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Phylogeny and Adaptive Radiation of the Neograptina (Graptoloida) During the Hirnantian Mass Extinction and Silurian Recovery

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SUMMARY: Cladistic analysis of some Hirnantian (latest Ordovician) and Rhuddanian–Aeronian (early Silurian) biserial graptolites and basal monograptids has been undertaken in order to test hypotheses of the relationships among the Neograptina ('normalograptids' and their descendents) and to provide a phylogenetic framework for understanding the early Silurian adaptive radiation of graptoloids. It is clear that Silurian graptolite faunas are dominated by two major clades, here named the superfamilies Retiolitoidea and Monograptoidea. Several other lineages whose basal relationships are unresolved, including *Normalograptus* and *Metaclimacograptus*, persisted through much of the Llandovery. The Retiolitoidea includes some taxa previously assigned to the Normalograptidae, as well as petalolithids and retiolitids. The Monograptoidea includes akidograptids, dimorphograptids, the uniserial monograptids, as well as stem taxa previously regarded as normalograptids. Both of these major clades had their origins in Late Ordovician time and began their diversification within the Hirnantian–early Rhuddanian, in step with the two main phases of the Hirnantian Mass Extinction. The Neograptina also exhibit an additional interval of accelerated turnover in the Rhuddanian during which the characteristic Silurian fauna largely replaced the Hirnantian Neograptina. One new family, Neodiplograptidae, and four new genera are described: *Avitograptus*, *Rickardsograptus*, *Korenograptus* and *Paramplexograptus*.

The pioneering work of Rickards *et al.* (1977) provided the first thorough synthesis of the early Silurian radiation of graptolites – a synthesis that lead to many hypotheses concerning the evolutionary relationships within these faunas. In addition, Dr. Rickards provided a rich legacy of morphologic and systematic work on early Silurian graptolites (e.g. Rickards 1970, 1972; Rickards & Hutt 1970; Rickards & Koren' 1974; Bulman & Rickards 1968; Hutt *et al.* 1970; Koren' & Rickards 1996, 2004). The early Silurian graptolite radiation followed from a profound evolutionary turnover during the Hirnantian mass extinction (Mitchell 1987, 1990; Melchin & Mitchell 1991; Fan and Chen 2007; Finney *et al.* 2007; Sadler *et al.* 2011). Several highly distinctive graptolite groups, most notably the monograptids but also dimorphograptids, petalolithids and retiolitids, all evolved during the early Silurian and appear to have arisen by the rapid adaptive radiation of a previously conservative lineage of species generally now referred to *Normalograptus*. Indeed, this radiation commenced *during* the Hirnantian mass extinction interval (e.g. Rickards *et al.* 1977), simultaneously with the preferential extinction of the previously dominant Ordovician clades (Chen *et al.* 2005a). A detailed reconstruction of the phylogeny of this radiation is an essential prerequisite for improving our understanding of the driving forces that determined this differential outcome and the adaptive radiation that accompanied the return to greenhouse conditions at the end of the Hirnantian glacial interval. Although our present understanding of the phylogeny of Hirnantian graptolites and their descendents is markedly different than initially envisioned, it is from the extensive foundation provided by Dr. Rickards and colleagues that this understanding arises.

Melchin (1998) was the first to attempt a phylogenetic analysis of these graptolites based on their astogenetic features. Previous work by Fortey & Cooper (1986) and Mitchell (1987) demonstrated the importance of features of the early (proximal) colonial development in the understanding of the evolutionary relationships among graptoloids; however, they dealt with Rhuddanian and younger species only superficially. This approach has been especially valuable in resolving the history of major shifts in colony structure and clade replacement (Fortey *et al.* 2005; Mitchell *et al.* 2007a; Maletz *et al.* 2009). Melchin's (1998) analysis, however, did not include characters of thecal form and his analysis of the distribution of characters was conducted manually, without the use of computer search algorithms that would ensure that all most parsimonious solutions were considered. One of the prime objectives of this study is to test the phylogenetic hypotheses proposed by Melchin (1998, text-fig. 5) using a full suite of astogenetic, rhabdosomal, and thecal characters, quantitative parsimony search methods, and tests for bootstrap support of resulting clades. In so doing, our intention is to elucidate the phylogenetic structure of this evolutionary radiation and thereby facilitate paleobiological analyses of the adaptive diversification of Silurian graptolites. We also examine the hypotheses of Mitchell (1987) and Melchin (1998) that suites of individual characters of the proximal development can be regarded to comprise coherent, recurring and readily recognizable astogenetic patterns among Hirnantian and early Silurian graptolites.

In the systematic section for this paper, we build upon the results of the phylogenetic analyses of Mitchell *et al.* (2007a) and Maletz *et al.* (2009). Maletz *et al.* (2009) employed the
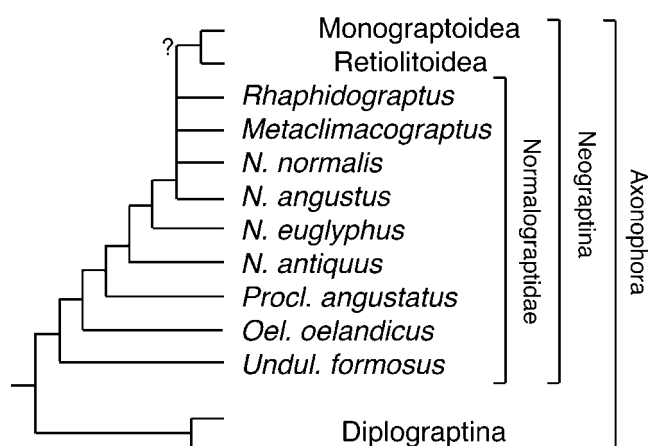
Fig. 1. Generalized cladogram showing the phylogenetic relationships between the Diplograptina and Neograptina within the Axonophora, based on Štorch *et al.* (2011, fig. 6). Also shown is the proposed relationship of the paraphyletic Family Normalograptidae to the monophyletic superfamilies Monograptoidea and Retiolitoidea, which are described and defined in the Discussion and Systematic Palaeontology sections.

name Infraorder Axonophora for a clade that includes the derived 'diplograptid' (including dicranograptids) and 'monograptid' graptolites. Like Mitchell *et al.* (2007*a*) they suggested that the Axonophora consists of two sister clades (Fig. 1). One of the two clades (the 'diplograptids') includes all of the taxa assigned by Mitchell *et al.* (2007*a*) to the Diplograptina: the Climacograptacea, Dicranograptacea, and Diplograptacea – which dominated the Late Ordovician graptolite assemblages. The second sister clade of the Axonophora (the 'monograptids', fig. 6 in Maletz *et al.* 2009) was named the Suborder Monograptina by Mitchell (1987) and Mitchell *et al.* (2007*a*). This clade includes many biserial and unibiserial forms including *Undulograptus formosus* and species of *Oelandograptus*, and *Proclimacograptus*, as well as all of the taxa assigned by Melchin (1998) to the Normalograptidae, Petalolithidae, Retiolitidae, Dimorphograptidae, and Monograptidae. Because this use of the name Monograptina refers to a group that contains many biserial genera, some of which first appeared in the early Mid Ordovician, many authors have not followed this usage, finding it confusing and contrary to nomenclatural stability. For this reason Štorch *et al.* (2011) renamed this clade the Infraorder Neograptina, sister to the Infraorder Diplograptina, within the Suborder Axonophora (Fig. 1). The basic phylogenetic structure of the Neograptina above the basal part of the tree described by Mitchell *et al.* (2007*a*) and Štorch *et al.* (2011) is the main subject of this paper. Based on the results of the analyses presented below, we identify and name the principle clades that comprise this most-derived portion of the graptolite phylogenetic tree. It is this clade that gives rise to the Silurian radiation of graptolites.

1. MATERIALS AND METHODS

1.1 Selection of Taxa

The list of taxa included in the present analyses and our sources of information pertaining to the morphology of these taxa are listed in Appendix 1. We coded a total of 58 species that span a range of thecal and rhabdosomal morphologies. The species included are representatives of most of the principal morphological species clusters of latest Ordovician and

early Silurian biserial graptolites (excluding Hirnantian survivors of the Diplograptina), as well as primitive representatives of the retiolitids and uniserial monograptids. The choice of taxa has also been driven by the phylogenetic scope of the problem at hand and the need to balance the number of taxa with the number of characters available to resolve this phylogeny. Accordingly, since the goal of this study is to resolve the relationships *among* the major Silurian clades, we have not included the many additional species that would be needed to resolve the internal relationships within some of these clades, particularly the akidograptids and dimorphograptids. For the following discussion of taxa included and coded (including Appendix 1) and in the presentation of the results of the cladistics analyses (Fig. 2), we have used the currently most widely accepted generic names for the studied taxa so that readers can easily identify these species in relation to previous literature and also so that readers can readily see how those traditional generic names are distributed on the cladogram. Indeed, the polyphyletic distribution of *Normalograptus* (for instance) is part of the rationale for several new genera. In Figure 3 we show both the currently employed generic names and also our proposed, revised classification of these taxa at the generic and higher levels. The revised classification is described in full in the systematic section below.

To elucidate the phylogeny of the dramatic radiation of early Silurian graptolites, we have particularly focused on those taxa for which we have information from chemically isolated specimens or from *in-situ* specimens that are very well preserved, often in full or partial relief. Thus, we did not include representatives of the genera *Talacastograptus*, *Victoriograptus*, *Dittograptus*, *Corbograptus*, or *Cephalograptus* because of a lack of detailed information concerning the astogeny, internal structure, and/or thecal morphology. We also excluded from the present analyses several taxa that are highly autapomorphic and thus are poorly suited to resolution of their phylogenetic position in a broad analysis of the sort conducted here. We did not include representatives of the genera *Pseudoglyptograptus* and *Clinoclimacograptus* or the related 'normalograptid', *N. scalaris*, even though their morphology is well known. These taxa show considerable and intergrading astogenetic variation in their thecal form (e.g. Bulman & Rickards 1968; Rickards 1972; Melchin 1998; Loydell & Maletz 2009), which makes unambiguous coding difficult. Whereas all species show some degree of intraspecific variation, particularly in thecal and rhabdosomal dimensions (characters not coded here), some show variation in features that we did include in the analysis and these are coded as polymorphic characters for those taxa (see Appendix 3). *Pseudoglyptograptus* in particular shows so many variable characters of thecal form, however, that coding all as polymorphic would have produced very little meaningful insight into its phylogenetic relations in the present analyses. Resolution of the relationships within the *Normalograptus-Pseudoglyptograptus-Clinoclimacograptus-Metaclimacograptus* group will require cladistic experiments using a more focused group of taxa.

The unique species *Rhaphidograptus toernquisti* presents similar difficulties and we did not include it in the final analyses presented here, although it was coded and included in test runs. We discuss its possible phylogenetic position following the presentation of results. *Neodicellograptus* is a monospecific genus that shares nearly all its features with derived species of *Metalclimacograptus* except for the possession of distally

diverging stipes (Melchin 1998), which would be an autapomorphic feature for this taxon. Thus, it too was not included in the cladistic analyses.

Finally, we did not include *Cystograptus*, which again is highly autapomorphic. The unique rhabdosome and thecae of *Cystograptus vesiculosus* and *C. penna* (e.g. Koren' & Rickards 2004) suggest that these species could not be reliably placed without including the less derived *C. ancestralis*. At this time too little is known of the proximal and internal structure of the latter species for adequate coding, unfortunately. For each of the genera not included in our analyses we discuss their possible phylogenetic position in the systematic section.

This paper provides a broad phylogenetic framework within which more detailed analyses of particular clades can be conducted using a larger number of more closely related species within each group, and documenting the full range of morphologic variation for each taxon.

1.2 Characters and coding

A description of the characters employed in the present analyses is given in Appendix 2. Our characters and character states are modelled after those employed by Mitchell *et al.* (2007a) but are modified to take account of the more limited range of variation seen in the proximal structure and different range of thecal form exhibited among normalograptids and their descendants, as compared with other Ordovician biserial graptolites. We were able to reliably distinguish a total of 55 characters. Most of these characters have two or three states but a few include as many as six states. We did not include characters of the prosicula for several reasons: all of the studied taxa in which the sicula can be seen have a complete prosicula, which does not vary in its general form; prosicular length does not seem to show any consistent pattern of variation in length among those species in which this parameter can be measured; and, the details of the prosicula are not visible in many of our studied taxa, even in some of the isolated forms, as a result of preservational circumstances.

1.3 Cladistic analysis methods

Preparation of the data matrix (Appendix 3) and analysis of trees resulting from the parsimony searches were conducted using MacClade 4.03 (Maddison & Maddison 2000). Heuristic parsimony searches and bootstrap analyses were conducted using PAUP* 4.10b (Swofford 2002). Starting trees were formed by stepwise addition of randomly selected taxa and 100 addition sequence replicates. Branch swapping was by tree-bisection-reconnection (TBR). Bootstrap analysis was conducted using 100 bootstrap replicates. In an initial analysis characters of thecal form were differentially weighted so that those features of the proximal thecae (determined at the second thecal pair) were weighted at 0.75 and those of distal thecae at 0.25. The rationale for this weighting pattern was to reduce the total weight of each thecal character to 1, equal to all characters not related to thecal form, while at the same time accounting for proximal to distal differences in thecal form. Features of the proximal thecae were weighted more heavily than those of distal thecae because the distal thecae are essentially serial homologues (although sometimes with variation) of the initial proximal form. We also analysed the same trees using 0.5 and 0.5 initial weights for the proximal and distal thecal characters and the resulting trees were identical and bootstrap support values varied only slightly.

After the initial analysis with these differentially weighted thecal characters, the character weights were then recalculated in proportion to the rescaled consistency index (RCI). The rationale for this procedure is extensively outlined by Donoghue *et al.* (2008, and references cited therein). After this second analysis the character weights were again recalculated by RCI and run again. This procedure was repeated until RCIs and tree length no longer changed between analyses, normally after a total of three or four runs.

During our experimentation we conducted several analyses with the full data set of 58 taxa and 55 characters. Although these analyses achieved a reasonably well resolved consensus tree in terms of its overall structure (Fig. 2A), there was a very large number (over 1000) of most parsimonious trees (MPTs), which are the product of the many possible arrangements of taxa at five polytomous nodes. In addition, it proved to be impossible to achieve good resolution of clades with significant bootstrap support. The essential problem relates to the fact that the number of characters available for this analysis was less than the total number of taxa we wished to study. This is a problem with graptolite phylogeny as a whole (and indeed in morphologically based phylogenetic analyses generally) that is exacerbated by the high level of homoplasy that occurs in thecal characters (e.g. Mitchell 1987; Mitchell *et al.* 2007a). In order to deal with this problem, we used the preliminary, whole-dataset tree, combined with the preliminary results of our previous analyses (Melchin *et al.* 2003, 2004, 2005) and preliminary runs using a variety of subsets of taxa to break the dataset into two segments that we analyzed separately. Donoghue *et al.* (2008) argued that in a large dataset a segmented analysis is more likely to produce reliable tree topologies for individual clades because they are less likely to be affected by spurious, inferred homologies with distantly related taxa. Our experience with analysis of Ordovician biserial taxa (e.g., Mitchell *et al.* 2007a) supports this conclusion.

The first segment consisted of all of the coded Neograptina known to occur in Hirnantian and Rhuddanian strata. This set included representatives of all of the major Silurian biserial clades that we had previously identified, except for the retiolitids *s.s.* (Fig. 2B). We added one Aeronian taxon, *Neodiplograptus magnus* (which is the type species of *Neodiplograptus*), to this analysis in order to help to resolve the relationships among biform "normalograptids" in relation to the currently accepted genera. The second segment included all of the Rhuddanian and younger taxa that formed the clade that included all of the aseptate species and their descendants (Node 4, Fig. 2C). This clade includes the taxa that Melchin (1998) included in the Petalolithidae and Retiolitidae. This analysis also included three of the species that appear to be part of the stem to that clade, as resolved in our previous studies and early trial runs (see Fig. 2C, and further discussion below).

The outgroup taxon chosen for the analyses of the whole dataset and the subset of Rhuddanian taxa was *Normalograptus angustus*. This species was chosen because compelling biostratigraphic evidence suggests that this was one of very few normalograptid taxa known to occur in mid-upper Katian strata, it possesses thecal and rhabdosomal features that appear to typify normalograptids immediately prior to and during the onset of the Hirnantian normalograptid diversification, and its morphology is relatively well known from specimens well preserved with varying degrees of relief.
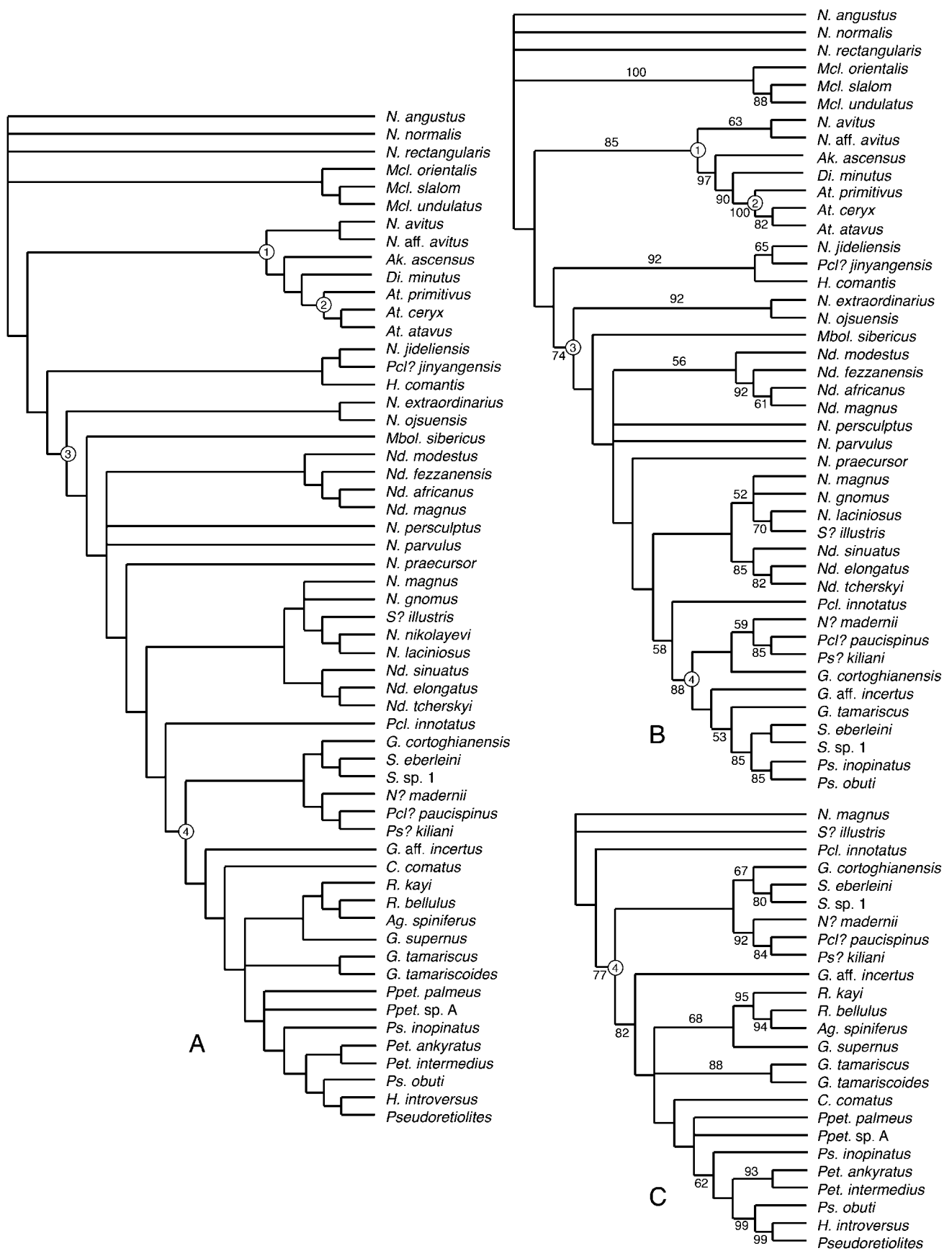
Experiments with different Upper Ordovician taxa as the outgroup yielded similar outcomes.

For the segmented analysis of the more derived clade above Node 4 (Fig. 2C) *Paraclimacograptus innotatus* was included because it is the sister taxon to that clade. In addition, *Normalograptus magnus* and ?*Sudburigraptus illustris* were selected as outgroup taxa because they are members of the next closest sister group to this clade, based on results of the analysis of the Rhuddanian taxon dataset, and because they show different thecal morphologies ('glyptograptid' and 'orthograptid') that both occur commonly among a wide range of taxa in the more derived group. *Normalograptus magnus* was previously described as a subspecies of *Glyptograptus tamariscus*, the type species of *Glyptograptus* (*G. tamariscus magnus* Churkin & Carter 1970), and ?*Sudburigraptus illustris* is one of the few septate taxa in our analysis that possesses 'orthograptid' thecae typical of many species of *Sudburigraptus*, *Pseudorthograptus*, and *Parapetalolithus*.

Bootstrap analyses were conducted on the two data subsets. The results of these analyses are here presented as a single tree (Fig. 3) in which the two segments have been merged in a way consistent with both the whole dataset tree (Fig. 2A) and the Rhuddanian subset (Fig. 2B) – all of the arrangements and bootstrap support values within the Retiolitidae (Fig. 3, see discussion below) were derived from the second segmented analysis.

2. RESULTS

The strict consensus tree resulting from the whole dataset analysis (Fig. 2A) and that of the Rhuddanian subset (Fig. 2B) reveal a basal polytomy from which several taxa emerge: those normalograptids that show simple climacograptid thecae (as in *N. normalis*, the type species of this genus); the clade that includes species of *Metaclimacograptus*; and a clade consisting of all other taxa in the dataset. However, the node that unites this last clade had less than 50% support in the bootstrap analysis of the Rhuddanian taxa. Likewise, the next higher node, which unites the small clade that includes *Hirsutograptus comantis* with the larger clade containing all other taxa above that node, also has low bootstrap support (<50%). Therefore, the branching relationships among the three clades that include *Atavograptus* (the earliest monograptid), *Hirsutograptus*, and *Metaclimacograptus*, respectively, cannot be considered to be confidently resolved in this analysis and are shown as emerging from a large basal polytomy in our composite bootstrap tree (Fig. 3).

The strict consensus trees for the whole dataset (Fig. 2A) and the Rhuddanian subset (Fig. 2B) show a well-resolved,

pectinate branching relationship among the paraphyletic group of taxa between *N. extraordinarius* and *Pcl. innotatus*. Many of the nodes in this portion of the tree, however, show <50% bootstrap support and we have collapsed those to a polytomy on our bootstrap tree (Node 3, Fig. 3). From this polytomy there emerge several small clades with variable bootstrap support, a number of individual taxa previously assigned to *Normalograptus*, as well as a relatively weakly supported clade (58% bootstrap support) that unites *P. innotatus* and the clade that emerges from Node 4, which we will hereafter refer to as the Retiolitidae (see Discussion below). In the analysis of the Rhuddanian subset, the clade Retiolitidae showed very strong bootstrap support (88%, Node 4, Fig. 3). The strict consensus trees obtained from the full dataset and from the retiolitid segment analysis show almost identical relationships among the taxa in the Retiolitidae. The only difference is the position of *Comograptus comatus* within the branching succession. The arrangement of the retiolitid taxa in the Rhuddanian subset analysis is significantly different. This suggests that the Aeronian taxa included in the other two segmented analyses helped to distinguish homologies from homoplasies and character polarity within clade Retiolitidae in relation to the more distantly related, non-retiolitid taxa.

As is the case for the other groups of taxa discussed above, a number of the nodes identified in the strict consensus trees for the retiolitid clade have less than 50% support in the bootstrap analysis, so the base of the clade is also marked by a succession of two polytomies on our composite bootstrap tree (Fig. 3).

3. DISCUSSION

3.1 Phylogeny and Classification

Two of the branches that emerge from the basal polytomy on our composite bootstrap tree (Fig. 3) lead to major clades that dominate graptolite faunas of the Silurian: these clades are here named the Monograptoidea (Node 1), and the Retiolitoidea (Node 3; see systematic section for formal definition of these taxa). The clade Monograptoidea has 85% bootstrap support and includes the uniserial monograptids (Pattern M), *Dimorphograptus* (Pattern J'), *Akidograptus* (Pattern J) and stem species previously assigned to *Normalograptus* or *Glyptograptus*, but here regarded as members of a new genus *Avitograptus*. In keeping with long-standing systematic practice, we propose that the Family Monograptidae should be the clade that includes only fully uniserial scandent species. At the present time, we do not believe that there are sufficient phylogenetic grounds for subdivision of distinct families Dimorphograptidae and Akidograptidae (Li & Ge 1981). We refer to the taxa within the Superfamily Monograptoidea that

Fig. 2. (**A**) Strict consensus of 1115 equally parsimonious trees resulting from the cladistic analysis by heuristic search of the whole taxon set (excluding *Rhaphidograptus toernquisti*), rooted using *Normalograptus angustus* as the outgroup and character weights proportional to the rescaled consistency index of each character. Tree length – 79.08; consistency index – 0.646; rescaled consistency index – 0.544; homoplasy index – 0.516. (**B**) Strict consensus of 40 equally parsimonious trees resulting from the cladistic analysis by heuristic search of the taxon set consisting only of Hirnantian and Rhuddanian taxa plus *Neodiplograptus magnus* (but excluding *Rhaphidograptus toernquisti*), rooted using *Normalograptus angustus* as the outgroup and character weights proportional to the rescaled consistency index of each character. Tree length – 69.86; overall consistency index – 0.722; overall rescaled consistency index – 0.612; overall homoplasy index – 0.451. (**C**) Strict consensus of 6 equally parsimonious trees resulting from the cladistic analysis by heuristic search of the taxon set consisting only of petalolithid-retiolitid (aseptate) taxa plus *Paraclimacograptus innotatus*, and *Normalograptus magnus* and ?*Sudburigraptus illustris* as outgroup taxa. Character weights proportional to the rescaled consistency index of each character. Tree length – 55.11; overall consistency index – 0.684; overall rescaled consistency index – 0.533; overall homoplasy index – 0.390. Numbers on branches show bootstrap support values for each node that has greater than 50% bootstrap support.
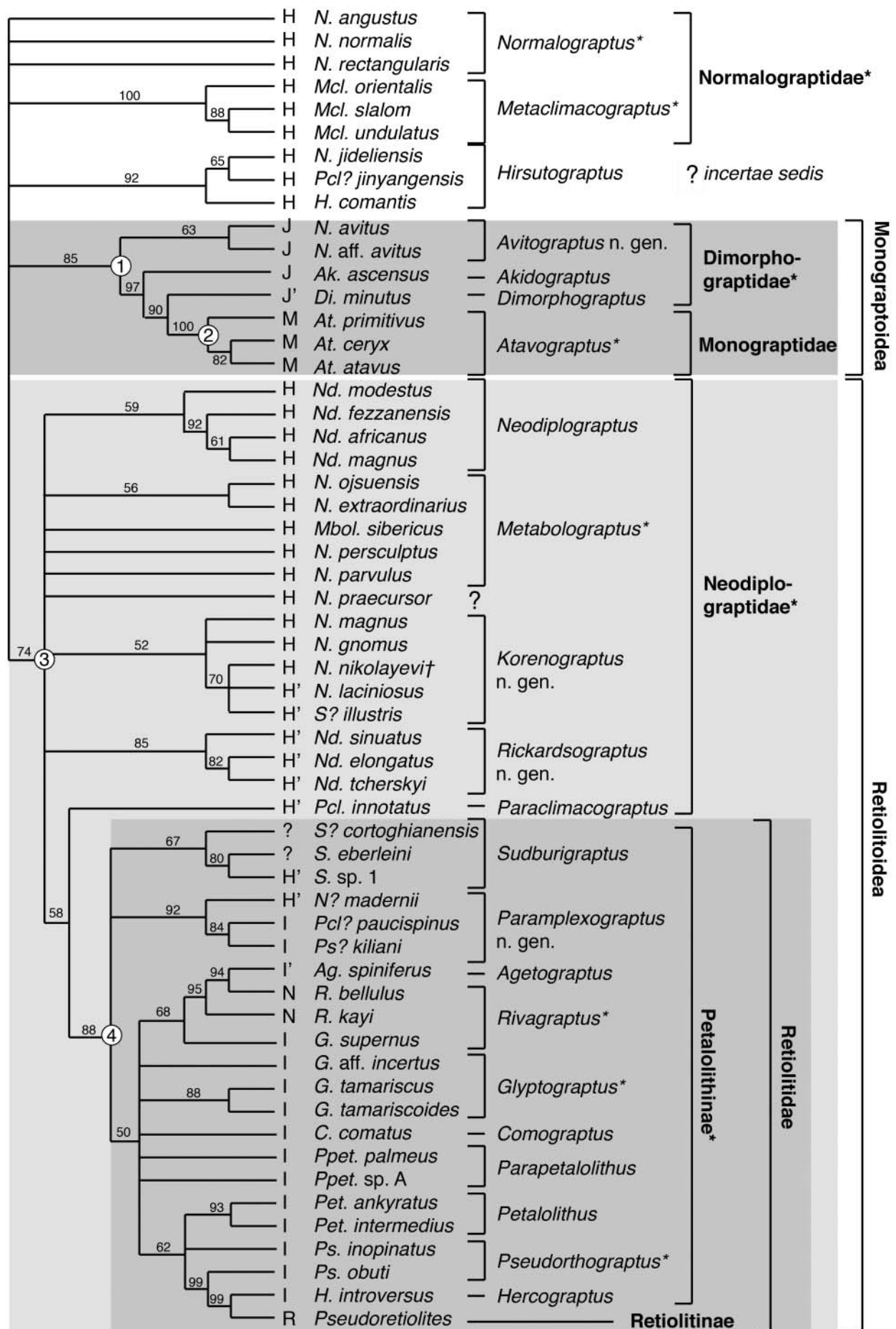
are stem to the Monograptidae as a paraphyletic Family Dimorphograptidae (Fig. 3). Further analysis will be required to determine if the akidograptids and dimorphograptids are paraphyletic or monophyletic groups arising from this stem lineage.

The clade Retiolitoidea has 74% bootstrap support (Node 3) and includes nested within it another well-supported clade, the Retiolitidae (Fig. 3, Node 4, 88% bootstrap support). The latter consists of aseptate (mostly Pattern I), fully biserial taxa with complete fusellar walls, which we include in the paraphyletic Petalolithinae, a group that forms a stem to the derived Retiolitinae. The Retiolitinae possess a thecal framework of lists with reduced thecal walls and includes both retiolitines and plectograptines (e.g. Lenz & Melchin 1997). *Pseudorthograptus obuti* occupies a position high in the stem to the Petalolithinae but reportedly possesses a full median septum distally (Koren' & Rickards 1996). That condition, therefore, must be a homoplasy.

Also within the Retiolitoidea is a series of taxa that had previously been variously assigned to *Normalograptus*, *Neodiplograptus*, *Sudburigraptus*, *Persculptograptus*, *Metabolograptus* and *Paraclimacograptus* that collectively are stem to the Retiolitidae (Fig. 3).We refer to this stem group as a new paraphyletic Family Neodiplograptidae within the Retiolitoidea. For reasons described in the systematic section below, we think that *Hirsutograptus* should not be included within the Retiolitoidea, even though it appears at the base of this clade in the strict consensus trees (Fig. 2A, B).

Our results support the hypothesis of Melchin (1998, text-fig. 5) that the combined Dimorphograptidae-Monograptidae (our Monograptoidea) and the combined Petalolithidae-Retiolitidae (our Retiolitidae) each form a clade that arose from 'normalograptid' ancestors. However, Melchin proposed that the clade Petalolithidae-Retiolitidae and the clade Dimorphograptidae-Monograptidae together formed a single larger clade with a shared a common ancestry from one normalograptid stem lineage. He suggested that the shortening of the downward growth of the first theca and the ancora-like structures seen in akidograptids and retiolitids and some petalolithids were uniting synapomorphies for this large clade. Our results suggest that these characters were independently derived in these two major groups, and that each of these two clades arose from different stem lineages each consisting of taxa previously regarded as normalograptids (Fig. 3) – *Avitograptus* for the Monograptoidea and the Neodiplograptidae for the Retiolitidae.

At the present time, we consider that it would be premature to refer the other clades that emerge from the basal polytomy of Fig. 3 to any taxon above the genus level. Koren' & Rickards (1996) named the Family Metaclimacograptidae, consisting only of the genus *Metaclimacograptus*. Results of the Melchin (1998) analysis suggest that *Neodicellograptus* belongs within this clade as well. Given that the phylogenetic relationships at the base of our tree remain unresolved, as is

the position of the morphologically similar genus *Clinoclimacograptus*, we do not favour the recognition of this small family at this time. Although there is currently no phylogenetic basis for recognition of a monophyletic group that could be referred to the Family Normalograptidae, we follow Štorch *et al*. (2011) and place all 'normalograptid' taxa outside of either the Monograptoidea or Retiolitoidea within the paraphyletic Family Normalograptidae.

Our present results support the suggestion by Melchin (1998) that the unibiserial (or 'dimorphograptid') condition in graptolites, with one or more uniserial proximal thecae followed by a biserial rhabdosome, was independently derived in at least three different graptolite groups. *Dimorphograptus s.s.*, which is stem to the monograptids, shows the derived features of *Akidograptus* (long sicula, short descending $th1^1$ that turns upward before reaching the sicular aperture) while retaining the dicalycal theca 2^1 and septate rhabdosome. In contrast, *Agetograptus* is characterized by a very short sicula and $th1^1$ that turns upward below the sicular aperture and an aspetate rhabdosome, similar to *Rivagraptus*. As noted above, the placement of *Rhaphidograptus toernquisti* in our analysis was inconsistent, depending on the details of other taxa included and character weighting. However, its most common placement in the latest runs was either directly from the basal polytomy or else from a separate node just below the base of the clade here referred to as the Retiolitoidea. Observations made by Hutt *et al*. (1970) suggest that it achieved its uniserial first theca by truncation of $th1^2$ rather than redirection as observed in *Dimorphograptus* and *Agetograptus*.

We have not included the unibiserial taxon referred to by Koren' & Rickards (1996) as *Pseudorthograptus (Dimorphograptoides) physophora* in our analysis. This species appears to be closely similar in many aspects of its thecal and rhabdosomal form to *Pseudorthograptus obuti*, except for a uniserial first theca. The growth pattern that resulted in this proximal development pattern is not clear, but this species may represent yet another independent origin for the unibiserial rhabdosome.

3.2 Proximal Development Patterns

As noted above, early attempts at phylogenetic classification of biserial graptolites relied heavily or exclusively on characters of early astogeny. Those studies proposed that suites of characters commonly co-occurred to form distinctive patterns of proximal development. Both Mitchell (1987) and Melchin (1998) used the distribution of these patterns as their primary basis for phylogenetic analysis and they named the patterns using letters (A–K, M, R). Mitchell *et al*. (2007a) showed that the individual characters that comprise these patterns do not always occur as coordinated entities, however, and that some homoplasy occurs among the characters that define these patterns. In this study we update the descriptions of those astogenetic patterns that occur among Hirnantian and younger Neograptina, and re-examine their distribution in

Fig. 3. Composite bootstrap support tree derived by combination of results from the bootstrap analysis of the Rhuddanian taxon set and that of the petalolithid–retiolitid taxon sets, joined in a manner consistent with the results of the whole taxon data set. All nodes that were not supported by both the strict consensus tree and >50% bootstrap support are collapsed to polytomies. Numbers on branches show bootstrap support values for each node. Also shown is our proposed grouping of taxa at the levels of genera, subfamily, family and superfamily. Letters at the tips of branches before species names refer to the proximal development pattern of that species. See text for discussion. Asterisks indicate taxa that are known or likely to be paraphyletic. [†]*Normalograptus nikolayevi* was placed on the tree based on its position in previous trial analyses.
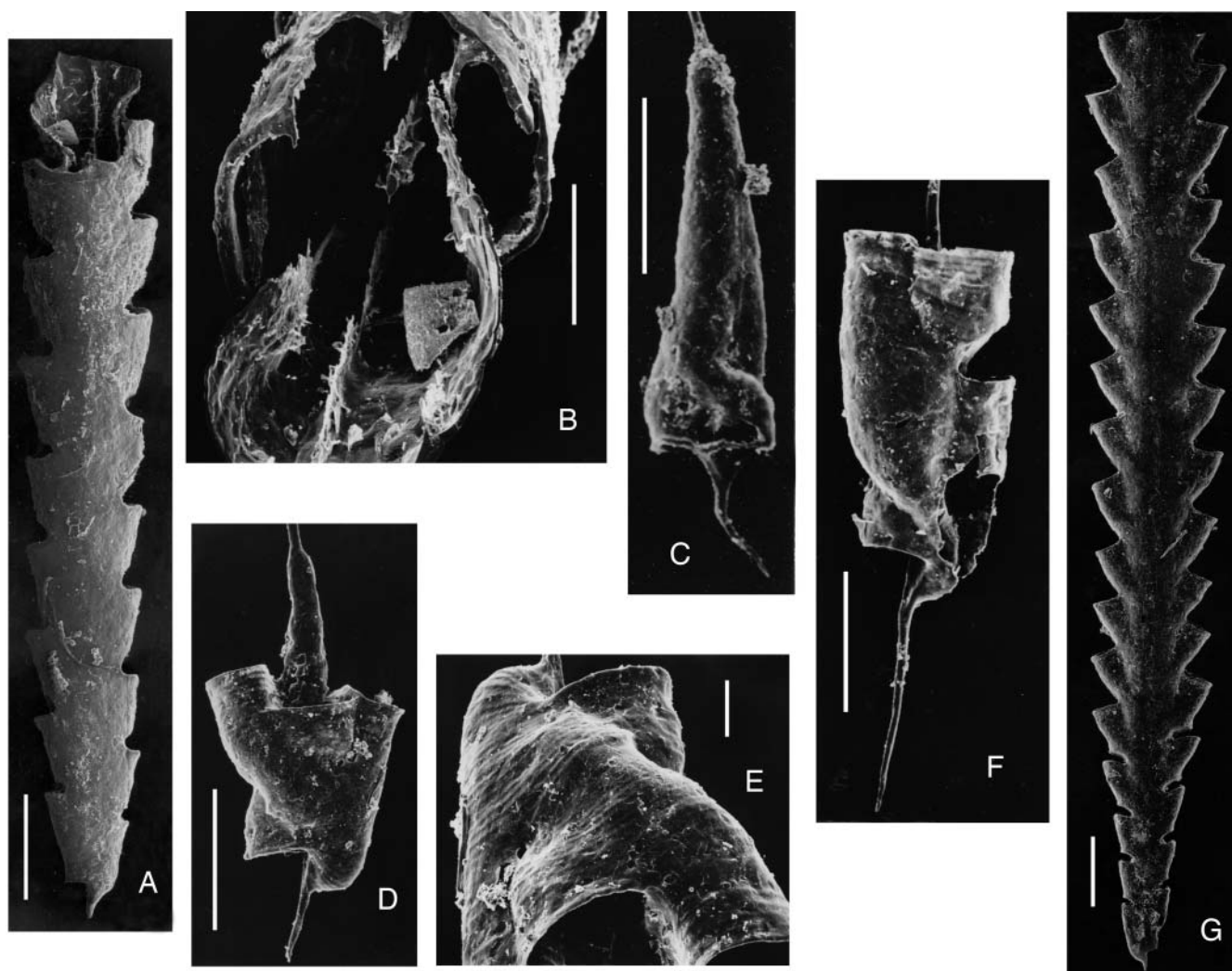
Fig. 4. Scanning electron microscope images. (**A–E**) *Korenograptus gnomus* (Churkin & Carter 1970), Cape Manning, Nunavut, Canada, *c.* 50–52 m above base of section as shown in Melchin & Holmden 2006, fig. 2; (**A**) mature rhabdosome; (**B**) distal end of (a) showing remnants of full median septum attached to obverse and reverse walls and nema, GSC135118; (**C**) sicula showing early downward growth of th1^1 with two terminal foramina separated by a list, GSC104820; (**D**) early growth stage specimen showing origin of th2^1 just above the base of th1^2, (**E**) oblique distal view of (d) showing line of truncation of fusellae at point of differentiation of th1^2, GSC135119; (**F–G**) *Rickardsograptus tcherskyi* (Obut & Sobolevskaya in Obut *et al.* 1967), Cape Manning, Nunavut, Canada, *c.* 50–55 m above base of section as shown in Melchin & Holmden 2006, fig. 2; (**F**) early growth stage showing delayed origin of th2^1 near aperture of th1^1, GSC104843; (**G**) mature rhabdosome, GSC135120. Scale bars: A, G, 1 mm; B, D, F, 0.5 mm; C, E, 0.1 mm. GSC, Geological Survey of Canada.

light of our phylogenetic analyses (Fig. 3). The descriptions of most of the patterns are based mainly on Melchin (1998), although some new observations are incorporated, based on observations made using infrared microscopy, and one new pattern is described. References are made to specific characters and states as described in Appendix 2: for example, Ch 11: 0 refers to character 11, state 0. The patterns described by Mitchell (1987) were renamed after characteristic taxa bearing those patterns by Koren' & Rickards (1996) and those names are included parenthetically here.

Pattern H (normalis Pattern). Sicula is conical with complete prosicula (Fig. 4C). Sicular aperture bears a straight downward-grown virgella, but not paired antivirgellar spines like those seen in the Diplograptoidea (=Diplograptacea of Mitchell *et al.* 2007*a*, who followed the rank endings employed by Bulman 1970, rather than current Linnaean convention). There are uncommon cases of taxa with other spines grown from the sicular rim. Th1^1 normally grows downward for 0.4 mm or more (Ch 11: 0) and turns upward below the sicular aperture (Ch 14: 0). Downward-grown prothecal tube terminates with two foramina (Figs 4C, 5A, B, H, I; Melchin 1998, pl. 1, fig. 5, pl. 3, fig. 3), one opening downward for th1^1 metathecae, and the other opening to the reverse side for growth of th1^2 (Ch 12: 0). Th1^2 grows straight or diagonally across the sicular aperture before turning upward (Ch 15: 0). The line of differentiation of th1^2 from th1^1 is marked by an abrupt line of condensed or truncated fusellae (Ch 13: 0 or 13: 1; Fig. 4E; Melchin 1998, text-fig. 4B, pl. 3, fig. 10), which is often manifest on the outer rhabdosomal surface as a line of change in relief (Fig. 6A). Th2^1 originates just above the base of th1^2 (Ch 16: 0; Fig. 4D, 5A, Melchin 1998, pl. 1, figs 3, 9). The majority of Pattern H species are septate (Fig. 4B) and th2^1 or some later theca is dicalycal (Ch10: 0). Among known Silurian Pattern H species where the dicalycal theca is delayed the proximal portion of the rhabdosome possesses a partial median septum on the obverse side of the rhabdosome that originates at the sicula (Ch 20: 0).

Pattern H'. Similar to Pattern H except that th1^2 shows a significant interval of upward growth before the point of differentiation of th2^1 (Ch 16: 1), usually near the level of the aperture of th1^1 (Fig. 4F, Melchin 1998, pl. 3, figs 7–9), although in a few species, this point is below the th1^1 aperture (Fig. 5B) and the distinction from Pattern H is subtle and sometimes difficult to discern. A few derived Pattern H' species show gradual divergence of th1^1 and th1^2 with interfingering fusellae (Ch 13: 2), e.g. *Paraclimacograptus innotatus* (Russel *et al.* 2000, fig. 1.5). Other species, such as *Paramplexograptus madernii* and *Sudburigraptus* sp. 1 *sensu* Koren' & Rickards (2004), show a complete loss of the median septum and dicalycal theca (Ch 10: 1; Fig. 5B, H). Thus, these characters, which Melchin (1998) regarded as collectively defining Pattern I, appear to have arisen separately during the evolutionary transition from Pattern H to Pattern I development.

Our results also suggest that the transition from Pattern H to H' may have taken place independently in several different clades within the Retiolitoidea, although considerable uncertainty remains regarding both the branching patterns within this group and the state of this character (Ch. 16) in some of our studied taxa.

Pattern I (tamariscus Pattern). Sicula is conical with complete prosicula and initially straight virgella and no paired antivirgellar spines. There are uncommon cases of taxa with other spines grown from the sicular rim (*Comograptus*, see Melchin 1998). Th1^1 normally grew downward for 0.3 mm or less (Ch 11: 1) and turned upward below the sicular aperture (Ch 14: 0). Downward-grown prothecal tube terminates with one foramen (Fig. 5D, F, Melchin 1998, pl. 4, figs 4, 12, pl. 5, figs 3, 10, pl.7, fig. 3), from which the th1^1 metatheca emerges. Th1^2 originates by divergence from the early, upward-grown part of th1^1 (Ch 12: 1), diagonally across the reverse side of the sicula (Ch 15: 0). The zone of divergence is often marked by interfingering fusellae (Ch 13: 2; Fig. 5J, Melchin 1998, pl. 5, fig. 7). There is normally no dicalycal theca (Ch 10: 1), although some derived forms (e.g. *Pseudorthograptus obuti*) appear to possess a full median septum distally, implying the presence of a distal dicalycal theca. The apex of sicula is free (Ch 20: 1; Melchin 1998, pl. 5, fig. 11) or marginal (Ch 20: 2; Melchin 1998, pl. 5, fig. 6). The nema may be internal and free (Ch 21: 4; Melchin, 1998, pl. 5, fig. 12), attached to the bases of the interthecal septa (Ch 21: 5; Fig. 5B, C, 6H, I, L–N), marginal (obverse side and attached to a narrow, partial median septum (Ch 21:1; Fig. 5E, Melchin 1998, pl. 4, fig. 2), or embedded in the obverse wall (Ch 21: 2; Melchin 1998, pl. 5, figs 5–7). Our phylogenetic analysis suggests that the single character that most precisedly defines this pattern, a descending th1^1 with only a single terminal foramen, may be derived independently more than once within the Retiolitidae (Fig. 3).

Pattern I'. Similar to Pattern I but the growth of the second theca is redirected above the first theca resulting in a uniserial first theca (Ch 15: 1; Melchin 1998, pl. 7, figs 2, 4, 5).

Pattern J (ascensus Pattern). Relatively long, straight or dorsally curved sicula with a complete prosicula and virgella, but no other apertural spines. The first theca has grown down to a point at or above the sicular aperture and then turns upward (Ch 14: 1 or 14: 2; Fig. 6B, C, G). It then grows upward for an interval before the second theca emerges from its dorsal wall (Ch 12: 2), apparently along a line of abrupt fusellar transition (suggesting condensed or truncated fusellae, Williams 1983, text-fig. 9f; Ch 13: 1). Th1^2 then grows across

the sicular aperture (Ch 15: 0). The fact that th1^2 emerges from the upward-grown part of th1^1 suggests that the downward grown portion of th1^1 terminates with a single foramen. No isolated specimens of Pattern J species are available, however, for us to confirm this suggestion. Th2^1 is dicalycal (Ch 10: 0) and there is a complete median septum.

Pattern J'. Similar to Pattern J but the growth of the second theca and usually additional thecae are redirected above the first theca resulting in a uniserial proximal end (Ch 15: 1; Fig. 6J). Biserial portion is septate.

*Pattern M (*ceryx *Pattern)*. First theca has no downward-grown portion (Ch 11: 2), but turns upward from its point of budding above the sicular aperture (Ch 14: 2), in some cases with a very short interval of outward growth. There is no dicalyc (Ch 10: 1), rhabdosome is uniserial throughout and the nema is normally embedded in dorsal wall (Ch 21: 3).

Pattern N (new). Very short sicula (*c*. 0.5 mm long) is conical with complete prosicula and initially straight virgella and no paired antivirgellar spines. Th1^1 has no downward-grown tube, but emerges from the sicular aperture, which shows a slight lateral flare (Ch 11: 2; Fig. 5J, K, M). Note that Melchin (1998, pl. 6, fig. 7) misinterpreted this slightly flared sicular aperture as a short downward-grown thecal tube. Taxa possessing this pattern also show early growth of the first thecal pair that almost fully encloses the sicula (Ch 3: 1; Fig. 5J, L). Th1^2 originates by divergence from the early, upward-grown part of th1^1 (Ch 12: 1), across the reverse side of the sicula (Ch 15: 0). The zone of divergence is marked by interfingering fusellae (Ch 13: 2; Fig. 5J). There is no dicalycal theca (Ch 10: 1). Apex of sicula is free (Ch 20: 1) and the nema is internal and free (Ch 21: 4; Fig. 5J, L, Melchin 1998, pl. 6, figs 9, 13).

Our results suggest that this pattern is derived from Pattern I by a change in the point of origin of th1^1, as well as the shortening of the sicula, which is almost completely enclosed by the growth of the first thecal pair. The origin of the first theca from the sicular aperture is unique for this group among biserial graptolites and is similar to the origin of sicular cladia in some derived monograptids, although in the latter case the emerging theca incorporates a pronounced sicular apertural spine as an axis for growth (Urbanek 1997).

4. HIRNANTIAN AND RHUDDANIAN RADIATION OF THE NEOGRAPTINA

We can employ the phylogenetic relationships revealed by the current analysis to explore the history of evolutionary radiation of the Neograpta. Melchin & Mitchell (1991) pointed out that the composition of graptolite communities underwent striking turnover during the Hirnantian mass extinction and recent studies (e.g., Underwood 1998; Chen *et al.* 2005*a,b*; Finney *et al.* 2007; Loydell 2007; Mitchell *et al.* 2007*b*; Štorch *et al.* 2011) reveal considerable detail about the timing and composition of this turnover event. We have constructed an evolutionary tree for the Neograptina (Fig. 7) based on our phylogenetic analyses and the known stratigraphic ranges of these graptolites. We also illustrate tentative hypotheses for the evolutionary position of a number of biserial genera (except derived retiolitines; see systematic descriptions for discussions of placement of these genera within our higher taxa) that we did not include in our present cladistic analyses. This evolutionary tree reveals a three-phased radiation of the Neograptina that proceeded in step with the Hirnantian mass extinction
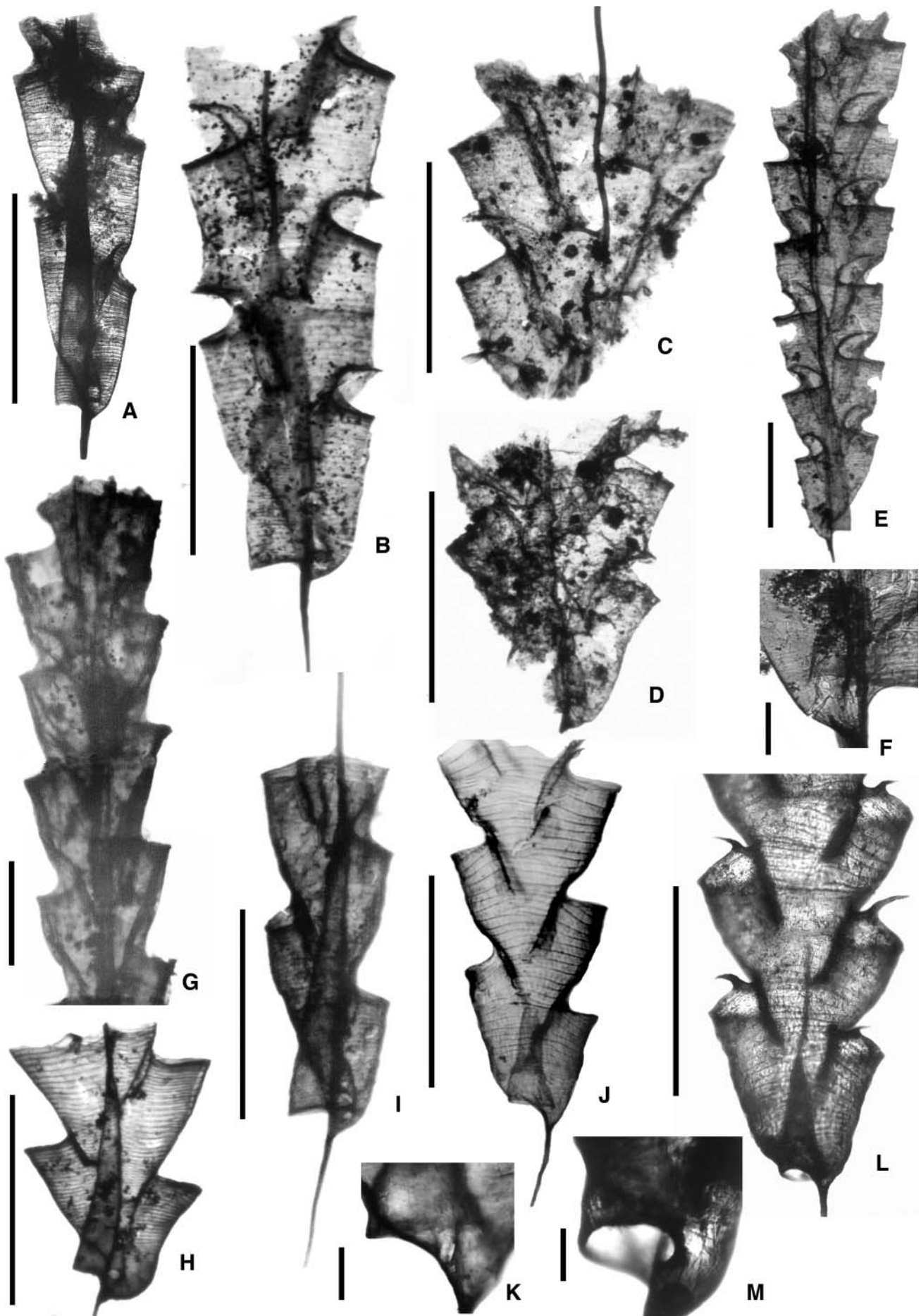
(HME) and continued turnover during the mid Rhuddanian: (1) an early radiation of Neograptina at the base of the Hirnantian coincident with the first phase of the HME; (2) a second radiation starting in the post-glacial, latest Hirnantian, coincident with the second phase of the HME and the following early Silurian recovery; and (3) an interval of accelerated turnover in the mid Rhuddanian, which ushered in the characteristic assemblage of taxa that we associate with the Silurian graptolite faunas.

The Ordovician Neograptina were represented in the late Katian primarily by a small number of species of *Normalograptus* (Goldman *et al.* 2011). They were joined by the archaic neodiplograptids *Neodiplograptus charis* and *Metabolograptus ojsuensis* in the very latest Katian and at the base of the Hirnantian by *Metabolograptus extraordinarius*. The precise biogeographic and phylogenetic origins of these neodiplograptids is unclear but present evidence suggests that they migrated into the paleotropics from mid to high latitudes during the onset of the first phase of the Hirnantian glaciation (see the recent summary by Goldman *et al.* 2011).

The early species of Retiolitoidea became abundant in the early Hirnantian and, as the previously dominant Diplograptina experienced preferential extinction (Chen *et al.* 2005a), underwent a modest radiation that produced a series of morphologically distinct lineages recognized here as seven different genera: *Neodiplograptus*, *Metabolograptus*, *Korenograptus*, *Paraclimacograptus*, *Sudburigraptus*, *Paramplexograptus*, and *Glyptograptus*. The evolutionary origin of several of these groups, based on our phylogenetic analysis and *Metabolograptus persculptus* Zone occurrences of the early petalolithine *Paramplexograptus madernii*, appears to have taken place within the mid to late Hirnantian (Fig. 7).

The radiation of the Monograptoidea was slightly delayed compared to the Retiolitoidea and appears to have commenced during the post-glacial sea level rise, triggered perhaps by conditions associated with the widespread return to black shales that characterize the later half of the *Mb. persculptus* Zone and the early *A. ascensus* Zone. The stem monograptids, the first true monograptids (*Atavograptus*), and also *Hirsutograptus*, *Metaclimacograptus* all appear in this interval. Koren' & Bjerreskov (1999) referred to this initial interval of monograptid radiation as the generative phase. These events also coincide with the final disappearance of nearly a dozen Diplograptina lineages, among them species of *Dicellograptus*, *Appendispinograptus*, *Anticostia*, *Rectograptus*, and *Phormograptus* that evidently persisted as sparse populations (and are now recovered only as rare individuals in large collections) through the entire Hirnantian glacial episode (Chen *et al.* 2005a; Mitchell *et al.* 2007b; Štorch *et al.* 2011).

Early lineages within the Retiolitoidea and Monograptoidea experienced high turnover rates at the end of the *P. acuminatus* Zone and into the *A. atavus* Zone, both at the generic level (Fig. 7) and at the species level (Melchin *et al.* 1998; Chen *et al.* 2005a). The Retiolitidae (including the petalolithines) and Monograptidae began their primary diversification in this third wave of radiation and generally replace the early members of the Retiolitoidea and Monograptoidea that had appeared during the Hirnantian. Koren' and Bjerreskov (1999) referred to this latter interval of monograptid diversification as the radiative phase. Thus, it was this third wave of neograpine radiation, some 4 million years after the end of the HME that produced the characteristic graptolite faunas of the Silurian to early Devonian. Although for many invertebrate clades, the HME produced only minor changes in clade abundance and composition, the HME produced a turnover in graptolite faunas that in terms of clade structure is perhaps comparable to the replacement of non-avian dinosaurs by birds at the end of the Maastrichtian.

5. SYSTEMATIC PALAEONTOLOGY

We have presented character-based diagnoses for genera herein. Some of these diagnoses are not substantively changed from those of Melchin (1998), although they may be paraphrased more concisely here. Those genera with substantively modified diagnoses are noted as emended herein. Higher taxa are defined on the basis of clade branching relationships, rather than diagnosed on morphological criteria. Characteristic synapomorphies are described in the remarks for each higher taxon.

Suborder AXONOPHORA Frech, 1897

Remarks. This taxon is used here in the sense of Maletz *et al.* (2009) and Štorch *et al.* (2011) encompassing all of the taxa assigned by Mitchell *et al.* (2007a) to the Diplograptina and Monograptina.

Infraorder NEOGRAPTINA Štorch, Mitchell, Finney & Melchin, 2011

Definition. The Neograptina is the total clade comprising all species sharing a more recent common ancestor with *Monograptus priodon* than with *Diplograptus pristis*.

Remarks. For a full discussion of this clade see Štorch *et al.* (2011). This clade is similar in concept to the Monograptina as defined by Mitchell *et al.* (2007a). For reasons noted above and

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Fig. 5. Transmitted infrared microscopy images. (**A**) ?*Metabolograptus praecursor* (Koren' & Rickards 2004), topotype (see Koren' & Rickards 2004), GSC135121; (**B**) *Paramplexograptus madernii* (Koren' & Mikhaylova 1980), Cape Manning, Nunavut, Canada, 2.1–2.3 m above base of section as shown in Melchin & Holmden 2006, fig. 2, GSC135122; (**C, D**) *Paramplexograptus paucispinus* (Li 1982), Cape Phillips South, Nunavut, Canada, 31.3–31.4 m above base of section as shown in Melchin & Holmden 2006, fig. 2, GSC135123; (**E, F**) *Glyptograptus incertus* (Elles & Wood 1907), Cape Manning, Nunavut, Canada, 44.1 m above base of section as shown in Melchin & Holmden 2006, fig. 2, GSC135124; (**G, I**) *Korenograptus magnus* (Churkin & Carter 1970), Cape Manning, Nunavut, Canada, 29.2 m above base of section as shown in Melchin & Holmden 2006, fig. 2, G, GSC135125, I, GSC135126; (**H**) *Sudburigraptus* sp. 1 *sensu* Koren' & Rickards 2004, topotype (see Koren' & Rickards 2004), GSC135127; (**J, K**) *Rivagraptus kayi* (Churkin & Carter 1970). (**K**) enlargement of proximal end showing origin of th1[1] from sicular aperture, Cape Manning, Nunavut, Canada, 54.5 m above base of section as shown in Melchin & Holmden 2006, fig. 2, GSC135128; (**L, M**) *Rivagraptus bellulus* (Törnquist 1890). (**M**) enlargement of proximal end showing origin of th1[1] from sicular aperture, both specimens from Cape Manning, Nunavut, Canada, 53.3 m above base of section as shown in Melchin & Holmden 2006, fig. 2, GSC135129, GSC135130. All scale bars 1 mm, except (**F, K, M**) 100 μm. GSC, Geological Survey of Canada.
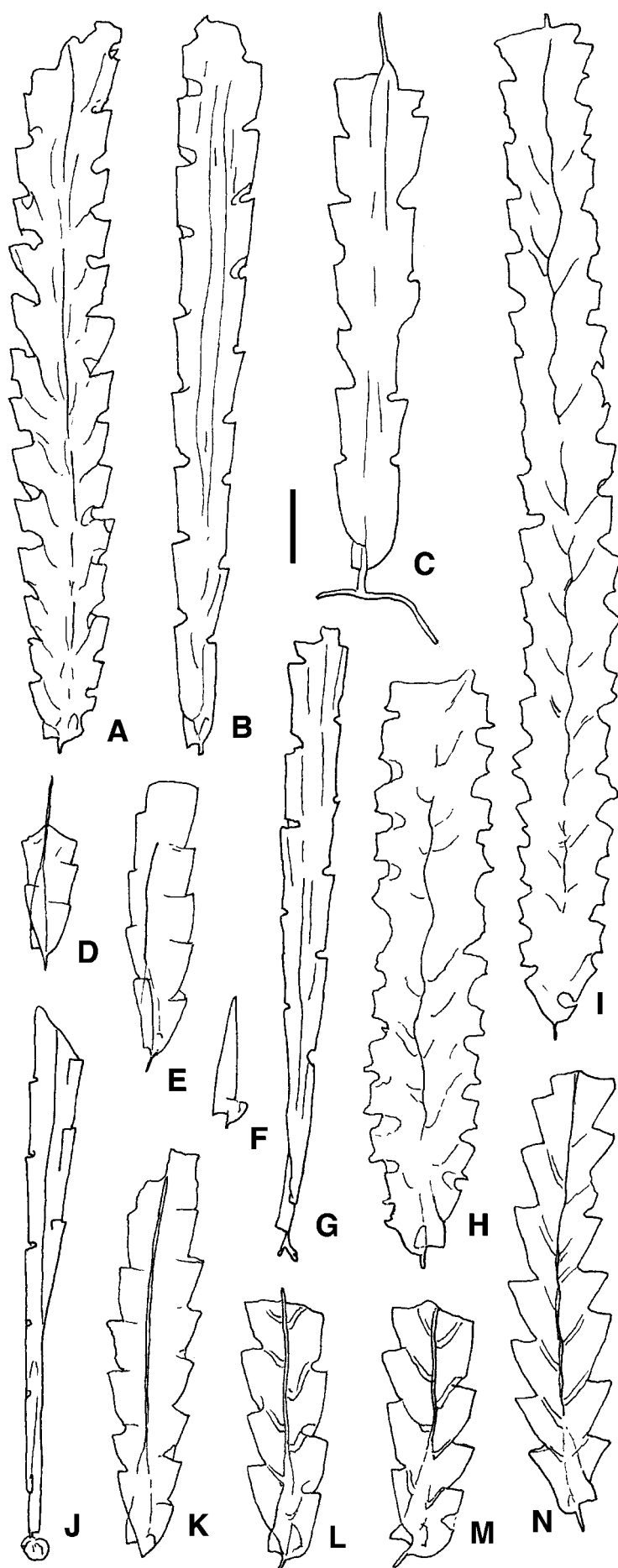
Fig. 6. *Camera lucida* drawings. (**A**) *Metabolograptus sibericus* (Obut 1955), holotype, Siberian Platform, Podkamennaya Tunguska River, Rhuddanian, Moyerokan Formation, moyeroensis Zone, locality 105 (Obut, 1955, pl. 61, fig. 5, O.I. Nikoforova's collection, 1951), CSGM211/6a; (**B**) *Avitograptus avitus* (Davies 1929), topotype, Dob's Linn, 1.6–1.65 m above base of Birkhill Shale, *ascensus* Biozone, GLAHM 131711; (**C**) *Avitograptus* aff. *avitus* (Davies 1929), Dob's Linn, Scotland, 1.3–1.37 m above base of Birkhill Shale, *persculptus* Biozone, GLAHM 131712; (**D–F, K**) *Glyptograptus* sp., Blackstone River, Yukon, Canada, 33.37–33.5 m above base of section shown in LaPorte *et al.* 2009, fig. 4. (**D**) GSC135131; (**E**) GSC135132; (**F**) GSC135133; (**J**) GSC135134 ; (**G**) *Akiograptus ascensus* Davies 1929, holotype, SM A10021; (**H, I**) *Paramplexograptus paucispinus* (Li *in* Anhui Geological Survey Team 1982), (**H**) topotype, NIGP154028I, lectotype, NIGP67260 (reillustrated *in* Li 1999, pl. 9, fig. 16); (**J**) *Dimorphograptus* cf. *minutus* (Chen & Lin, 1978), Dob's Linn, 2.17–2.35 m above base of Birkhill Shale, *ascensus* Biozone, GLAHM 131713; (**L, M**) *Sudburigraptus cortoghianensis* (Štorch & Serpagli 1993), UMC-IP457a (both specimens on counterpart slab to Štorch & Feist 2008, fig. 7.11); (**N**) *Sudburigraptus eberleini* (Churkin & Carter, 1970), holotype, USNM161783. Scale bar = 1 mm. CSGM, Central Siberian Geological Museum; GLAHM, Hunterian Museum; GSC, Geological Survey of Canada; NIGP, Nanjing Institute of Geology and Palaeontology; SM, Sedgwick Museum, University of Cambridge; UMC-IP, Université Montpellier II; USNM, US National Museum.
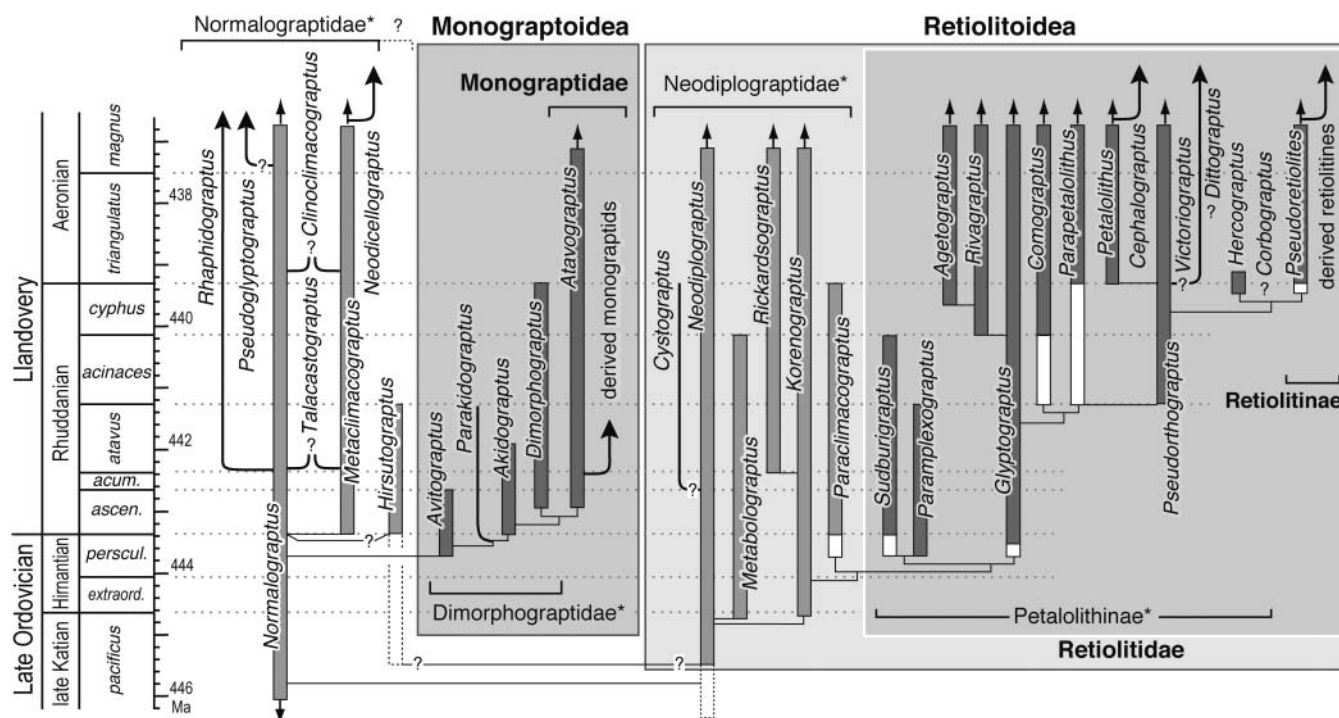
Fig. 7. Evolutionary tree of the Neograptina examined herein. The timescale is based on that of Sadler *et al.* (2009). Stratigraphic ranges of genera (filled bars) obtained from the literature and our unpublished data. History of evolutionary descent based on the present phylogenetic results combined with stratigraphic range. Ghost lineages (white bars) are range extensions implied by relationships in the phylogenetic analysis presented here and observed ranges of sister taxa. Budding speciation and direct ancestry postulated where not contradicted by known ranges or by autapomorphic features in the putative ancestor. Ranges that extend beyond the study interval are indicated by arrows.

described by Štorch *et al.* (2011) we do not favour the use of the name Monograptina for this clade.

Paraphyletic Family **NORMALOGRAPTIDAE** Štorch & Serpagli, 1993, emend

Emended definition. Paraphyletic taxon that includes all members of the clade Infraorder Neograptina excluding those included herein within the clades Superfamily Monograptoidea or Superfamily Retiolitoidea.

Remarks. This paraphyletic family includes the taxa that are stem to the clades Monograptoidea and Retiolitoidea (Figs 1, 3), which are likely sister taxa. The definition of the Superfamily Normalograptacea in Mitchell *et al.* (2007*a*, p. 337) was worded unclearly: as written, it appears that it was intended that the Normalograptacea should include all taxa included within the Monograptina, which was not the intent of the authors. Here we follow Štorch *et al.* (2011), who explicitly described the Family Normalograptidae as a paraphyletic stem lineage within the Neograptina.

The most primitive taxon known to be included within this family is *Undulograptus formosus*, which has a Pattern C astogeny (Mitchell *et al.* 2007*a*). The early Pattern H species, which originate in the Dariwillian and extend into the Late Ordovician include forms with both glyptograptid (e.g. ?*Normalograptus euglyphus*) and climacograptid (e.g. *Normalograptus angustus*) thecae. The phylogeny of these taxa is in need of study and further revision of the genera within the family may result. As a consequence of the variety of proximal and thecal morphologies found among taxa within this stem group, it is not currently possible to identify any morphologic criteria that can be used to uniquely characterize this taxon.

The fact that there seems to be a continuum in form between typical forms of *Normalograptus*, particularly *N. scalaris*, and *Pseudoglyptograptus* (Loydell & Maletz 2009) suggests that the ancestor of this group was derived directly and independently from a species of *Normalograptus* (Fig. 7) and should be included within the Normalograptidae. *Clinoclimacograptus* shows similarities with both *Pseudoglyptograptus* and *Metaclimacograptus* (Bulman & Rickards 1968) and likely falls within the Normalograptidae as well. The origin of *Talacastograptus* is even more problematic, since it possesses a unique internal structure with internal zig-zag lists (Rickards *et al.* 2002), but shows thecal forms similar to *Metaclimacograptus*, or possibly hooded species of *Hirsutograptus*.

Genus **NORMALOGRAPTUS** Legrand, 1987, emend.

Type species. Climacograptus scalaris var. *normalis* Lapworth 1877.

Emended diagnosis. Species with Pattern H rhabdosomes that possess unornamented climacograptid thecae with straight or concave interthecal septa throughout the rhabdosome and full median septum, which may be delayed.

Remarks. This concept of *Normalograptus* is very close to the original proposed by Legrand (1987). Melchin & Mitchell (1991) noted that many of the Silurian taxa that had previously been assigned to *Glyptograptus* could be shown to be aseptate with a Pattern H astogeny, not consistent with *G. tamariscus*, the type species of the genus. They recommended that until such time as the phylogeny of the Pattern H species with glyptograptid thecae was better resolved, these forms should be included within *Normalograptus*. Our present study

provides a phylogenetic basis for separation of Pattern H taxa into different genera based upon a combination of astogenetic, thecal and internal rhabdosomal characters and those forms with glyptograptid and biform thecae can now be grouped into genera distinct from *Normalograptus*.

As noted above, there are some pre-Hirnantian taxa currently assigned to this genus that have glyptograptid thecae and thus do not fit our revised generic diagnosis. Without further phylogenetic analysis it is not possible to tell if these are primitive members of the Neodiplograptidae (e.g. *Metabolograptus* or *Korenograptus*) or distinct taxa within the Normalograptidae.

Genus **RHAPHIDOGRAPTUS** Bulman, 1936, emend.

Type species. Climacograptus toernquisti Elles & Wood 1906.

Emended diagnosis. Species with Pattern H rhabdosomes modified by the presence of a uniserial theca one, produced by truncation of growth of th1^2; climacograptid thecae and full median septum distally.

Remarks. As noted above and by Melchin (1998), this taxon appears to be derived independently of species of *Dimorphograptus*, including other dimorphograptids with climacograptid thecae, such as *D. extenuatus* (Melchin 1998; Štorch & Feist 2008). Based on our present understanding, this appears to be a monospecific genus.

Genus **METACLIMACOGRAPTUS** Bulman & Rickards, 1968, emend.

Type species. Diplograptus hughesi Nicholson 1869.

Diagnosis. Species with Pattern H rhabododosomes with an undulose to zig-zag median septum, convex or concavo-convex subapertural thecal walls and apertural introversion (abbreviated from Melchin 1998).

Remarks. This genus forms a clear and distinctive taxon that has been widely and unambiguously recognized by many authors. Some of the earliest taxa that may be assigned to this genus (e.g. *M. fidus* and *M. pictus*, Koren' *et al.* 1980) show only very slight development of some of the key features of this genus, such as apertural introversion and subapertural wall curvature. Following Loydell (1992) and Melchin (1998), the genus *Lithuanograptus* Paškevičius (1976) is here considered a subjective junior synonym of *Metaclimacograptus*.

Also as noted by Melchin (1998) some of the more derived members of this genus show apertural hoods that are formed by growth of the dorsal wall of the underlying theca rather than simple genicular thickening.

Family *incertae sedis*

Genus **HIRSUTOGRAPTUS** Koren' & Rickards, 1996, emend.

Type species. Hirsutograptus longispinosus Koren' & Rickards 1996.

Emended diagnosis. Species with Pattern H rhabdosomes with climacograptid thecae bearing laterally and ventrally directed genicular hoods, genicular spines or both; full median septum.

Remarks. Although this genus was originally intended to include only species with Pattern H development and climacograptid thecae with genicular spines, Koren' & Rickards (1996) showed that the geniculae of these taxa are thickened and the spines tend to be basally expanded into hood-like structures. Our observations support this and suggest that the genicular hoods seen on some other 'normalograptids', which are extended onto both the lateral and ventral margins of the geniculae (e.g. '*Normalograptus*' *jideliensus* and '*Paraclimacograptus*' *jinyangensis*), may be homologous with the genicular spines, whose bases are expanded ventrally and laterally into small hoods. Our results also indicate that this group of hooded/spinose taxa with climacograptid thecae form a well supported clade. Therefore, we expand the concept of *Hirsutograptus* to include both the spinose and hooded forms.

Paraclimacograptus innotatus also shows a Pattern H astogeny but appears to be phylogenetically distinct from *Hirsutograptus*. In that taxon the hood extends only ventrally, not laterally, and appears to emerge from thecae that are otherwise glyptograptid in form (Russel *et al.* 2000). In addition, *P. innotatus* shows some details of its proximal development that are more derived (see below).

Although the small clade that defines *Hirsutograptus* in our study occurred at the base of the larger clade leading to the Retiolitidae in our strict consensus trees (Fig. 2A, B) this relationship had less than 50% bootstrap support (Fig. 3). Therefore, we cannot regard this genus as belonging to either the Retiolitoidea or the stem Normalograptidae with any degree of certainty. Only three characters unite *Hirsutograptus* with the Retiolitoidea. Two of these, the amount of proximal and amount of dorsal exposure of the sicula, show the same state changes in several places on the tree, are homoplastic characters among the Neograptina, and are therefore not likely to be reliable features on which to base phylogenetic position. The third character is angle of inclination of the th2^1 interthecal septum. The state of this character is difficult to judge in flattened specimens, but some of the species not included in our study that would otherwise be considered to fit well within *Normalograptus* (e.g. *N. mirnyensis*, see Koren' & Melchin 2000) show this character state on at least some specimens, so this feature may be variable within *Normalograptus* as a whole. These observations, together with the fact that the stratigraphic level of first appearance of *Hirsutograptus* is not consistent with it being a basal neodiplograptid (Fig. 7), suggest to us that this genus is more likely to be directly derived from *Normalograptus*. Although the spinose members of this genus are not known to occur below the *acuminatus* Biozone, hooded forms have been reported in the *ascensus* Biozone (e.g. Koren' & Melchin 2000).

Superfamily **MONOGRAPTOIDEA** Lapworth, 1873, emend.

Emended definition. The most recent common ancestor of *Avitograptus avitus* and *Monograptus priodon* and all of its descendants (Node 1, Figs 2, 3).

Remarks. The most basal members of this clade are characterized by the following synapomorphies (Node 1, Figs 2, 3): a slender, elongate, U-shaped proximal thecal pair; th1^1 turns upward at the sicular aperture, rather than below it; and the

th1^2 arises by abrupt lateral differentiation from the upward-grown portion of th1^1 (Pattern J; Fig. 6B, C). In all of the more derived members of this clade th1^1 turns upward above the sicular aperture and the downward grown portion is short (Fig. 6I) or absent (as in the Monograptidae).

Paraphyletic Family **DIMORPHOGRAPTIDAE** Elles & Wood, 1908, emend.

Emended definition. The partial clade that includes the common ancestor of *Avitograptus avitus* and *Monograptus priodon* and all of its descendents, including *Dimorphograptus elongatus,* but excluding those taxa included in the Family Monograptidae (i.e. excluding the uniserial monograptids).

Remarks. Melchin (1998) provided a diagnosis of this taxon that characterizes the species of the family as defined here. It includes Pattern J and J' species (biserial and unibiserial forms, respectively) that show the upward turn of growth of th1 at or, much more commonly, above the sicular aperture, but retain a biserial distal end that is fully septate. It should be noted that it is sometimes observed among Pattern I and N species that some individual specimens show the first theca turning upward at the sicular aperture (e.g. Koren' & Rickards 1996, text-fig. 13I, pl. 12, fig. 5), but this does not seem to be a consistent feature in these taxa. In addition, some petalolithids also show considerable elongation of the first thecal pair.

Genus **AVITOGRAPTUS** gen. nov.

Type species. Glyptograptus(?) *avitus* Davies 1929.

Diagnosis. Species with Pattern J rhabdosomes, th1^1 upturned at level of sicular aperture, th1^2 arises from a point low within the upward-grown portion of th1^1, geniculate, slightly to moderately inclined thecae, slightly elongated first thecal pair relative to subsequent thecae, full median septum.

Remarks. The species assigned to this genus differ from normalograptids and neodiplograptids in that species we assign to *Avitograptus* show a tendency toward early upward growth of the first thecae and also elongation of the first thecal pair relative to the following thecae. In particular, the upward-grown portion of th^1 is usually at least 1.4 times the length of the free ventral wall of th2^1. By contrast, in normalograptids and neodiplograptids, this ratio is normally 1.3 or less. Species of *Akidograptus* and *Parakidograptus* normally show even more proximal thecal elongation (and often proximal curvature) and a higher point of upward growth of both of the first two thecae, although the distinction is least clear in the stratigraphically lowest akidograptids. Thus, these species appear to be transitional in form between *Normalograptus* and *Akidograptus* in the degree of elongation of the proximal thecae and the position of origin and upward growth of these thecae. The two species that we assign to this genus were both assigned to ?*Glyptograptus avitus* by Williams (1983), although they differ somewhat in dimensions and also development of the virgella (Fig. 6B, C). Both species appear to show some degree of variation in these characters, particularly the point of upturn of th1^1. In some specimens it is below the thecal aperture (e.g. Williams 1983, plate 66, fig. 9), whereas in others it is at or even slightly above (Fig. 6B, C; Williams 1983, text-fig. 10a,b). We do not have any isolated specimens of species of *Avitograptus* so it is not possible to tell if the

downward-grown portion of th1^1 terminates with one foramen or two.

Genus **AKIDOGRAPTUS** Li & Ge, 1981, emend.

Type species. Akidograptus ascensus Davies 1929.

Diagnosis. 'Biserial rhabdosome with protracted proximal end and early upward growth of first two thecae (Pattern J). Thecae strongly geniculate (climacograptid)' (Melchin 1998).

Remarks. In addition to the characters noted in the diagnosis, species of this genus, and the similar *Parakidograptus*, often show dorsal curvature of the proximal end of the rhabdosome (Fig. 6G). *Parakidograptus*, which has not been included in this phylogenetic analysis, differs from *Akidograptus* in thecal form. Species of the former genus show more inclined thecae, often with concave subapertural walls.

Genus **DIMORPHOGRAPTUS** Lapworth, 1876, emend.

Type species. Dimorphograptus elongatus Lapworth 1876.

Diagnosis. Pattern J', unibiserial by redirection of growth of th2 above th1, biserial portion fully septate (abbreviated from Melchin 1998).

Remarks. The distinction of this genus from *Rhaphidograptus* and *Agetograptus* is discussed above. *Dimorphograptus* contains species with a wide variety of thecal forms, including isolate or slightly hooked thecae in the proximal end (Melchin 1998). Also, in contrast with other unibiserial taxa, most species of *Dimorphograptus* have more than one theca in the uniserial part of the rhabdosome.

Příbyl (1948) erected the subgenus *Bulmanograptus*, which was later raised to the level of genus, to distinguish dimorphograptids with orthograptid thecae, rather than glyptograptid as in the type species of *Dimorphograptus*. Few authors have made use of *Bulmanograptus*, however, and since we have not made any attempt to examine phylogenetic relationships among dimorphograptids in this study we cannot evaluate whether the set of species Příbyl had in mind forms a distinct clade.

A long-standing problem pertaining to the phylogenetic relationship between *Dimorphograptus* and the uniserial monograptids has been that the earliest species of *Atavograptus* was known from strata older than those of the oldest known *Dimorphograptus*. However, we have found specimens assignable to *Dimorphograptus* cf. *minutus* in the lowest Rhuddanian *asensus* Biozone in both Scotland (Fig. 6J) and South China (authors' unpublished data).

Family **MONOGRAPTIDAE** Lapworth 1873, emend.

Emended definition. The first species within the clade that contains *Monograptus priodon* to develop a scandent, uniserial rhabdosome and all its descendents (Node 2, Figs. 2, 3).

Remarks. The defining synapomorphies of this clade are the loss of the dicalycal theca, leading to a fully uniserial rhabdosome, and the loss of any downward growth in the first theca (Node 2, Figs 2, 3). Our present evidence suggests that all scandent, uniserial taxa comprise a monophyletic group,

although this hypothesis remains to be rigorously tested using cladistic analysis of a range of uniserial and stem monograptid taxa with differing thecal morphologies. Note that although Rickards & Hutt (1970) initially reported the oldest known monograptid, *Atavograptus ceryx*, from the upper Hirnantian *persculptus* Biozone, Harper & Williams (2002) showed that those occurrences were more likely within the lowest Silurian *ascensus* Biozone. All other known reports of *Atavograptus* are from early Rhuddanian and younger strata.

Superfamily **RETIOLITOIDEA** Lapworth, 1873, emend.

Emended definition. The most recent common ancestor of *Metabolograptus ojsuensis* and *Retiolites geinitzianus* and all of its descendants (Node 3, Figs 2, 3).

Remarks. There are several synapomorphies that appear near the base of this clade (Node 3), although none of these features are retained among all of the more derived members of the clade. The most characteristic synapomorphies that distinguish the basal members of the Retiolitoidea from *Normalograptus s.s.* are the presence of inclined distal thecal subapertural walls and interthecal septa. In most of the more derived Neo-diplograptidae and Petalolithinae the proximal thecae are inclined as well, and many show glyptograptid to orthograptid thecae. Another synapomorphy of the basal species of Retio-litoidea is the shape of the first thecal pair, which is cup-shaped (convex, inclined subapertural walls) as opposed to U-shaped (straight, parallel or only slightly inclined subapertural walls). In more derived Neodiplograptidae and Petalolithinae the first thecal pair may be V-shaped or flared. In addition, some the basal retiolitoids here assigned to the genus *Metabolograptus* possess sinuous interthecal septa and a sinuous median septum proximally, although these features are variable in some of the taxa, and are not seen in all of the taxa that emerge from Node 3 in the composite bootstrap tree (Fig. 3).

Our concept of the Retiolitoidea differs from that of Kozłowska-Dawidziuk *et al.* (2003) in that although the latter included some taxa with complete thecal walls, it encompassed only ancora-bearing taxa.

Paraphyletic Family **NEODIPLOGRAPTIDAE** fam. nov.

Definition. The partial clade that includes the most recent common ancestor of *Metabolograptus ojsuensis* and *Retiolites geinitzianus* but excluding those taxa included in the Family Retiolitidae.

Remarks. This taxon is intended to include all of the taxa within the Retiolitoidea that join the strict consensus and bootstrap cladograms below Node 4 (Figs 2, 3). As noted above, the phylogenetic origin of this clade within the Ordo-vician is not clear and requires further study of Katian and older 'normalograptids'. The oldest known species that we would assign to this clade are *Metabolograptus ojsuensis* and *Neodiplograptus charis*. Both appear to originate within the latest Katian, but the level of first appearance for the latter species is not precisely known (see Mitchell *et al.* 2011).

Although we did not include any species of *Cystograptus* in our analysis, the thecal form of the most primitive member of this genus, *C. ancestralis*, indicates that it was derived from within the Neodiplograptidae, likely from a species of *Neodiplograptus* or *Metabolograptus* (Štorch 1985).

Genus **METABOLOGRAPTUS** Obut & Sennikov, 1985, emend.

Type species. Diplograptus modestus sibericus Obut 1955.

Emended diagnosis. The partial clade that includes Pattern H species with sharp to bluntly rounded genicula, gently sinuous median septum proximally, sinuous interthecal septa, subaper-tural walls parallel to moderately inclined.

Remarks. Metabolograptus was originally intended to encom-pass many of the Hirnantian to early Silurian taxa with thecae that undergo a transition in thecal form from climacograptid proximally to glyptograptid distally. In the original descrip-tion, some of the species included were *N. modestus*, *N. ojsuensis*, and *N. tcherskyi*. From the point of view of thecal form alone, it could be regarded as a senior synonym of *Neodiplograptus*, although this has not been recognized by any subsequent authors. In fact, *Metabolograptus* has apparently not been recognized outside of the Russian literature.

The holotype of *Metabolograptus*, *Mbol. sibericus*, which is preserved as a low relief, bedding plane specimen, is reillus-trated here (Fig. 6A) and many of the details of proximal development and internal structure can be discerned. This specimen actually shows very little discernible change in thecal form along the length of the rhabdosome, unlike species currently assigned to *Neodiplograptus*. Our phylogenetic analy-sis suggests that *Mbol. sibericus* is part of a paraphyletic stem lineage that includes *N. ojsuensis*, *N. extraordinarius*, *N. par-vulus*, and *N. persculptus* (Figs 2B, 3). From this lineage four well supported clades arise: the clade that includes *Neodiplograptus magnus*, the type species of *Neodiplograptus*, the clade that includes *Neodiplograptus tcherskyi*, the clade including *Normalograptus gnomus*, and the clade that includes *Paraclimacograptus innotatus* and the petalolithids. Low boostrap support for this succession of nodes, however, indi-cates that there is substantial uncertainty about the sequence of derivation within this set of clades and their relationship to the basal retiolitoids. Accordingly we place all these taxa in a large polytomy in the bootstrap tree (Fig. 3). The most conservative option is to treat this entire suite of taxa between the root of the Retiolitoidea and *Paraclimacograptus* as a single genus, for which *Metabolograptus* would be the senior name. This taxon would be quite difficult to recognize in morphological terms while also obscuring the existence of the several distinct lineages that emerge from this stem lineage. Thus, we propose that the species that arise directly from this paraphyletic stem lineage be assigned to *Metabolograptus* and each of the well-supported separate clades that emerge from this stem be recognised as distinct taxa (Fig. 3). As redefined here, *Metabolograptus* is very similar in scope to *Persculp-tograptus* (Koren' & Rickards 1996) but the former name has priority and is based on sufficiently well preserved material that its type species can be readily recognized.

Genus **NEODIPLOGRAPTUS** Legrand, 1987, emend.

Type species. Diplograptus magnus (Lapworth 1900).

Diagnosis. Pattern H species with rapidly widening proximal end, thecae sharply geniculate proximally, thecal inclination increasing significantly through the proximal to mesial regions, full median septum distally.

Remarks. Species of this genus are distinguished from those of *Metabolograptus* by showing a more pronounced but gradual change in thecal inclination from the proximal to distal end. However, most species show at least somewhat geniculate thecae throughout, unlike species of *Rickardsograptus*, which show gently curved to orthograptid thecae at the distal end, although it should be noted that the geniculation on the distal thecae is not always evident in species of *Neodiplograptus*. More derived species of the genus, such as *Nd. africanus*, *Nd. fezzanensis*, and *Nd. magnus*, show very short, inclined subapertural walls at the end of very long, strongly inclined, geniculate thecae, as well as a rapid and even rate of widening through the proximal and mesial regions (Zalasiewicz & Tunnicliff 1994, text-fig. 7; Legrand, 1999, text-figs 3-2-60, 3-2-65, 3-2-67; Legrand 2002, fig. 5d,k). *Neodiplograptus modestus* shows a less even rate of widening (more rounded proximal end) and less elongate distal thecae, but Loydell (2007) noted that the distal thecae remain geniculate. Some early species that we suggest should be assigned to this genus, such as *Neodiplograptus charis* and *Nd. shanchongensis*, are very similar to *Nd. modestus* proximally but appear to show a change to more gently sinuous thecae distally (e.g. Chen *et al.* 2005*b*).

Genus **KORENOGRAPTUS** gen. nov.

Type species. *Glyptograptus gnomus* Churkin & Carter 1970. Holotype, Churkin & Carter (1970, pl. 2, fig. 16). Isolated, uncompressed specimens from Cornwallis Island, Arctic Canada, figured here Fig. 4A–E.

Derivation of name. Named in honour of the late distinguished graptolite worker, Dr. Tatiana Koren'.

Diagnosis. Pattern H or H' species with glyptograptid to orthograptid thecae throughout, with no thickening of the genicula; rhabdosome widens gradually from the proximal end.

Remarks. Many species that have previously been placed in *Glyptograptus*, *Normalograptus*, or *Sudburigraptus* (or formerly *Orthograptus*) that possess a Pattern H astogeny with a full median septum distally are assigned to this genus. Our analysis of Hirnantian and Rhuddanian species with this form suggests that they form a clade, although that clade shows only 52% bootstrap support. Nevertheless, this group of species is readily recognizable on morphological criteria. ?*Korenograptus praecursor* is only questionably assigned to this genus because unlike other species of the genus, its thecae show relatively sharp geniculae with slight genicular thickenings (Fig. 5A; Koren' & Rickards, 2004, text-fig. 4b). ?*Korenograptus praecursor* and *K. magnus* (Fig. 5G,I) were both initially named as subspecies of *Glyptograptus tamariscus*, but both show a downward-grown th1^1 that terminates in two foramina as well as a full median septum distally, indicating Pattern H astogeny (Nazck-Cameron 2000).

?*Glyptograptus telarius*, which we had included in our previous, preliminary studies (e.g. Melchin *et al.* 2004), is only known from relatively immature rhabdosomes. Therefore, we did not include this taxon in our final analyses. Our preliminary 2004 results, which included a much smaller set of taxa and somewhat different character coding scheme, and did not differentially weight or rescale any characters, showed ?*G.*

telarius as a derived taxon sister to species of *Rivagraptus*, clearly within the Petalolithinae. Similarities with *Rivagraptus* include a short sicula completely enclosed by the early growth of the first thecal pair and also cortical bandages with significantly thickened margins (Koren' & Rickards 2004). However, experiments with our current character coding scheme, taxon set, and analytical methodology unambiguously place this taxon among the Neodiplograptidae, owing to its other astogenetic features, which are characteristic of the Pattern H proximal development. ?*G. telarius* occurs in the subclade that also contains 'N.' *lacinious* and 'N.' *nikolayevi*, in all of our recent experiments. 'N.' *nikolayevi* appears only in Aeronian strata and thus was not included in the bootstrap analysis for the Rhuddanian segment but analysis of the full data set showed it to be sister to 'N.' *lacinious*. Like ?*G. telarius*, 'N.' *nikolayevi* shows a sicular apertural region completely enclosed by the proximal thecae as shown by Loydell & Maletz (2009). Thus, ?*G. telarius* and 'N.' *nikolayevi* are regarded here as species of *Korenograptus*. Loydell & Maletz (2009) also demonstrated that the specimens assigned by Melchin (1989, 1998) to *N. nikolayevi* are not that species. Those specimens, which are here assigned to *K. gnomus*, the type species of this new genus, show more upward growth of the first thecal pair and greater exposure of the sicula (Fig. 4A–E).

A number of Middle to early Late Ordovician graptolites (e.g. '*Glyptograptus*' *euglyphus* Elles & Wood and '*Glyptograptus*' *spiculatus* Keble & Benson) appear to resemble *Korenograptus* species closely. On morphological grounds alone they might be included in the genus, however, their much earlier and stratigraphically disjunct occurrence suggests that this similarity is homoplastic. Their relation to Ordovician normalograptids with more climacograptid thecae requires additional study but preliminary phylogenetic results suggest that species with these different thecal forms do not form separate clades (Mitchell *et al.* 2007*a*) and we recommend retaining these *Korenograptus* homeomorphs within *Normalograptus*.

Genus **RICKARDSOGRAPTUS** gen. nov.

Type species. *Diplograptus*(?) *tcherskyi* Obut & Sobolevskaya in Obut *et al.* 1967. Holotype Obut & Sobolevskaya (1967, pl. 3, fig. 1). Isolated, uncompressed specimens from Cornwallis Island, Arctic Canada, figured here (Fig. 4F, G).

Derivation of name. Named in honour of the late distinguished graptolite worker, Dr. R. Barrie Rickards.

Diagnosis. Pattern H' (primitive members may be Pattern H) species that show pronounced widening mesially, which corresponds to a change to more inclined and more gently sigmoidal to straight thecae.

Remarks. Species of this genus are distinguished from those of *Metabolograptus* and *Neodiplograptus* in possessing a relatively narrow proximal end that widens relatively abruptly mesially, in the same region where there is a relatively rapid change in thecal form to smoothly glyptograptid to orthograptid thecae (e.g. Fig. 4G; Melchin 1998, pl. 3, figs 4, 11, 12). The proximal thecae are parallel sided with a sharp or bluntly rounded geniculum. These characters are not as clearly developed in *R. elongatus* (Churkin & Carter 1970) as they are in the more derived forms such as *R. tcherskyi*. *Neodiplograptus lautus* of

Štorch & Feist (2008) is very similar to *R. elongatus* and likely belongs to *Rickardsograptus* although it shows a more gradual proximal widening and appears to be Pattern H rather than H' (early origin of th2^1).

Genus **PARACLIMACOGRAPTUS** Přibyl, 1947, emend.

Type species. Climacograptus innotatus Nicholson 1869.

Diagnosis. Species with Pattern H' rhabdosomes possessing thecae with bluntly rounded to sharp genicula that bear a ventrally projecting hood, wide apertural excavations, everted apertures, and slightly to moderately inclined supragenicular walls (slightly modified from Russel *et al*. 2000).

Remarks. This genus was described in detail by Russel *et al.* (2000) and its distinction from the revised *Hirsutograptus* and the new genus *Paramplexograptus* is discussed in the remarks for those genera.

Family **RETIOLITIDAE** Lapworth, 1873, emend.

Diagnosis. The first species that acquired a unistipular (aseptate) biserial rhabdosome in the clade that contains *Paramplexograptus madernii* and *Retiolites geinitzianus* and all its descendants (Node 4, Figs 2 & 3).

Remarks. Melchin (1998) considered a suite of characters to be characteristic of the Pattern I proximal development, including a short descending prothecal 1^1 ending in one terminal foramen, fusellar divergence of th1^2 from th1^1 at a point near its base, and loss of the dicalyc, resulting in an aseptate rhabdosome. Our study shows that these characters do not arise together. The gradual fusellar divergence of the second theca is observed in *Paraclimacograptus*, which is fully septate distally, as well as all of the aseptate taxa. In addition, some of the most basal aseptate forms show a long descending th1^1 (*Paramplexograptus madernii*, Fig. 5B) and two foramina at the base of th1^1 or both (e.g. *Sudburigraptus* sp. 1, Fig. 5H). In our study, the node that had the strongest bootstrap support was the node that corresponded with the loss of the dicalyc (Node 4, Figs 2 & 3). At this same node, we have observed that the following synapomorphy also occurs: the apex of the sicula is no longer central and attached to a partial median septum, but is either free, or, in more derived forms, laterally attached on the obverse side.

The scope of the Retiolitidae, as employed here, is very similar to the Retiolitidae of Mitchell (1987) and Štorch & Serpagli (1993).

Paraphyletic Subfamily PETALOLITHINAE Bulman, 1955, emend.

Emended definition. The partial clade that includes the first species that acquired a unistipular (aseptate) biserial rhabdosome in the clade that contains *Paramplexograptus madernii* and *Retiolites geinitzianus* and its descendants, but excluding the taxa included in the Subfamily Retiolitinae.

Remarks. The scope of the Petalolithinae, as employed here, is very similar to the Petalograptinae of Štorch & Serpagli (1993). The name is revised in accordance with the recognition that the valid name of the type genus is *Petalolithus* rather than *Petalograptus*.

In addition to the genera included in this study, it has been widely recognized that *Cephalograptus* likely descended from a species of *Petalolithus*, most likely *P. folium* (e.g. Rickards *et al*. 1977). In addition, Koren' & Rickards (1996) provided good evidence that *Victoriograptus* and *Dittograptus* were derived from a species of *Pseudorthograptus*. Therefore, all of these genera are here considered to belong to the Petalolithinae.

Genus **SUDBURIGRAPTUS** Koren' & Rickards, 1996, emend.

Type species. Orthograptus eberleini Churkin & Carter, 1970.

Emended diagnosis. Species with Pattern H' and possibly Pattern I, aseptate rhabdosomes with glyptograptid to orthograptid thecae. Colonies of species known to belong to this genus also show slight dorsal rhabdosomal curvature of the proximal end and a slightly flared dorsal sicular margin.

Remarks. This genus was originally intended to encompass non-spinose species with either Pattern H or I astogeny, orthograptid thecae, and a simple virgella (Koren' & Rickards 1996). The astogenetic pattern and internal structure of the type species *S. eberleini*, has hitherto been unknown, but our restudy of the type material shows that it is aseptate with the nema attached to the bases of the interthecal septa, and possesses a short descending th1^1 (Fig. 6N). Unfortunately, it is not possible to tell if the termination of the descending th1^1 possesses one or two foramina. *Sudburigraptus* sp. 1 (Koren' & Rickards 1996) shows a short descending th1^1 that possesses two foramina (Fig. 5H) whereas *S. cortoghianensis* has a long descending th1^1 (Fig. 6L, M). None of the species here assigned to *Sudburigraptus* clearly show the diagnostic feature of Pattern I – a descending th1^1 that terminates in a single foramen below the sicular aperture. However, all of these species are aseptate, which distinguishes them from other species previously (sometimes questionably) assigned to *Sudburigraptus*, such as *S. illustris* (e.g. Koren' & Melchin 2000) and ?*S. angustifolius* (e.g. Chen *et al*. 2005b), which instead belong to *Korenograptus*. In addition, the three species assigned to *Sudburigraptus* here also show a tendency toward slight dorsal curvature of the sicula and proximal end of the rhabdosome.

Genus **PARAMPLEXOGRAPTUS** gen. nov.

Type species. Paraorthograptus paucispinus Li, in Anhui Geological Survey Team 1982. Lectotype illustrated in Li (1999, pl. 9, fig. 16), reillustrated here Fig. 6I.

Diagnosis. Species that form an aseptate rhabdosome with Pattern H' or Pattern I proximal structure and the nema attached to the bases of the interthecal septa. Thecae have sharp genicula with thickenings or ventral flanges, and slightly to moderately inclined, usually concave subapertural walls. Sicular aperture shows slight dorsal flare.

Remarks. Members of this genus are distinguished from those in *Paraclimacograptus* and hooded forms of *Hirsutograptus* in being aseptate, with the nema attached to the bases of the interthecal septa (Figs 5B, C, 6H, I). In addition, the thecae of *Hirsutograptus* colonies are more typically climacograptid in

form and the hoods wrap around the lateral margins of the genicula. Legrand (1999) noted that there may be a partial median septum distally in some specimens of *Paramplexograptus kiliani*. Otherwise, our specimens of *P. kiliani kiliani* and *P. kiliani kuramaensis* differ from *P. paucispinus* primarily in their dimensions.

Paramplexograptus differs from *Sudburigraptus* in that the thecae are sharply geniculate, at least proximally, and possess ventral genicular flanges or thickenings. The thecal subapertural walls are also characteristically concave in *Paramplexograptus*.

Within the *Paramplexograptus* clade there is a transition from species with two foramina in the descending $th1^1$ (*P. madernii,* Fig. 5B) to those with a shorter descending $th1^1$ that has only a single foramen (*P. paucispinus,* Fig. 5D), which appears to arise independently in this group relative to the clade that includes *Glyptograptus* and *Petalolithus* (Fig. 3).

Genus GLYPTOGRAPTUS Lapworth, 1873, emend.

Type species. Diplograpsus tamariscus Nicholson 1868.

Emended diagnosis. Species with Pattern I aseptate rhabdosomes with glyptograptid to climacograptid thecae; nema embedded in the obverse rhabdosomal wall or with a narrow, obverse partial median septum.

Remarks. This is a paraphyletic genus that, as revised and restricted here, includes only those Pattern I species that have a nema embedded marginally either in a narrow partial median septum on the obverse side (Fig. 5E) or else in the obverse wall, as in *G. tamariscus* (Melchin 1998, pl. 5, figs 4–6). As noted below, our results suggest that those species previously assigned to *Glyptograptus* that show a free internal nema, such as *G. supernus*, occur in the clade with *Rivagraptus*. Further phylogenetic analysis incorporating a wider range of aseptate glyptograptid taxa will be required to test the relationships proposed here.

We have found a species that we refer to *Glyptograptus* sp. from the upper part of the *persculptus* Biozone in Yukon, Canada. Although flattened, this specimen appears to show a nema that is either embedded in the obverse rhabdosomal wall or a narrow partial median septum, and a short descending $th1^1$ (Fig. 6D–F, K). As far as we are aware, these are the oldest known specimens that fit our current definition of *Glyptograptus*.

Genus COMOGRAPTUS Obut & Soblevskaya, in Obut et al., 1968, emend.

Type species. Comograptus comatus Obut and Sobolevskaya, in Obut *et al.* 1968.

Diagnosis. Species with Pattern I rhabodosomes with at least three spines projecting outward from the sicular rim, thecae climacograptid to glyptograptid, nema free and central (Melchin 1998).

Remarks. See Melchin (1998) for discussion of this genus.

Genus RIVAGRAPTUS Koren' & Rickards, 1996, emend.

Type species. Diplograptus bellulus Törnquist 1890.

Emended diagnosis. Species forming aseptate rhabdosomes with Pattern I or N (new) proximal structure, glyptograptid to orthograptid thecae and free, central nema.

Remarks. Our new observations of *Rivagraptus bellulus* using infrared microscopy show that this species and *R. kayi* possess a unique proximal development (here named Pattern N, see above) in which $th1^1$ emerges from a flare in the margin of the sicular aperture and has no downward-grown protheca 1^1 outside of the sicula (Fig. 5J, K, M). On the other hand, *Rivagraptus supernus* (=*Glyptograptus elegans* subsp. nov. of Melchin 1998, pl. 5, figs 10, 13, pl. 6, figs 1–3) shows a typical Pattern I downward grown $th1^1$ with a single terminal foramen, but shares with *Rivagraptus bellulus* its internal structure with a central, free nema. Some of our specimens of *Rivagraptus supernus* also show a long virgella. These features of *Rivagraptus supernus*, the free, central nema and long virgella are shared with the other species of *Rivagraptus* studied here but not with *Glyptograptus tamariscus*. The result is that *Rivagraptus supernus* probably evolved within the same terminal clade as *Rivagraptus bellulus* despite the fact that the former does not share the unique proximal development features of the latter.

Genus AGETOGRAPTUS Obut and Sobolevskaya, *in* Obut et al., 1968, emend.

Type species. Agetograptus secundus Obut and Sobolevskaya, in Obut *et al.* 1968.

Diagnosis. Species forming aseptate rhabdosomes with Pattern I' proximal structure and glyptograptid to orthograptid thecae and a free, central nema. Uniserial first theca by redirection of growth of second theca (slightly modified from Melchin 1998).

Remarks. As noted above, species of *Agetograptus* have acquired the uniserial first theca by redirection of the growth of the second theca, as is the case in *Dimorphograptus*, but in all other aspects of the proximal development and internal rhabdosomal structure species of this genus resemble *Rivagraptus*. Also as in *Rivagraptus*, some species of *Agetograptus* possess a long, robust virgella, an unusually short sicula, and/or paired thecal apertural spines.

Genus PARAPETALOLITHUS Koren' & Rickards 1996, emend.

Type species. Parapetalolithus dignus Koren' & Rickards, 1996.

Diagnosis. Pattern I species with rhabdosomes that bear straight, V-shaped first thecal pair, straight, moderately inclined orthograptid thecae, nema free or obverse and embedded, and unbranched virgella (slightly modified from Melchin 1998).

Remarks. As with *Glyptograptus*, *Parapetalolithus* may be a paraphyletic genus. It is distinguished from *Petalolithus* and *Pseudorthograptus* by the lack of an ancora and by more V-shaped rather than flared first thecal pair (see Koren' &

Rickards 1996). In addition, rhabdosomes of *Petalolithus* species generally have more strongly inclined or more overlapping distal thecae or both. Colonies of *Pseudorthograptus* possess spines on the thecal apertures.

The species of *Sudburigraptus* encountered in this study show slight curvature of the sicula and proximal end and a more variable thecal form. In addition, the type species has a central nema that is attached to the bases of the interthecal septa.

The lack of resolution at the nodes from which the species of *Parapetalolithus* emerge do not permit unambiguous interpretation of the sister-group relationships of these taxa.

Genus PETALOLITHUS Suess, 1851, emend.

Type species. Prionotus folium Hisinger 1837.

Diagnosis. Rhabdosomes with Pattern I structure and elongate, weakly to strongly concave first thecal pair, straight to concave, strongly overlapping distal thecae, four-pronged ancora (after Melchin 1998).

Remarks. Distinction of this genus from *Parapetalolithus* is discussed in the remarks for that genus. Rhabdosomes of *Pseudorthograptus* species differ in possessing less strongly overlapping thecae, a more complex ancora, and spines on the thecal apertures.

Genus PSEUDORTHOGRAPTUS Legrand, 1987, emend.

Type species. Diplograptus insectiformis Nicholson 1869.

Diagnosis. A paraphyletic group of species bearing Pattern I colonies with concave first thecal pair, apertural thecal spines, straight to concave thecal walls, free nema proximally, ancora with four prongs and additional spiral lists and/or loops (slightly modified from Melchin 1998).

Remarks. Comparisons with the similar genera *Parapetalolithus* and *Petalolithus* can be found in the remarks for those genera, above.

Pseudorthograptus obuti, which has been regarded as a typical species of *Pseudorthograptus* (e.g. Koren' & Rickards 1996; Melchin 1998), forms a well supported clade with *Hercograptus* and *Pseudoretiolites* in this analysis. This is largely the result of the shared traits of an ancora that extends distally to enclose the proximal part of the rhabdosome (ancora sleeve), as well as the convexity of the thecal apertural margins. It is not clear whether the ancora sleeve attaches to the lateral margins of the thecae, however, and thecae still possess continuous, albeit somewhat thin, fusellar walls throughout (Koren' & Rickards 1996). Therefore, we tentatively retain *Ps. obuti* within *Pseudorthograptus*.

Genus HERCOGRAPTUS Melchin, 1999

Type species. Hercograptus introversus Melchin 1999.

Diagnosis. Species forming rhabdosomes with Pattern I, list framework and reduced fusellar periderm in thecal apertural regions, ancora with spiral lists extends to form ancora sleeve that is connected to lateral thecal apertural margins (abbreviated from Melchin 1999).

Remarks. The current study supports the hypothesis proposed by Melchin (1999) that *Hercograptus introversus* is sister to *Pseudoretiolites*. Bates *et al.* (2005) obtained a similar result in their broader study of retiolite phylogeny. Furthermore, we support the prediction that the common ancestor of these sister taxa should resemble *Hercograptus introversus* in all respects except for the isolation and introversion of the thecal apertures.

Subfamily RETIOLITINAE Lapworth, 1873, emend.

Emended definition. The first ancora-bearing graptolite species within the clade that includes *Retiolites geinitzianus* that acquired thecae constructed of a full framework of lists and reduced or absent fusellar walls, and all of its descendents.

Remarks. Melchin (1998) and Bates *et al.* (2005) considered that the key features defining the retiolites *s.s.*, were the presence of a full thecal framework of lists with reduced fusellar walls (periderm) and incorporation of the ancora into the development of the first thecal pair. These features are characteristic of the most primitive specimens of *Pseudoretiolites* that have been observed (e.g. Lenz *et al.* 2010) but are not seen in *Hercograptus* (Melchin 1999), which possesses an ancora sleeve that is connected to the thecal apertural margins, but the framework of thecal lists is restricted to the distal regions of the metathecae and is not connected to the ancora. The state of the relationship between the ancora and thecal lists in *Corbograptus* (Koren' & Rickards 1996) is not known so its phylogenetic position relative to *Hercograptus* and *Pseudoretiolites* is uncertain (Fig. 7). Previous work on the evolution of this clade indicates that it includes both the Retiolitinae and the Plectograptinae Bouček & Münch (1952), but excludes the Archiretiolitinae Bulman (1955), which is subclade within the Diplograptoidea (Bates *et al.* 2005, Mitchell *et al.* 2007*a*).

APPENDIX 1

Taxa included and sources of morphological information (note that the previously accepted generic names for taxa are used here to facilitate comparison with the literature sources listed).

Agetograptus spiniferus Obut & Sobolevskaya *in* Obut *et al.* 1968: Melchin (1998).

Akidograptus ascensus Davies 1929: Williams (1983); Melchin (1998); MJM unpublished observations of flattened and full relief, bedding plane specimens, mainly from South China and Scotland (Fig. 6G).

At. atavus (Jones 1909): Koren' & Bjerreskov (1997); Lukasik and Melchin (1997).

Atavograptus ceryx Rickards & Hutt 1970: Rickards & Hutt (1970); Williams (1983); Harper & Williams (2002); MJM unpublished observations of flattened and partial relief, bedding plane specimens from Scotland.

At. primitivus (Li *in* Nanjing Institute of Geology and Palaeontology 1983): Lukasik & Melchin (1994); Koren' & Bjerreskov (1997).

Comograptus comatus Obut & Sobolevskaya, in Obut *et al.* 1968: Melchin (1987); MJM unpublished observations of uncompressed, isolated specimens from Arctic Canada. The astogenetic, thecal and rhabdosomal form of this species very closely resembles that of *Comograptus gorbiachinensis*, which was illustrated by Melchin (1998).

Dimorphograptus minutus (Chen & Lin 1978): Melchin (1998); MJM unpublished observations. Note that we have recently discovered specimens very similar to *Di. minutus* in the *acensus* Biozone both in South China and Scotland (Fig. 6I).

Glyptograptus aff. *incertus* Elles & Wood 1907: Naczk-Cameron (2000), where this specimen was described as *G. incertus*. Our more recent comparison of our specimens described by Loydell (1992) show that *G. incertus* s.s appears to be aseptate with a central nema, whereas our specimens show a marginal nema attached to the obverse wall by a narrow, partial median septum, except at the sicular apex, where it is free (Fig. 5E, F).

G. supernus Fu, in Fu & Song 1986: Melchin (1998), where this taxon was identified at *G. elegans* n. subsp. (see Loydell 1992).

G. tamariscus (Nicholson 1868): Packham (1962); Melchin (1998).

G. tamariscoides (Packham 1962): Packham (1962); Naczk-Cameron (2000).

Hercograptus introversus Melchin 1999: Melchin (1999).

Hirsutograptus comantis (Chaletzkaya 1960): JL and MJM unpublished observations of isolated and bedding plane, compressed specimens from South China and Arctic Canada.

Metabolograptus sibericus (Obut 1955): Sennikov (1976); MJM study of excellent photographs of the holotype, a partial relief, bedding plane specimen, provided by Dr N. Sennikov (Fig. 6A).

Metaclimacograptus orientalis (Obut & Sobolevskaya 1966): Melchin (1998).

Mcl. slalom Zalasiewicz 1996: Zalasiewicz (1996), who noted that many specimens previously assigned to *Metaclimacograptus hughesi* belong to this species; MJM unpublished observations of isolated and bedding plane specimens from Arctic Canada.

Mcl. undulatus (Kurck 1882): Melchin (1998).

Nd. africanus (Legrand 1970): Legrand (1999, 2002); Loydell (2007).

Nd. elongatus (Churkin & Carter 1970): Churkin & Carter (1970); Melchin (1998); MJM unpublished observations of flattened, bedding plane and isolated specimens from Arctic Canada.

Nd. fezzanensis (Desio 1940): Štorch (1983); Legrand (1999, 2002).

Nd. magnus (H. Lapworth 1900): Zalasiewicz & Tunnicliff (1994).

Nd. modestus (Lapworth 1876): Zalasiewicz & Tunnicliff (1994); Melchin (1998); Loydell (2007); MJM unpublished observations of flattened, bedding plane specimens from Arctic Canada.

Nd. sinuatus (Nicholson 1869): Melchin (1998); Naczk-Cameron (2000).

Nd. tcherskyi (Obut & Sobolevskaya in Obut *et al.* 1967): Melchin (1998) (also illustrated here Fig. 4F, G).

Normalograptus angustus (Perner 1895): Štorch (1989); Loydell (2007); Štorch *et al.* (2011); MJM unpublished observations of flattened and partial relief, bedding plane specimens from South China and Arctic Canada.

N. avitus (Davies 1929): Williams (1983, text-fig. 7l) reillustration of holotype and MJM unpublished observations of flattened and partial relief, topotype, bedding plane specimens from Scotland (Fig. 6B).

N. aff. *avitus* (Davies 1929): Williams (1983), where specimens were identified as ?*Glyptograptus avitus*, except for the holotype, as noted above; MJM unpublished observations of flattened and partial relief, bedding plane specimens from Scotland (Fig. 6C).

N. extraordinarius (Sobolevskaya 1974): Koren' *et al.* (1980), where this species is identified as *Glyptograptus persculptus forma* A); Koren' *et al.* (1983); Chen *et al.* (2005b); Štorch *et al.* (2011); MJM unpublished observations of flattened and partial relief, bedding plane specimens from Scotland and northeastern Siberia.

N. gnomus (Churkin & Carter 1970): Churkin & Carter (1970); Melchin (1998) (also illustrated here Fig. 4A–E) and Naczk-Cameron (2000), where this species was identified as *N. nikolayevi*.

N. jideliensis (Koren' & Mikhaylova *in* Koren' *et al.* 1980): Koren' *et al.* (1980); Koren' & Melchin (2000); MJM unpublished observations of flattened, compressed specimens from Arctic Canada.

N. laciniosus (Churkin & Carter 1970): Churkin & Carter (1970); Naczk-Cameron (2000); MJM unpublished observations on compressed, isolated specimens from South China and Arctic Canada.

?*N. madernii* (Koren' & Mikhaylova *in* Koren' *et al.* 1980): Koren' *et al.* (1980); MJM restudy of holotype and paratype specimens, as well as other flattened and partial relief specimens on bedding planes from South China (identified by Chen *et al.* 2005b as *N.* aff. *N. indivisus*) and Scotland, as well as flattened bedding plane and isolated specimens from Arctic Canada (Fig. 5B).

N. magnus (Churkin & Carter 1970): Naczk-Cameron (2000) and MJM unpublished observations on uncompressed, isolated specimens from Arctic Canada (Fig. 5G, I). This species may be synonymous with *Glyptograptus rigidus* Fang *et al.* (1990).

N. nikolayevi (Obut 1965): Loydell & Maletz (2009) and MJM unpublished observations on additional specimens from their collections, provided by Dr J. Maletz.

N. normalis (Lapworth 1877): Loydell (2007); MJM unpublished observations of flattened and partial relief, bedding plane specimens from Scotland. Note that many of the specimens previously identified as this species have been recently found to be *N. ajjeri*, not *N. normalis*. However, these two species appear to differ only in dimensions and would be identical in our character coding scheme.

N. ojsuensis (Koren' & Mikhaylova *in* Koren' *et al.* 1980): Koren' *et al.* (1980); Koren' *et al.* (1983); Melchin (1998), where it was identified as '*Glyptograptus bohemicus*'; Chen *et al.* (2005b); Štorch *et al.* (2011); MJM unpublished observations of flattened and partial relief, bedding plane specimens from Bohemia, South China and Arctic Canada.

N. parvulus (H. Lapworth 1990): Williams (1983, identified as *Glyptograptus* cf. *persculptus*); Zalasiewicz & Tunnicliff (1994); Loydell *et al.* (2002); Chen *et al.* (2005b); Melchin (2008); MJM unpublished observations of flattened and partial relief, bedding plane specimens from South China and Arctic Canada.

N. persculptus (Elles & Wood 1907): Koren' *et al.* (1980), *Glyptograptus persculptus forma* B); Koren' *et al.* (1983); Williams (1983, type specimens reillustrated); Štorch & Loydell (1996); Štorch *et al.* (2011); MJM unpublished observations of flattened to full relief, bedding plane specimens from Bohemia and South China.

N. praecursor (Koren' & Rickards 2004): Koren' & Rickards (2004) and MJM unpublished observations on additional specimens from their collections, provided by Dr T. Koren' (Fig. 5A).

N. rectangularis (M'Coy 1850): Loydell (2007); Štorch & Feist (2008); MJM unpublished observations of flattened and partial relief, bedding plane specimens from Arctic Canada.

Paraclimacograptus innotatus (Nicholson 1869): Russel *et al.* (2000).

?*Pcl. jinyangensis* (Ye 1978): JL and MJM unpublished observations of flattened and partial relief, bedding plane and isolated specimens from South China and Arctic Canada.

?*Pcl. paucispinus* (Li 1982 *in* Anhui Geological Survey Team 1982): MJM and JF unpublished observations of flattened, bedding plane specimens, including the lectotype, from South China (Fig. 6H, I) and Arctic Canada, as well as fragmentary, flattened, isolated specimens from Arctic Canada (Fig. 5C, D).

Parapetalolithis palmeus (Barrande 1850): Loydell (1992); MJM unpublished observations of flattened bedding plane specimens from Arctic Canada.

Ppet. sp. A: Melchin (1998), where it was identified as *Parapetalolithus* sp.

Petalolithus ankyratus Mu *et al.* 1974: Melchin (1998).

Pet. intermedius Bouček & Přibyl 1941: Melchin (1998).

?*Pseudorthograptus kiliani* (Legrand 1977); Legrand (1999); MJM and JF unpublished observations of flattened, bedding plane specimens from South China and Arctic Canada, and one topotype specimen provided by Dr T. Koren'.

Ps. inopinatus (Bouček 1944): Melchin (1998).

Ps. obuti (Rickards & Koren' 1974): Štorch (1985); Koren' & Rickards (1996). Lenz & Melchin (1987, 1997).

Pseudoretiolites: Lenz & Melchin (1987, 1997).

Rhaphidograptus toernquisti (Elles & Wood 1906): Hutt *et al.* (1970); Bjerreskov (1975); Zalasiewicz & Tunnicliff (1994); Melchin (1998).

Rivagraptus bellulus (Törnqist 1890): Melchin (1998); Loydell & Maletz (2009) (Fig. 5K).

R. kayi (Churkin & Carter 1970): Churkin & Carter (1970); Melchin (1998); Naczk-Cameron (2000) (Fig. 5J).

?*Sudburigraptus cortoghianensis* (Štorch & Serpagli 1993): Štorch & Feist (2008) and MJM's restudy of specimens described in that paper (Fig. 6L, M).

S. eberleini (Churkin & Carter 1970): Churkin & Carter (1970); MJM restudy of holotype and paratype specimens (Fig. 6N).

?*S. illustris* (Koren' & Mikhaylova *in* Koren' *et al.* 1980): Koren' *et al.* (1980); MJM restudy of holotype and paratype specimens.

S. sp. 1: Koren' & Rickards (2004) and MJM unpublished observations on additional specimens from their collections, provided by Dr. T. Koren' (Fig. 5H).

APPENDIX 2

Descriptions of coded characters and their states.

1. Sicula length: 0 – long (>1.5 mm); 1 – medium (0.9-1.5 mm); 2 – short (<0.9 mm).
2. Dorsal flare of apertural region of sicula: 0 – absent; 1 – present.
3. Obverse exposure of sicula: 0 – fully exposed; 1 – enclosed by first thecal pair; enclosed by th1^2 and th2^1; enclosed by second thecal pair.
4. Exposure of dorsal margin of sicula: 0 – no exposure; 1 – exposed for a length <width of sicular aperture; 2 – ~ width of sicular aperture; 3 – > width of sicular aperture; 4 – exposed for at least ½ sicular length.
5. Sicular apertural spines (other than virgella); 0 – absent; 1 – present.

6. Virgella length; 0 – short (~ long as width of sicular aperture); 1 – medium (similar to length of sicula); 3 – much longer than sicula.
7. Virgellar elaborations: 0 – none; 1 – simple branching; 2 – 2nd order branching; 3 – distal vane or bulb; 4 – ancora. Note that through numerous trial analyses, we consistently found that when we coded ancora as the same feature as the second order branching seen in taxa such as *Akidograptus*, they were consistently found to be independently derived. In addition, the true petalolithid/retiolitid ancora is consistently strongly recurved, a feature not seen among akidograptids or normalograptids. Thus, we have coded them as separate characters.
8. Ancora umbrella: 0 – absent; 1 – 4-prong; 2 – 4-prong with spiral lists and loops; 3 – spiral basket.
9. Ancora sleeve enveloping rhabdosome: 0 – absent; 1 – present.
10. Dicalycal theca: 0 – present; 1 – absent.
11. Length of downward-grown protheca 1^1: 0 – long (> 0.3 mm); 1 – short (<0.3 mm); 2 – absent.
12. Point of differentiation of 2nd theca: 0 – from foramen in downward-grown th1^1; 1 – from near base of th1^1; 2 – from point in upward-grown part of th1^1.
13. Fusellar differentiation of 2nd theca: 0 – vertical unconformity at base of th1^1; 1 – abrupt line of differentiation (fusellar unconformity or densely packed, interfingering fusellae) diagonally crossing sicula; 2 – interfingering fusellae showing diverging thecae.
14. Point of upturn of th1: 0 – below sicular aperture; 1 – at level of sicular aperture; 2 – above sicular aperture.
15. Growth direction of 2nd theca: 0 – across sicula; 1 – above 1st theca; 2 – truncated (as described by Hutt *et al.* 1970, for *Rhaphidograptus toernqusti*).
16. Point of origin of th2^1 (th3 in uniserial taxa): 0 – proximal (near base of 2nd theca); 1 – delayed.
17. Proximal end shape (profile of 1st thecal pair): 0 – U-shaped (first thecal pair has straight, parallel subapertural walls); 1 – cup-shaped (convex, slightly inclined subapertural walls); 2 – V-shaped (straight, moderately inclined subapertural walls); 3 – flared (concave subapertural walls).
18. Elongate 1st thecal pair (relative to succeeding thecae): 0 – no; 1 – yes.
19. Proximal dorsal rhabdosomal curvature: 0 – absent; 1 – present.
20. Sicular apex: 0 – embedded in median septum, more-or-less central; 1 – free (unattached); 2 – marginal, obverse; 3 – in dorsal wall (uniserial).
21. Nema support (mesial-distal): 0 – embedded in median septum, central; 1 – marginal, supported by narrow, partial median septum; 2 – marginal, embedded in obverse thecal wall; 3 – embedded in dorsal wall (uniserial); 4 – internal, unattached (free); 5 – internal, attached to bases of interthecal septa.
22. Dorsal stipe wall, proximally (dorsal wall in uniserial forms, full medial septum in biserial, bistipular forms); 0 – alternating biserial (unistipular); 1 – straight; 2 – undulose; 3 – zig-zag.
23. Dorsal stipe wall change distally: 0 – no change; 1 – changes from undulose to straight; 2 – changes from alternating, unistipular to straight.
24. Stipe geometry: 0 – scandent biserial (unistipular or bistipular); 1 – unibiserial; 2 – uniserial.

25. Apertural thickening, 2nd thecal pair: 0 – none; 1 – apertural rim only; 2 – complete selvage (continuously thickened around apertural rim and geniculum); 3 – geniculum only.
26. Apertural orientation, 2nd thecal pair: 0 – horizontal (normal to rhabdosomal axis); 1 – everted; 2 – introverted.
27. Apertural shape, 2nd thecal pair: 0 – straight; 1 – concave; 2 – paired lateral lobes (convex).
28. Form of supra-apertural wall (wall above apertural rim but below geniculum, where present), 2nd thecal pair: 0 – straight, weakly inclined; 1 – straight, strongly inclined; 2 – concave.
29. Shape of geniculum (above apertural rim), 2nd thecal pair: 0 – absent; 1 – rounded; 2 – sharp.
30. Genicular flange, 2nd thecal pair: 0 – absent; 1 – ventral flange; 2 – flange extending laterally and ventrally (wrap-around); 3 – flange extending downward over apertural excavation.
31. Genicular spines, 2nd thecal pair: 0 – absent; 1 – ventral; 2 – paired, lateral or latero-ventral.
32. Apertural spines, 2nd thecal pair: 0 – absent; 1 – paired spines; 2 – paired branching spines.
33. Form of subapertural wall (wall below ventral apertural rim, above geniculum, where present), 2nd thecal pair: 0 – straight; 1 – concave; 2 – convex; 3 – sigmoidal.
34. Inclination of subapertural wall, 2nd thecal pair: 0 – parallel to rhabdosomal axis; 1 – inclined moderately outward; 2 – inclined strongly outward; 3 – inclined inward.
35. Inclination of interthecal septum, 2nd thecal pair: 0 – parallel to rhabdosomal axis; 1 – inclined outward.
36. Shape of interthecal septum, 2nd thecal pair: 0 – straight; 1 – concave; 2 – convex; 3 – sigmoidal.
37. Apertural thickening, distal thecae: 0 – none; 1 – apertural rim only; 2 – complete selvage (continuously thickened around apertural rim and geniculum); 3 – geniculum only.
38. Apertural orientation, distal thecae: 0 – horizontal (normal to rhabdosomal axis); 1 – everted; 2 – introverted.
39. Apertural shape, distal thecae: 0 – straight; 1 – concave; 2 – paired lateral lobes (convex).
40. Form of supra-apertural wall (wall above apertural rim but below geniculum, where present), distal thecae: 0 – straight, weakly inclined; 1 – straight, strongly inclined; 2 – concave.
41. Shape of geniculum (above apertural rim), distal thecae: 0 – absent; 1 – rounded; 2 – sharp.
42. Genicular flange, distal thecae: 0 – absent; 1 – ventral flange; 2 – flange extending laterally and ventrally (wrap-around); 3 – flange extending downward over apertural excavation.
43. Genicular spines, distal thecae: 0 – absent; 1 – ventral; 2 – paired, lateral or latero-ventral.
44. Apertural spines, distal thecae: 0 – absent; 1 – paired spines; 2 – paired branching spines.
45. Form of subapertural wall (wall below ventral apertural rim, above geniculum, where present), distal thecae: 0 – straight; 1 – concave; 2 – convex; 3 – sigmoidal.
46. Inclination of subapertural wall, distal thecae: 0 – parallel to rhabdosomal axis; 1 – inclined moderately outward; 2 – inclined strongly outward; 3 – inclined inward.
47. Shape of interthecal septum, distal thecae: 0 – straight; 1 – concave; 2 – convex; 3 – sigmoidal.
48. Inclination of interthecal septum, distal thecae: 0 – parallel to rhabdosomal axis; 1 – inclined outward.
49. Distal thecal overlap: 0 – small (< 1/3); 1 – moderate (1/3–2/3); 2 – large (>2/3).
50. Change in thecal form, proximal to distal: 0 – uniform (no change); 1 – gradual over proximal region; 2 – gradual over mesial region; 3 – abrupt, in proximal region.
51. Rhabdosomal widening: 0 – widens most strongly in proximal region; 1 – widens mainly in mesial regions; 2 – widens throughout rhabdosome; 3 – parallel-sided throughout.
52. Cortical bandages have thickened edges: 0 – no; 1 – yes.
53. Thickened list on median, ventral portion of thecae: 0 – absent; 1 – present.
54. Thecal apertural regions reduced to framework of lists: 0 – no; 1 – yes.
55. Whole thecae reduced to framework of lists: 0 – no; 1 – yes.

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APPENDIX 3

Matrix of taxa and character states used in the analysis in this study.

Taxa\Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
N. angustus	1	0	2	2	0	1&2	0	0	0	0	0	0	0	0	0	0	0	0&1	0	0	0	1&2	0&1	0	2	0&1	1	2	1&2	0	0	0	0	0	0	2	2	0	1	2	1&2	0	0	0	0	0	2	0/1	1	0	0	?	0	0	0
N. normalis	0&1	0	2	2	0	1&2	0	0	0	0	0	0	0/1	0	0	0	0	0	0	0	0	1	0	0	2	0	1	2	2	0	0	0	0	0	0	2	2	0	1	2	2	0	0	0	0	0	0	0	1	0	0	?	0	0	0
N. rectangularis	0&1	0	2	2	0	2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0&1	0&2	0	2	0	1	2	2	0	0	0	0	0	0	2	2	0	1	2	2	0	0	0	0	0	0	0	1	0	0	?	0	0	0
R. toernquisti	0	0	0	4	0	2	0	0	0	0	0	1	0&1	2	1	0	0	0	0	0	0	0&2	1&2	1	2	0	1	2	2	0	0	0	0	0	0	3	2	0	0	2	2	0	0	0	0	0	3	0	1	0	1	0	0	0	0
N. magnus	0	0	2	2&3	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	2	0	1	1	1	2	1	0	0	0	0	1	1	0	0	1	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0
N. praecursor	1	0	3	2	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	2	0	2	1	1	2	1	0	0	0	0	1	1	0	2	0&1	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0
N. gnomus	1	0	2	2	0	1	0	0	0	0	0	1	0	0&1	0	0	0	0	0	0	0	0	2	0	1	1	2	1	0	0	0	0	1	1	0	1	0	2	1	0	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0
N. laciniosus	1	0	2	2	0	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0	1	1	1	2	1	0	0	0	0	1	1	2	1	1	0	1	0	0	0	1	0	1	1	1	0	0	0	0	0	0	0	0
N. ojsuensis	0	0	3	2	0	1	0	0	0	0	0	?	1	0	0	0	0	0&1	0	0	0	0&2	0&1	0	2	0	1	2	2	0	0	0	0	0	1	3	2	0	0	2	1&2	0	0	0	0	1	3	1	1	0&1	0	?	0	0	0
N. extraordinarius	0&1	0	3&4	1&2	0	1	0	0	0	0	0	?	1	0	0	0	1	0	0	0	0	2	1	0	2	0	1	2	2	0	0	0	0	0	1	3	2	0	0	2	2	0	0	0	0	0&1	3	1	2	0	0&1	?	0	0	0
N. parvulus	0&1	0	2&3	1&2	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	2	0&1	0	2	1	1	2	2	0	0	0	0	1	1	3	2	0&1	1	2	1	0	0	0	0	1	3	1	1	0	0	?	0	0	0
N. persculptus	0&1	0	3	2	0	1	0	0	0	0	0	?	1	0	0	0	1	0	0	0	0	0&2	1&2	0	2	1	1	2	2	0	0	0	0	1	1	3	2	0&1	1	2	1	0	0	0	0	1	3	1	1	0	0	?	0	0	0
Mbol. sibericus	1	0	?	2	0	?	0	0	0	0	0	?	1	0	0	0	1	0	0	0	0	2	0&1	0	2	0	1	2	2	0	0	0	0	1	1	3	2	0	1	2	2	0	0	0	0	1	3	1	1	0	0	?	0	0	0
Nd. modestsus	1	0	2&3	2	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	?	?	0	2	1	1	2	2	0	0	0	0	1	1&3	2	0	0	2	1	0	0	0	0	1	0&3	1	1	1	1	0	?	0	0	0
Nd. africanus	0	0	3	1	0	1	0	0	0	0	0	?	1	0	0	?	1	0	0	0	0	2	0	2	1	1	2	2	0&1	0	0	0	1	1	3	2	1	1	2	2	0	0	1	1	3	1	2	1	0	?	0	0	0	0	0
Nd. fezzanensis	0	0	?	1&2	0	1	0	0	0	0	0	?	0	0	0	?	0	0	0	0	0	2	0	2	1	1	2	2	0	0	0	0	1	1	3	2	1	1	2	2	0	0	1	1	3	1	2	1	0	?	0	0	0	0	0
N. avitus	0	0	2	3	0	1	0	0	0	0	0	2	1	0&1	0	1	0	1	0	0	0	0	1	0	2	0	1	2	2	0	0	0	0	1	0	2	0	0	2	2	0	0	0	2	1	0	0	1&2	0	0	?	0	0	0	0
N. aff avitus	0	0	3	3	0	?	0	0	0	0	1	2	?	0&1	0	?	0	1	0	0	1	1	1	0	2	0	1	2	1&2	0	0	0	0	1	0	2	2	0	0	2	1&2	0	0	2	1	2	0	1	0	0	?	0	0	0	0
Nd. sinuatus	1	0	2	2	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	2	0&2	0	2	1	0	0	0	0	1	1	0	1	0&1	0	2	1	0	0	0	0&1	1&2	2	1	1	3	1	0	0	0	0	0
Nd. elongatus	1	0	2	2	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	2	0	0	2	2	0	0	0	0	0	0	0	1	0&1	0	2	1	0	0	0	2	1	?	1	1	2	1	0	0	0	0	0
Nd. tcherskyi	1	0	2	2	0	1	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	2	0	2	2	0	2	2	0	0	0	0	1	0	1	1	0	2	1	0	0	0	2	2	2	1	1	3	1	0	0	0	0	0	0
Nd. magnus	0	0	4	2	0	1	0	0	0	0	0	?	1	0	0	?	1	0	0	0	0	2	0	2	1	1	2	2	1	0	0	0	1	1	3	2	1	0&1	2	2	0	0	1	1	3	1	2	1	0	?	0	0	0	0	0
Mcl. orientalis	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	2	0	2	2	0	0	2	0	0	3	2	0	2	2	0	0	2	0	3	0	1	0	3	0	0	0	0	0	0	0	0
Mcl. slalom	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	2	0	2	2	3	0	2	0	0	3	2	2	2	3	0	0	2	0	3	0	1	0	3	0	0	0	0	0	0	0	0
Mcl. undulatus	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	2	2	0	2	2	3	0	2	3	0	3	2	2	2	3	0	0	2	3	3	0	1	0	3	0	0	0	0	0	0	0	0
S? illustris	1	1	2	2	0	1	0	0	0	0	0	?	0	0	1	1&2	0	0	0	0	0	2	0	1	1	0	?	0&1	0	0	?	?	1	0	1	1	0	0	0	0	0	0	?	?	1	1	0	0	0	0	0	0	0	0	0
N. jideliensis	1	0	3	2	0	1	0	0	0	0	0	1	0	0	0	0&1	0	0	0	1	0	2	0	1	2	2	2	0	0	1	0	1	0	2	0	1	2	2	2	0	0&1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Pcl? jinyangensis	0&1	0	3	2	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	2	0	1	2	2	2	0	0	1	0	1	0	2	0&1	1	2	2	2	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0

APPENDIX 3. *continued.*

Taxa\Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
H. comantis	0	0	3	2	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	2	0	1	2	2	2	2	0&1	0	0	1	0	2	0	1	2	2	2	2	0&1	0	0	0	0	1	0	0	0	0	0
N? madernii	1	1	3	2	1	1	0	0	0	1	0	0	2	0	0	1	1	0	0	1	5	0	0	0	2	1	1	2	2	0&1	0	0	0&1	1	1	3	2	0	1	2	2	0	0	0	1	1	3	1	1	0	0	0	0	0	0
Pcl? paucispinus	1	1	3	2	0	1	0	0	0	1	0&1	1	2	0	0	1	3	0	0	1	5	0	0	0	2	1	1	2	2	1	0	0	0&1	1	1	3	2	0	1	2	2	1	0	0&1	0	1	3	1	1	0	0	0	0	0	0
Pcl? kiliani	0&1	1	3	2	0	1	0	0	0	1	1	1	?	0	0	1	3	0	0	1	5	0	0	0	2	1	1	2	2	1	0	0	1	1	1	3	2	0	1	2	2	0&1	0	0&1	0	1	3	1	1	0	0	0	0	0	0
Pcl. innotatus	1	0	3	2	0	1	0	0	0	0	0	0	2	0	0	1	1&3	0	0	0	0	2	0	2	1	0&1	2	1	1	0	0	1	1	1	1	0	2	1	0	2	1	1	0	0	0	0	1	1	0	0	0	0	0	0	0
N. nikolaevi	1	0	1	1	0	2	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	1	1	1	2	1	0	0	0	0	1	1	2	1	1	1	2	1	0	0	0	0	1	2	1	1	0	0	0	0	0	0
R. bellulus	2	0	1	1	0	2	0	0	0	1	2	1	2	0	0	1	1	0	0	1	4	0	0	0	1	1	1&2	1	0	0	1	0	2	1	2	1	1	0	0	0	0	0	1	0	2	2	1	1	0	0	1	0	0	0	0
R. kayi	2	0	1	1	0	2	0	0	0	1	2	1	2	0	0	1	1	0	0	1	4	0	0	1	0&1	1	2	1	0	0	0&2	0	2	1	2	1	0&2	0	2	1	0	0	0	0	2	2	1	1	0	0	1	0	0	0	0
Ag. spiniferus	2	0	1	1	0	2	0	0	0	1	1	1	2	0	1	1	1	0	0	1	4	0	0	1	1	1	1&2	1	0	0	1	0	2	1	2	1	1	0	0	0	0	0	1	0	2	2	1	1	0	0	1	0	0	0	0
G. tamariscus	1	0	0	3	0	1	0	0	0	1	1	1	2	0	0	1	1	0	0	2	2	0	0	0	1	1	1	2	1	0	0	0	0	1	1	0	1	0	1	2	1	0	0	0	0	1	0	1	0	0	0	0	0	0	0
G. tamariscoides	1	0	0	3	0	1	0	0	0	1	1	1	2	0	0	1	0	0	0	2	2	0	0	0	1	1	1	2	1	0	0	0	0	0	1	1	1	0	1	2	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
G. aff incertus	0&1	0	3	3	0	1	0	0	0	1	1	1	2	0	0	1	1	0	0	1	1	0	0	0	2	1	0	2	1	0	0	0	0	1	1	0	2	0	0	2	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0
G. elegans	1	0	2	3	0	2	0	0	0	1	1	1	2	0	0	1	1	0	0	1	4	0	0	0	1	1	1	2	1	0	0	0	0	1	1	2	1	0	1	2	1	0	0	0	0	1	0	1	1	0	0	0	0	0	0
C. comatus	1	0	2	3	1	0	0	0	0	1	1	1	2	0	0	1	2	0	0	1	4	0	0	2	1	1	2	2	0	0	0	1	1	1	1	2	1	1	2	1&2	0	0	0	0	1	0&1	1	1	0	0	0	0	0	0	0
S? cortoghianensis	1	1	3	2	0	0	0	0	0	1	0	?	?	0	0	1	1	0	1	1	5	0	0	0	2	1	1	2	1	0	0	0	0	1	1	0	2	0	0	2	1	0	0	0	0	1	0	1	1	0	0	?	0	0	0
S. eberleini	1	1	?	2	0	0	0	0	1	1	?	?	0	0	1	2	0	1	1	5	0	0	0	1	1	1	0	1	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	1	0	1	1	0	0	?	0	0	0
S. sp. 1	1	1	3	2	0	0	0	0	0	1	1	0	2	0	0	1	3	1	1	1	1	0	0	0	1	0	1	0	0	0	0	0	2	1	0	?	0	1	0	0	0	0	0	2	0	1	1	0	0	0	0	0	0	0	0
Pet. ankyratus	0	0	3	3	0	1	4	1	0	1	1	1	?	0	0	1	3	1	0	2	1	0	0	0	1	1	1	1	0	0	0	0	1	2	1	2	1	1	1	1	0	0	0	0	0	2	1	1	2	0	0	0	0	0	0
Pet. intermedius	0	0	4	3	0	1	4	1	0	1	1	1	2	0	0	1	3	1	0	2	1	0	0	0	1	1	1	2	0	0	0	0	2	2	1	1	1	1	1	2	0	0	0	0	1	2	1	1	2	0	0	0	0	0	0
Ppet. sp. A	1	0	2	3	0	0	0	0	0	1	1	1	2	0	0	1	2	0	0	1	4	0	0	0	1	1	1	2	0	0	0	0	0	2	1	0	1	1	1	2	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0
Ppet. palmeus	1	0	2	3	0	1	0	0	0	1	1	?	?	0	0	1	2	0	0	2	1	0	0	0	1	1	1	0	0	0	0	0	0	2	1	0	1	1	1	0	0	0	0	0	1	0	1	2	0	0	?	0	0	0	0
A. ascensus	0	0	0	3&4	0	1	2	0	0	1	2	1	1&2	0	1	0	1	1	0	0	1	0	2	0	1	2	2	0	0	0	0	0	0	2	0	1	2	2	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0
Di. minutus	0	0	0	4	0	1	0	0	0	1	2	?	2	1	1	0	1	1	3	0	1	0	1	2	0	1	2	2	0	0	0	0	0	2	0	0	2	2	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0
At. primitivus	0	0	0	4	0	1	0	0	0	1	2	2	?	2	1	1	0	1	1	3	3	1	0	2	1	0	2	2	0	0	0	0	0	1	0	1	2	2	0	0	0	2	0	0	0	1	0	3	0	0	0	0	0	0	0
At. ceryx	0	0	0	4	0	1	0	0	0	1	2	2	?	2	1	1	0	1	1	3	3	1	0	2	1	0	0&1	2	1	0	0	0	0	0	0	0	1	0	0&1	2	1	0	0	0	0	2	0	0	1	0	3	0	0	0	0
At. atavus	0	0	0	4	0	1	0	0	0	1	2	2	?	2	1	1	0	1	1	3	3	1	0	2	1	0	1	2	1	0	0	0	0	1	0	0	1	1	1	0	1	0	0	0	0	1	0	1	1	0	2	0	0	0	0
Ps. inopinatus	1	0	3	3	0	1	4	2	0	1	1	1	2	0	0	1	3	0	0	1	4	0	0	0	1	0&1	0	1	0	0	0	0	2	0	2	1	0	1	0	0	1	0	0	0	0	2	0	2	0	1	1	0	0	0	0
Ps. obuti	0	0	0/3	2&3	0	1	4	3	1	0	0	1	2	0	0	1	3	0	0	?	?	0	2	0	1	1	2	1	0	0	0	1	1	2	1	0	1	1	2	1	0	0	0	1	1	2	0	1	1	0	0	0	0	0	0
H. introversus	0	0	3	2	0	1	4	3	1	?	0	1	2	0	0	1	3	0	0	1	4	0	?	0	1	2	2	1	0	0	0	1	3	2	1	0	1	2	2	1	0	0	0	1	3	2	0	1	1	0	0	0	1	1	0
Pseudoretiolites	1	0	?	2	0	1	4	3	1	1	0	1	?	0	0	1	3	0	0	1	2	0	0	0	1	2	2	1	0	0	0	1	1	2	1	0	1	2	2	1	0	0	0	1	1	2	0	1	0	0	0	0	1	1	1

REFERENCES

ANHUI GEOLOGICAL SURVEY TEAM (ed.) 1982. *Graptolites from Anhui*. Anhui Science and Technology Publishing House, Hefei.

BARRANDE, J. 1850. *Graptolites de la Bohême*. Published by the author, Prague.

BATES, D. E. B., KOZŁOWSKA, A. & LENZ, A. C. 2005. Silurian retiolitid graptolites: Morphology and evolution. *Acta Palaeontologica Polonica*, **50**, 705–720.

BJERRESKOV, M. 1975. Llandoverian and Wenlockian graptolites from Bornholm. *Fossils and Strata*, **8**, 1–93.

BOUČEK, B. 1944. O některých ostnitých diplograptidech českého a saského siluru. *Rozpravy České akademie věd a umění, Třída 2*, **53(25)**, 1–6.

BOUČEK, B. & MÜNCH, A. 1952. The Central European Retiolites of the Upper Wenlock and Ludlow. *Sborník ústredniho ústavu Geologickeho, oddíl paleontologicky*, **19**, 1–54 (Czech text), 55–103 (Russian text), 104–151 (German text).

BOUČEK, B. & PŘÍBYL, A. 1941. Über die Gattung *Petalolithus* Suess aus dem böhemischen Silur. *Mitteilungen der Tschechischen Akademie der Wissenschaften*, 1–17.

BULMAN, O. M. B. 1936. *Rhaphidograptus*, a new graptolite genus. *Geological Magazine*, **73**, 19–26.

BULMAN, O. M. B. 1955. Graptolithina with sections on Enteropneusta and Pterobranchia. *In:* MOORE, R. M. (ed.) *Treatise on Invertebrate Paleontology Pt. V*. Geological Society of America and University of Kansas Press, Boulder and Lawrence, 1–101.

BULMAN, O. M. B. 1970. Graptolithina with sections on Enteropneusta and Pterobranchia. *In:* TEICHERT, C. (ed.) *Treatise on Invertebrate Paleontology, Pt. V*. Geological Society of America and University of Kansas Press, Boulder and Lawrence, 1–163.

BULMAN, O. M. B. & RICKARDS, R. B. 1968. Some new diplograptids from the Llandovery of Britain and Scandinavia. *Palaeontology*, **11**, 1–15.

CHALETSKAYA, O. N. 1960. Novye vidy llandovereyski graptolitov Sredney Azii. *In:* MARKOVSKY, B. P. (ed.) *Novye Vidy Drevnikh Rastenii I Bespozvononochnykh SSSR, Chast' II*. Moskva, Gosudarstvennoe Nauchno-Teknicheskoje Izdatel'stvo, 373–375.

CHEN, X. & LIN, Y. K. 1978. Lower Silurian graptolites from Tongzi, northern Guizhou. *Memoirs of Nanjing Institute of Geology and Palaeontology, Academia Sinica*, **12**, 1–76 (in Chinese).

CHEN, X., MELCHIN, M. J., SHEETS, H. D., MITCHELL, C. E. & FAN, J.-X. 2005a. Patterns and processes of latest Ordovician graptolites extinction and recovery based on data from South China. *Journal of Paleontology*, **79**, 842–861.

CHEN, X., FAN, J.-X., MELCHIN, M. J. & MITCHELL, C. E. 2005b. Hirnantian (latest Ordovician) graptolites from the Upper Yangtze region, China. *Palaeontology*, **48**, 235–280.

CHURKIN, M. & CARTER, C. 1970. Early Silurian graptolites from southeastern Alaska and their correlation with graptolitic sequences in North America and the Arctic. *Professional Papers U.S. Geological Survey*, **653**, 1–51.

DAVIES, K. A. 1929. Notes on the graptolite faunas of the Upper Ordovician and Lower Silurian. *Geological Magazine*, **66**, 1–27.

DESIO, A. 1940. Fossili neosilurici del Fezzan occidentale. *Annali del Museo Libico di Storia Naturale*, **2**, 13–45.

DONOGHUE, P. C. J., PURNELL, M. A., ALDRIDGE, R. J. & ZHANG, S. 2008. The interrelationships of "complex" conodonts (Vertebrata). *Journal of Systematic Palaeontology*, **6**, 119–153.

ELLES, G. L. & WOOD, E. M. R. 1906. Monograph of British Graptolites, part V. *In:* LAPWORTH, C. (ed.) *Palaeontographical Society*. Monograph of the Palaeontolographical Society, Published by the Palaeontographical Society, London, 181–216.

ELLES, G. L. & WOOD, E. M. R. 1907. Monograph of British Graptolites, part VI. *In:* LAPWORTH, C. (ed.) *Palaeontographical Society*. Monograph of the Palaeontographical Society, Published by the Palaeontographical Society, London, 217–272.

ELLES, G. L. & WOOD, E. M. R. 1908. Monograph of British Graptolites, part VII. *In:* LAPWORTH, C. (ed.) *Palaeontographical Society*. Monograph of the Palaeontographical Society, Published by the Palaeontographical Society, London, 273–258.

FAN, J. X. & CHEN, X. 2007. Preliminary report on the late Ordovician graptolite extinction in the Yangtze region. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **245**, 82–94.

FANG, Y. T., LIANG, S. J., ZHANG, D. L. & YU, J. L. 1990. *Stratigraphy and graptolite fauna of Lishuwo Formation from Wuning, Jiangxi*. Nanjing University Publishing House, Nanjing, 1–155 (in Chinese).

FINNEY, S. C., BERRY, W. B. N. & COOPER, R. A. 2007. The influence of denitrifying seawater on graptolite extinction and diversification during the Hirnantian (latest Ordovician) mass extinction event. *Lethaia*, **40**, 281–291.

FORTEY, R. A. & COOPER, R. A. 1986. A phylogenetic classification of the graptoloids. *Palaeontology*, **29**, 631–654.

FORTEY, R. A., ZHANG, Y. & MELLISH, C. 2005. The relationships of biserial graptolites. *Palaeontology*, **48**, 1241–1272.

FRECH, F. 1897. *Lethaea geognostica oder Beschreibung und Abbildung für die Gebirgs-Formationen bezeichnendsten Versteinerungen. Herausgegeben von einer Vereinigung von Palaeontologen, 1. Teil – Lethaea Palaeozoica*. E. Schweizerbart'sche Verlagshandlung, Stuttgart, 544–684.

FU, L. P. & SONG, L. S. 1986. Stratigraphy and paleontology of Silurian in Ziyang Region (Transitional Belt). *Bulletin of the Xi'an Institute of geology and Mineral Resources, Chinese Academy of Geological Sciences*, **14**, 1–198 (in Chinese).

GOLDMAN, D., MITCHELL, C. E., MELCHIN, M. J., FAN, J. & WU, S. 2011. Biogeography and Mass Extinction: Extirpation and re-invasion of *Normalograptus* species (Graptolithina) in the Late Ordovician Palaeo-tropics. *Proceedings of the Yorkshire Geological Society*, **58**, 227–246.

HARPER, D. A. T. & WILLIAMS, S. H. 2002. A relict Ordovician brachiopod fauna from the *Parakidograptus acuminatus* Biozone (lower Silurian) of the English Lake District. *Lethaia*, **35**, 71–78.

HISINGER, H. 1837. Supplementum 1. *Lethaea Suecica seu Petrifacta Suecica*. D. A. Norstedt et filii, Stockholm, 1–24.

HUTT, J. E., RICKARDS, R. B. & SKEVINGTON, D. 1970. Isolated Silurian graptolites from the Bollerup and Klubbedden Stages of Dalarna, Sweden. *Geologica et Palaeontologica*, **4**, 1–23.

JONES, O. T. 1909. The Hartfell-Valentian succession in the district around Plynlimon and Pont Erwyd (North Cardiganshire). *Quarterly Journal of the Geological Society of London*, **65**, 463–537.

KEBLE, R. A. & BENSON, W. N. 1929. Ordovician graptolites of North-west Nelson. *Transactions of the New Zealand Institute*, **59**, 840–863.

KOREN', T. & BJERRESKOV, M. 1997. Early Llandovery monograptids from Bornholm and the southern Urals: taxonomy and evolution. *Bulletin of the Geological Society of Denmark*, **44**, 1–43.

KOREN', T. & BJERRESKOV, M. 1999. The generative phase and first radiation event in the early Silurian monograptid history. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **154**, 3–9.

KOREN', T. N. & MELCHIN, M. J. 2000. Lowermost Silurian graptolites from the Kurama Range, eastern Uzbekistan. *Journal of Paleontology*, **74**, 1093–1113.

KOREN', T. N., MIKHAYLOVA, N. F. & TSAI, D. T. 1980. Graptolity. *In:* APOLLONOV, M. K., BANDALETOV, S. M. & NIKITIN, I. F. (eds) *Granitsa Ordovika I Silura v Kazakhstane*. Nauka Kazakh SSR Publishing House, Alma-Ata, 121–170.

KOREN', T. N., ORADOVSKAYA, M. M., PYLMA, L. J., SOBOLEVSKAYA, R. F. & CHUGAEVA, M. N. 1983. *Granitsa Ordovika I Silura na Severo-Vostoke S.S.S.R.* Nauka Publishers, Leningrad, 1–205.

KOREN', T. N. & RICKARDS, R. B. 1996. Taxonomy and evolution of Llandovery biserial graptoloids from the southern Urals, western Kazakhstan. *Special Papers in Palaeontology*, **54**, 1–103.

KOREN', T. N. & RICKARDS, R. B. 2004. An unusually diverse Llandovery (Silurian) diplograptid fauna from the southern Urals of Russia and its evolutionary significance. *Paleontology*, **47**, 859–918.

KOZŁOWSKA-DAWIDZIUK, A., LENZ, A. C. & BATES, D. E. B. 2003. A new classification of ancorate diplograptids. *In:* ORTEGA, G. & ACEÑOLAZA, G. F. (eds) INSUGEO, Serie Correlación Geológica. *Proceedings of the 7th International Graptolite Conference & Field Meeting of the International Subcommission on Silurian Stratigraphy*. Cumunicarte Editorial, Tucumán, Argentina, 565–569.

KURCK, C. 1882. Några nya graptolitarter från Skåne. *Geologiska Föreningens i Stockholm Förhandlingar*, **6**, 294–304.

LAPORTE, D. F., HOLMDEN, C. *ET AL.* 2009. Local and global perspectives on carbon and nitrogen cycling during the Hirnantian glaciation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **276**, 182–195.

LAPWORTH, C. 1873. On an improved classification of the Rhabdophora. *Geological Magazine*, **10**, 500–504, 555–560.

LAPWORTH, C. 1876. On Scottish Monograptidae. *Geological Magazine*, **3**, 308–321, 350–360, 499–507, 544–552.

LAPWORTH, C. 1877. On the graptolites of County Down. *Proceedings of the Belfast Naturalists Field Club*, **1**, 107–147.

LAPWORTH, H. 1900. The Silurian sequence of Rhayader. *Quarterly Journal of the Geological Society of London*, **56**, 67–137.

LEGRAND, P. 1970. Les couches a *Diplograptus* du Tassili de Tarit (Ahnet, Sahara algerien). *Bulletin de la Societé d'Historire naturelle de l'Afrique du Nord*, **60**, 3–58.

LEGRAND, P. 1977. Contribution al'étude des graptolites du Llandoverien inferieur de L'Oued in Djerane (Tassili N'Ajjer oriental, Sahara algérien). *Bulletin de la Societé d'Historire Naturelle de l'Afrique du Nord*, **67**, 141–196.

LEGRAND, P. 1987. Modo de desarrollo del Suborden Diplograptina (Graptolithina) en el Ordovicico superior y en el Silurico. Implicaciones taxonomicas. *Revista Expanola de Paleontologia*, **2**, 59–64.

LEGRAND, P. 1999. *Approche stratigraphique de l'ordovicien terminal et du silurien inferieur du sahara algerien par l'etude des diplograptides (graptolites)*. Docteur d'Etat ès Sciences, Universite Michel de Montaigne, Bordeaux III, unpublished.

LEGRAND, P. 2002. La formation des argiles de Tedjert (?Ordovicien terminal-Silurien inférieur) au Tassili Oua-n-Haggar oriental (Sahara algerien) et sa faune graptolitique. *Annales de la Société Géolologique du Nord, Série 2*, **9**, 215–229.

LENZ, A. C. & MELCHIN, M. J. 1987. Silurian retiolitids from the Cape Phillips Formation, Arctic Islands, Canada. *Bulletin of the Geological Society of Denmark*, **35**, 161–170.

LENZ, A. C. & MELCHIN, M. J. 1997. Phylogenetic analysis of the Silurian Retiolitidae. *Lethaia*, **29**, 301–309.

LENZ, A. C., MELCHIN, M. J. & KOZŁOWSKA, A. 2010. Aeronian and lower Telychian retiolitid graptolites, Arctic Canada. 40. *The 20th Canadian Paleontology Conference and Canadian Association of Palynologists, Program and Abstracts*, September, 2010, Halifax, Canada.

LI, J. 1999. Lower Silurian Graptolites from Southern Anhui. *Bulletin of the Nanjing Institute of Geology and Palaeontology, Academia Sinica*, **14**, 70–157 (in Chinese, English summary).

LI, J. & GE, M. 1981. Development and systematic position of akidograptids. *Acta Palaeontologica Sinica*, **20**, 225–234 (in Chinese).

LOYDELL, D. K. 1992. Upper Aeronian and Lower Telychian (Llandovery) graptolites from western Mid-Wales. Part 1. *Monograph of the Palaeontographical Society*, **146**, 1–55, pl. 1.

LOYDELL, D. K. 2007. Graptolites from the Upper Ordovician and Lower Silurian of Jordan. *Special Papers in Palaeontology*, **78**, 1–66.

LOYDELL, D. K. & MALETZ, J. 2009. Isolated graptolites from the *Lituigraptus convolutus* biozone (Silurian, Llandovery) of Dalarna, Sweden. *Palaeontology*, **52**, 273–296.

LOYDELL, D. K., MALLETT, A. M., MIKULIC, D. G., KLUESSENDORF, J. & NORBY, R. D. 2002. Graptolites from near the Ordovician-Silurian boundary in Illinois and Iowa. *Journal of Paleontology*, **76**, 134–137.

LUKASIK, J. J. & MELCHIN, M. J. 1994. *Atavograptus primitivus* (Li) from the earliest Silurian of Arctic Canada: Implications for monograptid evolution. *Journal of Paleontology*, **68**, 1159–1163.

LUKASIK, J. J. & MELCHIN, M. J. 1997. Morphology and classification of some early Silurian monograptids (Graptoloidea) from the Cape Phillips Formation, Canadian Arctic Islands. *Canadian Journal of Earth Sciences*, **34**, 1128–1149.

MADDISON, D. R. & MADDISON, W. P. 2000. *MacClade 4*. Sinauer Associates, Sunderland, Massachusetts.

MALETZ, J., CARLUCCI, J. & MITCHELL, C. E. 2009. Graptoloid cladistics, taxonomy and phylogeny. *Bulletin of Geosciences*, **84**, 7–19.

M'COY, F. 1850. On Some New Genera and Species of Silurian Radiata in the Collection of the University of Cambridge. *Annual & Magazine of Natural History, ser. 2*, **6**, 270–290.

MELCHIN, M. J. 1987. *Late Ordovician and Early Silurian graptolites, Cape Phillips Formation, Canadian Arctic Archipelago*. Unpublished PhD thesis, University of Western Ontario, Canada.

MELCHIN, M. J. 1989. Llandovery graptolite biostratigraphy and paleobiogeography, Cape Phillips Formation, Canadian Arctic Islands. *Canadian Journal of Earth Science*, **26**, 1726–1746.

MELCHIN, M. J. 1998. Morphology and phylogeny of some Early Silurian 'diplograptid' genera from Cornwallis Island, Arctic Canada. *Palaeontology*, **41**, 263–315.

MELCHIN, M. J. 1999. Origin of the Retiolitidae: insights from a new graptolite genus from the early Silurian of Arctic Canada. *Lethaia*, **32**, 261–269.

MELCHIN, M. J. 2008. Restudy of some Ordovician-Silurian boundary graptolites from Anticosti Island, Canada, and their biostratigraphic significance. *Lethaia*, **41**, 155–162.

MELCHIN, M. J. & HOLMDEN, C. 2006. Carbon isotope chemostratigraphy of the Llandovery in Arctic Canada: Implications for global correlation and sea-level change. *GFF*, **128**, 173–180.

MELCHIN, M. J. & MITCHELL, C. E. 1991. Late Ordovician extinction in the Graptoloidea. *In:* BARNES, C. R. & WILLIAMS, S. H. (eds) *Advances in Ordovician Geology*. Geological Survey of Canada, Canada, Paper 90–9, 143–156.

MELCHIN, M. J., KOREN', T. N. & ŠTORCH, P. 1998. Global diversity and survivorship patterns of Silurian graptoloids. *In:* LANDING, E. & JOHNSON, M. E. (eds) *Silurian Cycles: Linkages of Dynamic Stratigraphy with Atmospheric, Oceanic, and Tectonic Changes, James Hall Centennial Volume*. New York State Museum, Bulletin, **491**, 165–182.

MELCHIN, M. J., NACZK-CAMERON, A. & KOREN', T. N. 2003. New insights into the phylogeny of Rhuddanian (Lower Llandovery) graptolites. *In:* ORTEGA, G. & ACEÑOLAZA, G. F. (eds) INSUGEO, Serie Correlación Geológica. *Proceedings of the 7th International*

Graptolite Conference & Field Meeting of the International Subcommission on Silurian Stratigraphy. Cumunicarte Editorial, Tucumán, Argentina, 67–68.

MELCHIN, M. J., NACZK-CAMERON, A. & KOREN', T. N. 2004. New insights into the phylogeny of Rhuddanian (Lower Llandovery) graptolites. 38. *Canadian Paleontology Conference, 2004*. St. Andrews, NB.

MELCHIN, M. J., NACZK-CAMERON, A. & KOREN', T. N. 2005. Phylogenetic Analysis of some Rhuddanian (Lower Llandovery, Silurian) Graptolites. *North American Paleontological Convention, Halifax, Nova Scotia, June 19–25, 2005, Program and Abstracts*, 84–85.

MITCHELL, C. E. 1987. Evolution and phylogenetic classification of the Diplograptacea. *Palaeontology*, **30**, 353–405.

MITCHELL, C. E. 1990. Directional macroevolution of the diplograptacean graptolites: a product of astogenetic heterochrony and directed speciation. *In:* TAYLOR, P. D. & LARWOOD, G. P. (eds) *Major Evolutionary Radiations*. Systematics Association Special Volume, Clarendon Press, Oxford, 235–264.

MITCHELL, C. E., GOLDMAN, D., KLOSTERMAN, S. L., MALETZ, J., SHEETS, H. D. & MELCHIN, M. J. 2007a. Phylogeny of the Ordovician Diplograptoidea. *Acta Palaeontologica Sinica*, **46** (supplement), 332–339.

MITCHELL, C. E., SHEETS, H. D., *ET AL.* 2007b. Species abundance changes during mass extinction and the inverse Signor-Lipps effect: apparently abrupt graptolite mass extinction as an artifact of sampling. *Acta Palaeontologica Sinica*, **46** (supplement), 340–346.

MITCHELL, C. E., ŠTORCH, P., HOLMDEN, C, MELCHIN, M. J. & GUTIÉRREZ-MARCO, J. C. 2011. New stable isotope data and fossils from the Hirnantian Stage in Bohemia and Spain: Implications for correlation and paleoclimate. 371–378. *In.* GUTIÉRREZ-MARCO, J. C., RÁBANO, I. & GARCIA-BELLIDO, D. (eds.), *Ordovician of the World*. Cuadernos del Museo Geominera, 14. Instituto Geológico y Minero de España, Madrid.

MU, E., LI, J., GE, M., CHEN, X., NI, Y., LIN, Y. & MU, H.-N. 1974. Silurian Graptoloidea. 211–231. *In:* NANJING INSTITUTE OF GEOLOGY AND PALAEONTOLOGY, A. S. (ed.) *A handbook of the stratigraphy and paleontology in southwest China*. Science Press, Nanjing.

NACZK-CAMERON, A. 2000. *Systematics and Phylogeny of some early Silurian graptolites:* Glyptograptus *and related genera*. Unpublished MSc thesis, St. Francis Xavier University, Canada.

NANJING INSTITUTE OF GEOLOGY AND PALAEONTOLOGY (ed.) 1983. *Palaeontological Atlas of East China, 1. Early Paleozoic*. Geological Publishing House, Beijing, 1–657 (in Chinese).

NICHOLSON, H. A. 1868. On the graptolites of the Coniston Flags; with notes on the British species of the genus *Graptolites*. *Quarterly Journal of the Geological Society of London*, **24**, 521–545.

NICHOLSON, H. A. 1869. On some new species of graptolites. *Annals and Magazine of Natural History, series 4*, **4**, 231–242.

OBUT, A. M. 1955. Graptolity. *Polevoy Atlas Ordovicoy y Silurskoy Fauny Siberskoy Platformy*. Gosgeoltechizdat, Moscow, 136–139.

OBUT, A. M. 1965. Graptolity silura omulevsky gor (bassein reki Kolymy). *Stratigrafiya y Paleontologiya Paleozoya Aziatskoy Chasti CCCP*, Moscow, 33–46.

OBUT, A. M. & SENNIKOV, N. V. 1985. Ocobennocti llandoveriyckich planktontovich coobschestv Sibirskoy Platformi. *In:* BETECHTUNA, O. A. & ZHURAVLEVA, I. T. (eds) *Sreda y Jizn v Geologichechom Proshlom (Paleobasseiny i ich Obitateli)*. Trudy Instituta Geologii I Geofiziki, Nauka Publishing House, Novosibirsk, **628**, 51–60.

OBUT, A. M. & SOBOLEVSKAYA, R. F. 1966. *Graptolitit rannego silura i Kazachstane*. Akademii Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii Geofiziki, Ministerstvo Geologii SSSR, Nauchno-issledovatelskie Institut Geologii Arktiki, 1–56.

OBUT, A. M., SOBOLEVSKAYA, R. F. & MERKUR'EVA, A. P. 1968. *Graptolity Llandoveri v kernach burovitch skvazhin Norilskogo raiona*. Akademia Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii I Geofiziki, Ministerstvo Geologii SSSR, Nauchno-Issledovatel'sky Institut Geologii Arktiki. Moscow, 1–137.

OBUT, A. M., SOBOLEVSKAYA, R. F. & NIKOLAEV, A. A. 1967. *Graptoliti y stratigrafiya nizhnego silura okainnykh podnyatii kolym-skogo massifa*. Akademiya Nauk SSSR, Sibirskoe Otdelenie, Institut Geologii I Geofiziki, Ministerstvo Geologii SSSR, Nauchno-Issledovatel'sky Institut Geologii Arktiki. Sibirskoe otdelenije, Institut Geologii I Geofiziki, Moscow, 1–162.

PACKHAM, G. H. 1962. Some diplograptids from the British Lower Silurian. *Palaeontology*, **5**, 498–526.

PAŠKEVIČIUS, J. 1976. On some new Llandoverian diplograptids of the eastern Baltic. *In:* KALJO, D. & KOREN', T. N. (eds) *Graptolites and Stratigraphy*. Academy of Sciences of Estonian SSR, Institute of Geology, Tallinn, 140–151.

PERNER, J. 1895. *Éstudes sur les Graptolites de Boheme: II Partie, Monographie des Graptolites de V Étage D*. Raimond Gerhard, Prague.

PŘÍBYL, A. 1947. Classification of the genus *Climacograptus* Hall 1865. *Bulletin International de l'Académie Tchèque des Sciences, Prague*, **48**, 1–12.

PŘÍBYL, A. 1948. Nekolik novych graptolitovych podrodu z celedi Dimorphograptidae a Diplograptidae. *Vestnik Statniho geologickeho ustavu Ceskoslovenske Republicky*, **23**, 37–48.

RICKARDS, R. B. 1970. The Llandovery (Silurian) graptolites of the Howgill Fells, northern England. *Palaeontographical Society Monograph*, **123**, 1–108.

RICKARDS, R. B. 1972. *Climacograptus scalaris* (Hisinger) and the subgenus *Glyptograptus* (Pseudoglyptograptus). Geologiska Foreningens Stockholm Forhandlingar, **94**, 271–280.

RICKARDS, R. B. & HUTT, J. E. 1970. The earliest monograptid. *Proceedings of the Geological Society of London*, **1663**, 115–119.

RICKARDS, R. B., HUTT, J. E. & BERRY, W. B.N. 1977. Evolution of Silurian and Devonian graptoloids. *Bulletin of the British Museum (Natural History), Geology*, **28**, 1–120.

RICKARDS, R. B. & KOREN', T. N. 1974. Virgellar meshwork and sicular spinosity in Llandovery graptoloids. *Geological Magazine*, **111**, 193–204.

RICKARDS, R. B., ORTEGA, G., BASSETT, M., BOSO, M. A. & MONALDI, C. R. 2002. *Talacastograptus*, an unusual biserial graptolite, and other Silurian forms from Argentina and Bolivia. *Ameghiniana*, **39**, 343–350.

RUSSEL, J. C., MELCHIN, M. J. & KOREN', T. N. 2000. Development, taxonomy, and phylogenetic relationships of species of *Paraclimacograptus* (Graptoloidea) from the Canadian Arctic and the southern Urals of Russia. *Journal of Paleontology*, **74**, 84–91.

SADLER, P. M., COOPER, R. A. & MELCHIN, M. J. 2009. A new approach to constructing high resolution time scales and an example from the Early Paleozoic. *Bulletin of the Geological Society of America*, **121**, 887–906.

SADLER, P. M., COOPER, R. A. & MELCHIN, M. J. 2011. Sequencing the Graptoloid Clade: building a global diversity curve from local range-charts, regional composites and global time-lines. *Proceedings of the Yorkshire Geological Society*, **58**, 329–344.

SENNIKOV, N. V. 1976. *Graptolity y stratigrafiya nizhnego silura Gornogo Altaya*. Akademiya Nauk SSSR, Sibirskoe otdelenie, Institut geologii i geofiziki, Trudy, 1–230.

SOBOLEVSKAYA, R. F. 1974. Novye Ashgillskie graptolity v basseine srednego techenia r Kolymy. *In:* OBUT, A. M. (ed.) *Graptolites of the USSR*. Nauka, Siberian Branch, Novosibirsk, 63–71 (in Russian).

ŠTORCH, P. 1983. The genu. *Diplograptus* (Graptolithina) from the lower Silurian of Bohemia. *Vestnik Ustredniho ustavu geologickeho*, **58**, 159–170.

ŠTORCH, P. 1985. *Orthograptus* s.l. and *Cystograptus* (Graptolithina) from the Bohemian lower Silurian. *Vestnik Ustredniho ustavu geologickeho*, **60**, 87–99.

ŠTORCH, P. 1989. Late Ordovician graptolites from the upper part of the Králův Dvůr Formation of the Prague Basin (Barrandian, Bohemia). *Vestnik Ustredniho ustavu geologickeho*, **64**, 173–186.

ŠTORCH, P. & FEIST, R. 2008. Lowermost Silurian graptolites of Montagne Noire, France. *Journal of Paleontology*, **82**, 938–956.

ŠTORCH, P. & LOYDELL, D. K. 1996. The Hirnantian graptolites *Normalograptus persculptus* and "*Glyptograptus*" *bohemicus*: Stratigraphical consequences of their synonymy. *Palaeontology*, **39**, 869–881.

ŠTORCH, P. & SERPAGLI, E. 1993. Lower Silurian graptolites from southwest Sardinia. *Bollettino della Societa Paleontologica Italiana*, **32**, 3–57.

ŠTORCH, P, MITCHELL, C. E., FINNEY, S. C. & MELCHIN, M. J. 2011. Uppermost Ordovician (upper Katian–Hirnantian) graptolites of north-central Nevada, U.S.A. *Bulletin of Geosciences*, **86**, 301–386.

SUESS, E. 1851. Über böhmische Graptolithen. *Naturwissenschaftliche Abhandlungen von W. Haidinger*, **4**, 87–134.

SWOFFORD, D. L. 2002. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods)*. Sinauer Associates, Sunderland, Massachusetts.

TÖRNQUIST, S. L. 1890. Undersökningar öfver Siljansområdets graptoliter, I. *Lunds Universitets Årsskrifter*, **26**, 33.

UNDERWOOD, C. J. 1998. Population structure of graptolite assemblages. *Lethaia*, **31**, 33–41.

URBANEK, A. 1997. The emergence and evolution of linograptids. *In:* URBANEK, A. & TELLER, L. (eds) *Silurian Graptolite Faunas in the East European Platform: Stratigraphy and Evolution*. Palaeontologica Polonica, **56**, 233–269.

WILLIAMS, S. H. 1983. The Ordovician-Silurian boundary graptolite fauna of Dob's Linn, southern Scotland. *Palaeontology*, **26**, 605–639.

YE, S. 1978. Class Graptolithina. *In:* CHENGDU INSTITUTE OF GEOLOGY AND MINERAL RESOURCES (ed.) *Part I. From Sinian to Devonian, Atlas of Fossils of Southwest China*. Geological Publishing House, Beijing, China, 431–686 (in Chinese).

ZALASIEWICZ, J. 1996. Aeronian (Silurian: Llandovery) graptolites from central Wales. *Geologica et Palaeontologica*, **30**, 1–14.

ZALASIEWICZ, J. & TUNNICLIFF, S. 1994. Uppermost Ordovician to Lower Silurian graptolite biostratigraphy of the Wye Valley, central Wales. *Palaeontology*, **37**, 695–720.