What is *Diplograptus*?

Charles E. Mitchell, Jörg Maletz & Daniel Goldman

Diplograptus pristis (Hisinger, 1837) is the type species of the genus *Diplograptus* and name bearer for Suborder Diplograptina. This species is primarily kown from the Dalarne region of Sweden, where it occurs in the *P. linearis* Zone. *D. pristis* exhibits a suite of features (particularly the shape of the proximal end, the configuration of proximal spines, and the gradient in thecal form) that is uniquely shared with a number of other late Katian and earliest Hirnantian species including *Glyptograptus nicholsoni* Toghill, 1970; *Glyptograptus posterus* Koren' & Tzai (*in* Apollonov *et al.* 1980); *Orthograptus maximus* Mu, 1945; and *Orthograptus truncatus rarithecatus* Ross & Berry, 1963. The phylogenetic affinities of the *Diplograptus* clade are equivocal, however. Two isolated, three-dimensionally preserved specimens of *D. pristis* from the Paasvere 309 core in Estonia reveal that the rhabdosome is aseptate and has a simple proximal structure comparable with a Pattern G astogeny. The pattern G astogeny, long, fully-sclerotized sicula, aseptate rhabdosome with free nema all point to its being a member of the derived orthograptids. On the other hand, the rapidly enclosed sicula and lack of antivirgellar spines together with the apertural spines on the first pair suggest archiclimacograptid affinity. Cladistic analysis supports orthograptid affinities. If these relations are correct, the Orthograptidae Mitchell, 1987, must be regarded as a junior synonym of the Diplograptidae Lapworth, 1873. • Key words: graptolite, phylogenetic systematics, biogeography, Ordovician, cladistics, Sweden, China, Scotland, Siberia, North America, Estonia.

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Prioniotis pristis Hisinger, 1837 is the type species of the genus *Diplograptus* McCoy, 1850, and name bearer for the Family Diplograptidae Lapworth, 1873, which historically has also been the root of the name applied to the entire clade of biserial graptoloids to which it belongs (excepting their uniserial descendents, which have generally been treated as a taxon of equivalent rank: the Monograptina; see Bulman 1970, for example). These graptolites dominated graptolite faunas from their origin in the early Mid Ordovician well into the early Silurian (at least through the Llandovery). Thus, a proper understanding of the detailed structure and phylogenetic relations of this particular species and its close relatives bears greatly on the taxonomy of the entire group. The intent of this present paper is several-fold. We first redescribe *Diplograptus pristis*, compare it to some related Katian and Hirnantian species, and then briefly review its phylogenetic affinities and discuss the implications of these observations for graptolite taxonomy.

Diplograptus pristis (Hisinger, 1837)

Material. – Hisinger (1837) described the species based on a single specimen from a small slab of shale from an exposure of the Trinucleusskiffer, near Draggabro in the Dalarne region of Sweden. The type specimen (Figs 1A, B, 2A) has been refigured twice, first by Tullberg (1881), and later by Přibyl (1949). During the nearly 70 years between Tullberg's and Přibyl's illustration of the holotype, a portion of the first theca has fallen off the slab. Both authors indicated that a more poorly preserved, additional specimen also occurred on the type slab and appeared to belong to this same species (Figs 1G, 2D). Tullberg also illustrated several additional specimens from the same region that he considered to belong to this taxon. These specimens all exhibit a broad rhabdosome with a bluntly rounded proximal end. The proximal thecae are strongly geniculate with shallow semicircular apertural excavations. The rhabdosome widens rapidly and thecae gradually become nearly straight tubes. A hint of an apertural spine is present on the first theca of the holotype (this is the region that is now broken away) and is well developed on both th1^1 and th1^2 in the other specimens. This broad colony shape with biform thecae has become the hallmark of the genus *Diplograptus*. Bulman (1955, 1970) reproduced Tullberg's figure of the holotype of *D. pristis* (albeit without attribution) in his synopsis of the genus.

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Table 1. Colony dimensions of type and other reference specimens employed in this description of *Diplograptus pristis* (Hisinger, 1837). The first six are specimens stored in the Natural History Museum, Stockholm. The Skoglund (1963) material is stored at the University of Uppsala Evolutionsmusset Paleontologi, and the Paasvere specimen at the Institute of Geology at the Tallinn University of Technology

Specimen	Widths				Sicula				2-theca repeat distance			
	th1	th3	th5	th10	lenght	ap width	dorsal exp	obv exp	th1	th3	th5	th10
Hisinger cn 59728												
Holotype	1.28	1.83		2.62	1.94	0.29	0.18		1.25	1.47	1.65	2.05
Paratype									1.41	1.7	1.89	2
Nilson specimens												
RM cn 996a					1.93				1.32	1.54	1.75	
RM cn 996b					1.95	0.35	0.30		1.35	1.45	1.7	2
RM cn 1001f	1.33	1.63	1.93		1.7	0.3		0.71	1.33	1.43		
Skoglund specimens (1963, Pl. 4)												
UMD1129			1.93	2.13							1.6	1.87
UMD1130	1.47	1.87	2.13		1.73	0.33	0		1.2	1.43		
UMD1131	1.55	2	2.5		1.9	0.3	0.15	0.4	1.4	1.6	1.75	
UMD1132									1.2	1.53	1.67	1.76
UMD1133	1.35	1.85	2.18		1.5				1.3	1.55	1.65	
Paasvere MS-504 46.0 m												
	1.39	1.56	1.53		1.91	0.36	0.14	0.63	1.33	1.5		
Average	1.4	1.79	2.03		1.82	0.32	0.15		1.31	1.52	1.71	1.94

In addition to the type specimens, the collections of the Swedish Museum of Natural History, Stockholm, contain additional specimens collected from the Dalarne region by R. Nilsson, two of which we illustrate here for the first time, so far as we are aware. Skoglund (1963) provided excellent figures of five additional specimens referred to *D. pristis* in his reassessment the graptolites of the Fjäka Shale and its equivalents in Västergötland and central Sweden. These specimens come from a level correlated with the upper *P. linearis* to lower *D. complanatus* zones. Finally, we have identified two specimens, one with five thecal pairs and a fragmentary growth stage in a set of graptolites etched from core samples in Estonia, in particular from the Paasvere 309 Core, Estonia (Vormsi Stage, F_1B ~ upper *P. linearis* Zone) which are understudy by D.G. and colleagues in Estonia. Since the type specimens provide a very limited foundation for detailed phylogenetic analysis, we base our description of *D. pristis* on all of this material. Several facts support this choice. First, the graptolite fauna in these strata in Sweden is of very low diversity (Skoglund describes eleven taxa in all) and offers few opportunities for confusion among its constituent taxa. Secondly, all of these putative *D. pristis* specimens share a suite of properties (particularly the geometry of the proximal end and the thecal architecture, as well as colony dimensions; Table 1) that is unique.

Rhabdosome form. – The sicular aperture is about 0.35 mm wide, bears a short stout virgella, and has no antivirgellar spines. The sicula is partly pressed through in several of the available specimens (Figs 1D, F, 2B) and its length may be approximated by the base of the pressed through nema in the holotype and several of the Skoglund specimens (1963, pl. 4, figs 2, 3, 5). In each of these, the sicula extends upward to a level between the apertures of th2^2 and th3^1 and is about 2 mm in length (see Table 1). The sicula is exposed on the obverse side of the rhabdosome for about 0.4–0.7 mm, where it is rapidly enclosed by th2^2 and th3^1 (Fig. 2F, G; Skoglund 1963, pl. 4, fig. 3).

The rhabdosome is 1.3–1.5 mm wide at the first thecal pair, increasing quickly to 2.1–2.6 at th10, with a maximum observed distal width of 2.6 mm. The proximal end is blunt and both of the first thecae are outwardly inclined at nearly 45° to the colony axis. The proximal thecae are also strongly outwardly inclined in flattened specimens and exhibit a two-theca repeat distance (2TRD) of 1.2–1.4 mm at the first pair, increasing to 2.0–2.1 mm in distal thecae (Table 1). The rhabdosome was aseptate with alternate thecae throughout. The thecal apertures are nearly horizontal, weakly lobate, and strongly thickened by an apertural selvage that forms a rim around the ventral margin of the aperture (*cf.* Figs 1A, D–F, 2D; Skoglund 1963, pl. 4, figs 1, 2, 5). The suprapertural wall is deeply concave. In

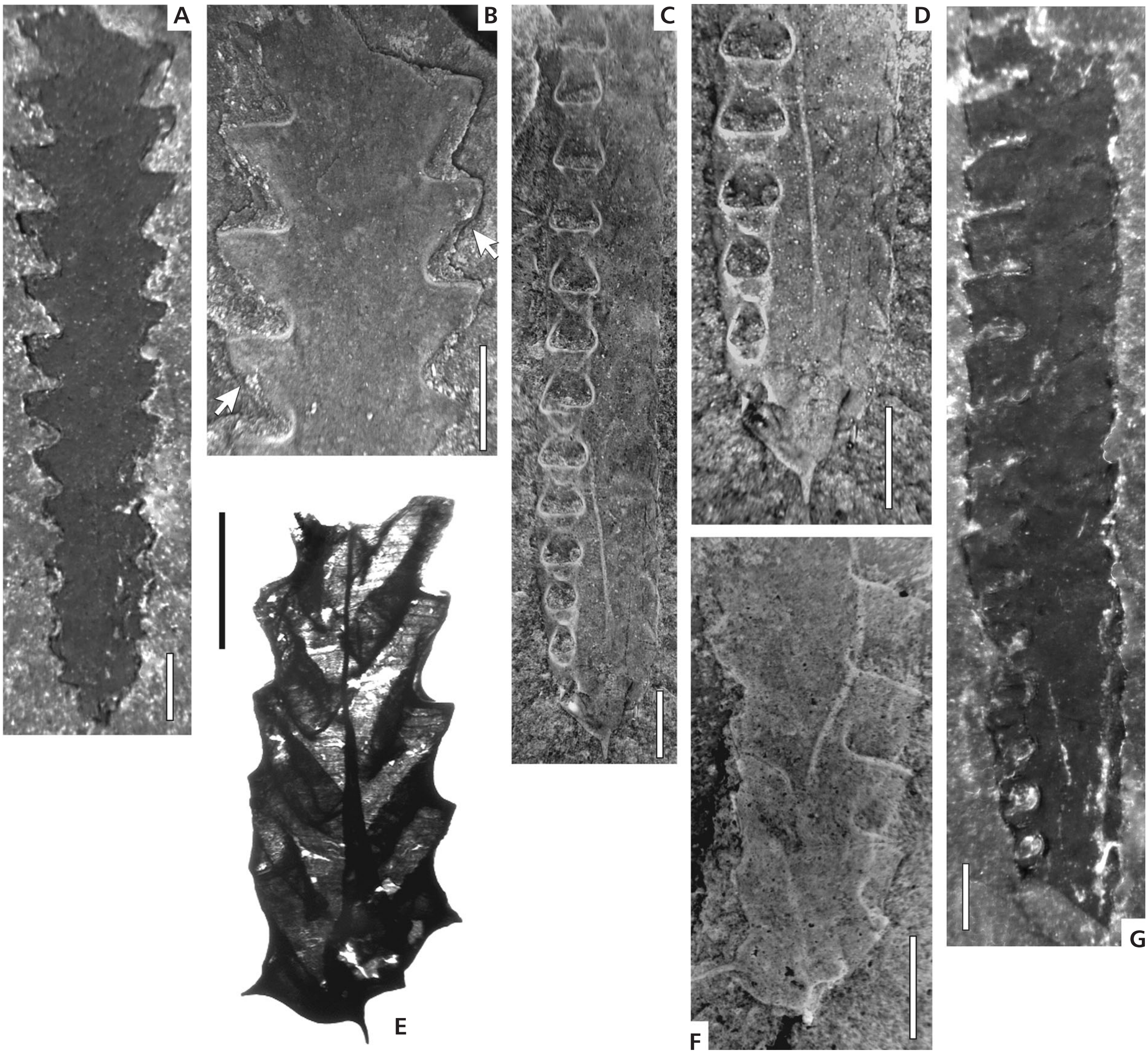


Figure 1. *Diplograptus pristis* (Hisinger, 1837). A–D, F, G from the Trinucleusskiffer, near Draggabro, Dalarne, Sweden; E from Vormsi Stage, Paasvere 309 core, Estonia. • A, B – holotype, cn 59728. A – obverse view of entire specimen, note broken first theca; *cf.* Fig. 2A. B – detail of distal end of same specimen whitened with ammonium chloride, showing pseudogeniculae (arrowed). • C, D – Nilsson specimen, cn 996b. C – subscalariform obverse view, showing strong thickening on thecal apertures. D – proximal detail of same, with sicula and nema pressed through and crushed subapertural spine on the first theca; note also the open U-shaped geometry of this theca. • E – MS-504a 46.0 m Paasvere 309; obverse view of etched, non-compressed specimen photographed in transmitted infrared light showing alternating thecae and long interthecal septa with strong aboral lists; *cf.* Fig. 2E, F. • F – ammonium chloride-whitened latex cast of Nilsson specimen, cn 1001f, in oblique ("box-flattened") obverse view with resulting "orthograptid" form of weakly geniculate thecae; note also rapid enclosure of sicula and wandering, free nema; *cf.* Fig. 2B. • G – second specimen on slab with holotype, cn 59728, *cf.* Fig. 2D. Scale bar in all images is 1 mm long.

proximal thecae, the apertural selvage continues up onto the suprapertural wall and across the geniculum, outlining the apertural excavation (*cf.* Figs 1C, G, 2D; Skoglund 1963, pl. 4, figs 3, 4). The proximal thecae are moderately strongly geniculate. The supragenicular wall is very short, roughly equal to the height of the apertural excavation. The geniculum becomes weaker distally and the supragenicular wall becomes increasingly short as a proportion of thecal length such that in distal thecae this structure is much closer to the overlying aperture than to the aperture below. We refer to this as a pseudogeniculum since its function may have been linked to that of the overlying aperture whereas a geniculum, *sensu stricto*, forms a part of the apertural restriction of the aperture it overarches. Distal thecae, therefore, have deep, long excavations of a somewhat triangular aspect (Figs 1B, 2A; Skoglund 1963, pl. 4, fig. 1).

The thecae have long interthecal septa and overlap about half their length. The aboral margin of the interthecal septa is thickened and inserted on the lateral walls of the colony but not connected to the nema (Fig. 1E). The nema was apparently free within the colony (Fig. 1E) and, consequently, the robust nema commonly shows a wandering course when pressed through the lateral wall of flattened specimens (Figs 1C, F, 2A; Tullberg 1881, pl. 1, fig. 6; Skoglund 1963, pl. 4, fig. 5).

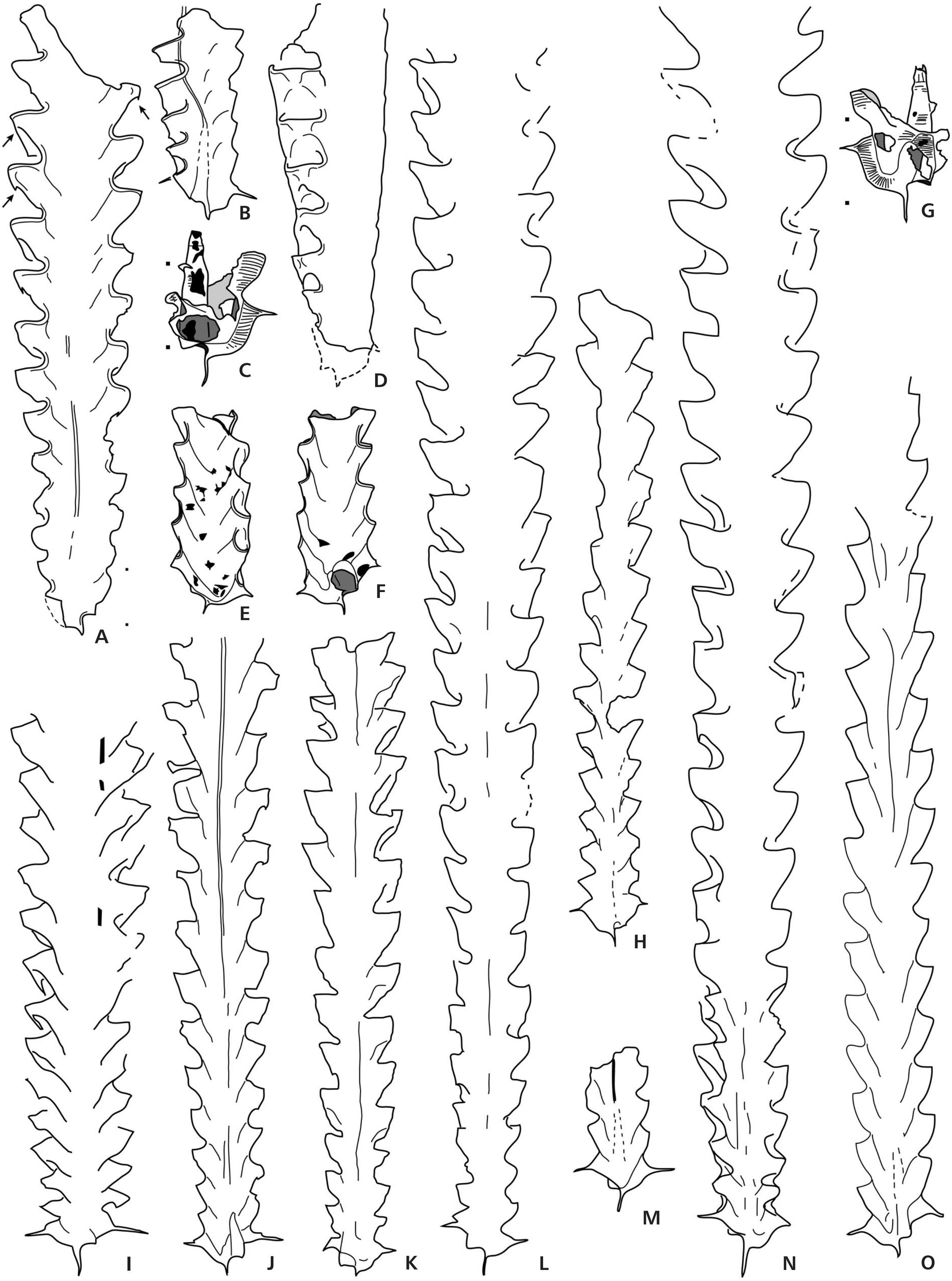
Flattened specimens display a range of thecal forms depending on their orientation and the degree of shearing that the rhabdosome experienced upon compression. Specimens in biprofile view (such as the holotype, Figs 1A, 2A but see also Skoglund 1963, pl. 4, figs 1, 5) exhibit a marked gradation from "amplexograptid" proximal thecae with nearly semicircular excavations to weakly "glyptograptid" distal thecae with open, elongate apertures and a barely visible pseudogeniculum at its apex (arrowed in Figs 1B, 2A). The uncompressed specimen illustrated in Fig. 1E and Fig. 2E, F suggests that all the thecae were in actuality relatively straight and that the "amplexograptid" appearance of the proximal thecae in compressed specimens is an artifact. Box-flattened specimens (those in which both the wide lateral surface of the rhabdosome, *i.e.*, the flat side of the box, and the lateral apertural margin, the shallower depth of the box, are visible) display a nearly orthograptid thecal shape throughout but also exhibit seemingly very shallow apertures, especially if only the thecal profile is clearly preserved (Figs 1F, G, 2B; Skoglund 1963, pl. 4, fig. 3). Subscalariform preservation is also common (Fig. 1C, D; Skoglund 1963, pl. 4, fig. 4) and these specimens, if they retain some relief, show the strong apertural thickening and its continuation with the geniculum/pseudogeniculum in proximal thecae, which is further linked by lateral thickenings to the overlying thecal aperture. This same range of preservation and thecal form is present in Tullberg's (1881) illustrations of *D. pristis*.

Proximal astogenetic structure. – The proximal structure of *D. pristis* cannot be fully determined based on the present material. Nevertheless, several useful features are evident. Th1^1 has an open, U-shaped form. The th1^2 crossing canal has a prosoblastic form (Fig. 2C) and reaches the dorsal side of the sicula very near the sicular aperture. Th2^1 arises from the left side of the th1^2 crossing canal forming a pair with its parent theca. Subsequent thecae are all upward growing and form in a simple alternate manner that is iterated through the remainder of the colony. Thus, there are only three primordial thecae and these are arranged in a fairly simple proximal structure reminiscent of that in species with a Pattern G (Mitchell 1987) primordial astogeny.

Phylogenetic Interpretation

The blunt, more or less symmetrical proximal end furnished with stout spines on the first thecal pair, the absence of antivirgellar spines, and gradient in thecal shape from vaguely "amplexograptid" with short supragenicular walls and semicircular apertures to more open "orthograptid" thecae distally all suggest affinities to *Pseudamplexograptus distichus* (Eichwald, 1840). Mitchell (1987) inferred from these similarities that *D. pristis* likely possessed a Pattern C proximal structure. This is clearly contradicted by the isolated Estonian specimens (Figs 1E, 2C, E–G). The *D. pristis* material differs from the archiclimacograptids in other ways as well. Among these differences the most striking is that the *D. pristis* specimens posses a quite simple proximal structure that is similar to that of Pattern G-bearing species of *Orthograptus* and their descendents. The aseptate colony structure with alternating thecae is also unknown among archiclimacograptids (which typically have a full median septum but in any case have a nema supported by robust crossbars) but is common among derived orthograptids such as *Rectograptus* and *Amplexograptus.* The free nema and long, straight interthecal septa that bear a prominent

Figure 2. *Camera lucida* sketches of *Diplograptus* species. Specimens A, B, E, F, H–O all x 10; C, G are x 15; paired dots near A, C, and G are 1 mm apart. • A–G – *Diplograptus pristis* (Hisinger, 1837); specimens A, B, D from the Trinucleusskiffer, near Draggabro, Dalarne, Sweden; C, E–G from Vormsi Stage, Paasvere 309 core, Estonia. A – holotype, cn 59728; obverse view showing gradient in thecal form (especially development of the geniculum and pseudogeniculum; arrowed) and strong apertural thickening visible in bi-profile view. B – cn 1001f. sketch of external mold of obverse side, box-flattened specimen. C, G – MS504b 46.0 m, Paasvere 309, reverse and observe sides, respectively, of early growth stage showing prosoblastic form of th1^2 and lateral origin of th2^1 from th1^2 protheca. E, F – MS504a 46.0 m, Paasvere 309, reverse and observe sides, respectively, of specimen showing early insertion of th2^2 interthecal septum suggesting alternation of the early thecae, note also absence of antivirgellar spines and rapid enclosure of sicula on obverse side. D – second specimen on slab with holotype, cn 59728, showing connection of thickened genicula to overlying apertures. • H – *Diplograptus nicholsoni* (Toghill, 1970), Hartfell Shales, Moffat, *D. anceps* Zone, Natural History Museum, London, Q27567, redrawn from Zalasiewicz (2000). • I – *Diplograptus rigidus* (Lee *in* Wang, 1974), Vinini Formation, Vinini Creek, Nevada, *P. pacificus* Zone, Univ. at Buffalo Cat. No. VC11.58CX. • J, K – *Diplograptus rarithecatus* (Ross & Berry, 1963), Vinini Formation, Martin Ridge, Nevada, *P. pacificus* Zone, California State Univ. at Long Beach, Cat. Nos 317 and 353, respectively. • L, N – *Diplograptus maximus* (Mu, 1945), Wufeng Formation, Yangtze Platform region, S. China, *P. pacificus* Zone, Nanjing Institute of Geology and Palaeontology, Cat. Nos 6621 (holotype) and 57003, respectively. • M, O – *Diplograptus posterus* (Koren' & Tzai *in* Apollonov *et al.* 1980), Mirny Creek, Siberia, *P. pacificus* Zone, Nos 11568/153 and 11568/155, respectively (redrawn from Apollonov *et al.* 1980).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post-apertural list are also features shared with orthograptids. To evaluate these conflicting similarities we have undertaken a cladistic analysis.

We conducted an analysis using PAUP* 4.0b10 for Macintosh (Swofford 2002) based on a data matrix of 117 discrete characters coded for 39 taxa. Eight of the characters describe sicula shape and condition, virgella development, and the geometric relation of the sicula to the stipes. Twenty characters describe proximal structure: the configuration of primordial thecae, pattern of prothecal budding, enclosure of sicula, and dicalycal position. Fourteen characters describe rhabdosome architecture: axial angle, presence or absence of cladia, scopulae, and lacinia, the form of nema support and development, distal dorsal wall shape, etc. A set of repeated characters describe thecal shape and spine development at four places along the rhabdosome: at th1^1, th1^2, th3^1, and distally. These characters plus several that assess gradients in shape and condition total to sixty-three characters. This is a large number of characters and likely includes a substantial degree of serial homology (non-independence in form arising from developmental process). To reduce the opportunity for these developmentally correlated characters to outweigh others in the analysis, we evaluated the degree of statistical correlation among the thecal character and we reduced the weights of those downstream characters in which the Pearson product moment correlation coefficient with upstream characters was significant. For example, if the apertural inclination of th3^1 was significantly correlated with that of th1^1, then the weight of the th3^1 character was adjusted. Adjusted weights were set to $1\text{-}r^2$, which is the amount of variance in the character unexplained by serial homology. Thus, 38 characters have reduced weights. Finally, twelve characters describe peridermal thinning, development of lists, *etc*. Most characters were unordered, but 32 characters in which states unambiguously imply a geometrical sequence of change (*i.e.*, the location of the first thecal bud from the upper 1/3 of the metasicula, from the middle third, or from the lower third), we used ordered states. The 39 included taxa are a broad sampling of Mid and Late Ordovician Diplograptacea *sensu* Mitchell *et al.* (2007). They include the stem-group species *Urbanekograptus retioloides* and *Pseudamplexograptus distichus*, as well as basal diplograptaceans (*e.g.*, *Hustedograptus uplandicus*) and representatives of all the derived subclades of the group. The taxa are primarily known from chemically isolated, three-dimensionally preserved specimens. A copy of the full data matrix is available from CEM upon request.

We analyzed this data matrix by heuristic search methods. Starting trees were obtained by stepwise addition with random branch addition and ten replicates per addition sequence. Branch swapping was by TBR. In this analysis 32 characters emerged as constant and 19 variable characters were parsimony uninformative, leaving 66 variable, parsimony informative characters with which to resolve the phylogeny. Repeated searches produced two equally most parsimonious trees. These have a retention index of 0.665 and rescaled consistency index of 0.299, which reflects the substantial degree of homoplasy in the character set. The strict consensus of these two MPT's place *Diplograptus pristis* as sister to derived orthograptids (*Rectograptus*, *Amplexograptus*, and their descendents), far removed from *Pseudamplexograptus* (Fig. 3). This placement is similar to the location of this species in the broader analysis of 87 taxa conducted by Mitchell *et al.* (2007), which included many archiclimacograptids and other early Diplograptina as well as a slightly different character set (characters were all unordered and did not include features of the distal thecae). In both cases, *D. pristis* nests among the orthograptids and their descendents and not with archiclimacograptids or the other species that Mitchell (1987) suggested were sister to *D. pristis*. Bootstrap analysis of the 39 taxon data set yields a 74% support level for the node uniting *D. pristis* and derived orthograptids (Fig. 3).

This relationship agrees much more closely with the known ranges of these graptolites than did Mitchell's (1987) placement of *D. pristis* among the archiclimacograptids. Like the other derived orthograptids, *D. pristis* is known from Late Ordovician (primarily Katian) strata whereas *Urbanekograptus retioloides* and *Pseudamplexograptus distichus* occur in Mid Ordovician (mid Darriwilian) strata. Thus, we conclude that the consensus of the available evidence points toward *Diplograptus* being a member of the clade of derived orthograptids.

Other *Diplograptus* species

Among the Katian and Hirnantian graptolite faunas known from around the globe there appear to be several other species that closely resemble *Diplograptus pristis* in having a blunt proximal end with a strongly outwardly inclined first thecal pair that bear stout apertural spines, a sicula with virgella only, and the unusual *D. pristis*-like thecal form (modestly to weakly geniculate proximal thecae with concave, reinforced thecal excavations that grade into nearly orthograptid thecae distally while retaining the somewhat thickened but now quite delayed pseudogeniculum). These species, like *D. pristis*, also appear to be aseptate and have a simple proximal structure (see Koren' & Tzai *in* Apollonov *et al*. 1980). Considerable research is needed to work out the possible synonymies among the named forms. Species of this group present a bewildering array of thecal forms as a consequence of the somewhat thin-walled thecae that bear a concave suprapertural wall and weak to moderately strong geniculum. Flattening, both in the form of compression and lateral shearing, induce a range of artifacts in thecal profile such that proximal thecae may appear simple and straight (orthograptid), weakly rounded (glyptograptid), or sharply geniculate (amplexograptid). This fact, combined with an intrinsically large range of variation in rates of rhabdosome widening (which is common in many Diplograptidae) has lead to the establishment of a large number of species spread among several genera. It appears to us from a preliminary assessment of the described forms that the known material of *Diplograptus* from the late Katian of the paleotropics can be grouped roughly into five taxa in addition to *D. pristis*:

1. *Diplograptus rarithecatus* (Ross & Berry, 1963);
2. *Diplograptus maximus* (Mu, 1945), which is the senior synonym of *Diplograptus ostreatus* Lin (*in* Mu *et al.*, 1993), and *Orthograptus xinanensis* Li (*in* Mu *et al.*, 1993);
3. *Diplograptus rigidus* (Lee *in* Wang, 1974), which may be the senior synonym of *Orthograptus augescens* Li (*in* Mu *et al.*, 1993), *Orthograptus mirus* Mu & Li (*in* Mu *et al.*, 1993), and *Orthograptus yangtziensis* Li (*in* Mu *et al.*, 1993);
4. *Diplograptus posterus* (Koren' & Tzai *in* Apollonov *et al.*, 1980);
5. *Diplograptus nicholsoni* (Toghill, 1970).

A complete redescription of these taxa is beyond the scope of this paper, however, some notes about the distinctive features of these species may be of value here. *D. nicholsoni* (Toghill, 1970) is a diminutive form (Fig. 2H) with closely space thecae and a narrow rhabdosome that is unlike any other *Diplograptus* species (see also Zalasiewicz 2000). It is known only from Scotland and appears to be rare even there (Toghill 1970).

Diplograptus maximus (Mu, 1945) is most similar to *D. rarithecatus* (Ross & Berry, 1963; Fig. 2L, N and 2J, K, respectively), but differs in having more widely spaced proximal thecae in comparison to colony width, which gives the proximal end in particular a protracted appearance that Mu noted in his description of the species. Both species are present in the Wufeng Formation of the Yangtze region and are also present in equivalent strata along the Cordilleran margin of North America.

Diplograptus rarithecatus (Ross & Berry, 1963) unfortunately is based on deformed material from the Phi Kappa Formation of Idaho. This collection also includes the type specimens of "*Glyptograptus*" *teretiusculus occidentalis* Ruedemann, 1947, which it closely resembles in some respects. Further study of the type specimens of these species is needed to determine their relationships.

Diplograptus posterus (Koren' & Tzai *in* Apollonov *et al.*, 1980) has even more widely space proximal thecae than *D. maximus* and tends to have a more "orthograptid" thecal profile and is narrower distally than *D. maximus* (Fig. 2M, O). Material referred to *Diplograptus rigidus* (Lee) by Mu *et al.* (1993), on the other hand (Fig. 2I), has a substantially wider proximal end than any of these species and has more strongly outwardly inclined thecae that, relative to colony width, are slightly more closely spaced. Thus, proximal ends in this species have a more blunt, dense appearance.

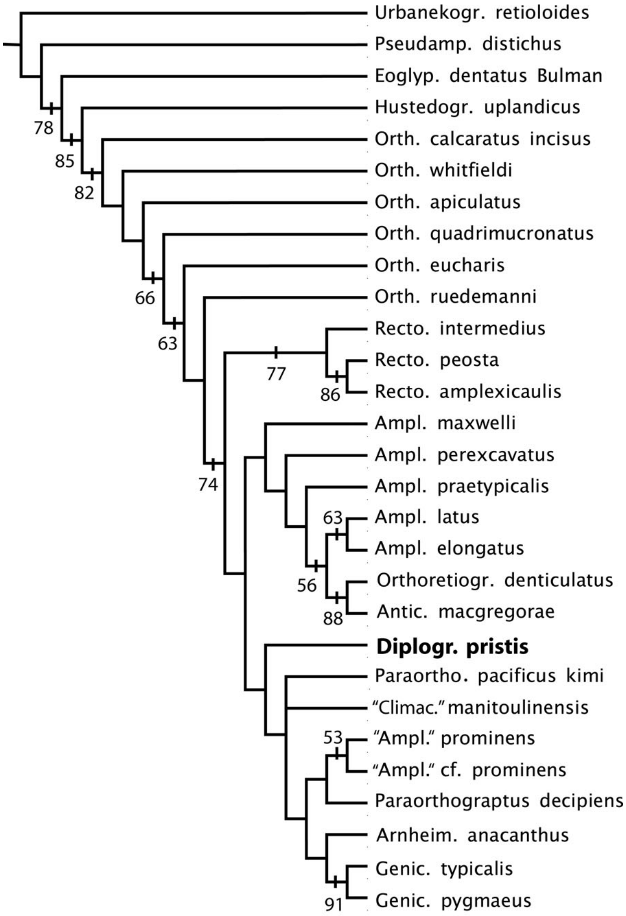

Figure 3. Cladogram depicting phylogenetic history of the Diplograptidae plus outgroup taxa *Urbanekograptus retioloides* and *Pseudamplexograptus distichus*. Bootstrap support values given for all nodes where support > 50%. *Diplograptus pristis* nests among the descendents of the common ancestor of *Rectograptus* and more derived 'amplexograptid'-like species, however, its precise location within this clade (which itself has a moderate bootstrap support value of 74%) is not well constrained. See text for further discussion.

Diplograptus pristis, which is known from the mid Katian *P. linearis* Zone in Baltica, is the first appearing of all these species. The remaining species are all confined to late Katian (*D. complanatus* to *P. pacificus* zones) and Hirnantian strata and have been described from sites that occupied a tropical location during the Late Ordovician. Whether this represents a migration into the tropics from a center or origin in mid to high latitudes requires further study. Late Katian and Hirnantian faunas are presently known from very few sites outside the paleotropics.

Conclusions

The small *Diplograptus* clade is a widespread and distinctive element in Late Ordovician faunas of the paleotropical and subtropical regions. Phylogenetic analysis indicates that *Diplograptus* is likely to be most closely related to a species ancestral to *Rectograptus* and its descendents. The precise origin of the clade is unknown but on present evidence it appears likely to lie among the still poorly understood Katian faunas of the extra-tropical world. In any event, the revised systematic position of *Diplograptus pristis* means that the Family Orthograptidae Mitchell, 1987, is a junior synonym of the Diplograptidae Lapworth, 1873. Finally, this result suggests the name Climacograptidae Frech, 1897, is the senior family group name for the clade that Mitchell (1987) referred to as the Diplograptidae.

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