.
TEXT-FIG. 7. Camera lucida drawings of species exhibiting Pattern D and Pattern E primordial astogenies. All illustrations are reverse views unless noted otherwise. See text-fig. 2 for explanation of abbreviations and specimen repositories.

A, *Pseudoclinacograptus* (Pseudoclinacograptus) scharenbergi (Lapworth), BMNH GS 74247, Balelatchi beds, Caradoc Series ('D.' multidentatus Zone), Laggan Burn, Ayrshire, Scotland; note origin of th2 at point of fusion between upward-growing flange of reverse prothecal wall and crossing canal of th2; sicula apex sealed but lacking normal prosicula.

B, C, P. (P.) elevensis Skoglund, Fjäcka Shale, Jonstorp, Västergötland. B, Vg 757, semi-relief specimen with prominent list scar (ls) where list that links crossing canal of th2 to reverse prothecal wall has been pressed through. C, Vg 758, obverse view; th2 rapidly encloses strongly deflected sicula.
Following its origin, th1² continues the trend of the right lateral wall of th1¹ and grows strongly upward, often reaching the dorsal side of the sicula well above the latter's aperture. This origin of th1² is quite late (in some species it does not appear until after the protheca of th1¹ has reached the dorsal side of the sicula) compared to other diplograptid astogenetic patterns. The differentiation of th1² follows a developmental pattern like that of all later thecae. Thus, Pattern I exhibits only one primordial theca and no crossing canals. Although generally aseptate, some Pattern I species have a straight median septum and a dicalycal th2¹ or some later theca. In at least some dimorphograptids (e.g. Rhaphidograpus toernquisti) the metatheca of th1² appears to be suppressed (text-fig. 12n) but th2¹ develops from the protheca of th1² in the normal fashion.

The proximal end is sharply fusiform to acicular. In reverse aspect, a substantial portion of the dorsal side of the sicula is visible. The combined right lateral wall of th1¹ and ventral wall of th1² often have a concave curvature (especially in species with orthograptid or petalograptid colonies). In obverse view the sicula is commonly exposed for most or all of its length. Nevertheless, thecae are sufficiently elongate that it is usually enclosed by the level of the aperture of th1¹ or, more rarely, by a level slightly below that of the aperture of th1². Also in obverse view, th1¹ often appears to grow directly upward from near the sicular aperture because of its enclosure of the short descending portion of the protheca of th1¹. Pattern I species (all are Silurian in age) possess post-primordial thecae ranging in shape from climaclograptid to orthograptid and petalograptid.

**PHYLOGENY AND CLASSIFICATION OF THE DIPLOGRAPTACEA**

Suborder VIRGELLINA Fortey and Cooper, 1986

*Diagnosis.* Graptoloids with a virgella. Primordial astogeny is of isograptid type or modified to 'diplograptid', 'hemagraptid', or 'monograptid' type. Rhabdosomes extensiform to reclined or platyacalycal scendent.

Superfamily DIPLOGRAPTACEA Lapworth, 1873, emend.

*Diagnosis.* Horizontal to reclined and partly to wholly scendent, dipleral biserial and monoserial virgellinids with a single dicalycal theca, delayed to th2¹ or some later theca, and three crossing canals; th1¹ with metasclerotic origin and th1² arising right-handedly from th1¹.

*Discussion.* Text-fig. 13 depicts the cladistic relationships among the major diplograptacean taxa (typified in the diagram by their astogenetic patterns), the stem group *Oelandograptus* gen. nov. ('Of',—see below), and the other taxa of the Virgellina Fortey and Cooper, 1986. The Phyllograptidacea, which possess an isograptid primordial astogeny (denoted by 'I' in text-fig. 13), form a convenient outgroup for comparisons among the Diplograptacea (see Cooper and Fortey 1983 for a discussion of the primitive status of this astogenetic pattern).

---

D-1, *Climacograptus* (Diaplanocragnostus subgen. nov.) *spiniferus* Ruedemann, Viola Springs Formation, Maysvillian Stage ('C7' pyrmacras Zone), Arbuckle Mns., Oklahoma; MCZ 9466 from 51 m above base of section along Interstate Highway 35, adjacent to section H; MCZ 9467 from 104-5 m above base of section H; MCZ 9468 from 36-5 m above base of section J; MCZ 9469 from 30-5 m above base of section H (Alberstadt 1973). D, MCZ 9466/1, early th1¹ stage; note set of prosicular rods in place of normal prosicula and dorsal deflection of metasicula. E, MCZ 9467/1, ventral view; note stirrup-like form of prosicula rods and prosoblastic crossing canal of th1¹. F, MCZ 9466/2, ventral view; note characteristic twisted, asymmetric form of sicula, × 40. G, MCZ 9468/1, th1² formed by upward-growing flange. H, I, MCZ 9466/3, oblique reverse and left-lateral views; flange of th1² originates on reverse lateral wall of th1¹, not in continuity with earlier segment of its crossing canal. J, MCZ 9469/1; note origin of th2¹ by simple differentiation from distal portion of protheca of th1², × 40. K, L, MCZ 9467/2, reverse and obverse views; note dicalycal th2¹ and strongly deflected sicula visible for its entire length on obverse side.

All except F and I × 32.
TEXT-FIG. 8. Camera lucida drawings of species exhibiting Pattern F primordial astogeny. All illustrations are reverse views unless noted otherwise. See text-fig. 2 for explanation of abbreviations and specimen repositories.

A–D, H–J, O, P, Genticulograpus (gen. nov.) pygmaeus (Ruedemann), Viola Springs Formation, Maysvillian Stage ('C. pygmaeus Zone), Arbuckle Mts., Oklahoma; MCZ 9427 from 51 m above base of section along Interstate Highway 35, adjacent to section H and MCZ 9470 from 104.5 m above base of section H (Alberstadt 1973). A, B, MCZ 9470/1, obverse and reverse views of specimen in early phase of formation of foramen of th₅₂. C, MCZ 9470/2. D, MCZ 9427/4, completed foramen of th₂₂ and metatheca of th₁₁ nearing maturity. E, MCZ 9427/2, early th₂₁ stage showing division of crossing canal of th₁₂ to form metatheca of th₁₂ and protheca of th₂₁. F, MCZ 9427/1. I, MCZ 9427/3, stage showing construction of protheca of th₁₁ by upward-
The cladistic relationships depicted in text-fig. 13 provide an outline of the branching history of the group. It includes three alternative interpretations, differing in their treatment of the Dicranograptinae and the Nemagraptinae. The basis for these alternatives is discussed below. As is readily apparent from the cladograms (and as Bulman had suspected in 1963a, b), the Diplograptacea comprises three large primary divisions: the Diplograptidae, the Monograptidae, and the Orthograptidae. The roots of these families lie deep within the early history of the clade. Each family exhibits a striking degree of parallelism during its evolutionary history and each includes a subgroup that is characterized by a highly derived and highly simplified astogenetic pattern that becomes dominant among the family's representatives in Upper Ordovician or Silurian faunas. The highly derived uniserial monograptines also belong taxonomically among the Diplograptacea, as do the Dicranograptidae (see below).

Previously, when most graptolitologists considered the Monograptina to be a grade of organization that stood above that of the Diplograptina (one which was achieved repeatedly by several lineages), the ranking of these two taxa at the same level was appropriate (see Rigby 1986). However, the monograptid condition is a synapomorphy that characterizes a subclade of the Diplograptacea and is not a grade of organization. The close structural and cladistic relationships between the traditional Monograptina and their antecedents among the morphograptines and glyptograptines (discussed below in the section ‘Monograptidae’) indicate that there is no longer sufficient justification for the retention of the high taxonomic rank usually accorded to this subclade. Instead, I propose here a classification that emphasizes their evolutionary derivation from among the diplograptaceans. In as much as the ICZN has extended the principle of priority to encompass family monograptinae, the entire family to which the monograptines belong must take the most senior available name—the Monograptidae. The Monograptidae, thus, includes Arenig biserial species as well as the traditional Silurian and Devonian monograptine and cyrtograptine species.

It is very difficult to establish a well-corroborated hierarchical branching among the three original families. Archaic monograptids (e.g. ‘Glyptograptus’ dentatus, with a Pattern B astogeny) and archaic diplograptids (in the form of Pseudolimacograptus cumbrensis and related forms, with a Pattern C astogeny) each differ from the primitive diplograptaceans (Pattern A representatives of the ‘G. australodontatus’ species group, herein recognized as Oelandograptus gen. nov.) in a unique suite of derived characters. All astogenetic similarities that they exhibit with Pattern A are symplesiomorphic, regardless of the cladistic position of the Dicranograptidae relative to other diplograptaceans. However, data on the character of the thecal apertures among these graptolites appear to be helpful. Very early in the history of the Orthograptidae, this group acquired a cuspathe thecal aperture (text-fig. 2t, m). An identical thecal form is present in ‘G. dentatus’ (text-fig. 3t) and ‘G. cerasus’ and suggests that the Orthograptidae (excluding the stem group Oelandograptus gen. nov.) and the Monograptidae are sister groups, and that the Diplograptidae branched from the stem group lineage prior to the appearance of this thecal form and the separation of the Monograptidae and Orthograptidae. Given the small size of the group and their paraplythic status, the members
TEXT-FIG. 9. Camera lucida drawings of species exhibiting Pattern G primordial astogeny. All illustrations are reverse views unless noted otherwise. See text-fig. 2 for explanation of abbreviations and specimen repositories.

A–D, F–H, Orthograptus quadrimerconatus (Hall), sp. Viola Springs Formation (51 m above base of section along Interstate Highway 35, adjacent to section H; Alberstadt 1973), Maysvillian Stage (*C. pygmaeus* Zone), Arbuckle Mtns., Oklahoma. A, C, MCZ 9471/1, reverse and obverse views; note fusion of hood with upward-growing flange of prosoblastic crossing canal of th1₂. B, D, MCZ 9471/2, proximal view illustrating origin of flange of th1₂, D, MCZ 9471/3; note paired growth of th1₂ and th2₂ following fusion of hood and flange. E, MCZ 9471/4, th2₂ arises from distal portion of protheca of th2₁ by simple differentiation. G, H, MCZ 9471/5, reverse and obverse views; note extensively exposed scutula and delayed dicalycal theca, ×12.

E, *Amplexograptus leptotheca* (Bulman), SM A. 723040, Balclachie beds, Caradoc Series (*D. multidentis* Zone), Laggan Burn, Ayrshire, Scotland; showing presence of upward-growing flange in ontogeny of th1₂; also note growth of protheca of th2₁ back upon crossing canal of th1₂.

J, A. bekkerti (Opik), Cn. 59938, Kukruse Stage, (*N. gracilis* Zone), Estonia; formation of prosoblastic th1₂.

All except G and H, × 26.
TEXT-FIG. 10. Camera lucida drawings illustrating Pattern G primordial astogeny in Amplexograptus bekkeri (Opik); Kakruse Stage (X. gracilis Zone), Estonia (Holm Collection). All illustrations are reverse views unless noted otherwise. See text-fig. 2 for explanation of abbreviations and specimen repository.

A. Cn 59909; note upward growing flange. B, C. Cn 59939, obverse and reverse views, showing fusion of hood-like crossing canal with small flange and early growth of protheca of th2r. D, Cn 59942. E, Cn 59943; note origin of th2 still in early prothecal stage, while th1 is nearly complete. F. Cn 2474c, obverse view; note strong gradient in thecal form from orthograptid through lastiograptid to amplexograptid in distal thecae, ×12. G. Cn 59941; note post-primordial pattern of differentiation in th2r and th3r. H. Cn 59940, broken specimen showing course of internal canals.

All except F × 26.
Text-fig. 11. Camera lucida drawings illustrating Pattern H primordial ontogeny in Glyptagnostus kuckersi ansa (Wiman); Kukruse Stage (N. graecis Zone), Estonia (Holm Collection). All illustrations are reverse views unless noted otherwise. See text-fig. 2 for explanation of abbreviations and specimen repository.

A, B, Cn 59933, ventral and reverse views; note form of sicular aperture. C, D, E, Cn 59930, obverse, reverse, and oblique dorsal views, illustrating enclosure of foramen of th1² by the metatheca of th1¹. F, Cn 59931, crossing canal of th1² formed by upward growing flange. G, H, Cn 59932, obverse and reverse views; note origin of protheca of th2¹ by zigzag suturing of fuselli below interthecal septum. I, Cn 59934, J, Cn 54606, obverse view; note rapid enclosure of sicula by level of aperture of th1¹. K, L, Cn 59935, reverse and obverse views, × 12. M, Cn 59936, bleached specimen showing details of dicalycal budding and distal thecal ontogeny. All except K and L, × 26.
of the *Oelandograptus* gen. nov. *austrodonatus* species group are treated as *Incertae familiae* within the classification presented here.

**Family dicranograptidæ** Lapworth, 1873, emend. Fortey and Cooper, 1986

*Diagnosis.* Diplograptaceans with uniserial and uni-biserial, partly scandent to reclinod or extensiform rhabdosomes with three crossing canals and dicalycal th2	extsuperscript{1}; sicula with aperture notched on dorsal side and with paired clefts adjacent to the lanceolate virgella; thecae exhibit strong morphological gradient along stipes, with proximal-most thecae at least having isolate, introverted apertural regions; all thecae with sharp fusellar disconformity within the prothecal segment (see Finney 1985).

*Discussion.* Among the traditional Diplograptina, the Dicranograptidae, and in *Nemagraptus* (see Finney 1985), the first dicalycal theca is delayed from its primitive position at th1	extsuperscript{2} to a position at th2	extsuperscript{1} or later, producing three crossing canals. Unlike *Phyllograptus* and the multi-stiped dichograptids, no further dicalycal thecae occur in any of these taxa. As Finney (1985) has shown, the lateral branches of *Nemagraptus* are cladia and are produced in a quite different way from the branch dichotomies of the anisograptids and dichograptids. The possession of a delayed single dicalycal theca distinguishes the advanced Virgellina from all previous Graptoloidea. An additional synapomorphy is the metasicular origin of th1	extsuperscript{1}.

*Nemagraptus* shares a unique configuration of the sicural aperture with the Dicranograptidae Lapworth, 1873, emend. Fortey and Cooper, 1986: the sicural aperture bears two broad lappets that are separated from one another on the antivirgellar side of the sicula by a broad notch. These lappets are also separated from the virgella by a pair of clefts that possess a flared lip (see text-fig. 2H, 8). This synapomorphic condition is unknown in other Virgellina, including the traditional Diplograptina, and unites the Dicranograptinae and the Nemagraptinae as the Dicranograptidae, emend. However, the relationship of the Dicranograptidae to the rest of the Diplograptacea and its status as a clade or paraclade are problematic. In addition to the dicalycal th2	extsuperscript{1} mentioned above, the traditional Diplograptina (or 'diplograptids' in the following discussion) and the Dicranograptinae share additional unique agenetic features — yet these are not shared with *Nemagraptus*: 1, in contrast to the right-handed origin of th1	extsuperscript{2} from th1	extsuperscript{1} in the isograptid pattern, this theca arises left-handedly in 'diplograptids' and dicranograptines; and 2, th1	extsuperscript{2} then follows a convoluted S-shaped course that Bulman referred to as streptoblastic. Despite vague similarities in thecal form or more intriguing similarities in growth direction, no dichograptid or other virgellinid is known to possess these features. The dicranograptines possess a primordial astogeny that, apart from the form of the sicural aperture, is indistinguishable from that of the primitive diplograptaceans — members of the 'G.' *austrodonatus* group (see Bulman 1945, 1947). These similarities (the left-handed origin of th1	extsuperscript{2} from th1	extsuperscript{1}, and the streptoblastic form of this second theca), together with the dipleural scandent rhabdosome architecture of *Dicranograptus* and the 'diplograptids', may be interpreted in several ways (cf. text-fig. 13A–C).

First, they may be synapomorphies (text-fig. 13B). If so, this indicates that the 'diplograptids', as traditionally construed, and the Dicranograptinae of the Dicranograptidae are sister groups. It further implies that the 'diplograptids' have lost the unique form of the sicural aperture characteristic of the paraclade Dicranograptidae. The clade 'diplograptids' + Dicranograptinae, in turn, shares with the Nemagraptinae the synapomorphies of three crossing canals and a dicalycal th2	extsuperscript{1}. However, as Fortey and Cooper (1986) noted, this cladistic sequence conflicts sharply with the stratigraphic order of appearance of these taxa. The diplograptids proceed the earliest dicranograptines or nemagraptines by at least the entire duration of the Llanvirn (Bulman 1960; Finney 1985). Furthermore, Finney has found that the thecae of *Nemagraptus*, like those of the Dicranograptinae, are highly complex with a number of unique features that make them unlikely to be ancestral to the 'diplograptid' thecal structure.

Secondly, the Dicranograptidae as a whole may be a sister group to the 'diplograptids' (text-fig. 13C), but this does not alleviate the problems posed by the stratigraphic record of these graptolites. Furthermore, it requires either that the similarities in proximal end structure and colony architecture
TEXT-FIG. 12. Camera lucida drawings of species exhibiting Pattern H and Pattern I primordial astogenies. See text-fig. 2 for explanation of abbreviations and specimen repositories.

A, B, Pelagograptus sp. 1, Cn 54917 and Cn 54916, lower Klubudden Stage (M. turriculatus Zone), Dalarna, Sweden; reverse views (after Hutt et al. 1970); note metatheca of th1 in contact with reverse side of sicula; also note pattern of simple differentiation of th1 from protheca of th1; dorsal side of sicula extensively exposed; ×32.

C, D, Rhuphidograptus toernquisti Elles and Wood, Cn 54910 and Cn 54915, upper Bollery Stage (M. gregarius Zone), Dalarna, Sweden; obverse and reverse views (after Hutt et al. 1970); note form of th1 and absence of metatheca of th1; ×12 and ×18.
between the dicanograpitinae and the 'diplograptids' are parallelisms, or that the ostensibly primitive astogenetic and other features of Nemagraptus are not primitive but derived.

Thirdly, the Dicranograpitidae may be a sister group of the Orthograptidae (text-fig. 13A). In this case the unique dicanograpitid scutar form must have been derived from the simple scutar of the 'diplograptids'. In addition to the better fit of this hypothesis with the stratigraphic data, there are two further lines of morphological evidence in its support: 1, several Llanvirn–Llandeil species among the archaic orthograptids, such as 'G.' vikarbyensis Jaanusson and 'G.' teretiusculus sensu Jaanusson, which exhibit a Pattern A astogeny, have a flared scutar aperture (text-fig. 2t); this flair is strongest on the dorsal side of the scutar and consists of two lobes separated by a broad, shallow notch; this structure may be homologous with the unique lappet and dorsal notch of the dicanograpitid scutar; and 2, in N. gracilis the first two thecae have isolated, introverted apertures quite like those of Dicellograptus (see Finney 1985), while later thecae have simpler apertural regions that are neither isolated nor introverted. If this condition, like the astogenetic pattern, is primitive relative to the condition in Dicellograptus (in which all thecae have isolated and introverted apertures), then this complex thecal form must have arisen at the proximal end and spread distally during the course of evolution. This, however, conflicts sharply with the general conservatism of the primordial thecae in virgellinid colonies. Alternatively, if the thecal characters in N. gracilis are derived relative to those of early dicanograpitids like D. vagus Hadding, then the complexity of th1 and th2 may be the result of conservatism in the proximal end while distal thecae became simplified.

Subfamily DICRANOGRAPTINAE Lapworth, 1873, emend. Finney, 1985

**Diagnosis.** Dicranograpitids with Pattern A astogeny; complex introverted, introverted thecae with isolated apertures and lateral apertural processes; reclined uniserial unbranched stipes to uniserial, partly scanty rhodosomes, at least some of which possess a virgella.

**Generic group taxa.** Dicranograptus Hall, Dicellograptus Hopkinson, and Leptograptus Lapworth.

---

f–g, Petalograptus sp. 2 (after Hutt et al. 1970), t. Trinity College Dublin, TCD 8272a, a, Balbriggan Co., Dublin, Eire (M. turriculatus Zone); obverse view; note simple form of scutar aperture, ×9. p, g, Cn 54920 and Cn 54921, lower Klubudden Stage (M. turriculatus Zone), Dalarna, Sweden; reverse views; note narrow, acicular proximal end and short interthecal septum between th1 and th2 (cf. text-fig. 12A), ×11.

h, P. insectiformis (Nicholson), Cn 54913, Bollerup Stage (M. gregarius Zone), Dalarna, Sweden; obverse view (after Hutt et al. 1970); note short downward-growing portion of protheca of th1 and strongly upward-growing metatheca of th1; virgella with ancora, ×30.

i, P. obtus (Rickards and Koren), Tchernyhev Central Geol. Mus., Leningrad (topotype collection), Sakhalin Formation, Llandovery Series, Mugodiary Range, South Ural, USSR; reverse view (after Rickards and Koren 1974); note form of th1, which arises well above scutar aperture, and growth lines that suggest late differentiation of th1, ×10.

j, P. palmaeus (Barrande), USNM 161811, Descon Formation, Llandovery Series (M. gregarius Zone), south-eastern Alaska; reverse view (after Churkin and Carter 1970), ×6.

k, o, Glyptograptus sp. cf. G. scalaris, Birmingham University unnumbered, Jupiter Formation, Llandovery Series, south shore Anticosti Island, Quebec. k, (after Barrass 1954) reverse view of proximal end fragment showing origin of th2 and probable dicalycal th2; ×36. o, ventral view of scutar fragment with protheca of th1; note absence of distinct crossing canal of th1, ×36.

L, Paraelmograptus innatus obesus (Churkin and Carter), USNM 161611, Descon Formation, Llandovery Series (M. cyphus Zone), south-eastern Alaska; obverse view (after Churkin and Carter 1970); note strongly acicular proximal end and absence of antivirgellar spines, ×7.

m, 'Diplograptus' modestus diminutus Churkin and Carter, USNM 161701, Descon Formation, Llandovery Series (P. acuminatus and C. vesicularis zones), south-eastern Alaska; obverse view (after Churkin and Carter 1970), ×7.

TEXT-FIG. 13. Cladograms illustrating the possible general relationships among the major virgellinid clades, symbolized by the letter designation of their primordial astogenetic pattern (see text-fig. 1; Is, isogaptid; M, monogaptid; Ol, Oelandogaptus (gen. nov.) austrodentatus and related species) and their classification.

A, preferred relationships with the Dicranogaptididae as sister group to the Orthogaptididae. Synapomorphies: I, virgella present; II, dichotomy d3 suppressed (see Fortey and Cooper 1986); 1, metasomal origin of th1; 2, dichotomy d1 delayed to th2; 3, dichotomy d2 suppressed; 4, th1 with left-handed origin from th1; 5, metatheca of th2 and protheca of th2 arise from paired foramina formed by fusion of downward-growing crossing canal of th2 with upward-growing flange; 6, scendent diplural rhabdosome architecture; 7, capacity for cladia generation; 8, sigmoidal thecae; 9, cuspathe thecal apertures; 10, right-handed origin of th2; 11, sharply geniculate thecae; 12, introverted thecal apertures; 13, asymmetrical proximal end; 14, origin of th2 delayed to distal portion of protheca of th2 and removed from set of primordial thecae; 15, elaborated siculare aperture; 16, asymmetrical proximal end among advanced species; 17, paired antivirgellar spines among advanced species; 18, delay of dicalytal theca to th3 among advanced species; 19, complex notched and lappet-bearing siculare aperture; 20, colony achieves capacity for wholly or partially uniserial stipes; 21, isolated,
Diagnosis. Dicranograpitids with horizontal, cladia bearing, uniserial stipes; primordial astogeny nemagrapitid (see Finney 1985) with right-handed origin of th1 from th1².

Generic group taxa. Nemagraptus Emmons. Nemagrapitine status of Amphagraptus Lapworth, Pleurograptus Nicholson, and Symdagraptus Ruedemann is probable but remains to be demonstrated.

Family Orthograpitidae fam. nov.

Diagnosis. Diplograptaceans with Pattern A astogeny or the derived Patterns G or F; sicular aperture simple or with antirviggellar spines; thecae sigmoidal primitives but becoming orthograpitid or ampliesgroupitid among forms with fully sclerotized periderm, and lysiograpitid to retolittid among others; generally with cuspile apertures or with paired apertural spines.

Discussion. Text-fig. 14 presents a detailed cladogram that includes representatives of the broad range of orthograpitids. Text-fig. 17 illustrates the approximate geochronological range of the redefined and new orthograpitid genera. Among species with Pattern A astogeny, several (e.g., 'Diplograptus' uplandicus Wiman; see text-fig. 2) exhibit a markedly asymmetrical proximal end; th1² is prosoblastic or nearly so; the crossing canal of th2¹ is quite short and the sicular bears a

introverted thecal apertures; 22, genulate dicanograpitid thecae with prominent growth line unconformity in protheca; 23, uni-biseria condition; 24, metatheca of th1 and th1² horizontal, forming uniserial, reclined to horizontal stipes; 25, th1² with right-handed origin from th1¹; 26, introversion and apertural isolation of post-th1² theca reduced or lost; 27, cladia present; 28, sicular extensively exposed on obverse side; 29, th1³–th2¹ form as a pair and with th2¹ non-primordial; 30, second and third crossing canals lost; 31, metatheca of th1² and protheca of th2¹ formed by fusion of upward-growing flange and hood-like crossing canal of th1²; 32, protheca of th1² is simple upward-growing flange that is not connected to its reduced hood-like crossing canal; 33, metatheca of th1² and protheca of th2¹ formed by division of protheca of th1²; 34, th1¹ with metatheca closely pressed against its protheca; 35, crossing canal of th1² suppressed; 36, protheca of th1¹ partly surrounded by its metatheca; 37, th2¹ no longer a primordial theca; 38, protheca of th1² forms from isolated, upward-growing flange; 39, reverse wall of metatheca of th1¹ commonly free prior to growth of th1¹; 40, reverse lateral wall of metatheca of th1¹ in contact with reverse side of siculo; 41, th1² no longer a primordial theca; 42, capacity to produce proximally uniserial, scendent colonies; 43, sicular extensively exposed along its obverse side; 44, capacity to produce ancora from virgella; 45, uniserial rhodosome; 46, th1 no longer a primordial theca; 47, siculo with porus and lacuna stages in formation of foramen of th1; 48, crossing canal of th2¹ visible as oval or diamond-shaped patch positioned on or near median plane of rhodosome; 49, th2² no longer primordial; 50, dicalyval theca delayed to th2² or later; 51, asymmetrical siculo strongly deflected to dorsal side; 52, metascula with bands comprising condensed fuselli; 53, prosticka commonly absent; 54, crossing canal of th2² reduced to hood-like form; 55, protheca of th2¹ formed by upward-growing flange that does not fuse with crossing canal; 56, crossing canal of th1² suppressed; 57, protheca of th1² formed from isolated, upward-growing flange; 58, th2¹ no longer primordial; 59, virgella reflected across sicular aperture; 60, undulating median septum; 61, sigmoidal thecae with short, nearly vertical suprageneric wall and genule genculum. Retained primitive characters: a, quasi-symmetrical proximal end; b, left-handed origin of th2¹; c, paired origins of metatheca of th2¹ and protheca of th2¹ (see 5, above); d, left-handed origin of th1² from th1¹; e, broad proximal end with th2¹ occupying region between protheca and metatheca of th1¹; f, th2² with descending crossing canal; g, retained characters 10–12 (see above).

a, alternative cladogram with Dicranograpitidae as paraphyletic stem-group occupying intermediate position between 'dicranograpitids' and Phylograpitidae. Synapomorphpies 1–20, 22–25, 27–61 as in a; 21, th1¹ and th1² introverted with isolated, introverted apertures; 26, thecal characteristics of th1¹ and th1² extended throughout rhodosome; 62, loss of complex features of sicular aperture; 63, loss of prothecal folds and fusellar unconformity in protheca. Retained primitive characters a–g as in a; h, horizontal to reclined stipes (24 of a, above); i, right-handed origin of th1² (25 of a, above).

C, second alternative cladogram with Dicranograpitidae as sister-group to traditional 'dicranograpitids', but requiring several parallelisms. Synapomorphies and retained primitive characters as in a.
prominent pair of antivirgellar spines. These species are combined in the new genus *Hustedograptus* defined below. The overall configuration of the proximal end of *Hustedograptus* gen. nov. is remarkably similar to that of species of *Orthograptus* (particularly species of the *O. calcarius* group) and *Amplexograptus* with their Pattern G astogeny (compare text-fig. 2r, k with text-figs. 9g and 10f). While not exactly identical in these advanced Pattern A species and in *Orthograptus* etc., I believe that this complex form produces a gestalt (*sensu* Fortey and Jeffries 1982) which, together with the presence of the paired antivirgellar spines, constitutes a high burden synapomorphy between these groups. This gestalt synapomorphy is maintained largely intact throughout the group of orthograptid species. Such a relationship is also supported by similarities in the form of the thecal apertures among these taxa. The orthograptid cuspathe thecal aperture, which is prominently displayed in species of *Hustedograptus* gen. nov., is similarly developed in species of *Amplexograptus* and most of the other Peiragraphtinae. In the distal thecae of *H. uplandicus*, these cusps develop into prominent lateral apertural spines of the same form and construction as those on the thecae of species in the *O. calcarius* and *O. quadririncicoronatus* groups. I see no justification for segregating such species as *O. gracilis*, which lack apertural spines, into *Rectograptus* Pfibyl. This taxon is defined on the basis of the loss of a single, relatively simple character, and there is no reason to assume that such a loss should be unique.

Pattern G species are linked, in turn, to those with Pattern F ("Climacograptus" typicalis Hall and relatives; see Table 1 and text-fig. 8) by the shared presence of paired antivirgellar spines, extensive exposure of the sicula for most of its length in obverse view, the possession of three primordial thecae, and only one crossing canal. These synapomorphies are further strengthened by the great thecal similarities between these 'climacograptid' and peiragraphtine such as *A. leptotheca* Bulman. Indeed, the generic placement of such species as "C." inuiti Cox has been a persistent problem that reflects their close relationship.

Several of the genera included within this family require significant revision and restriction in their scope. *Orthograptus* does not properly include the Silurian species that have been referred to it. *Orthograptus* Lapworth, with type species *O. quadririncicoronatus* (Hall), is a well-known genus comprising a coherent set of similar species, all of which possess a Pattern G astogeny. The Silurian species that have been referred to *Orthograptus* (e.g. "O." obuich Rickards and Koren’) exhibit a Pattern I astogeny and consequently have a narrow, acicular proximal end. These forms may be subsumed within *Petalograptus* Sues, among the *Monograptidae*.

*Amplexograptus* has been a source of persistent confusion. The type species *A. perexcavatus* Lapworth has no holotype and Bulman (1962) selected a neotype (Birmingham University specimen BU 1297) from among the specimens referred to this species and figured by Elles and Wood (1907). As Bulman noted, two distinct species have been confused under this name. Bulman chose a neotype that matches well with the age and morphology of Lapworth’s original taxon (Lapworth 1876, 1877). However, it is clearly the other species, *A. fallax* Bulman, that Lapworth (1880) had before him when he made the distinction between typical *Diplograptus* species and members of the species group that Elles and Wood (following Lapworth’s lead) later named *Amplexograptus*. Thus, although it has been referred to as *A. perexcavatus* Lapworth, the type species of *Amplexograptus* is in fact the biological entity *A. fallax* Bulman. The species group associated with *A. fallax* is by far the better known. Consequently, the interests of taxonomic stability will be best served by retaining the name *Amplexograptus* for these species, rather than for the "A." perexcavatus group. According to ICZN guidelines, I am preparing an application requesting that the Commission exercise its plenary powers to suppress *A. perexcavatus* and establish *A. fallax* as the neotype of the genus. The biological entity originally described by Lapworth (1877) as *D. perexcavatus* is probably not an orthograptid. Rather, both it and *D. pristis* (Hisinger) (the type species of *Diplograptus* M’Coy) appear to have a Pattern C astogeny similar to that of "C." distichus (see the discussion for the Family *Diplograptidae*).

The genera *Glyptograptus* and *Climacograptus*, as presently used, are extremely heterogeneous and include species from each of the three superfamilies. Among the orthograptids, at least two separate species groups with glyptograptid thecae exist: 1, the ancestral diplograptidians of the
TEXT-FIG. 14. Cladogram and classification of the Orthograptidae, including its relationship to the stem group Oelandograptus gen. nov. and the other diplograptacean families. Synapomorphies 1–61 as in text-fig. 13A; 64, orthograptid thecae; 65, sharply geniculate thecae with long straight infragenicular wall, short supragenicular wall, and prominent genicular spines; 66, amplexigraptid thecae with genicular flanges present in distal thecae; 67, amplexigraptid thecae throughout; 68, asetate; 69, th1 sharply upturned at dorsal side of sicula; 70, genicular spines; 71, uni-biserial; 72, gymnograptid thecae with lists; 73, elongate climaigraptid thecae in proximal end; 74, glyptograptid thecae; 75, lasiigraptid thecae; 76, thecae with reduced fusellar periderm and clathria; 77, lateral (septal) spines or scopulae; 78, bifid genicular spines on post-th1 thecae; 79, lacinia developed from genicular spines; 80, fusellar periderm of all thecae reduced to clathria except for sicula and initial bud; 81, archeinolitid-like clathrial astogeny; 82, loss of septal spines and scopulae; 83, reduction of flange in ontogeny of crossing canal of th1; 84, fusellum of all post-th1 thecae reduced to clathria; 85, loss of reverse wall of th1 in region of foramen of th1; 86, pioigraptid thecae; 87, loss of lacinia; 88, simplification of clathria to produce ‘orthograptid’ thecae; 89, nema in obverse wall; 90, loss of septal spines. Retained primitive characters: j, sigmoidal glyptograptid thecae; k, amplexigraptid thecae.
Subfamily ORTHOGRAPTINAe subfam. nov.

_Diagnosis_. Aseptate to septate species with straight median septum; Pattern A or Pattern G astogeny; strongly asymmetrical proximal end with sícula extensively exposed on obverse side; sícula commonly bearing paired antivirgellar spines.

_Generic group taxa_. _Hustedograptus_ gen. nov.; _Orthograptus_ Lapworth (= _Rectograptus_ Pribyl, non _Dittoograptus_ Obut and Sobolevskaia).

**Genus HUSTEDOGRAPTUS** gen. nov.

_Type species_. _Diplograptus uplandicus_ Wiman, 1895, from erratic boulders of _Chasmops_ (= Dalby) Limestone, Upland, Sweden; Viruan Series (N. gracilis Zone ?). The reported occurrence of this species in boulders of _Centauros_ Limestone (= Folkeslunda Limestone, in part) (Wiman 1895) has not been confirmed by subsequent studies of this unit.

_Diagnosis_. Thecae smoothly sigmoidal glyptograptid in the proximal end, becoming orthograptid distally; thecal apertures normal to rhabdosome axis or slightly introverted, with prominent paired cusps or spines on lateral margin and with concave ventral apertural margin; median septum straight with dicalyval theca th21 or substantially delayed; primordial astogeny follows Pattern A but with short descending portion in crossing canal of th22; proximal end broad and weakly to markedly asymmetric; sícula with simple aperture, or aperture bearing paired lappets, or antivirgellar spines flanking concave dorsal margin.

_Species included_. _D. notabilis_ Hadding, _D. propinquus_ Hadding, _G. teretiusculus_ (senso Jaanusson 1960), _D. uplandicus_ Wiman, and _G. vikarbyensis_ Jaanusson.

_Discussion_. Based on a restudy of the type specimens, the proximal end structure of ‘_D._ uplandicus’ given by Wiman (1895) appears to be inaccurate. The structure is correctly illustrated in text-fig. 2, based on abundant and excellently preserved material isolated from a limestone sample in the Holm collections of the Naturhistoriska Riksmuseum, Stockholm. This sample is labelled ‘_Diplograptus_, Kuckers C2b’ and is lithologically identical to the distinctive Kukruse Limestone of Estonia. It is my intention that the type species of the genus _Hustedograptus_ gen. nov. be the biological entity embodied by the Estonian material, an entity that I believe to be synonymous with Wiman’s _D. uplandicus_.

_Hustedograptus_ gen. nov. differs from _Orthograptus_ Lapworth in its primordial astogeny (Pattern A as opposed to Pattern G), the exposure of the sícula only to the level of the aperture of th12 on the obverse side of the rhabdosome, and by the presence of glyptograptid proximal thecae. Additionally, in _Orthograptus_ the dicalyval theca is never as early as the second thecal pair (in the type species, _O. quadrimorcoratus_ Hall, th52 or a later theca is dicalyval) and the sícula always bears paired antivirgellar spines, while in many species of _Hustedograptus_ gen. nov. antivirgellar spines are absent. For comparisons with _Oelandograptus_ gen. nov. and _Eoglyptograptus_ gen. see discussion of these taxa below.
Subfamily PEIRAGRAPTIINAe JARNUSSON, 1960, emend.

Diagnosis. Orthograptids with Pattern G or Pattern F primordial astogeny; strongly geniculate thecae bearing genicular spines or flanges or both; rhabdosome generally aseptate and with fully sclerotized periderm.


Discussion. The Peiragraptinae comprises two informal generic groups. Within Group 1 (peiragraptids), Paraorthograptus and Peiragraptus are little modified from Amplexograptus and both retain the basic amplexograptid theca. Within Group 2 (geniculograptids), all three genera share the unique Pattern F astogeny and narrow, gradually widening proximal end, but exhibit variously modified thecal forms.

Genus AMPLEXOGRAPTUS Elles and Wood, 1907

Proposed Neotype species. Amplexograptus fallax Bulman, 1962 (subject to approval by the ICZN), Hartfell Shales, Scotland; Caradoc Series (principally C. wilsoni Zone).

Emended diagnosis. Thecae amplexograptid with short, slightly outwardly inclined supragenicular walls, sharp geniculum bearing a genicular flange, and with cuspate thecal apertures horizontal to slightly everted. Rhabdosomes may be partly septate, with th35 or some later theca dicalycal, but are more commonly aseptate. Primordial astogeny follows Pattern G. Paired antivirgellar spines generally present on dorsal margin of sicural aperture. Th11 invariably bears a subapertural or mesial spine but th12 commonly does not.


Discussion. This name is here applied only to forms with amplexograptid thecae and a Pattern G astogeny (see discussion of the Family Orthograptidae above). Amplexograptus is most similar to Geniculograptus gen. nov. but differs in the form of its proximal end. Geniculograptus species such as G. inuiti (Cox), possess a narrow proximal end based on a Pattern F astogeny in which the first theca is tightly upturned and closely pressed against its protheca. Its metatheca extends distally to the level of the bud of th1 or beyond. In contrast, in Pattern G proximal ends th11 is always separated from its protheca by a gap through which th21 develops, and its aperture seldom reaches the level of its primary bud (cf. text-figs. 8f, L, O, 9d, b, F, h, 10e, f, H). Homeomorphic members of the Diplograptidae (e.g. 'A.' munimentus Berry or 'A.' confertus Lapworth) differ in their possession of simple, semicircular to introverted thecal apertures that lack the lateral lappets of amplexograptid thecae, and a Pattern C astogeny with dicalycal th21, as well as by the rapid enclosure on the obverse side of the colony of the sicula, which lacks antivirgellar spines.

Genus GENICULOGRAPTUS gen. nov.

Type species. Climacograptus typicalis Hall, 1865, Lexington Limestone and Kope Formation, Cincinnati Region, USA; Blackriveran to Maysvillian Stages (C. americana to A. manitoulinensis zones).

Diagnosis. Aseptate, gradually widening rhabdosomes with narrow proximal end; slightly outwardly inclined amplexograptid thecae bearing a variably prominent genicular flange; primordial astogeny follows Pattern F; sicula is extensively exposed on the obverse side of the rhabdosome and bears paired antivirgellar spines in addition to the virgella. Th11 may or may not bear a mesial spine. Th12 bears no spines.

Discussion. Species of *Geniculograptus* gen. nov. most resemble those of *Amplexograptus* in the form of their thecae, but they differ astogenetically (see discussion above for *Amplexograptus*). They also resemble certain members of the Monogriptidae, such as *Paraclimacograptus innotatus* and *P. nevadensis*, which also possess amplexograptid-like thecae with prominent generical flanges, but again these taxa differ in the form of their proximal end and rhabdosome architecture. Among *Geniculograptus* species, the sicula bears prominent antivirgellar spines and is extensively exposed on the obverse side of the rhabdosome, which is asceptate. Those of *Paraclimacograptus*, with their Pattern H astogeny, are generally septate, the sicula is rapidly enclosed by the early thecae, and there are no antivirgellar spines (see Table 2).

**Genus Arnheimagraptus** gen. nov.

*Type species.* *Glyptograptus lorrainensis anacanthus* Mitchell and Bergström, 1977, Arnheim Formation, Cincinnati Region, USA; Richmondian Stage (*A. manitoulinensis* Zone).

*Diagnosis.* Minute asceptate species with glyptograptid thecae; thecal apertures undulating to cuspate; th1 may or may not possess a mesial spine; primordial astogeny follows Pattern F.

*Species included.* *G. anacanthus* Mitchell and Bergström, *G. hudsoni* Jackson, and *G. lorrainensis* Parks.

*Discussion.* The rhabdosomes of these species exhibit a proximal end which is nearly identical to that of *Geniculograptus* gen. nov. species. The common ancestor of the *Arnheimagraptus* species probably arose from one of these by the loss of the distinctive generical flanges, converting the amplexograptid thecae of *Geniculograptus* gen. nov. to the glyptograptid thecae of *Arnheimagraptus*. Also like *Geniculograptus* gen. nov., this taxon differs from similar looking species of *Glyptograptus* in being asceptate, by exhibiting a long slender sicula that is extensively exposed on the obverse side of the colony, and in possessing antivirgellar spines on the dorsal margin of the sicula.

**Genus Gymnograptus** Bulman, 1953, emend.

*Type species.* *Gymnograptus linnarssoni* (Moberg, 1896), *Ogygiocaris* Shale, Crassicauda (= Furudal) Limestone, Baltoscandia; Uhakuan Stage (*H. teretiuscula* Zone).

*Discussion.* Taxon remains as described by Bulman except that it is here restricted to species which, like the type species, possess a Pattern F primordial astogeny. Thus, species such as *G. retioloides* (Wiman), with its Pattern C astogeny, belong among the Diplogriptidae (see below). *G. linnarssoni* differs from typical Pattern F proximal form in that the sicula possesses only a single dorsal antivirgellar spine.

*Subfamily Lasioigraptinae* Lapworth, 1879, emend.

*Diagnosis.* Species with Pattern G primordial astogeny; thecal periderm reduced to absent; thecae with prominent lists and commonly bearing lacinia derived from generical and lateral spines; thecae lasioigraptid to highly stylized, polygonal clathrium.


*Discussion.* This subfamily includes two generic groups that are clearly related but none the less distinct in their colonial architecture. Group 1 (lasioigraptids) consists of forms exhibiting lasioigraptid to *Pipigraptus*-like thecae with prominent generical spines; sicula and at least th1 partly sclerotized; typical Pattern G astogeny; clathria, lateral (septal) spines, and at least partial lacinia common. *Halloegraptus* has the appearance of a primitive stem group with respect to the core of this assemblage because of its lack of a lacinia and somewhat better sclerotized thecae (which resemble the proximal thecae of *A. bekkeri* and possess weaker clathria than the main group of
lasioeirotritids]. [I consider the absence of a lacinia and the generally simple architecture of Ortho-
reitolites to be a derived condition based on considerations discussed more fully elsewhere.] This
group includes several retiolitid-like taxa formerly classed in the polyphyletic Archiretoiilitinae
Bulman, 1955. Nymphograptus is included here with some reservation because its structure is very
incompletely known.

Group 2 (archiretoiilitids) comprises retiolitid rhabdosomes with a sclerotised sicula bearing
antivirgellaeal spines; thecal fusellum represented only by clathria; clathrium generally irregularly
organized and complexly connected with well developed lacinia; primordial astogeny like that of
Archiretoiilites. Although the phylogeny of these highly derived and structurally reduced archiretoi-
litid colonies is somewhat difficult to evaluate, their orthograptid sicula with antivirgellaeal spines and
a lacinia derived from paired genicular or subapertural spines allies the archiretoiilitids with the
lasioeirotritids among the Orthograptidae, and clearly separates them from any close phylegenetic
relationship with the Silurian Retiolititinae.

The Lasioeirotritinae include an unusually large number of monotypic genera and it is quite likely
that, as these taxa become better known, several may prove to be synonymous (e.g. Pipiodiagrapus with
Neurograptus). As discussed by Finney (1980) the abgraptid Reteograptus of the Phyllograptidae
Lapworth (emend. Cooper and Fortey, 1982) is distinguished from the archiretoiilitids by its pos-
session of an isograptid primordial astogeny and a small, simple sicula that lacks antivirgellaeal
spines.

Incertainae familiae

Genus Oelandograptus gen. nov.

[= Undulograptus partim Jenkins, 1980; non Undulograptus Bouček, 1973]

Type species. Glyptograptus austrodentatus oelandicus Bulman, 1963a, Holen Limestone (= Glaukonithalitig
grä Vagnatumkalk of Holm and Bulman), Oland; Ontikan Series, Kunda Stage (D. hirundo and D. bifidus
zones).

Diagnosis. Median septum undulatory, weakly sigmoidal thecae with long, outwardly inclined
infragenicular wall, sharply rounded geniculum and short, nearly vertical supragenicular wall.
Theccal apertures slightly everted and undulatory with a concave ventral margin. Sicural aperture
simple. Primordial astogeny follows Pattern A and the proximal end is evenly rounded to somewhat
blunt and nearly symmetrical.

Species Included. G. a. americanus Bulman, G. austrodentatus Harris and Keble, G. a. oelandicus Bulman, and
G. sinodentatus Mu and Lee; G. curvithecatus Mu and Lee is imperfectly known but may also belong here.

Discussion. Oelandograptus gen. nov. differs from its contemporaries Hustedograptus gen. nov.,
Undulograptus Bouček, and Pseudoclimagrapus (Archilimagrapus) subgen. nov. in several
respects. Species of Oelandograptus gen. nov. are most similar to the archaic Pseudoclimagrapus
species of P. (Archilimagrapus) subgen. nov. but differ in possessing a Pattern A astogeny, an
undulatory median septum, and weakly geniculothece with apertures normal to the rhabdosome
axis; the latter exhibit a Pattern C astogeny (see Table 2), generally have a sharply zigzag median
septum, and pseudoclimagraptid thecae with introverted apertures. Undulograptus Bouček, as
redefined here, is a monotypic taxon with a narrow proximal end based on primordial astogenetic
Pattern B and a climagograptid thecal form exhibiting a nearly vertical supragenicular wall. Hustedo-
graptus gen. nov. has more strongly glyptograptid proximal thecae, thecae with prominently cuspate
apertures, and a more asymmetrical proximal end (still based on Pattern A), together with a straight
median septum.

Orthograptid history. The Orthograptidae were an important constituent of graptoloid faunas from
the early Llanvirn to the late Ashgill. Their initial diversity was eclipsed by that of the Diplograptidae
but advanced orthograptids dominated the faunas of the Upper Ordovician. This situation changed
radically at the end of the Ordovician when the orthograptids appear to have become extinct. All of the early Silurian diplograptaceans, based on their possession of astogenetic Patterns H and I, were monograptids. [I am indebted to Anton Kearsley who pointed out to me, in 1981, the magnitude of these late Ordovician and early Silurian extinctions and their effects on the taxonomic composition of the Silurian diplograptacean radiation.] Thus, the Silurian species currently referred to the genera ‘Amplexograpthus’ and ‘Orthograptus’ are not particularly closely related to the species of these Ordovician taxa.

One outstanding problem for the systematics of Ordovician diplograptaceans is the fact that our knowledge of the astogeny of many of the Arenig to Llandeilo species previously included in Diplograptus, Glypiograptus, and Amplexograpthus is quite limited. Some of these species may possess either a Pattern A or G astogeny, while others will certainly be found to exhibit a Pattern C or perhaps even a Pattern B proximal end structure. Additional study of material from this interval, preserved in relief or in isolated preparations, is needed to resolve the cladistic relationships and systematic associations of the early diplograptaceans. Such study is of particular importance because it is in just this interval that several of the fundamental steps in diplograptacean evolution occurred, including the establishment of all four of the diplograptacean families.

**Family diplograptidae** Lapworth, 1873, emend.

*Diagnosis*. Rhabdosomes generally septate with pseudoclimategraptid to climaceograptid and amplexograpit to orthograptid (rarely gymnograptid or lasiograptid) thecae, and with promidial astogenetic Pattern C or its derivatives D and E. Siculo commonly deflected toward its dorsal side and rapidly sealed by the second thecal pair. Sicular aperture simple, lacking paired antivirgellar spines. Many species with a three-vaned nematularium formed from an intact nema.

*Discussion*. The second major subclade among the Diplograptaceae is the pseudoclimategraptines and their descendants, the diplograptines and true climaceograptines. Text-fig. 15 presents a cladogram of the branching history of the taxon. The primitive diplograptid astogenetic pattern, Pattern C, differs from the ancestral diplograptacean Pattern A in the right-handed rather than left-handed origin of th2'. The crossing canal of th2', on its way toward the virgella, grows out from the siculo and arcs around the crossing canal of th12 (text-figs. 2l, o, p, and 4). This peculiar origin of th2' (best known in *P. eurystoma* Jaanusson, *P. angulatus*, ‘C.’ *distichus* Eichwald, and ‘G.’ retioloides) is shared with the advanced diplograptid pattern, Pattern D (e.g. *P. scharenbergi*, cf. text-fig. 6), clearly indicating that these two groups share a close common ancestry. This relationship is also fully corroborated by the correspondence in thecal form and rhabdosome architecture among these graptolites. Indeed, the form of the thecae and shape of the proximal end indicate that the advanced pseudoclimategraptines, such as *P. scharenbergi*, appear to be directly descended from an archaic form with a Pattern C astogeny (e.g. *P. eurystoma*). The species ‘L.’ *haplus* Jaanusson, with its compact proximal end and Pattern C astogeny, also appears to be very closely allied to pseudoclimategraptines like *P. eurystoma*.

Primordial astogenetic Pattern D is not confined to species with pseudoclimategraptid rhabdosomes. It is also present in *C. bicornis* (Hall), the type species of *Climaceograptus* (text-fig. 6l–p), and several other related species (see text-fig. 15). This high burden synapomorphy unambiguously allies *Climaceograptus, sensu stricto*, with the advanced pseudoclimategraptines and removes them from the possibility of any close phylogenetic relationship to species of either the *Geniculograptus typicus* group (see above) or the ‘C.’ *brevis’/‘C.’ *normalis* group, which possess a Pattern H development and are allied to the Monograptidae (see below). Finally, several species such as ‘C.’ *distichus*, ‘C.’ meridianalis Ruedemann, and ‘A.’ *munimentus* Berry possess a Pattern C astogeny. Given the relationships of *C. bicornis* to advanced pseudoclimategraptids with a Pattern D astogeny, these species must have acquired their climaceograptid thecae independently of *C. bicornis* and related species (in contrast to Riva’s 1976 suggestions). Hence, they too must be classified separately from the true climaceograptines. However, it should not be difficult to recognize these as a separate group, given their proximally zigzag median septum and broad, blunt proximal end.
Species of the *C. spiniferus* Ruedemann species group, with their Pattern E astogeny, share with *C. bicornis* and *C. cf. caudatus* (Strachan 1974, cf. pl. 6, figs. 1, 7, 9 with figs. 2 and 3, and text-fig. 7 herein) an unusual sicula: the prosicula is absent and replaced by a stirrup-like set of rods; the metascula is strongly deflected to the dorsal side and bears a series of regularly spaced dark bands. These synapomorphies link the *C. spiniferus* and *C. bicornis* species groups. Based on the overall morphology, proximal end structure, and stratigraphic occurrence of these species, Riva (1976) arrived at the conclusion that *C. spiniferus* is descended from *C. bicornis*. A similarly close relationship is shown in text-fig. 15. Despite the highly simplified astogeny of the distinctive Pattern E species, they are best retained within Hall’s genus, although they can easily and usefully be recognized as a subgenus: *C. (Diplacanthograptus)* subgen. nov.
The taxa *Metaclimacograptus* and *Clinoclimacograptus*, recognized by Bulman and Rickards (1968) and included as subgenera of *Pseudoclimacograptus*, appear to possess a Pattern H astogeny. Michael Melchin (pers. comm.) has acquired numerous isolated growth stages of several metaclimacograptid and clinoclimacograptid species during his studies of Llandovery biserial diplograptaceans from arctic Canada. These specimens confirm that even the most pseudoclimacograptid-like of these species, *M. orientalis* Obut and Sobolevskaya, possess a Pattern H astogeny. They are, thus, homeomorphic with Ordovician pseudoclimacograptines and represent a Silurian 're-invention' of this rhabdosome architecture among the Monograptidae, following the extinction of pseudoclimacograptine diplograptids in the latest Ordovician.

The Diplograptidae appear to have undergone a significant dichotomy early in their history. In the second branch of the family, th1 and th12 acquired a more horizontal growth form with only the apertural regions sharply upturned. This configuration gave these diplograptids a broad and rather blunt proximal end that commonly attains widths nearly as great as the maximum colony width. This group, the subfamily Diplograptinae, includes species with a much broader range of thecal types than exist among the Climacograptidae. Within the subfamily occur several species-groups in which rhabdosomes exhibit thecae homeomorphic with those of such orthograptid taxa as *Amplexograptus, Orthograptus, Hallograptus*, and *Gymnograptus*. The most important of these taxa are *Diplograptus* M'Coy and *Pseudoplexograptus* gen. nov. The latter comprises the archaic amplexograptid-like species, such as *A. confertus* (Lapworth), *A. munimentus* Berry, and *C. distichus* (Eichwald), and it includes most of the species from the Arenig to the Llandoil that have formerly been assigned to *Amplexograptus*—where they have resided uncomfortably (see Bulman 1962).

The status of *Diplograptus* remains particularly problematic. *D. pristis* (Hisinger) is known only from flattened material, but Skoglund’s (1963) preparations of isolated, flattened specimens from the type area in Sweden provide useful information. Its broad, blunt proximal end that rapidly encloses a short, stout sicula lacking antivirgellar spines suggests a Pattern C astogeny. Thecal characters of the proximal end are also like those of *Pseudoplexograptus* gen. nov. This suite of characters exhibited by *D. pristis* appears to be shared with many other species assigned to this genus. Additionally, I have isolated specimens of a species similar to *D. decoratus* Harris and Thomas from the Table Head Formation, Western Newfoundland, and its growth stages exhibit a Pattern C astogeny. Finally, it is noteworthy that, like many pseudoclimacograptines, species of *Diplograptus* (sensu stricto) often possess a retina, three-veaned nematularium derived from the distal extremity of their intact nema (see Ruedemann 1904; Mitchell and Carle 1986). To my knowledge, nematularia of the *comulare*-type (Müller and Schauer 1969) do not occur in other diplograptacean families during the Ordovician.

Not all of the Arenig to Caradoc species that have been classed with *Diplograptus* exhibit these features, however. *D. propinquus* Hadding and *D. notabilis* Hadding belong among the Pattern A-bearing *Hustedograptus* gen. nov., in which weak thecal gradients encompass glyptograptid to orthograptid shapes. Still others (e.g. *D. toernquisti* Hadding) possess a Pattern H astogeny that places them among the Monograptidae. Considerable additional work needs to be done on this group.

Subfamily CLIMACOGRAPTINAE Frech, 1897, emend.

*Diagnosis.* Diplograptids with zigzag to straight median septum and pseudoclimacograptid to climacograptid thecae; th1 and th12 grow distally in a gentle arc producing a rounded proximal end. Primordial astogeny is Pattern C or D.

*Generic group taxa.* *Pseudoclimacograptus* Prüby, s.s. (non *Metaclimacograptus* Bulman and Rickards; non *Clinoclimacograptus* Bulman and Rickards), comprising the subgenera *P.* (*Pseudoclimacograptus*) Prüby and *P.* (*Archioclimacograptus*) subgen. nov.; *Prolasiograptus* LeC. *Climacograptus* Hall, 1865, emend., comprising the subgenera *C.* (*Climacograptus*) Hall and *C.* (*Diplocanithograptus*) subgen. nov.; *Diciacograptus* Rickards and Bulman.

*Type species.* *Climacograpthus scharenbergi* Lapworth, 1876, Bulclatchie beds and Lower Hartfell Shale, Scotland; Caradoc Series ('D.' multidentes and 'C.' wisoni zones).

*Diagnosis.* Climacographtines with narrow, rounded proximal end and Pattern D astogeny, including a dicalycal th2. Region between the metatheca of th1 and th12 on the reverse side occupied by the protheca of th2.

*Species included.* Those few species known to possess this suite of characters include *P. scharenbergi* (Lapworth) and *P. evensis* Skoglund.

Subgenus *Pseudoclimacograpthus* (Archiclimacograpthus) subgen. nov.

*Type species.* *Pseudoclimacograpthus angulatus sebysensis* Jaanusson, 1960, Grey Seby Limestone, Seby and Folkeslunda Limestone, Sjötorp, Öland; Viruan Series, Lasnamägi Stage (*D. murchisoni* Zone).

*Diagnosis.* Taxon with broadly rounded proximal end and Pattern C astogeny; median septum sharply zigzag to undulatory. Th2 generally dicalycal and with the region between the metatheca of th1 and th12 on the reverse side occupied by an exposed patch of the right-handed crossing canal of th21 flanked or enclosed by the prothicae of both th21 and th22.

*Discussion.* *P. (Archiclimacograpthus)* subgen. nov. differs from the nominate subgenus by its possession of a relatively broad and blunt proximal end, based on a Pattern C astogeny, and a dicalycal th2, in contrast to the rather more narrow and evenly rounded proximal end of *P. (Pseudoclimacograpthus)*, with its Pattern D astogeny and dicalycal th2 (see Table 2). It differs from *Pseudamplexograpthus* gen. nov. in the form of the thecae and median septum (see below). Species of *Metaclimacograpthus* and *Climoclimacograpthus* exhibit a Pattern H astogeny that produces a slender, nearly parallel-sided rhabdosome and allies them unambiguously with the Monograptidae. They also possess a complexely folded, rather than strictly zigzag, median septum.

Although the species *P.? camptochnus* Skevington and *P.? formosus* Mu and Lee are known from isolated and well-preserved relief material, respectively, and possess the thecal characters of the genus, they are doubtfully included in *P. (Archiclimacograpthus)* subgen. nov. The symmetrical form of their proximal end, in which the descending crossing canal of th2 lies along the mid-line of the colony and is extensively exposed, suggests a Pattern A rather than Pattern C astogeny. This remains to be confirmed from the study of early growth stages, however. In any event, their primitive geometry places this species group as a paraphyletic stem group in text-fig. 15.

*Species included.* Structurally well-known members of this taxon include *P. angulatus angulatus* (Bulman), *P. a. sebysensis* Jaanusson, *P. lapusae* Jaanusson, *P. marathoneis* Clarkson, *P. modestus* (Ruedemann), and *P. oliveti* Boué. The form of the proximal end of *P. eurytoma* Jaanusson closely resembles that of typical members of *P. (Pseudoclimacograpthus)*, differing only in its retention of a Pattern C astogeny with an exposed patch of the crossing canal of th2 between the apertures of th1 and th1 of the reverse side of the rhabdosome.


*Type species.* *Lasiorapgratus retusus* Lapworth, 1880, 'upper Llandeilo shales of the neighbourhood of Llandrindod Wells, Radnorshire', Wales; Llandeilo Series (*N. gracilis* Zone?).

*Diagnosis.* Taxon restricted to Climacographtinae with Pattern C astogeny, lasiorapgraptid thecae, and without lacina.

*Discussion.* Distinguished from similar looking species of *Lasiorapgratus* by its proximal end structure, absence of antivaginal spines, and simple thecal apertures.

*Species included.* Known to include *L. hapsus* Jaanusson, 1960, in addition to the type species.
Genus climacograptus Hall, 1865, emend.

Type species. Graptolites bicornis Hall, 1848, Austin Glen Greywacke, Norman's Kill, New York (but also common in equivalent units world wide); Mohawkian Series, Blackriveran to Shermanian stages (N. gracilis and 'D.' multidens zones).

Emended diagnosis. Climacograptines with climacograptid thecae, bearing semicircular thecal excavations that lack apertural cusps, nearly vertical suprageneric walls, and a sharp geniculum without genicular flanges. Proximal end narrow, evenly rounded to blunt, based on a Pattern D or Pattern E astogeny. Sicula strongly deflected toward its dorsal side, generally lacking a normal prosicula, and with an aperture bearing only a prominent virgella. Rhabdosome septate with proximally zigzag to straight median septum. Th2^2 generally dicalycal.

Discussion. Species of Climacograptus Hall differing from similar looking taxa in Geniculograptus gen. nov., Glyptograptus, Pseudoplexograptus gen. nov., and Undulograptus in the form of the thecae, or the proximal end (including the configuration of the sicula), or both. Genus consists of two subgenera.

Subgenus CLIMACOGRAPTUS (CLIMACOGRAPTUS) Hall, 1865, emend.

Type species. Graptolites bicornis Hall, 1848, see above.

Diagnosis. Characters of genus, but restricted to species with Pattern D astogeny.

Species included. Species well enough known to be assigned with confidence include C. caudatus Lapworth, C. hastatus T. S. Hall, C. raricaudatus Ross and Berry, C. tubuliferous Lapworth, Diplograptus minimus Carruthers, and G. puillus Hall.

Discussion. Among species of the nominate subgenus the crossing canal of th1^2 exhibits an evenly rounded curvature and constant diameter as it sweeps across the reverse side of the sicula at the level of the sicural aperture. The globular protheca of th2^1 occupies the region encircled by th1^2 and commonly bears a distinct dimple that corresponds to the end of a list which links the enclosing protheca with the hood-like crossing canal below (see text-figs. 5 and 6). The sicula commonly bears a long stiff virgella that projects downward. The first thecal pair may be without spines, or th1^1 alone, or both it and th1^2 may possess prominent mesial spines.

C. (Climacograptus) is most similar to Pseudoplexograptus gen. nov. but differs in that the latter, despite their climacograptid thecae, retain a Pattern C astogeny, which produces a broad, blunt proximal end and a rather wide, tubular rhabdosome (see also Table 2). The sicular form of Climacograptus is highly distinctive but difficult to observe. Some species of C. (Climacograptus), such as C. (C.) caudatus (see text-fig. 6R), exhibit a proximally zigzag median septum, but in all species the median septum is straight after the first few thecal pairs, thus distinguishing them from species of Pseudoclimacograptus.

Subgenus CLIMACOGRAPTUS (DIPLOCANThOGRAPTUS) subgen. nov.

Type species. Climacograptus spiniferus Ruedemann, 1908, lower Utica Shale, Hudson and Mohawk River valleys; Mohawkian and Cincinnati Series, Blackriveran to Edenian Stages (C. americanus to C. pygmaeus zones).

Diagnosis. Species of Climacograptus with Pattern E primordial astogeny and a narrow, asymmetrical proximal end with the sicula lying almost entirely to the right of rhabdosome mid-line in obverse view; sicural aperture oriented at about 70° from the rhabdosome axis and bearing a stout (but not necessarily long) virgella deflected across the sicural aperture. Virgella commonly matched by a long mesial spine on th1^1 such that they form a pair which, in an undeformed state, is symmetrical about the rhabdosome axis. More rarely th1^2 bears a small mesial spine as well.

Species included. C. dorothaeus Riva and C. spiniferus Ruedemann. At present, the astogenetic details of C. venustus Hsu, C. longispinus T. S. Hall, and related species are unknown, but their possession of a reflected
virgella that is symmetrical with a mesial spine on th1, plus a strongly asymmetrical proximal end, both suggest that they belong here rather than in C. (Climacograptus).

**Discussion.** Differs from C. (Climacograptus) in its possession of a Pattern E astogeny and in the unique configuration of its sicula.

Subfamily *Diplograptinae* Lapworth, 1873, emend.

**Diagnosis.** Diplograptids with a broad and blunt proximal end that arises from a strong lateral component in the growth of the first thecal pair and a Pattern C primordial astogeny; thecae amplexograptid to orthograptid, or rarely gymnograptid.

**Generic group taxa.** *Diplograptus* McCoy, *Pseudoplexograptus* gen. nov., and *Urbanekograptus* gen. nov. The status of *Diplograptus* remains uncertain due to our poor understanding of the type species, *D. pristis* (Hisinger) (see discussion of Diplograptidae). The species of the 'L. armatus-porrectus' Bulman group may also belong in this family. These species appear to combine amplexograptid thecae bearing prominent genicular spines with a diplograptid-like proximal end, but the details of their development are unknown. Similarly, many of the other species referred to 'Lastiograptus' and 'Hallograptus' among the Llanvirn and Llandeilo faunas will probably prove to belong here.

**Genus Pseudoplexograptus** gen. nov.

*Type species.* *Lomatoceras distichus* Eichwald, 1840, Lasnamägi strata, Estonia, but best known from the Seby and Folkeslunda Limestones, Öland, Sweden; Lasnamägi Stage (upper *D. murchisoni* Zone).

**Diagnosis.** Species having broad, tabular, and nearly parallel-sided rhabdosomes with amplexograptid thecae throughout. Thecal excavations deep and semicircular to somewhat restricted, commonly with strong apertural selvage; apertures horizontal to introverted and lacking lateral cusps. The suprageneric wall is short and commonly of similar height to that of the thecal excavation; geniculum sharp and frequently with genicular flange. Proximal end blunt and nearly as wide as distal colony width. Primordial astogeny follows Pattern C; th21 generally dicalycal with proximally zigzag to straight, complete median septum. Sicula exposed on obverse side only to level of th12 aperture, or slightly above, and bearing only a stout virgella.


**Discussion.** *Pseudoplexograptus* differs from *Amplexograptus* in its proximal end structures (Pattern C rather than Pattern G astogeny and morphological correlates; see Table 2), absence of antivirgellar spines, extent of exposure of the sicula, and in the simple thecal excavations. For comparison with *Climacograptus* and *Pseudoclaimacograptus* see discussion of these taxa above.

**Genus Urbanekograptus** gen. nov.

*Type species.* *Climacograptus retioloideus* Wiman, 1895, from erratic boulder of Scandinavian origin but probably from the *Crassicauda (= Furudal) or Ludibundus (= Dulby)* Limestones, Sweden; Uhaku or Kukruse Stages (H. teretiusculus or N. gracilis zones).

**Diagnosis.** Diplograptines with gymnograptid thecae bearing complex spinose genicular processes, Pattern C primordial astogeny, and nearly symmetrical, blunt proximal end. Th13 and th12 with orthograptid shape and prominent apertural spines.

**Discussion.** Taxon distinguished from homeomorphic *Gymnograptus* by its astogeny, the broad shape of the proximal end with its subhorizontal first two thecae and by the absence of antivirgellar spines. Taxon presently monotypic.

**Summary history of the Diplograptidae**

Compared to the other diplograptacean superfamilies the Diplograptidae form a relatively small and close-knit assemblage. They appear to have achieved their maximum diversity and peak abun-
dance early in the history of the diplograptaean radiation—during the Llanvirn and Llandoilo (text-fig. 17), when members acquired a range of thecal shapes and rhabdosome designs that are strikingly similar to those evolved later among the Orthograptidae. But by the mid-Caradoc, the diplograptids had begun to wane in importance, losing their status as common and numerous components of the diplograptid fauna. Species of Climacograptus (particularly in the subgenus Diplacanthograptus), however, did remain as highly distinctive elements and continued to evolve rapidly (hence their common use in zonation and chronostratigraphic correlation). Yet, they too were extinguished in the Ordovician-Silurian mass extinction. The Diplograptidae, like the Orthograptidae, apparently made no contribution to the great Silurian diplograptid radiation.

**Family Monograptidae** Lapworth, 1873, emend.

*Diagnosis.* Rhabdosomes with narrow, asymmetrical proximal end and simple sicula; colonies may be biserial, uni-biserial, or fully uniserial. In biserial taxa the first two thecae are closely pressed to the sicula and lack mesial spines. Primitively, thecae are glyptograptid to climacograptid, but are modified to petalograptid, pseudoclimacograptid, or variously isolate, lobate, hooked, or triangular—particularly among the Monograptinae. Primordial astogeny is Pattern B, modified to Patterns H, I, or the monograptid pattern. Silurian representatives develop vengellar meshworks and anchor-based retiolitid colonies while others develop thecal and sicular cladia to re-establish multi-stiped, spreading colony forms.

*Discussion.* The fourth major division of the Diplograptacea encompasses *G.* dentatus Brongniart, its congeners, and their descendants. Bulman (1963b) considered the prosoblastic form of th1 in the astogeny of *G.* dentatus to be distinctive of that species and all its descendants. This has proved not to be true, however. Derived members of both the Orthograptidae and Diplograptidae also develop a prosoblastic th1, i.e. species with Patterns E, F, and G. The distinctive elements of a Pattern B astogeny, of which *G.* dentatus is the prime example, comprise the suppression of the upward-growing flange present in the ontogeny of th2 in the primitive diplograptid pattern (Pattern A), the consequent J-shaped growth of the crossing canal of th2, and the late origin of th2 by a pattern of differentiation like that of distal thecae. Thus, this pattern has only two crossing canals and three primordial thecae, compared to the primitive pattern of three and four respectively. The Llanvirn–Llandoilo species that possess this pattern accordingly exhibit a relatively advanced proximal structure compared to their contemporaries among the Orthograptidae and Diplograptidae.

Text-fig. 13 indicates that the species group with Patterns H and I shares a common ancestry with Pattern B species. Since Pattern I is restricted to Silurian species, I have based the inference of common ancestry on characters shared between Patterns B and H. Pattern H astogeny is highly simplified and possesses few unique characters apart from the loss of the more complex features of other diplograptidae astogenies. Thus, establishing the sister group relations of Pattern H species poses a difficulty. The overall shape of the proximal end, as well as the ontogeny of th1, are like those in species with astogenetic Patterns E and F—both of which are also highly derived and simplified patterns. However, species with Patterns E and F primordial astogenies exhibit distinctive, derived features of the sicula or of its relationship to the colony that unambiguously ally them with the orthograptids or diplograptids and exclude any close relationship with Pattern H species. For instance, in the geniculograptes (Peiragrapinae, generic group 2), which possess a Pattern F astogeny, the sicula is extensively exposed on the obverse side of the colony and its aperture bears a pair of antivirgellar spines—all synapomorphies shared among the Peiragrapinae as a whole. In contrast, species with Pattern H retain the primitive conditions: the sicula is rapidly enclosed by th1 and th2 on the obverse side of the rhabdosome and its aperture does not bear antivirgellar spines. These are also still present in *C.* (Diplacanthograptus) spiniferus (the only species with a Pattern E astogeny in which the details of its course are known), but, once again, the sicula exhibits a suite of unique features: the metascula is strongly deflected toward its dorsal side and exhibits a series of regularly spaced bands comprising condensed fuselli, while the prosicula is replaced by a set of rods.
that unite to form the nema. These characters are shared with C. (Climacograptus) bicornis and other species with a Pattern D astogeny. Since this suite of synapomorphies appeared among the Climacograptinae prior to the derivation of the Pattern E astogeny, and since the species with a Pattern H astogeny lack all of these characteristic sicula features, the similarity between these highly simplified primordial astogenetic patterns must be analogous and must have been derived in parallel. Furthermore, th₁ is commonly the dicalylic theca in Pattern H species, but all known Pattern F species are aseptate and no species of Climacograptus s.s. (whether with a Pattern D or E astogeny) is known to have a dicalylic theca earlier than th₂.

The combination of a prosoblastic th₂ which gives rise to th₂ from its upward-growing segment, and which is also dicalylic, is found only in species with a Pattern H or a Pattern B astogeny. Additionally, a thecal form strikingly like that of the early glyptograptines of the G. euglyphus group is present in 'G.' jaroslovi (Bouček). Contrary to the inexplicable thecal diagram given by Bouček (1973, text-fig. 36d), 'G.' jaroslovi appears to exhibit a Pattern B proximal end structure. Given these resemblances, I conclude that Glyptograptus s.s. (but including members of the 'C.' brevis-, 'C.' normalis and related lineages) is the sister group of the primitive, Glyptograptus-like, and Pattern B-bearing species (e.g. 'G.' dentatus and 'G.' jaroslovi) grouped below as Eoglyptograptus gen. nov.

It is among species with a Pattern H astogeny that we last encounter the diplograptaceans with glyptograptid thecae that are congeneric with Diplograptus tamariscus Nicholson, the type species of Glyptograptus Lapworth. The Diplograptus-like species of this group, however, are only homeomorphic with C. bicornis and not closely related to it, as discussed above. Pfibyl's (1947) taxon Paraclimacograptus, with 'C.' innotatus as its type, is available to accommodate those Silurian (and possibly Ordovician) glyptograptines with climacograptid thecae and prominent genicular flanges. However, it is unclear to what extent the other Silurian and Ordovician 'climacograptines' such as 'C.' rectangularis, 'C.' normalis, 'C.' mohawkensis, and 'C.' brevis constitute a true clade separate from Glyptograptus (see Bulman 1963b, p. 413; 1970, p. V103). Among the many Llandoveryian glyptograptine species the distinction between Glyptograptus and 'Climacograptus' is entirely arbitrary (see Rickards et al. 1977, p. 19). At the present time, it seems preferable to group all these species together under the genus Glyptograptus Lapworth. Detailed morphometric studies may help to delineate some useful and recognizable subclades within this complex array of structurally simple taxa.

Pattern I-bearing species, which comprise the Retiolitinae (including Petalographus and Cephalograptus, as well as the 'retiolitids' themselves: see text-fig. 16) and the Dimorphograptinae, share with Pattern H-bearing species, the Glyptograptinae: 1, the propensity of the right lateral wall of the metatheca of th₁ to be free of its protheca on the reverse side, and thus to form a free-standing edge, as in 'C.' brevis, or a broad reverse wall that extends on to the sicula, as in Petalographus (see text-fig. 12A, B); 2, the tendency for the left lateral wall to enclose much or all of the descending portion of its protheca on its obverse side; and 3, the continued presence of the plesiomorphic dicalylic th₂. The primordial astogenetic Patterns H and I characterize all of the biserial Silurian diplograptaceans with the exception of the retiolitines. Silurian species currently identified as Diplograptus, Amplexograptus, or Orthograptus will have to be either subsumed by Glyptograptus or Petalographus or renamed if their heritage is to be properly reflected and justice done to the true magnitude of the Late Ordovician extinction. None possess the characteristic astogeny of their Ordovician homeomorphs. Obut (1949), Obut and Sobolevskaya (1968), and others have erected a number of genera based on these unique Llandoveryian glyptograptines and their phylogenetic significance needs to be established.

The retiolitines have an even more highly derived proximal end structure than the other monograptids. Since the early thecae and even the metasicula are wholly unsclerotized, apart from the stylized clathrium, it is hardly possible to compare their primordial astogeny with that of the non-retiolitid diplograptaceans. None the less, they too possess proximal end structures that ally them with a sister group—in this case Petalographus. In their recent work on the retiolitines, Bates and Kirk (1984) demonstrated that several Petalographus species, such as 'O.' obuti, possess an ancora.
TEXT-FIG. 16. Cladogram and classification of the Monograptidae. Synapomorphies 1-61 as in text-fig. 13a; 107, th2; J-shaped and without upward growing flange in its prothecal ontogeny; 108, thecal elongation to produce double sigmoidal curvature; 109, undulatory median septum; 110, thecal apertures hooded by overhanging genicular flanges; 111, orthograptid thecae; 112, strongly arcucular proximal end with dorsal side of isca free for nearly its entire length; 113, metatheca of th1 becomes upturned well above apical aperture; 114, metatheca of th1 reduced; 115, metatheca of th1 absent but protheca retained; 116, th1 absent; 117, thecal incline at high angle to axis of rhabdosome and with everted aperture; 118, th1 and th2 with concave ventral walls; 119, rhabdosome asceptate; 120, thecal elongate and with great overlap; 121, anchora incorporated into thecal clathria; 122, fusellar periderm reduced to clathria; 123, metasclera suppressed; 124, clathrial elements corresponding to edges of interthecal septa present; 125, ‘reticulum’ that forms separate, lacina-like mesh which encloses, but is free of, clathria along median region of rhabdosome; 126, clathria lacks elements showing any clear correspondence with interthecal septa; 127, reticulum entirely dependent on clathria; 128, cladia present. Retained primitive character as in text-fig. 134; n, dicycical th2; o, fusellar periderm present.

The conformity between the complex structures of the Petalograptus ancora and the anchora of the Silurian retiolitids suggests that these structures are homologous. This relationship raises questions about the nature of the so-called clathria of these graptolites. If their anchora is derived phylogenetically not from the fusellum of the theca, but rather from a lacina-like set of rods that arise from the virgella independently of the theca, then the retiolite skeletal framework can hardly be considered a clathria in the same sense that it is among the Lasiorigraptinae or the Abrograptinae. This appears to be the case at least in 'O.' obtusit, where the anchora produces a lacina-like structure that grows upwards to enclose an otherwise non-retiolitid-like and fully sclerotized rhabdosome. In
any case, the morphogenesis of these retiolite colonies must be quite different from that of the Lasioograptinae (including the archiretiolitids). Not only is the proximal end structure of the Ordovician retiolite-type diplograptaceans derived from that of Orthograptus and related taxa, but here the lacinia is developed primarily from bifurcated thecal spines and lateral spines located along the dorsal clathria, and is anchored to an otherwise normal set of virgellar and antivirgellar spines.

Text-fig. 16 presents the Monograptinae as a sister group to the Retiolitinae plus the Dimorphograptinae, with their Pattern I astogeny, because in all these taxa th1 is no longer a primordial theca. As discussed below, this relationship explains many of the troubling similarities between the Monograptinae and the Dimorphograptinae—similarities that are not accounted for in the phylogenetic hypotheses advanced by Rickards and Hutt (1970) and Rickards, Hutt and Berry (1977). It also provides insights into the significance of some of the unique features of the Monograptinae that previously did not appear to be directly related to their origins.

As Bulman (1970, pp. V108–V109) noted, the elimination of th1 from the astogenetic sequence has been a stumbling block to theories concerning the origin of the monograptine design. He pointed out that the suppression of the dicalycal theca is not sufficient to produce a monograptid rhabdosome and cited the partly monoserial species *Peiragruptus fallax* as an example. Indeed, the suppression of the dicalycal theca is not sufficient, but neither is its location or suppression of critical significance to this problem. Nevertheless, the structure of *P. fallax* is helpful in understanding the evolution of a fully monograptid rhabdosome.

In *P. fallax* the proximal end consists of three alternate thecae, th1, th1, and th2, after which the rhabdosome is uniserial. This condition, in which th1 is retained while th2 is lost, is not the consequence of the suppression of the second bud of the dicalycal theca. In no species with a Pattern G astogeny is th2 dicalygal; *A. bekkeri* has a dicalycal th3 and this is the earliest dicalycal theca of any Pattern G species known to me. Furthermore, all of the advanced peiragruptine species to which *P. fallax* is most closely related are aseptate, e.g. *A. prominens* Barrass and *Paraorthograptus pacificus* (Ruedemann). The proximal end configuration of *Peiragruptus fallax* suggests that it is not the location or presence of a dicalycal theca that is problematic. Rather, the cause of this proximally biserial and distally uniserial rhabdosome form appears to be the configuration of the highly conservative primordial thecae. Both this species and all others with a Pattern G astogeny possess three primordial thecae, and it is precisely these three that are retained in their primitive alternating form in *P. fallax*. Th2 may be the first theca to be suppressed because it is the first non-primordial theca. Th1 is an older uniserial sections than do those of succeeding zones, suggesting that evolution in this groupfavoured the accumulation of more fully biserial rather than monoserial species.

The fully monograptid condition of the Monograptinae arose through the loss of the characteristic primordial features of th1. The morphogenesis of the sicula and the mode of origin of th1 reflect the loss of the primordial status of th1. In all of the Graptoloidea except the Monograptinae, the first theca arises through a resorption foramen. Among the Monograptinae a sinus forms in the aperture as the metatheca grows. The protheca of th1 crosses the virgella and then grows directly upward without any noteworthy ontogenetic specializations. This coincidence between the occurrence of a wholly unprecedented structural change in the sicula and the early ontogeny of th1 on the one hand, and the possession of a radically new rhabdosomal form on the other, could be unrelated to the acquisition of the monograptid condition but this is unlikely. The sicula is the most structurally and morphologically conservative portion of graptolite colonies. The resorption
foramen is plesiomorphic with respect to the entire Graptolithina and the nematophorous sicula, with a primordial th1, is plesiomorphic to the Graptoloidea. The shift from a resorption foramen did not involve the simple loss of that feature but, rather, required an alteration of metasclerotic ontogeny.

The fusellar morphology of the metasclera provides some information about the origins of the monograptine sicular ontogeny: the configuration of growth lines during the sinus and lacuna stages of porus formation are remarkably like the corresponding stages in the formation of the foramen for th1 in the descending protheca of th1 among other diplograptaceans. The metasclerotic fusellae are out from the sicula profile and loop back distalward. They make contact with previous fusellae before reaching the virgella (e.g. Bulman 1970, fig. 48.9; Walker 1953, text-fig. 2). In this way the siculoszoid formed a hooded foramen. The metasclera's contribution to the hood ceased when the next fusellae reached directly around to the virgella and so closed the open proximal end of the sinus. The th1 protheca arises unconfornmly from this hooded foramen. The configuration of its protheca and metaexa are like those of all subsequent theca.

I propose that this similarity between the sicular structures and mode of origin of th1 in the Monograpinae and the structure of the protheca of th1 in diplograptines is more than analogy—it reflects a common origin. The monograptid condition, like that of the other fundamentally distinct primordial astogenetic patterns among graptolites, appears to have arisen by an abrupt shift in the timing or coordination of a crucial event in the astogenetic sequence: by a kind of colonial heterochrony. Beginning with a primordial astogeny in which only th1 retained its specialized role in astogeny, as in Pattern I, the essential primordial feature of the protheca of th1 (the hooded foramen for th1) was accelerated (displaced to an earlier stage in astogeny) into the ontogeny of the sicula, th1 was liberated from its role as a primordial theca and the previously fully biserial colony acquired a fully uniserial architecture.

Rickards et al. (1977, pp. 36–39) advanced the theory that the monograptines arose in a saltatory fashion within a dithyridial population of a glyptograpine species similar to G. persculptus in the G. persculptus Zone. Although a plausible suggestion, their theory lacked both a convincing mechanism and predictions by which it could be tested. Derived along a different route and based on a different logic, the theory I have outlined above postulates a similar mode of origin for the monograptines. It provides a mechanism for their proposed origin and a means of testing its explanatory power. It differs only in suggesting an ancestor with a Pattern I primordial astogeny like that of a Petalographus or Parakidographeus species rather than the Pattern H-bearing glyptograpine favoured by Rickards et al.

Rickards and Hutt (1970) were unable to determine whether Atavographeus cerxy exhibited a descending portion in the ontogeny of th1 and whether this theca developed from a primary notch rather than a resorption foramen. If the theory presented above is correct, then suitable material should reveal the astogeny and sicula of A. cerxy to be fully monograptid. If it proves not to have a primary notch and a non-primordial th1, then the theory is wrong. The proposed relationships also imply that monoseriality of the monograptines and the dimorphographtines may be a parallelism that reflects the highly simplified character of the primordial astogeny of their common ancestor (an astogeny in which th1 was no longer a primordial theca), which established the necessary preconditions for a shift to uniserial colonies.

This mode of transformation from one primordial astogenetic pattern to another is not unique to the Monograpitidae. The shift from a Pattern A to a Pattern G astogeny, for example, can be explained as the consequence of the acceleration of the upward-growing flange from the ontogeny of th2 (where it had fused with the crossing canal of th2 to form the pair of foraminia through which the prothecae of th2 and th2 arose) into the ontogeny of th1 (where it fused with the downward-growing crossing canal of th1 to form the metasclera of th1 and the foramen from which th1 developed). The result is a simpler, less crowded proximal end in which there are now only three primordial thecae rather than four. The sequence of changes leading from a Pattern C to a Pattern D and thence to a Pattern E primordial astogeny (and likewise from Pattern G to Pattern F) also appears to have required only the relatively straightforward acceleration, mutatis mutandis,
to earlier astogenetic stages of the upward-growing flange of th2 and the consequent reduction or suppression of the corresponding descending crossing canal. Such a shift in the timing of primordial astogenetic features, and particularly their transferral to an earlier stage in astogeny, appears to be the principal means by which the Diplograptacea achieved simplified astogenetic patterns.

Subfamily GLYPTOGRAPTINAE subfam. nov.

Diagnosis. Monograptids with glyptograptid to climacograptid or pseudoclimacograptid thecae; median septum straight to complexly folded and with a Pattern H primordial astogeny.

Generic group taxa. Glyptograpthus Lapworth, Climacograptus Bulman and Rickards, Cystograptus Hundt, Lithuanograpthus Puškevičius, Metaclimacograptus Bulman and Rickards, Paraclimacograptus Přibyl, Pseudoglyptograpthus Bulman and Rickards [= ?Comograptus Obut and Sobolevskaya]. May include other taxa such as Hetrograptus Obut, but the phylogenetic status of these taxa remains to be established.

Genus GLYPTOGRAPTUS Lapworth, 1873, emend.

Type species. Diplograptus tamariscus Nicholson, 1868, Birkhill Shale, Southern Uplands, Scotland; Llandovery Series (M. cyphus to M. turriculatus zones).

Diagnosis. Species with glyptograptid to climacograptid thecae having relatively narrow geniculum and nearly straight suprageneric wall; proximal end generally narrow and fusiform, with strongly alternating thecae; generally septate with straight median septum and th2 or some later theca dicalyceal, but may be aseptate; sicula simple, generally short and broad, lacking antivirgellar spines.

Species included. Taxa assigned to this genus are too numerous to list but include: G. euglyphus, G. simuatus, G. tenuissimus, G. persculptus, ‘C.’ brevis, ‘C.’ rotundatus, and ‘C.’ scalaris.

Discussion. The genus is here expanded to encompass the Ordovician and Silurian species formerly included in Climacograptus that possess a Pattern H astogeny (see discussion of Monograptidae, above), but restricted to apply only to those species with a Pattern H astogeny. This and other features distinguish the taxon from similar looking species in Eoglyptograpthus gen. nov., Hustedograptus gen. nov., Climacograptus, and Arnrheimograptus gen. nov. (see discussion of these taxa). Glyptograpthus differs from Paraclimacograptus Přibyl in its lack of prominent genicular flanges.

Subfamily RETILOTINAE Lapworth, 1873, emend.

Diagnosis. Monograptids with sharply acicular proximal end based on a Pattern I astogeny among forms with fully sclerotized proximal end or with ancora-based retioliid astogeny; ancora common. Primitively with orthograptid thecae but elaborated to glyptograptid, climacograptid, or to a stylized clathrial framework.

Generic group taxa. Subfamily comprises three generic groups: Group 1 (petalograptids), Petalograptus Suess and Cephalograptus Hopkinson; Group 2 (retioliids), Retioliites Barrande, Pseudoleptomatograptus Přibyl, Sinostomatograptus Huo Shih-Cheng, and Stomatograptus Tullberg; Group 3 (petalograptids), Petalograptus Moberg and Törnquist, Agastograptus Obut and Zaslavskaya, Gothograptus Frech, Holoretioliites Eisenack, Parapetalograptus Přibyl, and Spinograptus Bouček and Münch.

Genus PETALOGRAPTUS Suess, 1851, emend.

Type species. Prionitis folium Hisinger, 1837, Rasstrites Shale?, Sweden; Llandovery Series (M. leptotheca and M. convolutus zones).

Emended diagnosis. Monograptids with orthograptid thecae disposed at a high to moderate angle to the colony axis and with extensive overlap. Thecal apertures everted. Thecae commonly with concave ventral walls that may lead to apertural isolation. Distally, thecal inclinations commonly
increase and the rhabdosome becomes broad and tabular. Ancora commonly present and some species exhibit additional spines on thecal apertures.

Species included. Representative species include *P. folium*, *P. ovatoelongatus*, *P. elongatus*, ‘O.’ eberleini, ‘O.’ insectiformis, and ‘O.’ mutabilis.

Discussion. Genus is here expanded to include the Silurian species with a Pattern I astogeny formerly referred to *Orthograptus* [≡ *Dittograptus* Obut and Sobolevskaya].

Subfamily *DIMORPHOGRAPTIINAE* Elles and Wood, 1908

Diagnosis. Monograptids with th1 reduced or absent, with proximally uniserial rhabdosomes. Length of the uniserial portion variable. Rhabdosome commonly septate with straight median septum. Astogeny of Pattern I. Sicula commonly with ancora.


Discussion. In the light of studies by Li (1985) and Rickards et al. (1977), which suggest that several of the genera in this family are polyphyletic, and the several additional taxa that have been proposed for various species with different thecal shapes (e.g. *Bulmanograptus* Přibyl, *Agetograptus* Obut and Sobolevskaya, and *Metadimorphograptus* Přibyl) the phylogenetic status of the entire Dimorphograptinae needs to be re-examined.

Subfamily *EOGYLPTOGRAPTIDAE* subfam. nov.

Diagnosis. Archaic monograptids with glyptograptid to climacograptid thecae, straight to undulating median septum, and Pattern B primordial astogeny.


Genus *EOGYLPTOGRAPTUS* gen. nov.

Type species. *Fucoideas dentatus* Brongniart, 1828, Upper Lévis Shale, Point Lévis, Quebec; Whiterockian Series (*Isoograptus* and *P. etheridgei* zones).

Diagnosis. Monograptids with glyptograptid thecae having a gentle geniculum located about halfway along the theca. Thecae overlap about one half their length and commonly bear cuspate apertures. Narrow, gradually widening rhabdosomes are septate with a straight median septum. The dicalycal theca may be th2 or a later theca. The strongly asymmetric proximal end is broadly rounded and exhibits a Pattern B astogeny. Th1 may possess a subapertural spine or the proximal end may be without spines apart from the virgella.

Species included. ‘G.’ *dentatus* Brongniart, ‘Pseudoclimacograptus’ jaroslavi Bouček, and ‘G.’ *cerrus* Jaanusson.

Discussion. Skewington’s (1965, fig. 61a) illustration of the *E. dentatus* specimen, Ól 1228, is inaccurate: the specimen does not possess a th2 crossing canal where shown on this figure. The illustrated structure is wholly incompatible with his fig. 62a and with Bulman’s (1936, 1963a) wax model reconstructed from serial sections. Text-fig. 3r is a new illustration of Ól 1228.

Eoglyptograptus gen. nov. differs from other Glyptograptus-like taxa principally in the form of its proximal end and primordial astogeny. Species of *Glyptograptus* sensu stricto lack the apertural cusps present on the thecae of *E. dentatus* and *E. cerrus* and exhibit a narrower and more fusiform proximal end based on a Pattern H astogeny. Among the Orthograptidae, species of *Arnheimograptus* gen. nov. resemble the eoglyptograptids in their rhabdosome form and proximal end shape, but possess a Pattern F primordial astogeny and an extensively exposed sicula with antivirgellar spines.
Type species. Climacograptus paradoxus Bouček, 1944 [= C. pauperatus Bulman, 1953], Šárka Formation, Kršná hora Mt. region, Bohemia; Llanvirn Series (lower D. bifida Zone).

Emended diagnosis. Taxon here restricted to forms like the type species, which exhibits climacograptid thecae, a weakly undulating median septum, and a Pattern B astogeny (= Undulograptus Jenkins, 1980, partim).

Species included. If one accepts Bouček’s (1973) determination that ‘C.’ pauperatus is synonymous with the type species, this taxon is presently monotypic. ‘C.’ pauperatus occurs in the Ogygiocaris Series, Norway and in the Seby Limestone, Öland; both occurrences are equated with the D. marchisoni Zone.

Discussion. The narrow proximal end and Pattern B astogeny of the type species is quite unlike those of Oelandograptus austrodenatus and congeners. Jenkins’s (1980) expansion of Bouček’s taxon to encompass these species was ill advised. However, Bouček (1973) also included several species in Pseudoclimacograptus (Undulograptus) that are indeed pseudoclimacograptines of the group P. (Archiclimacograptus), and that exhibit no close similarity to U. paradoxus other than their possession of an undulating median septum. E. jaroslovi, on the other hand, does seem to possess a similar proximal end structure but lacks the undulating median septum and has glyptograptid rather than climacograptid thecae. Thus, confusion about the scope of this taxon dates from its inception.

Subfamily Monograptinae Lapworth, 1873

Diagnosis. Monograptids with fully uniserial stipes; some with cladia formed by secondary budding from a mature zooid or sicula; proximal end development highly simplified, having no primordial thecae; thg grew upwards from a primary porous produced by the metascula during its ontogeny.

Discussion. Rickards et al. (1977) presented a detailed study of monograptid phylogeny which indicated that the divisions Monograptidae and Cyrtograptidae of the Monograptina (see Bulman 1955, 1970) are not phylogenetically meaningful units. They did not present an alternative classification, however. Thus, the systematic subdivision of the Monograptinae based upon the group’s evolutionary history remains to be accomplished.

MACROEVOLUTIONARY PATTERNS

My intention here has been to present a phylogenetic classification of the Diplograptacea. Accordingly, consideration of their evolutionary history forms an integral part of this endeavour. It is not primarily my intention to review the history of the classification (but see Rigby 1986) or to speculate about the causes that may have underlain diplograptacean macroevolutionary patterns. Considerable work remains to be conducted in deciphering the details of this history. Nevertheless, a number of large scale features of diplograptacean phylogeny are now apparent. These have implications for both systematic practice and for future studies of graptolite colonial evolution.

The course of graptolite evolution has generally been traced on the basis of similarity in thecal characters and in the disposition of the stipes, following the suggestions of Nicholson and Marr (1895; see also Bulman 1970, p. V102). Neither when Nicholson and Marr wrote nor at any time since has there been any compelling biological justification for this preference among the suite of characters available for study in flattened graptolites. Rather, the demands of pragmatism, combined with the attractively anti-Darwinian phylogenies that the method generated, led to a general acceptance of Nicholson and Marr’s proposals among their contemporaries. The major works on graptolite phylogeny (e.g. Elles 1898, 1922; Bulman 1933a, b, 1936; Bouček and Přibyl 1951) and systematics (e.g. Elles and Wood 1901–1918; Ruedemann 1904, 1908; Mu 1950) followed their recommendations. The conception of graptolite evolutionary history that subsequently emerged was one characterized by a confusing array of parallel trends, each leading in Lamarkian fashion
to the progressive improvement of the lineage. These trends manifested themselves not only in astonishly similar colony designs within independent lineages but also in their often contemporaneous appearance (Elles 1898, 1922; Ruedemann 1904; Bulman 1933b; Rickards et al. 1977). Within this framework, primordial astogeny has been seen as simply another of the many features of graptoloid colonies that underwent extensive parallel change. Thus, Bulman (1933a, p. 2) while discussing Elles’s developmental types, cautioned that ‘. . . they represent simply grades of evolution, probably reached or passed through quite independently in many different lineages. What is here assembled as a purely morphological series, without strict reference to phylogeny, is believed to represent an ‘orthogenetic’ trend, comparable with the stipe reduction trend and others described by Elles. . . .’

Graptolite evolutionary history became one of the prime examples of orthogenesis (Bulman 1933b). Urbanek (1959, p. 326) and others have expressed a similar attitude with regard to the phylogenetic significance of astogenetic similarities. Although Bulman (1960, 1963a, b) later retreated from his statements on the importance of orthogenesis as an explanation for the observed trends, the present graptoloid classification remains one that is conceptually more compatible with Osborn’s theory of aristogenesis than with Darwinian theory. This systematic history, combined with the inherent difficulty of producing a phylogenetic classification of these organisms from their often inadequately preserved and incomplete remains (see Bulman 1963b, pp. 413–416) has prevented the establishment of an integrated graptoloid systematics that is in step with both the group’s probable evolutionary history and with contemporary evolutionary thought.

The results of the present studies of diplograptacean astogeny and thecal form show that graptolite evolution was strikingly directional and exhibited distinct phases. The major diplograptacean clades were founded through apparently rapid structural reorganizations. The Diplograptaceae differ from all other virgellinids in a substantial suite of features involving characters of the primordial astogeny, thecal form, and rhabdosome architecture. The nature of these structural changes, like those that occurred in the transitions from one primordial astogenetic pattern to another (such as from Pattern D to Pattern E, or from Pattern A to Pattern C), indicate that they were not gradual transitions made through a series of intermediate steps. Rather, they were achieved abruptly over a short interval of time (as in a single allopatric speciation event) compared to the millions of years over which they remained stable. This is also illustrated by the total lack of any preserved intermediates between diplograptaceans and non-diplograptaceans (despite nearly ninety years of searching) or between the groups of species characterized by the nine diplograptacean astogenetic patterns.

Following several of these rapid structural reorganizations (as in the case of the Orthograptidae, following the origin of the Pattern G astogeny), the new clade apparently underwent an evolutionary radiation. During its radiation the clade’s members achieved a substantial diversity of thecal form and colony design, often exhibiting close analogy with species of other clades. The radiations of the Orthograptidae and the advanced climacograptines in the late Llandoilo and early Caradoc appear to have coincided with the waning of their predecessors among the primitive diplograptaceans (particularly Oelandograptus gen. nov. and Hustedograptus gen. nov.) and among the pseudoclimacograptids and diplograptines (see text-fig. 17). The appearance is one of a relay in which a dominant and diverse clade or set of clades is succeeded by another set which is itself succeeded. Hence, the faunas of the late Arenig to late Llandoilo were dominated by the archaic diplograptids (the Diplograptidae and, to a lesser degree, Oelandograptus and Hustedograptus). The late Llandoilo to latest Ashgill witnessed the proliferation of the advanced Orthograptidae, Climacograptinae (especially in the form of Orthograptus, Ampelograptus, and Climacograptus), and the Dicranograptidae. Following the near total extinction of diplograptaceans the Monograptidae underwent an explosive evolutionary diversification in the Llandovery. These intervals of successive clade dominance are more or less equivalent to the diplograptid subfaunas that Bulman described (1970, p. V99).

In the course of these three successive major radiations, homeomorphism arose in thecal form and rhabdosome architecture with a bewildering frequency. Furthermore, this pattern of radiations
TEXT-FIG. 17. Evolutionary tree showing pattern of descent among the generic group taxa of the Diplograptidae in the interval of the upper Arenig to the base of the Wenlock Series. The nemagraptids and retiliolitids are shown as family group taxa because of the remaining uncertainty about evolutionary relationships within them. The relationships among the generic group taxa of the Monograptinae are beyond the scope of the present study. Patterning within the range bars of each taxon indicates the astogenetic pattern exhibited by its constituent species and its family membership according to the inset key. The absence of patterning in range bars among the archiretiolitids (Orthograptidae) and retiliolitids (Monograptidae) corresponds to the highly stylized clathral architecture of these taxa that consequently does not fit within the astogenetic patterns defined herein. The plotted stratigraphic ranges of the taxa are approximate due to uncertainty about their species membership.
and rampant homeomorphism was not confined to the Diplographtacea. A number of authors (but especially Cooper and Fortey 1982) have recently completed work on the Arenig graptoloids that has revealed a surprisingly complex history. Early Arenig (Bendigonian Stage) faunas are dominated by *Pendiograptus* and an early proliferation of *Pseudophylograptus* species. These are succeeded in the Chewtonian to early Castlemainian (Ca1) by pendent didymographtids (mostly *D. (Didymograptella)* with an isographtid primordial astogeny and *Phyllograptus* sensu stricto. Later in the Castlemainian, as the isographtids begin their main radiation, the pendent didymographtids vanish and *Phyllograptus* is succeeded by a second radiation of *Pseudophylograptus*. Finally, there occurs the now well known sudden re-emergence, just prior to the beginning of the Darriwillian, of pendent didymographtids in the form of *D. (Didymograptus)*. This time, however, the rhabdosomes of these ‘tuning fork’ graptolites appear to be based for the most part on an *artus*-type primordial astogeny (see Cooper and Fortey 1983). To what degree this seemingly endless playing out of variations on a few themes reflects the action of either adaptive or constructional constraints (producing convergence), or channelling by historical constraints (leading to parallelisms) is an important area for further research—an area that may shed as much light on the processes of evolution as on the palaeobiology of graptoloids.

The nature of the causal connection, if any, between the waxing of one clade and the waning of another is unknown. This issue is likely to be intimately related to the source of the overall directional history of diplographtacean evolution. Ostensibly, their history exhibits a strong birth-bias in favour of more simplified astogenetic patterns. Following the establishment of the superfamily and the Pattern A primordial astogeny, ten of the eleven transitions to new primordial astogenetic patterns among the three lineages of fully scindent diplographtaceans (including the transitions to the clathril agestones of the archiretiolitids and retiolitids) resulted in astogenies less complex than the patterns that preceded them. (Relative complexity may be gauged by comparing the number of crossing canals and primordial thecae, as well as the mode of thecal construction, *vis.* the ‘direct’ growth pattern of the ontogeny of *th1* in Pattern F compared to the ‘indirect’ mode of construction seen in Pattern G.) Only Pattern C is no simpler than its predecessor, Pattern A, but neither is it more complex. Furthermore, this trend toward greater astogenetic simplicity affected all three of the dominant Ordovician families: the Orthographtidae, Diplographtidae, and Monographtidae. Accepting the cladogenetic history depicted in text-fig. 13A, the Dicranographtidae underwent little change in primordial astogenetic structure during their range, except to give rise to the Nemagraptinae with their right-handed origin of *th1*. Transitions to astogenetic patterns of greater complexity either did not occur among the diplographtaceans or were so unsuccessful that they left no known record. Thus, the source of the variance that underlay the directional trends in astogeny and colonial architecture of the Diplographtacea was strongly channelled by directed speciation.

Apart from the observation that loss of complexity is in some way ‘easier’ to achieve than is an increase in complexity (consider the host of extant albino creatures, from cave crickets and white rabbits to the Indian pipe, *Monotropa uniflora*, and the multitude of independent paths by which they arrived at this lack of pigmentation), we have only speculative answers to the question of why this bias should exist. Nevertheless, I am convinced by the frequent coincidence of a radiation in thecal form and an increase in the clade’s diversity with the origin of a new, less complex astogeny that these astogenetic changes were associated with a selective advantage in favour of graptolites with a simplified pattern.

Differential rates of origination or extinction, or both, may also have contributed to the observed replacement of clades with a complex astogeny by clades with a less complex astogeny. During the course of diplographtacean evolution the changes in character distribution that accompanied the astogenetic trends involved characters for which variance existed only at the clade level. It is now clear that, phenemologically at least, these trends seem to be the result of sorting among clades.
TABLE 2. Key to the identification of diplagnostid astogenetic pattern on the basis of features visible in mature rhabdosomes well preserved in semi- or full relief, or in isolated preparations. These features are not a substitute for the study of isolated growth stages but are guides to the distinctive features of the modal proximal-end architecture associated with each astogenetic pattern. Sketches in the panels labelled II to VIII provide illustrations, in otherwise similar rhabdosomes, of the contrasting features under consideration in the corresponding key statement. For example, statement II asks the user to decide whether or not the prothecae of th21 and th22 arise as a symmetrical pair from the descending portion of the crossing canal of th22; the sketches in panel II illustrate proximal ends with a paired and an unpaired th21 and th22. Abbreviations: a, apertural thecal spine; av, antirhizellar pegs on apertural aperture; m, mesial thecal spine; v, virgella. Diagonal or horizontal ruling highlights the theca or thecae that are the focus of comparison; vertical ruling highlights the sicula.
APPENDIX

Application of classification to non-isolated graptolites

The circumstances described above make a thorough study of the evolutionary history of graptolites essential and justify a revision of their classification, despite the temporary hardship it may impose in the day to day practice of classification. Furthermore, I am confident that, with patience and attention given to the descriptions and figures provided here, most well-preserved flattened and semi-relief graptolite specimens can be placed within the new taxonomic system.

There are several features of the present situation that should ease the application of this classification to non-isolated material. First, although the diplograptacean astogenetic patterns initially could only be recognized through the study of isolated graptolite growth stages, now that they have been defined it is clear that each primordial astogenetic pattern exhibits a number of reliable morphological correlates visible in well-preserved, semi-relief, and flattened, mature specimens. Table 2 presents a key to these features and their correspondence with the diplograptacean astogenies. Given a working knowledge of the diplograptacean astogenetic patterns, it is possible to recognize many of their distinctive features in the flattened growth stages and sub-mature rhosoasomes that generally accompany fully developed colonies on shale surfaces. This is especially true if the age of the specimens at hand is known. Since many of the new and redefined taxa have shorter stratigraphic ranges than the previous form genera, this knowledge can be used to considerably narrow the range of possible astogenetic patterns that a species might possess (see text-fig. 17).

Secondly, scientists with the good fortune to have among their collections material preserved in semi- or full relief should begin the process of re-examining and re-illustrating the proximal ends and growth stages of the species so represented. Through the publication of such studies the list of species with known astogenetic patterns (Table 1) can be augmented. Although Table 1 does not include a majority of diplograptacean species, it nevertheless does represent a broad spectrum of diplograptacean diversity. By the association of morphologically similar but less well-preserved species with those in Table 1, the new classification can be extended to these other species.

Thirdly, the present situation is similar in many respects to the continuing reorganization of conodont form taxonomy. An interim device, like that used by conodont workers, can be employed in cases where the astogenetic pattern, and hence the generic classification, of a particular species is uncertain: where the generic affiliations of a species are ambiguous or unknown, the species name can simply be combined with a name corresponding to one of the traditional diplograptacean form-taxa, e.g. 'Diplograptus' compactus (with the generic name enclosed in quotation marks to indicate that the name is being used as a form-taxon rather than in its phylogenetic sense). In cases where uncertainty about the generic assignment remains, but where the author considers it probable that the assignment of a species to a particular phylogenetic taxon is correct, this may be indicated as Amplexograptus? arcticus. With these conventions, authors should be able to describe any diplograptacean fauna that is well enough preserved to support specific identification.

Finally, note that this revision only affects genera and higher taxonomic units. Astogenetic features are seldom of importance in the definition of graptolite species: not because astogeny is non-adaptive or inconsequential to the biology of the species, but because little variance in astogeny exists at this level in the taxonomic hierarchy. Thus, individual species will be identified as before and their use in biostratigraphy will remain unchanged.

Acknowledgements. The present study is part of a project begun as my doctoral dissertation at Harvard University. I thank Mr Anton Kearsley for his willingness to discuss work in progress on Orthograptus and diplograptacean systematics, and also Drs Anthony Arnold, Roger Cooper, Peter Crowther, Stan Finney, Richard Fortey, Valdar Jaanusson, Michael Melchin, John Riva, and Henry Williams for their discussions of some of the ideas and data presented, and their willingness to share their own ideas and data with me. I also thank Drs Jaanusson, Barrie Rickards, and Isles Strachan for their help and for allowing me to examine collections of isolated, three-dimensionally preserved graptolites in the collections of the Naturhistoriska Riks museum, Sedgwick Museum, Cambridge, and the University of Birmingham, respectively. I thank my dissertation advisor, Dr Steven J. Gould, for guidance and encouragement. My dissertation research was supported by National Science Foundation Dissertation Improvement Grant EAR 8115100 and by grants from the Department of Geological Sciences, Harvard University and the Royal Society of London.
MITHCHEL: GRAPTOLITE EVOLUTION AND CLASSIFICATION

REFERENCES


— 1933a [dated 1932]. Notes on the evolution and morphology of certain graptoloids. Ibid. (13), 1-37.


— 1963a. On Glyptagnostus dentatus (Bromignart) and some allied species. Palaeontology, 6, 665-689.


— 1985. A new phylogeny of diplograptid graptoloids, and their classification based on proximal and thecal construction. Ibid. 6, 8-22.


— 1877. On the graptolites of County Down. In Systematic lists illustrative of the flora, fauna, palaeontology and archaeology of the North of Ireland by the members of the Belfast Naturalists Field Club, Vol. 1, Append. IV, 126-144, pls. v-vii.


— 1908. Graptolites of New York, Pt. II. Graptolites of the higher beds. Ibid. 11, 1-583, pls. 1-31.


Typescript received 26 March 1986
Revised typescript received 18 September 1986