The classification of the Pterobranchia (Cephalodiscida and Graptolithina)

JÖRG MALETZ

This paper presents a proposal for a taxonomic approach to the classification of the Pterobranchia (Cephalodiscida and Graptolithina) to be adopted for the revision of the *Treatise on Invertebrate Paleontology, Part V (Hemichordata)*, currently in preparation. A combination of traditional Linnaean taxonomy, supported by cladistic analyses in some groups is proposed herein as a *practical solution* for the classification of the Graptolithina as for many groups a cladistic analysis has never been attempted and is unlikely to be undertaken in the near future. The number of ranked taxa has been kept as low as possible, with all genus level taxa referred to a family. All families and higher taxonomic units are discussed, but new taxa have not been introduced. Paraphyletic (but not polyphyletic) taxa are accepted as useful units in this classification. A number of recently introduced taxonomic units, based on cladistic analyses (*e.g.* Eugraptoloida, Pan-Reclinata, Pan-Bireclinata), are discussed in the context of this classification and the usefulness of these taxa is critically evaluated. The solution proposed here opts not to name a number of nodes from the published cladistic analyses that potentially could be named and in some cases have been named – not to inflate the hierarchy of the used taxonomic system. Taxa are kept as close as possible to their original definition and not unnecessarily expanded or restricted. The taxonomy proposed here for the Graptolithina indicates that the extensive use of higher level taxa, *e.g.* orders for small groups of genera as has been done for many benthic graptolite groups in the past is unnecessary and should be avoided.
• Key words: Hemichordata, Pterobranchia, Graptolithina, taxonomy, evolution.

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Graptolites represent one of the most important groups of Palaeozoic fossils for a number of geological applications, most particularly biostratigraphy and biogeography. They are also, if well preserved, beautiful and complex fossils and can be used to document and understand evolutionary patterns. For all graptolite studies and applications, a precise and workable taxonomy is essential. During the last half century, the two *Treatise* editions (Bulman 1955, 1970) have been the standard for all taxonomic work on graptolites, but these are now outdated and a revision is necessary. New insight gained over more than 40 years has to be integrated.

In recent years, cladistic approaches to the interpretation of general taxonomy and of phylogenetic relationships have taken over the field almost entirely with the naming convention introduced as the PhyloCode (latest version: Cantino & de Queiroz 2010) aimed at revolutionizing naming procedures. PhyloCode is a nomenclatorial concept intended to be applied to naming clades, and only clades, above the species level and used parallel to the concurrent rank-based codes (PhyloCode 4c, Preamble). Interpretations of clades in cladistics are stable by their definition and its link to a specific cladistic diagram (PhyloCode; Cantino & de Queiroz 2010). A different cladogram (a different hypothesis) involving an identical list of taxa would require completely different names (see discussion in Kojima 2003). In the Linnaean System, taxa are not defined, but are labels for communication (Kojima 2003) and, therefore, are flexible. Over the years, a duality has been established and available taxonomic concepts for graptolites are difficult to conjoin.

One of the main problems for palaeontologists in dealing with taxonomy is the lack of information at all levels (see Padian *et al.* 1994). Our fossils are poor representations of ancient life and provide very little evidence for any taxonomic interpretation (Fig. 1A, C, D). For example, the soft tissue of the graptolite zooids is barely preserved in the fossil record and we have to work with the secreted housing construction only. Crowther & Rickards (1977) introduced the currently accepted interpretation of the graptolite colony with its inhabiting zooids (Fig. 1B). In this interpretation the zooids are based on the extant pterobranch

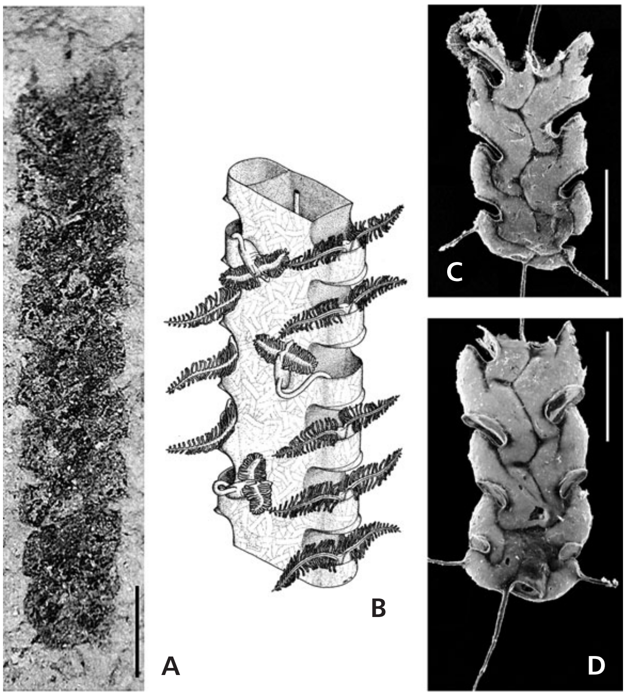

Figure 1. Various axonophoran specimens showing preservation and availability of taxonomically important details. • A – NMV P 31933 holotype of *Archiclimacograptus modicellus*, flattened and weathered. • B – reconstruction of part of a biserial rhabdosome, based on Crowther & Rickards (1977, fig. 2). • C, D – *Archiclimacograptus* sp., Darriwilian, western Newfoundland, SEM images in reverse (C) and obverse (D) views, showing relief specimen for comparison with A. JM 24/01, JM 24/02. Scale bar represents 1 mm.

Rhabdopleura. Recently, *Rhabdopleura* was identified as a living graptolite (Mitchell *et al.* 2013), validating the interpretation of Crowther & Rickards (1977).

The quality of the type material of many graptolite genera may serve as a warning here. Too many genera, especially of dendroid graptolites, are described from fragments and the morphological details of the complete colonies cannot be estimated from these. This is the case also and especially with most of the benthic encrusting taxa described by Kozłowski (1949) and referred to a number of graptolite orders at the time. The material usually consists of small fragments of colonies without preservation of the sicula or any view of the precise shape and development of the colonies.

Graptolite taxonomy through time

The available morphological information represents the basis for the scientific concept of a taxon, species, genus or other type. Increasing knowledge has invariably resulted in the splitting and introduction of new taxa, the normal procedure in Linnaean taxonomy and an expression of scientific improvement. A single genus, *Graptolithus* Linnæus, 1758, was enough in the early years of graptolite taxonomy, but obviously is not now. Linnæus (1735, 1768, p. 173) established the genus *Graptolithus* and thus is responsible for the name that we use for the graptolites. The name was initially intended to describe inorganic markings on rocks and is no longer used as a graptolite genus (see Bulman 1929, p. 170). Bronn (1849, p. 149) referred the graptolites (as the Graptolithina) to the Anthozoa (corals) and included the only available genus, *Graptolithus*. Here, the graptolites resided for some time. It is the success of Linnaean taxonomy, that the graptolites are not still associated with the corals and that the extant pterobranchs are no longer identified as a strange group of bryozoans ("Polyzoa") (Sars 1872, M'Intosh 1882).

Graptolite taxonomy progressed with a single family, Graptolitidae (*e.g.* Hall 1858, 1865; Törnquist 1865; Nicholson 1872a, b), and a small number of genera. Erection of additional genera originally was not deemed necessary and most were introduced only much later, leading to the more than 600 genera now available. Today, more than 275 years after Linnaeus, we understand the graptolites to be a group of pterobranch hemichordates with numerous extinct and a few extant taxa (Mitchell *et al.* 2010, 2013). We have learned a lot about their evolutionary patterns over more than 500 million years from the Early to Middle Cambrian until today (Maletz 2014).

A number of higher-level taxon names have been introduced over the centuries by various authors, showing the improvement in our taxonomic understanding. Examples of names that today are unfamiliar include the Monophyontes, Mono-Amphiphyontes and Amphiphyontes of Tullberg (1883) (Table 1) and the differentiation of the Axonophora and Axonolipa of Frech (1897). However, Frech's Axonophora is used in modern graptolite taxonomy, re-introduced by Maletz *et al.* (2009). Some of the early taxonomic concepts show some remarkable insight and a deep understanding of the differentiation of the major groups of graptolites. Even though some of the family level names in Tullberg's (1883) taxonomy may be unfamiliar, their content still makes sense today. The taxonomy and evolutionary understanding of the Graptolithina evolved from the early works of Lapworth (1873a, b, 1879a–d, 1880a–e), Tullberg (1883) and Frech (1897) among others, to the now quite outdated approach in two editions of the *Treatise* (Bulman 1955, 1970). The general differentiation of the graptolites into a number of families seems to have been the main goal of most early authors. It was an attempt to determine the useful characters to define easily recognizable groups among the Graptolithina and to understand their phylogenetic relationships. Initially, this taxonomic approach was not necessarily based upon the most reliable features, but recognizing this is a modern achievement.

Even though the idea of naming only clades (monophyletic groups) and not grades (polyphyletic groups) is

Table 1. Early example of classification of the graptolites by Tullberg (1883), including a number of unfamiliar family names.

- Graptolitidae Hall, 1858, p. 6
  - Monophyontes Tullberg, 1883, p. 12
    - Family Dictyograptidae Tullberg, 1883, p. 12
      - Genera: *Dictyonema*
    - Family Dichograptidae Lapworth, 1873b, p. 555
      - Genera: *Bryograptus*, *Clematograptus*, *Pleurograptus*, *Cladograptus*, *Dichograptus*, *Tetragraptus*, *Phyllograptus*, *Didymograptus*
    - Family Nemagraptidae Lapworth, 1873b, p. 556
      - Genera: *Leptograptus*, *Amphigraptus*, *Coenograptus (C. gracilis)*, *Nemagraptus*
    - Family Monoprionidae Hopkinson, 1869, p. 157
      - Genera: *Rastrites*, *Monograptus*, *Cyrtograptus*
    - Family Mono-diprionidae Hopkinson, 1869, p. 160
      - Genera: *Dicellograptus*, *Dicranograptus*
    - Family Diprionidae Hopkinson, 1869, p. 157
      - Genera: *Climacograptus*, *Diplograptus*
  - Mono-Amphiphyontes Tullberg, 1883, p. 13
    - Family Heteroprionidae Tullberg, 1883, p. 13
      - Genera: *Dimorphograptus*
  - Amphiphyontes Tullberg, 1883, p. 13
    - Family Glossograptidae Lapworth, 1873b, table 1 facing p. 555
      - Genera: *Glossograptus, Lonchograptus*, *Retiograptus*, *Gymnograptus*, *Lasiograptus*
    - Family Retiolitidae Lapworth, 1873b, table 1 facing p. 555
      - Genera: *Trigonograptus*, *Clathrograptus*, *Retiolites*, *Stomatograptus*

implemented and strongly promoted by cladistics and in the PhyloCode, it is not a new idea (*e.g.* Haeckel 1866, 1868; Gegenbaur 1870, pp. 78–81). It has been the underlying, even though rarely explicitly stated, aim of every taxonomic approach and every evolutionary interpretation since the introduction of the Linnaean System. Certainly, at the beginning of taxonomic and evolutionary research, knowledge and understanding of synapomorphic characters (a term unknown at the time of Linnæus) was just starting to emerge and taxonomy developed via a "trial-and-error" system, using characters that appeared important and meaningful. This is clearly visible in early graptolite work (*e.g.* Lapworth 1873b, Tullberg 1883, Gürich 1908), where the number of stipes and uniseriality or biseriality of the stipes were used as the main characters for taxonomic differentiations (*cf.* Table 1), but see also Yu & Fang (1979) for a modern example. Many of the graptolite genera described in these taxonomies were soon identified as polyphyletic. This can easily be seen in the statement of Nicholson & Marr (1895, p. 538), that "the single genus *Monograptus* may contain descendants of more than one 'family'", and Ruedemann (1904, p. 478: "Their results point also to a polyphyletic origin of the large genera of this family and especially of *Tetragraptus* and *Didymograptus*") among others. Every specialist on these graptolite taxa would have to agree with the statement of Ruedemann. Jaeger (1978) discussed the trends ("Entwicklungszüge") in the evolution of graptolites following similar ideas, but clearly stated that the trends are descriptional and identical patterns appear often independently in various groups. Thus, he did not emphasize a phylogenetic meaning of these trends.

Over the years a considerable divergence of taxonomic approaches on graptolite classification evolved in various countries (Rigby 1986), resulting from language barriers, differing taxonomic concepts and lack of communication. This division has not yet ended as is seen in several newer approaches (*cf.* Mu *et al.* 2002, Mitchell *et al.* 2007, Maletz *et al.* 2009). Especially in the western hemisphere, the taxonomy and evolution of the Graptolithina has been hotly debated in recent decades with the increasing popularity of cladistics and the availability of cladistic analyses for a number of groups within the Graptolithina (*e.g.* Fortey & Cooper 1986, Mitchell 1987, Bates *et al.* 2005, Mitchell *et al.* 2007, Maletz *et al.* 2009, Melchin *et al.* 2011, Štorch *et al.* 2011). This approach has helped us to understand the general relationships of certain groups better, but a complete analysis of all graptolite taxa has not been attempted. The most important results of the cladistic analyses include the recognition of Anisograptidae as ancestors of all planktic graptolites and their inclusion in Graptoloidea (Fortey & Cooper 1986). Through recognition of the proximal development types of the axonophoran graptolites by Mitchell (1987) and Melchin (1998), a better understanding of many biserial graptolites was achieved. The most recent improvement is the recognition of *Rhabdopleura* as an extant graptolite (Mitchell *et al.* 2010, 2013), following a similar, but not identical suggestion by Beklemishev (1951a, 1951b [various later editions in Russian, English and German]) who included the pterobranchs in the class Graptolithoidea.

Of the more than 600 genera of graptolites described, not many are known in enough detail to be useful for any phylogenetic analysis, as they often consist of fragmentary material lacking taxonomically relevant details. Therefore, cladistic approaches are still limited to a few well-known groups, such as the retiolitids (Lenz & Melchin 1997, Bates *et al.* 2005) and the Ordovician to lower Silurian biserial axonophorans (Mitchell 1987, Mitchell *et al.* 2007, Melchin *et al.* 2011, Štorch *et al.* 2011). In these groups, enough taxa are available as isolated or relief specimens, yielding the morphological details necessary for a reasonable cladistic analysis. Even though they represent one of the morphologically and taxonomically most varied groups of graptolites, monograptids have not been subjected to a detailed cladistic analysis, but Muir (1999) provided data for a limited number of Llandovery monograptids.

The resolution of the early Graptolithina is poor in the analysis of Mitchell *et al.* (2013) and a number of formerly established benthic graptolite orders (*e.g.* Kozłowski 1949, Bulman 1970, Bates & Urbanek 2002) have been dissolved. There is no doubt, however, that many of the high level taxonomic units (orders) of Kozłowski (1938, 1949) may be unnecessary and the benthic taxa are in dire need of a modern taxonomic revision.

Systematics

Ranks are useful and convenient when we want to talk about larger groups of taxa (*e.g.* genera, species) using a Linnaean taxonomy, but we all know that they represent highly artificial concepts. A family of radiolarians is not comparable to a family of graptolites or any other group of organisms. These ranks are interpretations based on an understanding of taxonomic and evolutionary relationships and represent a simplification based on an evolutionary tree or a cladistic analysis. They evolved over time with the increase of knowledge as we have seen in the example of the family Graptolitidae.

In cladistics, the diagrams represent distributions of characters, analysed step by step, character by character. They reflect general phylogenetic relationships, but do not represent them in detail. Pushing a (named) ranked system upon this analysis could lead to the erection of numerous named and ranked taxa (see Maletz *et al.* 2009) as potentially every node can be named. Thus, a cladistic system works best without explicit ranking, but every cladistic diagram includes an implicit ranking through the fixed succession of nodes. The arbitrary decision to name only certain nodes on a cladistic diagram (*cf.* Fig. 2) – and not all nodes – would be an exact equivalent of the "artificial" concept of defined ranks in higher level taxonomic units that exists in a Linnaean System.

It is suggested here to use the Linnaean System approach with the minimum number of taxonomic ranks (Table 2) that is sufficient to express the general relationships between the easily recognizable individual groups of graptolites. A system with a higher number of specified ranks may better represent the detailed evolutionary history, but may overburden our taxonomic system with names and being less practical. The extreme pectinate form of the results of the recent cladistic analyses of graptolite taxonomy (Mitchell *et al.* 2007, Maletz *et al.* 2009) already led to an increasing number of proposed taxonomic ranks within the Graptolithina, most fully expressed in Maletz *et al.* (2009). The ranked and named taxa in Maletz *et al.* (2009), however, show genuine taxonomic relationships and strictly describe monophyletic clades in a stacked succession. These taxa show details of the evolutionary relationships not explicitly stated in the taxonomic system. It is an arbitrary decision to use or not use any of these taxa and to add hierarchical levels or not to the taxonomy.

Monophyly is the central dogma of modern taxonomy (*e.g.* Hennig 1950, 1965; PhyloCode), but so many previously established taxa have been shown to be paraphyletic or polyphyletic and to make our taxonomic approach a nightmare. Mitchell *et al.* (2007) and Maletz *et al.* (2009) largely avoided the problem of paraphyly in graptolites by naming only monophyletic groups and extracting paraphyletic taxa as unnamed stem groups. Whilst there is no doubt that polyphyletic taxa should be avoided at all costs, the question is whether we should abandon all paraphyletic taxa. The discussion is not restricted to fossil taxa. There are several supporters of paraphyly in plant taxonomy for example (Brummitt 1996, 2003; Brummitt & Sosef 1998; Sosef 1997; Zander 2007; Farjon 2007) and the debate has been quite heated (see Nordal & Stedje 2005, Ebach *et al.* 2006). Even though these references refer to botany, not surprisingly, the arguments are the same than the ones used in zoology and show that the same discussion is happening everywhere where taxonomy is used.

The recognition of taxa as monophyletic or paraphyletic is seemingly easy in cladistics. However, the recognition of monophyletic and paraphyletic taxa often rests on the taxonomic resolution of the particular cladistic tree that is produced. Depending upon the number of end-branches in a tree/diagram (resolution), a taxon defined the same way through a synapomorphy-based definition can become monophyletic or paraphyletic in an analysis. The differentiation of Plectograptinae and Retiolitinae may be regarded as a useful example (Fig. 3). These two subfamilies of retiolitids have generally been recognized as separate and easily identifiable (Bouček & Münch 1952; Lenz & Melchin 1987, 1997), even though this separation appeared somewhat blurred in a more recent analysis (Bates *et al.* 2005). Its separation was based mainly on the recognition of a single character, the pustulose surface of the bandages in the Plectograptinae. In this case, the pustulose surface

Table 2. Proposed classification of the Pterobranchia.

- Phylum Hemichordata Bateson, 1885, p. 111
  - Class Enteropneusta Gegenbaur, 1870, p. 158
  - ?Class Planctosphaeroidea van der Horst, 1936, p. 612
  - Class Pterobranchia Lankester, 1877, p. 448
    - Subclass Cephalodiscida Fowler, 1892, p. 297
      - Family Cephalodiscidae Harmer, 1905, p. 5
    - Subclass Graptolithina Bronn, 1849, p. 149
      - *Incertae sedis* Family Rhabdopleuridae Harmer, 1905, p. 5
      - *Incertae sedis* Family Cysticamaridae Bulman, 1955, p. 42
      - *Incertae sedis* Family Wimanicrustidae Bulman, 1970, p. 52
      - *Incertae sedis* Family Dithecodendridae Obut, 1964, p. 295
      - *Incertae sedis* Family Cyclograptidae Bulman, 1938, p. 22
      - Order Dendroidea Nicholson, 1872b, p. 101
        - Family Dendrograptidae Roemer, 1897 *in* Frech (1897), p. 568
        - Family Acanthograptidae Bulman, 1938, p. 20
        - Family Mastigograptidae Bates & Urbanek, 2002, p. 458
      - Order Graptoloidea Lapworth, 1875 *in* Hopkinson & Lapworth (1875), p. 633
        - Suborder Graptodendroidina Mu & Lin, 1981 *in* Lin (1981), p. 244
          - Family Anisograptidae Bulman, 1950, p. 79
        - Suborder Sinograpta Maletz *et al*., 2009, p. 11
          - Family Sigmagraptidae Cooper & Fortey, 1982, p. 257
          - Family Sinograptidae Mu, 1957, p. 387
          - Family Abrograptidae Mu, 1958, p. 261
        - Suborder Dichograptina Lapworth, 1873b, table 1, facing p. 555
          - Family Dichograptidae Lapworth, 1873, p. 555
          - Family Didymograptidae Mu, 1950, p. 180
          - Family Pterograptidae Mu, 1950, p. 180
          - Family Tetragraptidae Frech, 1897, p. 593
        - Suborder Glossograptina Jaanusson, 1960, p. 319
          - Family Isograptidae Harris, 1933, p. 85
          - Family Glossograptidae Lapworth, 1873b, table 1 facing p. 555
        - Suborder Axonophora Frech, 1897, p. 607
          - Infraorder Diplograptina Lapworth, 1880e, p. 191
            - Family Diplograptidae Lapworth, 1873b, table facing p. 555
              - Subfamily Diplograptinae Lapworth, 1873b, table facing p. 555
              - Subfamily Orthograptinae Mitchell, 1987, p. 380
            - Family Lasiograptidae Lapworth, 1880e, p. 188
            - Family Climacograptidae Frech, 1897, p. 607
            - Family Dicranograptidae Lapworth, 1873b, table facing p. 555
              - Subfamily Dicranograptinae Lapworth, 1873b, table facing p. 555
              - Subfamily Nemagraptinae Lapworth, 1873, p. 556
          - Infraorder Neograptina Štorch *et al*., 2011, p. 368
            - Family Normalograptidae Štorch & Serpagli, 1993, p. 14
            - Family Neodiplograptidae Melchin *et al*., 2011, p. 298
              - Subfamily Neodiplograptinae Melchin *et al*. 2011, p. 298
              - Subfamily Petalolithinae Bulman, 1955, p. 87
            - Superfamily Retiolitoidea Lapworth, 1873b, table 1 facing p. 555
              - Family Retiolitidae Lapworth, 1873b, table 1 facing p. 555
                - Subfamily Retiolitinae Lapworth, 1873, table 1 facing p. 555
                - Subfamily Plectograptinae Bouček & Münch, 1952, p. 10
            - Superfamily Monograptoidea Lapworth, 1873, table facing p. 555
              - Family Dimorphograptidae Elles & Wood, 1908, p. 347
              - Family Monograptidae Lapworth, 1873b, table 1 facing p. 555
                - possibly several subfamilies

texture is a synapomorphy of Plectograptinae. If only a single genus taxon of Retiolitinae and Plectograptinae is used in an analysis, both would end up as monophyletic sister groups (Fig. 3A).

A different scenario, in which several other retiolitid taxa are added to provide a higher resolution of the analysis (Fig. 3B), shows Retiolitidae as a paraphyletic taxon from which the derived Plectograptinae originate as a monophyletic taxon. The alternative would be to define an [informal] paraphyletic stem group that includes the group formerly called Retiolitinae and separate the derived Plectograptinae from these. Lenz & Melchin (1997) took a slightly different route and regarded *Pseudoretiolites* as a paraphyletic stem group and recognized two monophyletic subfamilies, the Retiolitinae and Plectograptinae. A similar "trick" was used by Maletz *et al.* (2009) for several groups of early Graptoloidea, by routinely identifying informal, paraphyletic stem groups of formally defined monophyletic taxa.

Cannon *et al.* (2009, figs 3, 4) discussed the molecular phylogeny of the Hemichordata and provided a number of trees to demonstrate the relationships of modern enteropneusts. Their diagrams show a number of paraphyletic families like the Harrimaniidae and Ptychoderidae, from which other family taxa originate (the Saxipendiidae and Torquaratoridae). Even Pterobranchia is shown (Cannon *et al.* 2009, fig. 4) as originating as a sister group to Harrimaniidae + Saxipendiidae from within Enteropneusta. So it seems that there is no problem to accepting paraphyletic taxa.

It is advisable to discuss or at least state the paraphyletic nature of a taxon in the descriptions or remarks. Melchin *et al.* (2011), in their paper on the Neograptina indicated in their definition the mono- or paraphyly of some of their taxonomic units and this approach may be used as a guide here.

Systematic palaeontology

The duality of the available taxonomic approaches, a morphological or Linnaean style diagnosis of the taxa (based on Bulman 1955, 1970) and a definition based on a particular cladogram following de Queiroz & Gauthier (1990), makes it difficult to generate a useful and consistent taxonomy. Morphological diagnoses are often impossible to be connected precisely to a phylogenetic definition. Clearly defined synapomorphies can be used in some cases to diagnose taxa and may help to integrate cladistic analyses into the here presented taxonomic approach. Melchin *et al.* (2011) provided definitions for family level taxa, which are based on a particular cladogram, but these can be translated into a diagnosis by using the defining synapomorphies. As a decision had to be made, cladistic definitions are used when available and remarks on the diagnostic features are provided in the discussions. Taxa, for which cladistic definitions are not available, are only diagnosed.

The family is regarded as the most useful rank to combine genera, as they combine a number of genera on morphological criteria and indicate a taxonomic and evolutionary relationship. Sepkowski (1979) for example, used families for his study of the early Phanerozoic diversity of the metazoans, as it was less likely to produce biases due to the lack of a fossil record or poor preservation of fossils. Many of the numerous families that have been established for graptolites may not be useful at all, as they were established on extremely poor material or because of the, at the time, unknown phylogenetic relationships of individual species and genera (*e.g.* Peiragraptidae: Jaanusson, 1960: Kalpinograptidae Jiao, 1977), but others may be referred to here also. Mu *et al.* (2002) for example described 62 family level taxa (families and subfamilies), many of questionable value for modern taxonomy. Subfamilies have been erected in a number of families, of necessity, as a great many genera would otherwise be included in a family and sufficient knowledge is available to effect subdivision (*e.g.* Cucullograptinae, Neocucullograptinae in Monograptidae: Urbanek 1958, 1966), but elevation of these to family level is not advisable at present.

Genera are listed under the families to which they are referred. All genera that I am aware of have been included in the lists, generally in alphabetical order and in their original spelling (*e.g. Tetragrapsus*, not *Tetragraptus*) for easy access to original literature, even though later name changes are sanctioned by ICZN (ICZN 1963) and should be followed. Taxa originally erected as subgenera are listed as if of full generic status for easy access only. No indication is provided regarding the synonymy of taxa, even though numerous synonyms have been established and a number of the genus names listed here may be quite unfamiliar, therefore. Often, taxa based on incomplete, fragmentary and macerated material have been described validly as new genera; for example, the "hydroid" fragments described by Kozłowski (1959), now in part recognized as stolonal fragments of rhabdopleurids (*e.g.* Mierzejewski 1986a). A specific identification of these may never be possible, however. I have, nevertheless, indicated their relationships by including them in families and accepting the interpretation of Mierzejewski (1986a) and others.

The inclusion in families is uncertain for a number of genera and the list provided here may have to be seen as preliminary, prone to revision. It is based on new information and suggestions and does not necessarily follow the previous *Treatise* editions of Bulman (1955, 1970). Due to space limitations, it is not possible to discuss each taxon and its inclusion in a certain group here. This should be the task for the next edition of the *Treatise*.

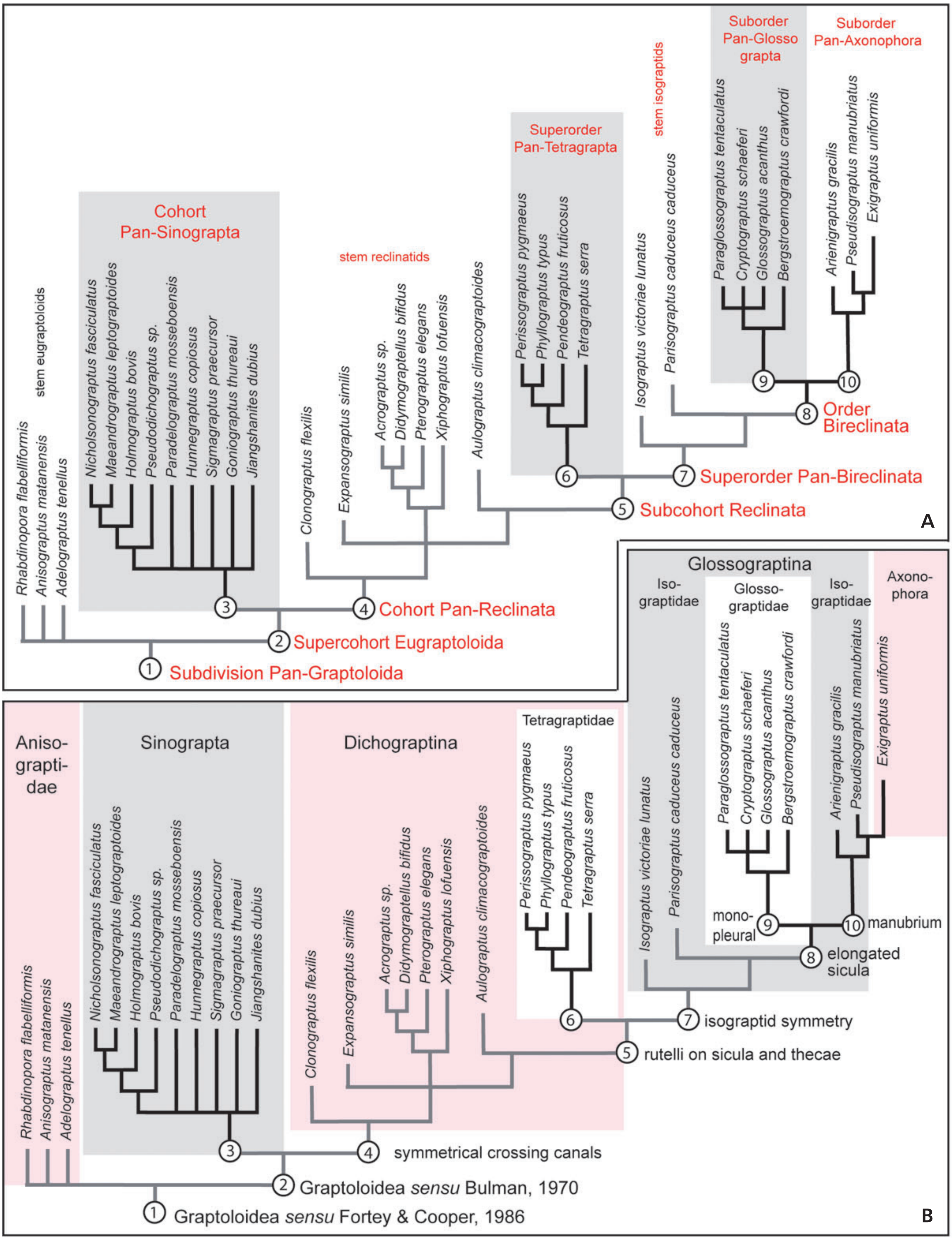

Figure 2. The Pan-Graptoloida (A), based on Maletz *et al.* (2009, fig. 2) with partial re-labeling (B). New taxa of Maletz *et al.* (2009) labelled in red in A. Coloured boxes for easier access only. Version B is preferred here. Inclusion of several taxa is questioned in text.

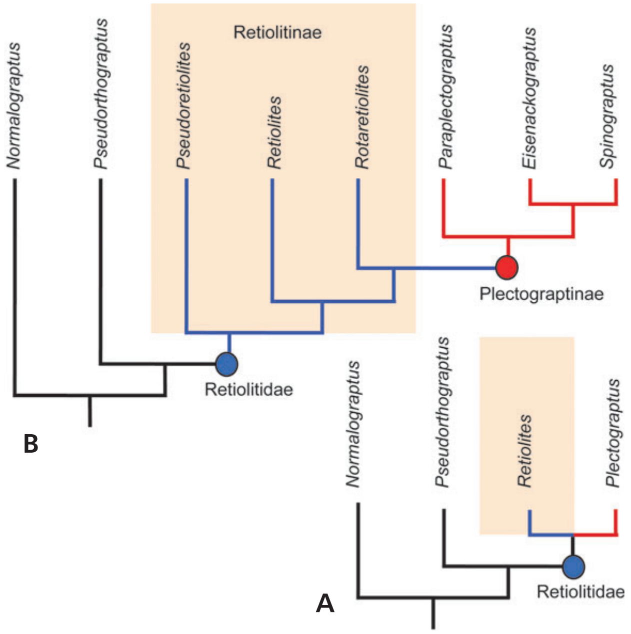

Figure 3. Cladistic relationship of the Retiolitidae, diagrams based on data from Bates *et al.* (2005). Retiolitine taxa in blue, Plectograptine taxa in red. • A – Retiolitinae (*Retiolites*) and Plectograptinae (*Plectograptus*) as monophyletic sister taxa. • B – a monophyletic Plectograptinae derived from a paraphyletic Retiolitinae.

Repositories

Illustrated specimens are in the following collections: CEGH-UNC – CICTERRA University of Cordoba, Argentina; GSC – fossil type collection of the Geological Survey of Canada, Ottawa, Ontario, Canada; IANIGLA – Department of Paleontology, Mendoza, Argentina; LO – Department of Geology, Lund University, Sweden; MB.G. – Museum für Naturkunde, Berlin, Germany; NMV – National Museum, Victoria, Australia; NMW – National Museum and Gallery of Wales, Cardiff; NYSM – New York State Museum, Albany, N.Y., U.S.A.; PMO – National History Museum, Oslo, Norway; SGU – Sveriges Geologiska Undersökning, Uppsala, Sweden; SMF – Forschungsinstitut Senckenberg, Frankfurt, Germany. All other specimens in collection of Jörg Maletz (Berlin, Germany).

Phylum Hemichordata Bateson, 1885 (p. 111)
Class Enteropneusta Gegenbaur, 1870 (p. 158)
Class Planctosphaeroidea van der Horst, 1936 (p. 612)

Discussion. – The taxonomy of the Hemichordata in general is not discussed herein. The classes Enteropneusta and Pterobranchia are well established, while the Planctosphaeroidea is an uncertain taxonomic unit, possibly based on the planktic larvae of some unknown enteropneusts (Spengel 1932, Hyman 1959, Cameron *et al.* 2000). Enteropneusta are marine worms with a tripartite body and may be seen as a sister group to the Pterobranchia (Fig. 4), but do not produce a domicile or tubarium.

Some authors considered Pterobranchia and Enteropneusta as monophyletic taxa of the Hemichordata (*e.g.* Winchell *et al.* 2002, Cameron *et al.* 2005), while others suggested that the Enteropneusta are a paraphyletic group with the family Harrimaniidae as a sister group to the monophyletic Pterobranchia (Halanych 1995, Cameron *et al.* 2000, Bourlat *et al.* 2006, Cannon *et al.* 2009). Recently, however, Peterson *et al.* (2013) provided MicroRNA support for a monophyly of Enteropneusta.

Class Pterobranchia Lankester, 1877, p. 448
(= Graptolithoidea Beklemishev, 1951a, p. 269)

Definition. – (Mitchell *et al.* 2013, p. 52) The least inclusive clade containing *Rhabdopleura normani* Allman, 1869 (*in* Norman 1869), and *Cephalodiscus dodecalophus* M'Intosh, 1887.

Discussion. – Pterobranchia is regarded as a monophyletic taxon with the presence of the tubarium, a variably shaped domicile, as the defining synapomorphy. The tubarium is secreted from glands on the cephalic shield of the zooids. Pterobranchia are characterised through a colonial or "pseudo-colonial" lifestyle, originating from a sexually formed initial zooid. Additional zooids are asexually budded from the founding member. They show a constant organic connection (Graptolithina) or develop into separate individuals when mature (Cephalodiscida).

The zooids of Pterobranchia have a tri-partite body, differentiated into the cephalic shield, the collar with the arms and the trunk regions, differing considerably from the elongated worm-like body of the Enteropneusta (see Fig. 4). The cephalic shield bears the glands from which the tubarium is secreted. One (*Rhabdopleura*) or several (*Cephalodiscus*) pairs of arms with paired tentacles characterise the collar. The trunk is short and bears a u-shaped gut. A contractile stalk or stolon connects the individual zooids of *Rhabdopleura*, while in *Cephalodiscus* the stalk is short and provided with an attachment disc from which also new zooids are formed. These separate from their mother zooid when mature.

Lankester (1877) erected Pterobranchia for a single genus, *Rhabdopleura* and referred it to the Bryozoa, named Tentaculibranchia by him. He did not refer to the fossil graptolites, even though Allman (1872) and Nicholson (1872a, p. 80) already suggested a possible relationship between graptolites and the extant *Rhabdopleura*. At that time, the genus *Cephalodicus* was unknown to Science.

A close phylogenetic relationship of the Graptolithina and the Pterobranchia has been postulated through investigation of the tubarial tissues (*e.g.* Andres 1977, 1980; Crowther 1981) and was discussed in some detail by Urbanek (1986). Mitchell *et al.* (2013) provided strong support for this relationship through a cladistic analysis of the tubarium characteristics including extant pterobranchs and fossil graptolites (Fig. 5). The results indicate an inclusion of the extant *Rhabdopleura* with the otherwise extinct group of the benthic graptolites.

Beklemishev (1951a, b, 1964, 1970) had already used the class Graptolithoidea with the orders Rhabdopleuroidea and Cephalodiscoidea and including the graptolite orders Stolonoidea, Camaroidea, Tuboidea, Dendroidea and Graptoloidea. Beklemishev, thus, did not include the extant pterobranchs in the graptolites, but extended the concept of the "graptolites" and synonymised the Pterobranchia with his more extensive class Graptolitoidea. Some graptolite workers followed his classification (see discussion in Urbanek 1986). It is here preferred to keep the name Pterobranchia as an umbrella for all hemichordates secreting a tubarium (termed rhabdosome in planktic Graptoloidea) and use the term Graptolithina for its colonial members (following Mitchell *et al*. 2013).

Dramatic differences in organismal size, and especially the development of a secreted housing construction, the tubarium (rhabdosome) generally differentiate the Pterobranchia from the worm-like Enteropneusta; however, extremely small members of the Enteropneusta have been discovered recently (Worsaae *et al*. 2012). All Graptolithina are also colonial, but the Cephalodiscida have a pseudo-colonial life style with unconnected mature zooids asexually budding new zooids from the short stalk (Fig. 6F). This interpretation differs little from the Bulman (1955, 1970) concept of an extinct class Graptolithina, separate from the extant Pterobranchia. It makes it possible to understand the graptolites from a modern point of view. As the zooids of the recent *Rhabdopleura* are well known (Fig. 6H, I), they can now be used as a model for the zooids of the extinct taxa also (as was done by inference earlier: Crowther & Rickards 1977) (Fig. 1B).

Subclass Cephalodiscida Fowler, 1892 (p. 297)
(= Cephalodiscoidea Beklemishev, 1951)

Diagnosis. – Same as family.

Family Cephalodiscidae Harmer, 1905 (p. 5)
(incl. Eocephalodiscidae Kozłowski, 1949, p. 195)

Diagnosis (herein). – Pterobranchia with separate mature zooids, forming "pseudo-colonies" in various complex shapes from assemblages of individual, separate tubes to communal tubaria; one genus (*Atubaria*) without known tubarium; a differentiation of a sicular zooid or a sicular tubarium is not present; zooids with several pairs of tentaculated arms; tips of arms sometimes with club-like extensions.

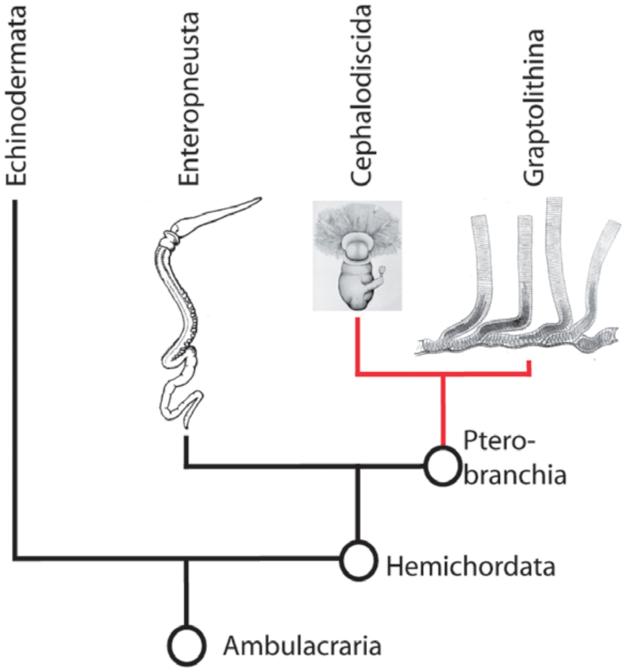

Figure 4. Cladistic diagram (based on Maletz 2013, fig. 2) showing the general phylogenetic relationships of the Hemichordata.

Genera included. – *Acoelothecia* John, 1931; *Aellograptus* Obut, 1964; *Atubaria* Sato, 1936 (Fig. 6G); *Cephalodiscus* M'Intosh, 1882 (Fig. 6C, E, F) [*non Cephalodiscus* Berlese, 1916; Arachnida], *Demiothecia* Ridewood, 1906; *Eocephalodiscus* Kozłowski, 1949; *Idiothecia* Lankester, 1906 *in* Ridewood (1906) (Fig. 6A, B); *Melanostrophus* Öpik, 1930; *Orthoecus* Andersson, 1907; *Pterobranchites* Kozłowski, 1967.

Discussion. – The Cephalodiscida may be recognized as a monophyletic taxon based on the available data (see Cannon *et al.* 2009, Mitchell *et al.* 2013). The group is known from a few extant taxa and some possible fossil cephalodiscid tubaria, but the phylogenetic relationships to the Enteropneusta are uncertain. Rickards & Durman (2006) indicated that Cephalodiscidae is more closely related to the "graptolites" than Rhabdopleuridae, suggesting that the non-colonial organisation is a secondary development. However, Mitchell *et al.* (2013) re-analysed the data and found that *Cephalodiscus* and *Rhabdopleura* were part of an unresolved basal polytomy.

Cephalodiscida includes all pterobranchs with a non-colonial lifestyle. The zooids of a cephalodiscan "pseudo-colony" originate through asexual budding from each other, but separate when mature. The tubaria consist of individual tubes, closed at the origin or of communal tubaria shared by their members (Fig. 5M, N). Taxa with communal tubaria may be difficult or even impossible to separate from Graptolithina in the fossil record when the anatomy of the zooids is unknown.

The inclusion of the extant genus *Atubaria* (Sato 1936, Komai 1949) is based on the zooidal anatomy (Fig. 6G) as the taxon is only known from individual, separate zooids without any indications of the secretion of a tubarium. The anatomy of the *Atubaria* zooids differs little from that of *Cephalodiscus* (see Fig. 6F, G). It is uncertain, whether *Atubaria heterolopha* produces a tubarium or not. A stolon system connecting the individual mature zooids is lacking in Cephalodiscida.

The inclusion of fossil taxa in Cephalodiscida is often difficult, as details of the tubarium design are often not available and the individuality of the mature zooids cannot be ascertained. In modern cephalodiscid taxa the colony design is highly variable in the various subgenera (see Figs 5M, N, 6A, C, E), even though zooidal morphology varies little. Thus, a detailed comparison of extant and extinct taxa is not possible. It is not necessary to subdivide the Cephalodiscida or introduce any additional higher-level taxon units, as a single family is included. The description of the Eocephalodiscidae in Kozłowski (1949) is in all details comparable with the diagnosis of the Cephalodiscidae. Therefore, there is no reason to keep a separate family Eocephalodiscidae for fossil cephalodiscids.

Subclass Graptolithina Bronn, 1849 (p. 149)

Definition. – (Mitchell *et al.* 2013, p. 52) Graptolithina is defined as a lineage-based taxon that includes all taxa sharing a more recent common ancestry with *Rhabdopleura* than with *Cephalodiscus*.

Discussion. – The name Graptolithina originates from the genus name *Graptolithus*, introduced by Linnæus (1735) for a feature "resembling a fossil". For a long time *Graptolithus* was used for numerous graptolite species and only a few additional genera were created (*e.g.* by Hall 1865). It later became the general term for graptolite fossils and was not used in publications as a genus name any more (see Elles & Wood 1902, Bulman 1929 for discussion). Gurley (1896, p. 98) was first to suggest abandoning it as a generic name.

The monophyletic Graptolithina includes all pterobranchs with a colonial development as the defining synapomorphy (Fig. 5). Mitchell *et al*. (2013) indicated the "serial budding from an interconnected stolon system" as the defining synapomorphy of all Graptolithina. The presence of a larval vesicle or prosicula and the regular zigzag fusellae are more difficult to establish from fossil taxa. However, also the presence of a stolon system is in most cases also inferred only through the interconnection of the individual thecae of the tubaria (see remarks on communal tubaria in Cephalodiscidae). A precise construction of thecal tubes with a zigzag suture as in creeping tubes of *Rhabdopleura* and in derived Graptolithina may not be developed in early taxa (see Durman & Sennikov 1993).

The extant *Rhabdopleura* is included in Graptolithina, following Mitchell *et al*. (2013), but Cephalodiscida is not. This inclusion of *Rhabdopleura* in Graptolithina is a major step in the understanding of the fossil Graptolithina of which it is the only modern representative.

The differentiation of benthic taxa above the family level within the early Graptolithina is fairly poor (Fig. 5) and a formal differentiation of higher-level taxonomic units is not advocated at the moment. The families Rhabdopleuridae, Cysticamaridae and Wimanicrustidae are here provisionally separated using previously established family group taxa (see Kozłowski 1949, Bulman 1970). They are not included in Dendroidea or Graptoloidea, as they do not possess the defining characteristics of these, especially the thecal differentiation and triad budding system. Mitchell *et al.* (2013) show *Bulmanicrusta* and *Bithecocamara* as sister taxa (Fig. 5), but very few taxa of the camaroids and crustoids were analysed due to lack of morphological data and a conclusion of their phylogenetic relationships is impossible to gain.

Graptolithina *incertae sedis*

Discussion. – The inter-relationships of the benthic families Rhabdopleuridae, Cysticamaridae, Wimanicrustidae, Dithecodendridae and Cyclograptidae are unclear. They are here not referred to a defined order of the Graptolithina, and are listed under the heading Graptolithina *incertae sedis* to show the uncertainty of their status. Further research may provide a better understanding of the evolutionary status and differentiation of these taxa. There is no doubt, however, that the taxa can be referred to the Graptolithina and that they represent basal members of the taxon.

Family Rhabdopleuridae Harmer, 1905 (p. 5)

Diagnosis (emended). – Colonial pterobranchs with encrusting tubular constructions with irregular fusellar rings or regular zigzag sutures in creeping and erect tubes; resorption porus for the origination of new tubes; erect thecal tubes parallel-sided or slowly widening, with unornamented apertures; zooids connected through robust stolon system (black stolon); sicular zooid secretes featureless domal prosicula.

Genera included. – ?*Archaeocryptolaria* Chapman, 1919; *Calyxhydra* Kozłowski, 1959; *Chitinodendron* Eisenack,

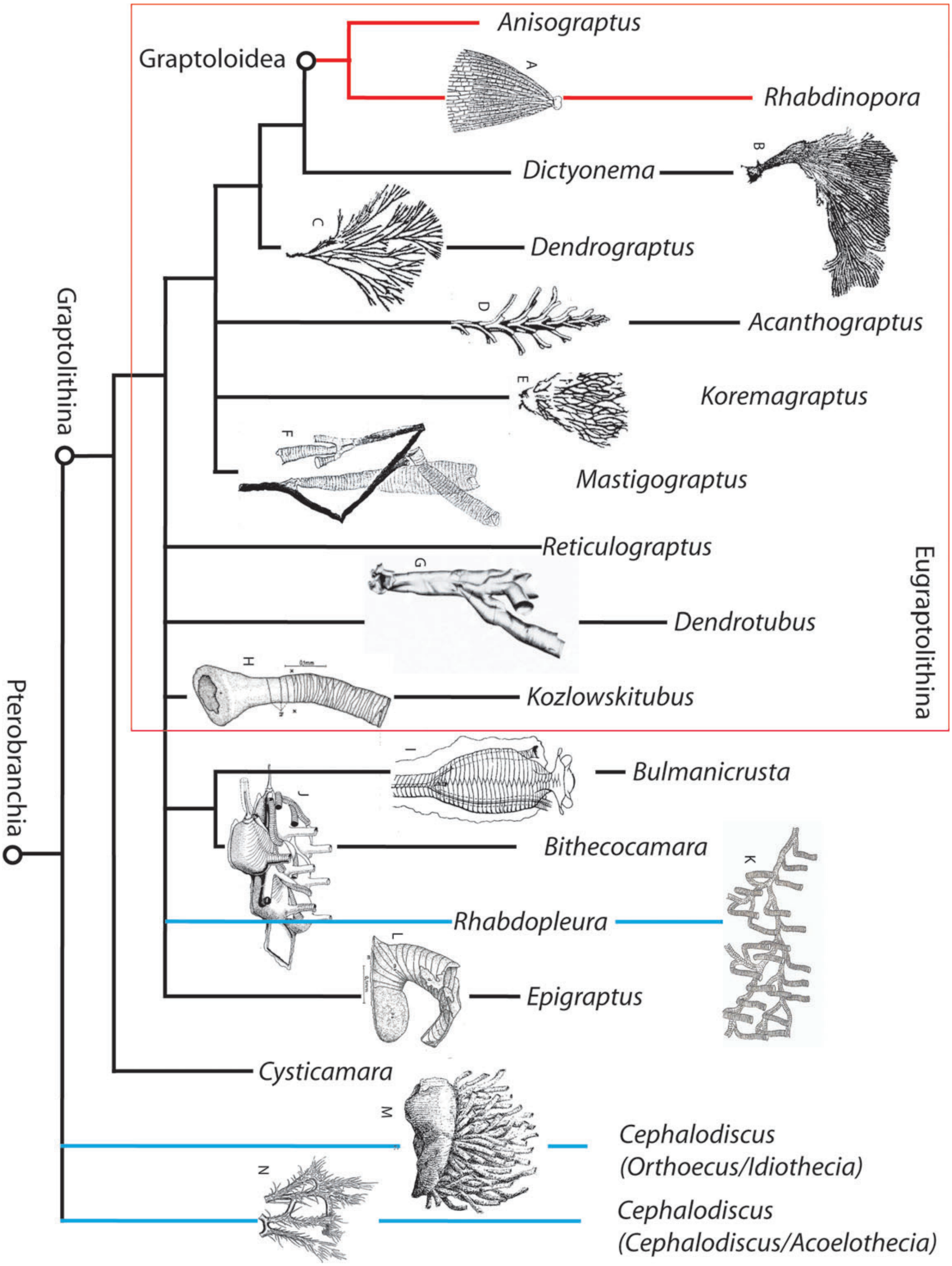

Figure 5. The Graptolithina, based on data and interpretations in Mitchell *et al.* (2013), showing the inclusion of *Rhabdopleura* and the poor resolution of the early graptolites.

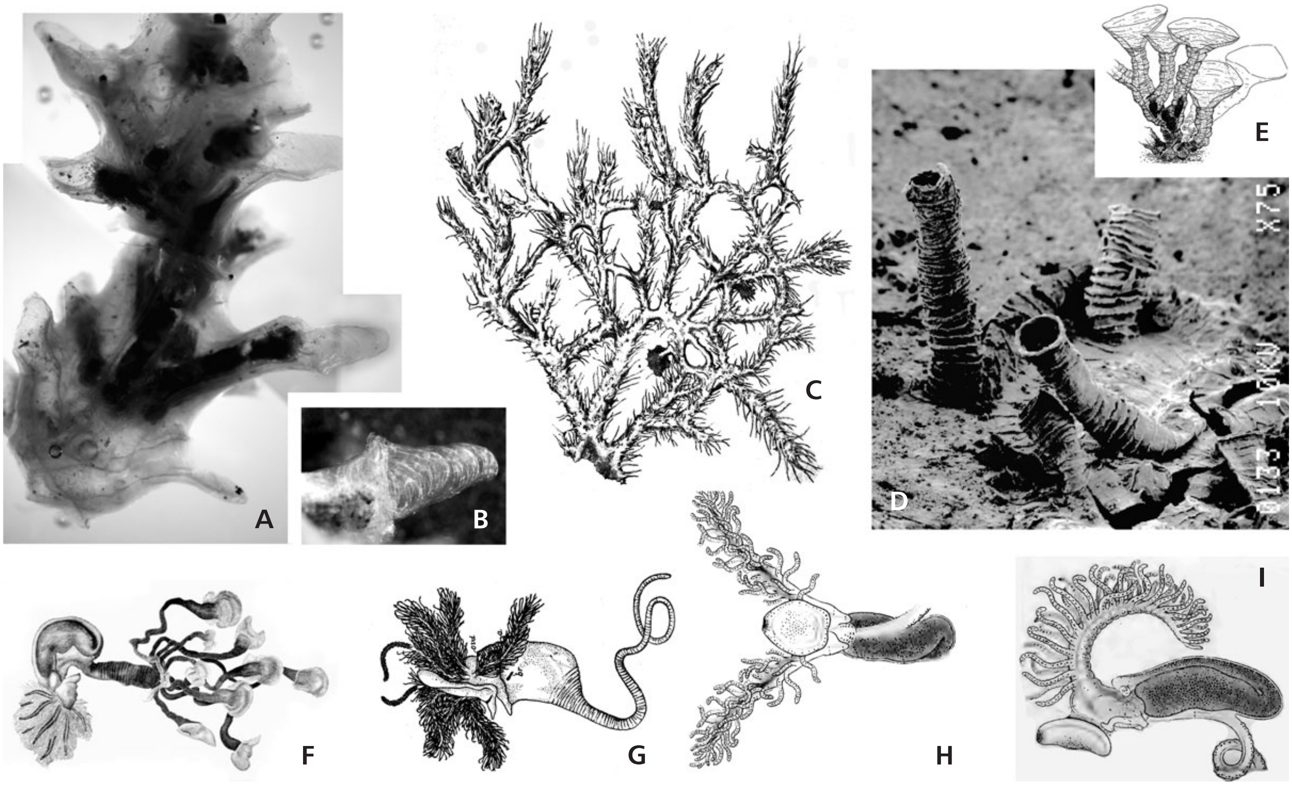

Figure 6. A. Tubaria and zooids in modern Pterobranchia. • A, B – *Cephalodiscus* (*Idiothecia*) *levinseni* Harmer, SMF 75728, part of colony (A) and rutellum with fusellar structure (B), dark spots are preserved zooids. • C – *Cephalodiscus dodecalophus* M'Intosh, part of large branched tubarium with numerous apertural spines (from M'Intosh 1887, pl. 1). • D – *Rhabdopleura compacta* Hincks, SMF 75727, SEM photo showing encrusting tubes with zigzag sutures and erect tubes with full fusellar rings. • E – *Cephalodiscus calciformis* Emig with widening openings, based on Emig (1977). • F – *Cephalodiscus fumosus* John, mature zooid with budding individuals (from John 1931). • G – *Atubaria heterolopha* Sato, mature zooid (from Komai 1949, fig. 1). • H, I – *Rhabdopleura normani* Allman, dorsal (H) and lateral (I) views of single zooid (after Sars 1874, pl. 1).

1937; *Cylindrohydra* Kozłowski, 1959; *Diplohydra* Kozłowski, 1949; *Eorhabdopleura* Kozłowski, 1970; *Epigraptus* Eisenack, 1941; *Fasciculitubus* Obut & Sobolevskaya, 1967; *Graptovermis* Kozłowski, 1949 (Fig. 7C); *Haliolophus* Sars, 1868; ?*Haplograptus* Ruedemann, 1933; *Idiotubus* Kozłowski, 1949 (Fig. 7E); *Kystodendron* Kozłowski, 1959; *Lagenohydra* Kozłowski, 1959; ?*Malongitubus* Hu, 2005; *Palaeokylix* Eisenack, 1932; *Palaeotuba* Eisenack, 1934; *Rhabdopleura* Allman, 1869 *in* Norman (1869) (Fig. 6D, H, I); *Rhabdopleurites* Kozłowski, 1967; *Rhabdopleuroides* Kozłowski, 1961; *Rhabdotubus* Bengtson & Urbanek, 1986 (Fig. 8A, B); ?*Sphenoecium* Chapman & Thomas, 1936; *Sphenothallus* Chapman, 1917 (*non Sphenothallus* Hall, 1847: uncertain tubular fossil, see Fatka *et al.* 2012), *Stolonodendrum* Kozłowski, 1949a; *Xenotheca* Eisenack, 1937; ?*Yuknessia* Walcott, 1919.

Discussion. – Rhabdopleuridae is a taxon including graptoloids with simple, parallel-sided encrusting tubes and erect, parallel-sided or slowly widening zooidal tubes with unornamented apertures. The encrusting tubes show either irregularly placed sutures or distinct dorsal zigzag sutures (*Rhabdopleura*). The erect zooidal tubes have irregular sutures or fusellar halfrings and may possess distinct collar structures. A featureless dome in place of a sicula is known from a few taxa (*Rhabdopleura*, *Epigraptus*), but for most taxa the development is uncertain as the available material consists of fragments of the tubes or the stolons only (see Mierzejewski 1986a).

The Rhabdopleuridae includes *Rhabdopleura* the only genus in which zooidal anatomy is known, and thus, the only graptoloid of which we have any information of the zooidal development. The zooids of *Rhabdopleura* show the tri-partite body development known from *Cephalodiscus*, but differ from those and from *Atubaria* by the development of only a single pair of arms (Fig. 6H, I) and the constant, life-long connection to the stolon system. Additional minor anatomical differences exist.

Mitchell *et al.* (2013) indicated the possible differentiation of an informal group of "rhabdopleurids" as a paraphyletic taxon (Mitchell *et al.* 2013, fig. 6c) including *Rhabdopleura*, *Epigraptus* and *Cysticamara*.

The proximal dome is known in *Rhabdopleura* and *Epigraptus* (Fig. 5L) only, but the complete tubarium development is uncertain for most members. Therefore, early taxa are largely included due to their benthic, creeping

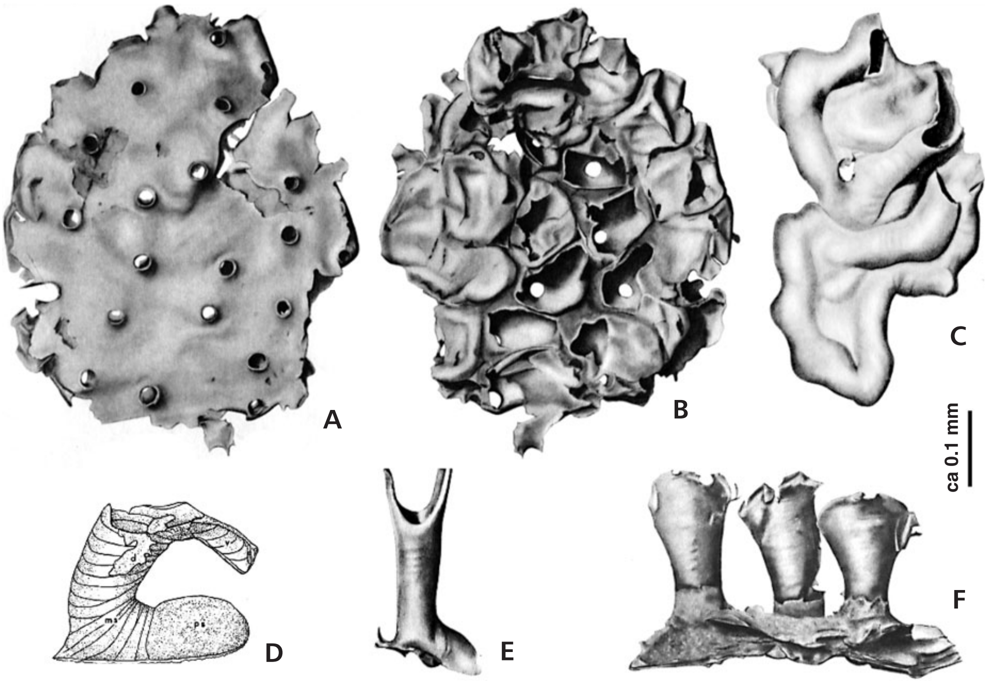

Figure 7. Encrusting graptoloids showing the fragmentary preservation of colonies (based on Kozłowski 1949, 1971). • A, B – *Cysticamara accolis* Kozłowski. • C – *Graptovermis intestinalis* Kozłowski. • D – *Epigraptus* sp., showing domal prosicula. • E – *Idiotubus bilinguis* Kozłowski. • F – *Tubicamara coriacea* Kozłowski. Magnification approximate only.

habit and the simple style of their thecal tubes. Rhabdopleuridae is here strongly extended to include early encrusting taxa with considerable differences in tubarium construction to the extant members.

The Middle Cambrian "*Rhabdopleura*" *obuti* Durman & Sennikov, 1993 is one of the earliest known members of the Rhabdopleuridae, but lacks most of the characters of the tubarium in *Rhabdopleura*, even the regular zigzag sutures on the dorsal side of the creeping tubes and the collars of the erect tubes, so typical of the modern, extant *Rhabdopleura* (Fig. 6D). Both features may have been derived late in the evolution of the group and are recognizable first in Lower Ordovician taxa (*e.g.* Mierzejewski 1986a). The presence of colonies with full fusellar rings and collars as in *Rhabdopleura* and *Kystrodendrum* is therefore regarded as a character of derived rhabdopleurids.

Mierzejewski (1986a) suggested the inclusion of a number of hydroids described by Kozłowski (1959) as stolonal remains of rhabdopleurids. This is supported here, but a synonymy with *Rhabdopleura* is not proposed and may be impossible to establish.

The precise age of the oldest rhabdopleurids is still uncertain. Steiner & Maletz (2012) referred the Middle Cambrian ?*Cephalodiscus* sp. of Maletz *et al.* (2005) to the earliest members of the group and recognized *Yuknessia* from the Burgess Shale as one of the earliest pterobranch hemichordates. According to the authors, also the Burgess Shale taxon *Dalyia* Walcott and the genus *Malongitubus* Hu from the Chenjiang Biota of China may belong to the Pterobranchia.

Family Cysticamaridae Bulman, 1955 (p. 42)

Diagnosis (emended). – Encrusting Graptolithina with the characteristic camara, an inflated chamber and an erect neck; stolon system with modified diad budding, forming a bifurcating network above camarae or represented by extracameral tissue surrounding stolons.

Genera included. – *Bithecocamara* Kozłowski, 1949; *Cysticamara* Kozłowski, 1949 (Fig. 7A, B); *Erecticamara* Mierzejewski, 2000; *Flexicollicamara* Kozłowski, 1949; *Graptocamara* Kozłowski, 1949; *Syringataenia* Obut, 1953; *Tubicamara* Kozłowski, 1949 (Fig. 7F).

Discussion. – Cysticamaridae (= order Camaroidea Kozłowski, 1938) is characterized by the typical camara, a creeping tube with a considerable inflation (Fig. 10A, B) and an erect neck with the thecal aperture (Fig. 7F). All members of the order Camaroidea Kozłowski, 1938 are included herein. Bulman (1955) differentiated *Bithecocamara* (Fig. 5J) in its own family Bithecocamaridae. Only parts of the colonies are known and the housing of the initial zooid, the sicula, has not been described from any of the taxa. A further differentiation of the camaroids into families is not advocated here, nor is the retention of the camaroids in their own order. The combined "Camaroidea" and "Crustoidea" might actually represent a single group of encrusting graptolites. Both possess inflated thecae (camearae) and differences are found in the shape of thecal apertures in the development of the stolon systems. The importance of these differences cannot be estimated at the moment.

The status of the Cysticamaridae is unclear. It may be a completely artifical unit, based on the assumption of the homology of the camara by Kozłowski (1938), but the presence of bifurcating ("diad budding") of the stolons may indicate their closer relationships. Mitchell *et al.* (2013, fig. 6c) included two cysticamarid taxa in their analysis, but the closer relationships between both still remain uncertain. The authors included *Cysticamara* in the informal "rhabdopleurids" and referred *Bithecocamara* together with the crustoid *Bulmanicrusta* to a possibly monophyletic group, the informal "camarates" not further mentioned in their text. This appears questionable, as *Bulmanicrusta* was described to show triad budding (Kozłowski 1949, Bulman 1970), but was coded as having diad budding by Mitchell *et al.* (2013) and it is here preferred to keep *Cysticamara* and *Bithecocamara* in one group. *Bulmanicrusta* with a typical triad budding system then has to be referred to the crustoids (family Wimanicrustidae).

Family Wimanicrustidae Bulman, 1970 (p. 52)

Diagnosis (emended). – Encrusting Graptolithina with the characteristic camara an inflated chamber and an erect neck with often complex apertural modifications; stolon system with triad budding

Genera included. – *Bulmanicrusta* Kozłowski, 1962 (Fig. 5I); *Ellesicrusta* Kozłowski, 1962; *Graptoblastoides* Kozłowski, 1949; *Graptoblastus* Kozłowski, 1949; *Holmicrusta* Kozłowski, 1962; *Hormograptus* Öpik, 1930; *Lapworthicrusta* Kozłowski, 1962; *Maenniligraptus* Mierzejewski, 1986b; *Ruedemannicrusta* Kozłowski, 1962; *Thallograptus* Öpik, 1928 (*non Thallograptus* Ruedemann, 1925: algae), *Urbanekicrusta* Mierzejewski, 1986b; *Wimanicrusta* Kozłowski, 1962; *Xenocyathus* Eisenack, 1982.

Discussion. – Like Cysticamaridae, Wimanicrustidae may be an artificial taxonomic unit, based on Kozłowski (1938) and includes material of fragments of encrusting graptoloids with inflated camarae and a triad budding. Bulman (1970, p. 52) described the family Hormograptidae based on the single, poorly known genus *Hormograptus*. Mitchell *et al.* (2013) included *Bulmanicrusta* as the only genus of the group in their analysis and referred the genus to the informal "camarates" indicating a possible close relationship to the Cysticamaridae.

The Wimanicrustidae is known only from very fragmentary material, often of isolated single thecae. Thus, the development of the colonies and their shapes is impossible to judge for most taxa included in the crustoids. The differentiation of Wimanicrustidae and Cysticamaridae can be based on the presence of a triad budding system of the stolons in the crustoids and a diad budding in camaroids. While Wimanicrustidae are represented largely by runner-type colonies, Cysticamaridae are more compact or thigmophylic. The initial part of the colony, the sicula, is unknown in both groups, but Kozłowski (1971) referred an isolated sicula to the Crustoidea.

Family Dithecodendridae Obut, 1964, p. 295

Diagnosis. – Erect Graptolithina with a slender, often branching stem with thick cortical cover; slender and long tubular metathecae individual to multiple, slowly widening, formed of thin fusellum with irregular sutures.

Genera included. – Archaeolafoea Chapman, 1919; *Bulmanidendrum* Obut, 1974; ?*Dalyia* Walcott, 1919; *Dithecodendrum* Obut, 1964; *Karasidendrum* Sennikov, 1998; *Ovetograptus* Sdzuy, 1974; *Protodendrum* Sennikov, 1998; *Siberiodendrum* Obut, 1964; *Sibiriograptus* Obut, 1964; *Sotograptus* Sdzuy, 1974; *Tarnagraptus* Sdzuy, 1974.

Discussion. – Dithecodendridae represents a difficult taxonomic unit of erect, benthic taxa, of which the colony construction is very poorly known. None of the taxa was well enough known to be included in the analysis of Mitchell *et al.* (2013). Rickards & Durman (2006) included number of taxa in the order Dithecoidea and showed the genera *Archaeolafoea*, *Mastigograptus* and *Sotograptus* as a clade in their diagrams. Of these, *Mastigograptus* has here been excluded from the Dithecodendridae due to the recognition of a triad budding system and is referred to the Mastigograptidae. The development of the stolons is unclear in the remaining taxa.

It is currently uncertain, whether the Dithecodendridae belong to Eugraptolithina of Maletz *et al.* (2009) or should be considered as basal Graptolithina. None of these taxa is known from relief or isolated material, and the sicular development is completely unknown. A number of taxa can be shown to be graptolites based on the presence of fuselli (Rickards & Durman 2006), while the rest is included only due to the general shape of the colonies. Previously, Mierzejewski (1986a) referred several Middle Cambrian genera to the hydroids.

The taxa in general possess slender stipes with an alternating origin of the long and slender, often slightly widening metathecae, in part similar to those of the genus *Mastigograptus*, but the presence of a triad budding system is unlikely due to the alternation of thecae along the stipes. Dithecodendridae includes the earliest erect growing benthic graptolites and precedes most of the encrusting taxa described by Kozłowski (1949) and others. Johnston *et al.* (2009) illustrated a number of erect "dithecoid"-like bushy graptolites from Burgess Shale-type biota at Haiduk and Tangle Peaks, British Columbia, which may represent the oldest taxa of this group. The material originates from the

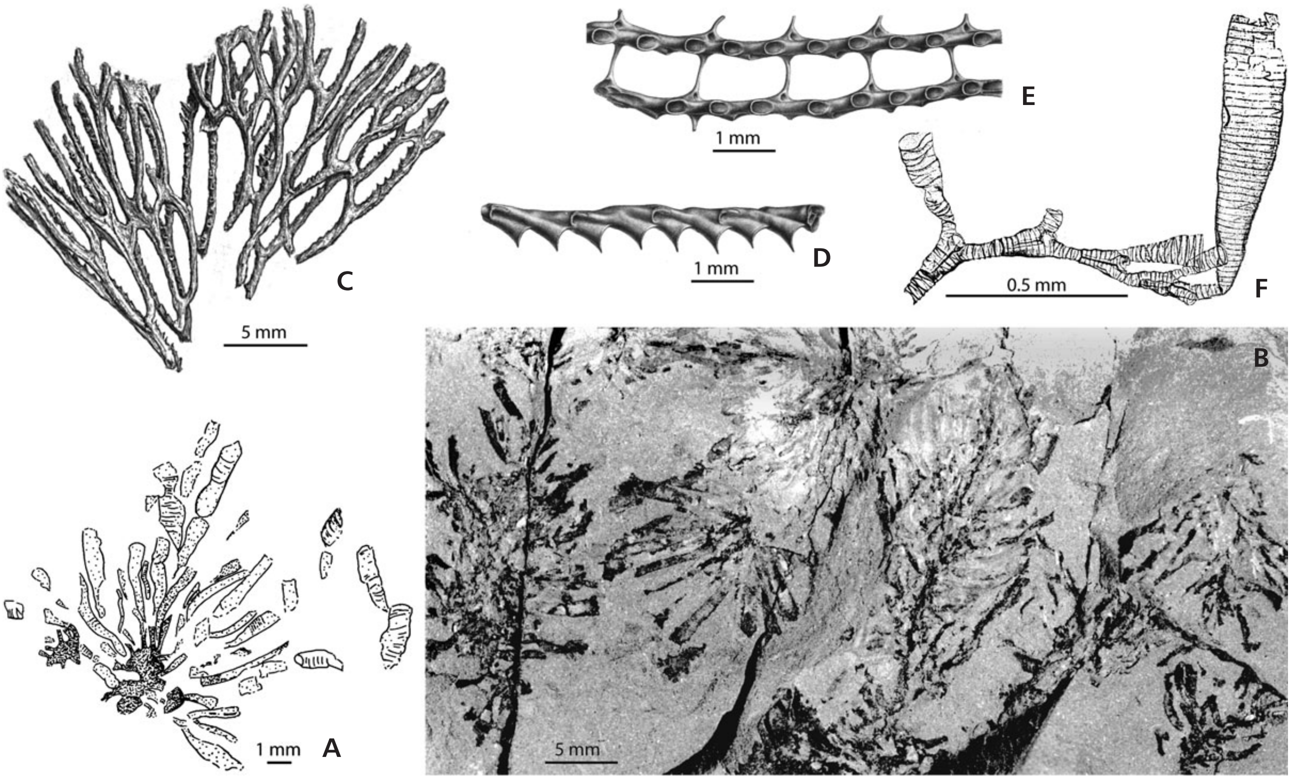

Figure 8. Encrusting and dendroid graptoloids. • A, B – *Rhabdotubus robustus* Maletz, Steiner & Fatka (Maletz *et al.* 2005), colonies with encrusting thecorhiza and erect tubes, showing fuselli. • C – *Desmograptus idoneus* Bulman (Bulman 1933, pl. 4), part of colony. • D, E – *Rhabdinopora flabelliformis* (Eichwald) (Bulman 1933, pl. 1), showing development of autothecae and bithecae. • F – *Micrograptus* sp. (Andres 1977) showing triad budding and form of isolated thecae.

Bolaspidella trilobite zone of Drumian age and is thus slightly younger than the Burgess Shale from which graptolites have not been identified with certainty.

Family Cyclograptidae Bulman, 1938 (p. 22)
[= Tubidendridae Kozłowski 1949, p. 160;
homonym of Tubidendridae Nutting, 1905, p. 940:
Hydrozoa]

Diagnosis (emended). – Largely encrusting Graptolithina with tubular thecae; often forming short erect branches in which the thecae are serially arranged; thecal development in diads with autothecae and bithecae, the latter often restricted to the thecorhiza.

Genera included. – ?*Alternograptus* Bouček, 1956; ?*Callodendrograptus* Decker, 1945; *Calycotubus* Kozłowski, 1949; *Camarotubus* Mierzejewski, 2001; *Conitubus* Kozłowski, 1949; *Cyclograptus* Spencer, 1883; *Dendrotubus* Kozłowski, 1949; *Discograptus* Wiman, 1901; *Dyadograptus* Obut, 1960; *Galeograptus* Wiman, 1901; *Kozlowskitubus* Mierzejewski, 1978 (Fig. 5H); *Marsipograptus* Ruedemann, 1936; *Multitubus* Skevington, 1963; *Parvitubus* Skevington, 1963; *Reticulograptus* Wiman, 1901; *Rhiphidodendrum* Kozłowski, 1949; *Rodonograptus* Počta, 1894; *Siberiodendrum* Obut, 1964; *Syrriphidograptus* Poulsen, 1924; *Tubidendrum* Kozłowski, 1949.

Discussion. – As Bulman (1938) already established the family Cyclograptidae for this group, the Tubidendridae Kozłowski, 1949, a homonym of Tubidendridae Nutting, 1905, becomes a junior synonym of this taxon. Bulman (1955, p. 22) quoted the Cyclograptidae, but did not use the name in the taxonomic part and did not refer to it in the second edition of the Treatise (Bulman 1970).

Cyclograptidae includes a number of benthic graptolites with encrusting to erect, bushy colonies and tubular thecae with a diad budding system. Mitchell *et al.* (2013, fig. 6) recognized an informal group, the "tuboids" including the genera *Kozlowskitubus* and *Reticulograptus* in their analysis, but did not discuss the group.

The taxa included in Cyclograptidae were previously referred to the two families Tubidendridae and Idiotubidae (Kozłowski 1949, Bulman 1970). They are here combined into one group based on their encrusting habit and the presence of groups of tubular erect thecal tubes. Quite a number of the genera may actually belong to other groups such as are Rhabdopleuridae, Cysticamaridae or Wimanicrustidae, but details of their initial colony growth are unknown.

Cyclograptidae, thus, can be seen as a "portmanteau" for benthic, encrusting graptolite taxa. The sicular (initial) development is barely known in any of these taxa. Kozłowski (1963, fig. 1) and Kozłowski (1971, fig. 5) illustrated bottle-shaped siculae with partial helical line in the prosicula and referred it to *Dendrotubus* (now *Kozlowskitubus*) *erraticus* (Fig. 8H).

Mitchell *et al*. (2013) separated the first taxon with a helical line in the prosicula and all its descendants as the paraphyletic Eugraptolithina. The authors included the three genera *Dendrotubus*, *Kozlowskitubus* and *Reticulograptus* in their analysis and referred to these taxa as the basal Eugraptolithina.

Eugraptolithina Mitchell *et al*., 2013 should not be confused with Eugraptoloida Maletz *et al*., 2009. Mitchell *et al.* (2013, p. 53) erected the Eugraptolithina as the holophyletic, apomorphy-based taxon that includes the first graptolite that acquired a prosicula with a helical line and all its descendants, basically including all Dendroidea and Graptoloidea as defined herein. The origin and early evolution of this feature, however, is quite unclear, as its presence can be ascertained in very few benthic taxa only, while it is present in all planktic graptolites. The presence of a helical line on the sicula is based on three isolated siculae referred to *Kozlowskitubus* (Kozłowski, 1963: *Dendrograptus erraticus* Kozłowski), of which two specimens show this possible helical line. The sicula and its development are not known from any other Cyclograptidae. Therefore, the basal members of this clade, identified as members of the Cyclograptidae herein, cannot be identified with any confidence. Mitchell *et al.* (2013), especially discuss the genus *Dendrotubus* and its influence that its inclusion or exclusion in the analysis has. The sicula is not known in *Dendrotubus*, but the cladistic analysis indicates the inclusion of the genus in the Eugraptolithina (Mitchell *et al.* 2013, p. 47). Interestingly, an exclusion of *Dendrotubus* increases the resolution of the eugraptolithines in the analysis.

The introduction of a helical line in the prosicula (see Fig. 5H) may potentially be an important event in graptoloid evolution, but at the moment, it is not useful at all, questioning the value of the taxon Eugraptolithina. Too few juvenile specimens of benthic, dendroid graptolites are known to show the construction of the initial colony and to interpret the evolutionary patterns. The presence of the helical line in the prosicula may also be related to an upright, erect growth of the colonies, which appears to be typical of the Dendroidea. However, some taxa of the Cyclograptidae already possess an erect growth of the stipes and overlap in their tubarium features with the Dendroidea.

The triad budding of many dendroid graptolites may be more useful to delimit the group, but its phylogenetic origins are shrouded in mystery. Most geologically important graptolites belong to the Eugraptolithina. Two main groups, Dendroidea and Graptoloidea can be differentiated, based on the presence of a nematophorous sicula (Graptoloidea) or a tubular sicula (Dendroidea), leading to the interpretation of a benthic, sessile (Dendroidea) or planktic (Graptoloidea) lifestyle. It is useful to keep these two main taxon names as they are well established and useful and their definition has not changed considerably from previous use (*e.g*. Bulman 1970).

Mitchell *et al.* (2013, fig. 6) indicated an informal paraphyletic group as the "dendroids", but did not discuss the group further. The group also included the genus *Mastigograptus*, here referred to the Mastigograptidae and several taxa of the Acanthograptidae.

Order Dendroidea Nicholson, 1872b (p. 101)
(= Cladophora Hopkinson, 1875
in Hopkinson & Lapworth 1875, p. 634)

Diagnosis (emended). – Benthic graptoloids with variable colony shape; erect, bushy or fan-shaped tubarium; thecae serially arranged along the stipes with regularly placed bithecae based on a triad budding concept; thecal development variable from tube-shaped to distinctly widening and with ventral rutellum; anastomosis or dissepiments present in some taxa; sicular development largely unknown.

Discussion. – Dendroidea includes most of the non-nematophorous graptoloids with a bush- or tree-shaped colony development, possessing a triad-budding system and a distinct thecal differentiation. Bushy growth, however, also appears in some Cyclograptidae, in which the encrusting part may be reduced in size. The genera are usually defined from tubarium fragments, based on general constructional features. Proximal ends and siculae are rarely known in enough detail to understand the real phylogenetic relationships. The taxon is used for stability (of nomenclature) reasons. A phylogenetic analysis of all groups of these benthic graptolites and their relationships does not exist and is unlikely to be provided soon.

Mitchell *et al*. (2013) did not provide any indication or opinion on the differentiation of the "dendroid", benthic graptolites. The earlier differentiation into several families (see Chapman *et al.* 1993) indicates, that differences and similarities can be used to group the individual genera into higher rank taxa, but little information on the important initial colony development exists.

Family Dendrograptidae Roemer, 1897
in Frech (1897) (p. 568)
(incl. Pseudodictyonemidae Chapman *et al.* 1993,
Stelechocladiidae Chapman *et al.* 1993).

Diagnosis (emended). – Benthic graptoloids with variable colony shape; erect, bushy or fan-shaped tubarium; thecae serially arranged along the stipes with regularly placed bithecae based on a triad budding concept; anastomosis or dissepiments present in some taxa; sicular development largely unknown; autothecae widening towards the apertures, possessing a vental lip or rutellum, sometimes with complex apertural modifications.

Genera included. – *Airograptus* Ruedemann, 1916; *Aspidograptus* Bulman, 1934; ?*Cactograptus* Ruedemann, 1908; *Callograptus* Hall, 1865; *Calyxdendrum* Kozłowski, 1960; *Capillograptus* Bouček, 1957; *Dendrograptus* Hall, 1858 (Fig. 5C); *Denticulograptus* Schmidt, 1939; *Desmograptus* Hopkinson *in* Hopkinson & Lapworth, 1875 (Fig. 8C); *Dictyonema* Hall, 1851 (Fig. 5B); *Graptolodendrum* Kozłowski, 1966; *Licnograptus* Ruedemann, 1947*;* *Odontocaulis* Lapworth, 1881; *Ophigraptus* Jaeger, 1992; *Ophiograptus* Poulsen, 1937; *Pseudocallograptus* Skevington, 1963; *Pseudodictyonema* Bouček, 1957; *Ptilograptus* Hall, 1865; *Ptiograptus* Ruedemann, 1908; *Rhabdinopora* (*Dictyograptus*) Paškevičius, 2011; *Rhizograpsus* Spencer, 1878; ?*Ruedemannograptus* Termier & Termier, 1948; *Stelechiocladia* Počta, 1894; *Streptograptus* Ruedemann, 1947 [*non Streptograptus* Yin, 1937: see Monograptidae], *Zigzagigraptus* Yu, 1962.

Discussion. – Dendrograptidae may represent a paraphyletic taxon from which the derived planktic graptoloids originated. Mitchell *et al.* (2013, fig. 6) showed the "dendroids" as a paraphyletic unit including a number of genus level taxa that are here informally referred to a variety of family level taxa (*e.g.* Acanthograptidae, Mastigograptidae) between which the precise phylogenetic relationships are unclear.

Most taxa are poorly known, from flattened shale material or isolated stipe fragments. Thus, their proximal end development and sicular construction are unknown. The erect growth of their colonies may be regarded as a defining character of Dendrograptidae. The thecae are generally serially arranged on the stipes and possess the typical triad budding with alternate bithecae (Fig. 8D, E). Branching is often irregular and secondary connections between stipes through dissepiments and anastomosis is common, but not present in all taxa.

Planktic dendroids (Kraft & Kraft 2008) have been described from a number of occurrences. They may possibly be referred to the genus *Calyxdendrum* Kozłowski, a genus that Bulman (1970) identified as a member of the planktic Anisograptidae. The taxon *Pseudocallograptus* cf. *salteri* (Skevington 1963) from the Middle Ordovician of Öland has a sicula with a free nema, indicating a possibly planktic taxon. These planktic taxa should not be placed in the planktic Graptoloidea, as they likely represent a secondary, independent origination of a planktic life style. It is preferred here to keep them with the benthic Dendrograptidae, as they do not possess the defining characters of the planktic Anisograptidae. They may have to be referred to their own family when better known.

Family Acanthograptidae Bulman, 1938 (p. 20)
(= Inocaulidae Ruedemann, 1947, p. 230)

Diagnosis (emended). – Benthic graptoloids with variable shape of colonies, from erect, bushy or fan-shaped; thecae elongated, tube-shaped with a non-serial organisation; complex stipe development of ropy appearance and isolated autothecal apertures or development of twigs; regularly placed bithecae based on a triad budding concept, but no size differentiation of bithecae; anastomosis or dissepiments present in some taxa; sicular development largely unknown.

Genera included. – *Acanthograpsus* Spencer, 1878; *Archaeodictyota* Obut & Sobolevskaya, 1967; *Boiophyton* Obrhel, 1959; *Coremagraptus* Bulman, 1942; *Koremagraptus* Bulman, 1927b (Fig. 8E); *Palaeodictyota* Whitfield, 1902; *Saxonia* Roselt, 1962; *Trimerohydra* Kozłowski, 1959.

Discussion. – Rickards & Durman (2006, fig. 18) included a number of taxa of the Acanthograptidae in their study (*Acanthograptus*, *Thallograptus*, *Koremagraptus*, *Palaeodictyota*) and showed them as a monophyletic group. The presence of multiserial stipes was regarded as the main synapomorphy of the group. The monophyly of the taxon cannot be proven due to the lack of structural information on most taxa and the family is therefore regarded as a preliminary taxonomic unit until more details on the colony development of its members are available. The family includes a small number of taxa with complex stipe development and tubular thecae with isolated apertures (Fig. 5D). The proximal development and sicula are unknown for all included taxa. A number of taxa previously included in the Inocaulidae may turn out to represent algae, including the type species of the genus *Inocaulis*, *Inocaulis plumulosa* Hall.

Maletz & Kozłowska (2013) illustrated partial relief specimens of *Acanthograptus sinensis* Hsü & Ma, with slender and parallel-sided, tube-like thecae, typical of Acanthograptidae. The specimens show paired thecal origins, but a differentiation of potential autothecae and bithecae is impossible. The thecae are generally straight and curve outwards only at their apertures, but a number of thecae can be seen to produce irregular curved paths.

Acanthograptidae can easily be misidentified as landplants if only the outline of the specimens is preserved. This may be the case with the genera *Boiophyton* and *Saxonia*, two poorly known acanthograptid genera from Ordovican to Silurian strata. Kenrick *et al*. (1999) have convincingly documented the graptolitic relationships of *Boiophyton*.

Ruedemann (1947) introduced the family Inocaulidae for taxa with complex stipes formed from numerous slender tubular thecae. Mierzejewski (1986) discussed the genus *Inocaulis* in some detail and questioned the inclusion in the graptolites. He restricted the family Inocaulidae to a single genus, *Inocaulis*. Muir *et al.* (2013) referred a single stipe fragment from the Middle Ordovician of Guizhou, China to the genus *Inocaulis*, and suggested the recognition of *Inocaulis* as a graptolite. There is no evidence of a graptolitic nature of the type *Inocaulis plumulosa* Hall, 1852, however, and the inclusion of *Inocaulis* in the graptolite must be questioned. The specimen of Muir *et al.* (2013) may be identified as a taxon of the Acanthograptidae.

Family Mastigograptidae Bates & Urbanek, 2002 (p. 458)

Diagnosis (emended). – Bushy dendroid colonies with slender stipes formed from stolonal strands; metathecae arranged in pairs, distinctly widening; fuselli formed as complete fusellar rings with irregularly placed sutures, not regular half-rings; triad budding present; auto- and bithecae not differentiated by size; sicular development poorly known.

Genera included. – *Mastigograptus* Ruedemann, 1908; *Micrograptus* Eisenack, 1974

Discussion. – Mastigograptidae is likely to be monophyletic. The family is based on two closely related genera with a typical triad budding system. The taxa are known from isolated three-dimensionally preserved specimens, found in glacial boulders in northern Germany and Poland. Their origin and phylogenetic relationships are uncertain, but the development of a typical triad budding system demands an inclusion in the derived Eugraptolithina (see Mitchell *et al.* 2013), and here in Dendroidea. Rickards & Durman (2006), however, included *Mastigograptus* in Dithecoidea.

Mastigograptidae differ from all other graptolites through their slender stems with a tightly adhering tube covering the stolon system and the thin-walled distinctly widening and completely isolated metathecal tubes (Fig. 8F). Similarities can be seen only to Dithecodendridae, but isolated material is not available from the latter group. This small, but well-defined family shows clearly the difficulties in our taxonomy. Few taxa are well enough known for a detailed analysis. Bates & Urbanek (2002) introduced a new order, Mastigograptida, for these taxa.

Bates & Urbanek (2002) provided some general information on the "initial segment" of the *Mastigograptus* colonies, which they presumed to represent the sicula. However, details of the sicular development are not available due to the cortical overgrowth of the proximal ends and the presence of a prosicula and metasicula is unknown. The authors interpreted the structure as a cylindrical sicula similar to the sicula of the dendroid graptolites, different from the embryonic vesicle of *Rhabdopleura* or the conical sicula of *Dendrotubus*.

Order Graptoloidea Lapworth, 1875 *in* Hopkinson & Lapworth (1875) (p. 633)

(= Rhabdophora Allman, 1872, p. 380;
= Division Graptoloida Mitchell *et al*., 2013, p. 53)

Definition. – (Mitchell *et al.* 2013, p. 53: Division Graptoloida) Graptoloida is the total clade descended from the first graptolite to possess a sicula with a caudal apex.

Discussion. – The Graptoloidea may be diagnosed as nematophorous graptoloids with serially budded autothecae and triad budding or derived development. They have highly variable colony shapes and are generally symmetrically organized. Their thecal construction varies from simple to complex. Graptoloidea (Graptoloida in Maletz *et al.* 2009 and Mitchell *et al.* 2013) represents a monophyletic taxon. Graptoloidea (Figs 2, 5) is used here in the same sense as in Fortey & Cooper (1986), to include all planktic, "nematophorous" graptoloids or Graptoloida of Maletz *et al.* (2009, p. 9) and Mitchell *et al.* (2013), while Bulman (1955, 1970) excluded Anisograptidae from Graptoloidea and referred the family to Dendroidea. Due to the complexities in colony development and its rapid evolutionary changes, a characterization of Graptoloidea is difficult to provide. Limitation of the colony shape is due to the planktic lifestyle of the organisms and their clonal, colonial organization. Early taxa (*Rhabdinopora* Eichwald) closely resemble benthic taxa (*Dictyonema* Hall), but new colony shapes and developments quickly evolved after the origin of the planktic graptoloids in the basal Tremadocian.

Secondarily derived planktic taxa of the Dendroidea have been discussed earlier (see Dendrograptidae). As long as information on the development of their siculae and proximal development is not available, a comparison with the Graptoloidea is impossible and the interpretation of these taxa as independently derived may be conjectural.

The Supercohort Eugraptoloida Maletz, Carlucci & Mitchell, 2009, p. 11 (= Graptoloidea *sensu* Bulman, 1970). – Maletz *et al.* (2009, p. 11) defined the clade Eugraptoloida as the common ancestor of *Nicholsonograptus fasciculatus* Nicholson and *Exigraptus uniformis* Mu *in* Mu *et al.* and all its descendents. The authors indicated as a defining synapomorphy the loss of the bithecae along the stipes (synapomorphy 2). Eugraptoloida, thus, include the same group of taxa included in the order Graptoloidea by Bulman (1955, 1970). Interestingly,

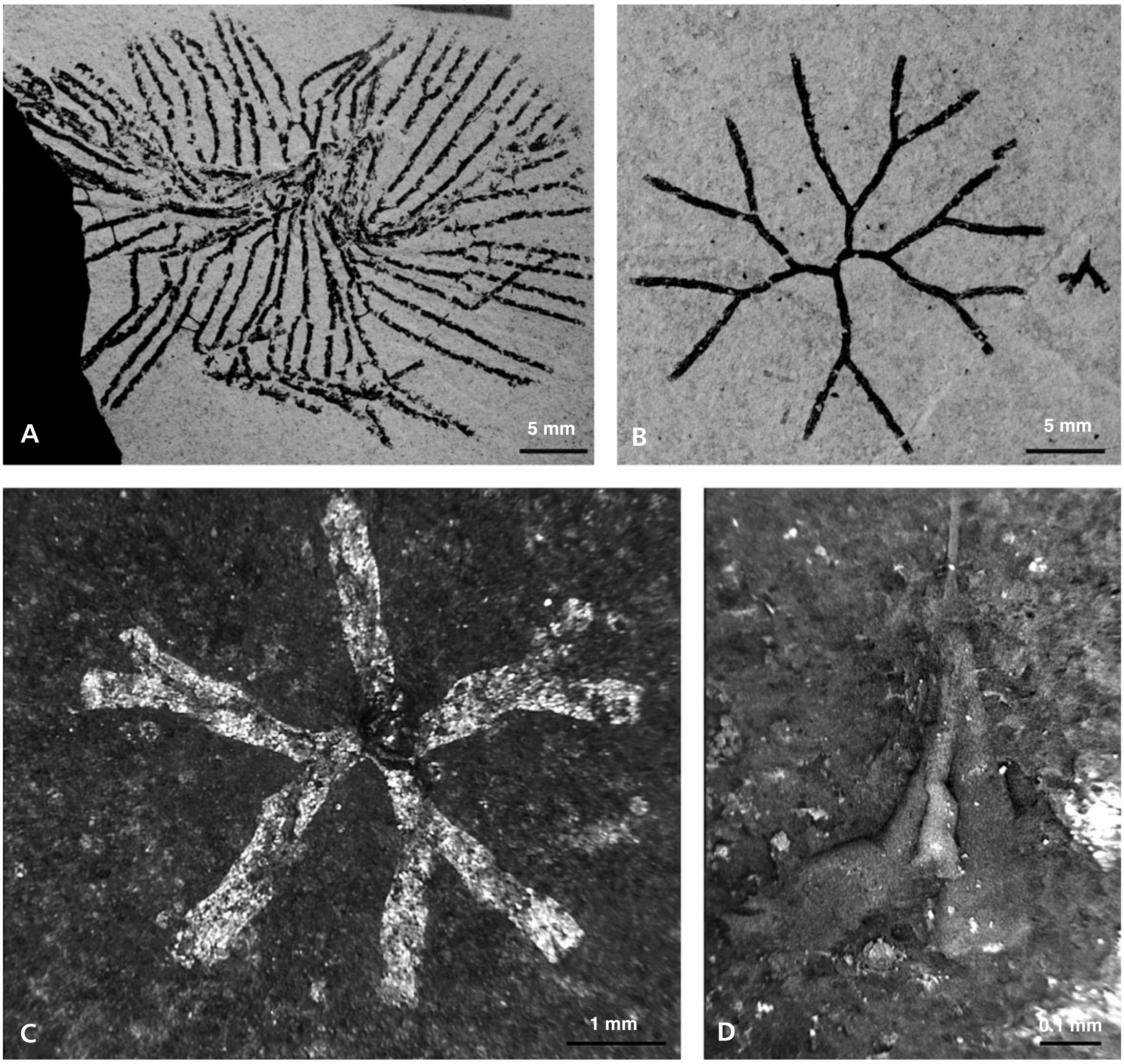

Figure 9. Examples of Anisograptidae, showing rhabdosome shapes and development. • A – *Rhabdinopora flabelliformis anglica* Bulman, Erdtmann collection, specimen showing conical shape of rhabdosome and presence of dissepiments connecting stipes. • B – *Anisograptus matanensis* Bulman, Erdtmann collection, horizontal, triradiate taxon, see juvenile to the right. • C – *Staurograptus dichotomous* Emmons, NYSM 6016 (Ruedemann 1904, pl. 2, fig. 9), small specimen with impression of sicula in centre. • D – *Staurograptus dichotomous* Emmons, NYSM 6011, latex cast of juvenile showing sicular bitheca (Ruedemann 1904, pl. 2, fig. 4).

the cladistic analysis of Fortey & Cooper (1986, fig. 3) showed Graptoloidea *sensu* Bulman (1970) as polyphyletic, a notion that has never been rejected entirely, but was not discussed in Maletz *et al*. (2009). Fortey & Cooper (1986) analyzed the anisograptids in aim to understand the transition of the bithecate to non-bithecate taxa. Thus, their analysis was able to shed some light on the roots of the non-bithecate graptoloids (now the Eugraptoloida). The conclusion shows an at least triphyletic origin of non-bithecate graptoloids and the authors concluded that an inclusion of the Anisograptidae in the Graptoloidea was more useful.

Lindholm (1991, p. 289), also discussing the finds of Williams & Stevens (1991), suggested a loss of bithecae "along different lineages in a rather restricted time period" within the anisograptids, based on the investigation of the late Tremadocian *Hunnegraptus copiosus* Biozone fauna. Lindholm (1991) included the genus *Hunnegraptus* Lindholm, in which the sicular bitheca is the only bitheca of the colony, in the Dichograptidae and referred *Paradelograptus* Erdtmann, Maletz & Gutiérrez-Marco to the Sinograptidae.

Maletz *et al*. (2009) used *Rhabdinopora* Eichwald as the outgroup and added two further anisograptid taxa (*Anisograptus* Ruedemann, *Adelograptus* Bulman) to their analysis. Due to the low number of anisograptid taxa, the authors were unable to trace the origins of the Eugraptoloida. However, their intention was to differentiate clades within the Eugraptoloida and not to find the eugraptoloid roots.

The value of the clade Eugraptoloida (see Fig. 2) is questionable, as the transition from the bithecate to the non-bithecate graptolites is still not resolved. The main difficulty in understanding these early planktic graptoloids and their evolutionary relationships is the rarity of well-preserved and isolatable material or relief specimens showing the thecal details of the transitional taxa (Lindholm 1991). Sadler *et al.* (2011, fig. 13) showed a crisis in graptolite evolution during the Tremadocian, in which an extremely low diversity has been demonstrated. This "crisis", however, may be based on the lack of sections of this age, which contain well-preserved or investigated graptolite faunas, and thus may be an artefact. The sudden appearance of Sinograpta and Dichograptina in the basal Floian (and possibly in the upper Tremadocian) indicates an independent origin of at least these two groups from Anisograptidae.

Suborder Graptodendroidina Mu & Lin, 1981 *in* Lin (1981) (p. 244)

Diagnosis. – See diagnosis of family Anisograptidae.

Discussion. – Lin (1981) introduced the Graptodendroidina to accommodate the bithecate planktic graptoloids of the Anisograptidae. Mu (1974, p. 229), previously, used the term "graptodendroids" for the Anisograptidae, but referred the taxon to the Dendroidea. Erdtmann (1988) emended the Graptodendroidina and discussed its early members in some detail. The Graptodendrodina is here understood as a paraphyletic taxon from which all derived graptoloids originate.

Family Anisograptidae Bulman, 1950 (p. 79)

Diagnosis (emended). – Planktic, multiramous graptoloids with triad budding; colony shape reclined, horizontal to declined and bell-shaped; origin of first theca in the median part of the prosicula; proximal development isograptid, quadriradiate to biradiate, variably dextral and sinistral; distinct size differentiation of autothecae and bithecae; bithecae initially regular, irregular and often reduced or even lost in later taxa; autothecae simple, aperturally widening tubes, sometimes aperturally isolated; ventral rutelli common; dissepiments in a few taxa.

Genera included. – *Adelograptus* Bulman, 1941; *Aletograptus* Obut & Sobolevskaya, 1962; *Ancoragraptus* Jackson & Lenz, 2003; *Anisograptus* Ruedemann, 1937 (Figs 9B, 11B); *Aorograptus* Williams & Stevens, 1991; *Araneograptus* Erdtmann & VandenBerg, 1985; *Bryograptus* Lapworth, 1880; *Chigraptus* Jackson & Lenz, 1999; *Choristograptus* Legrand, 1964; *Damesograptus* Jahn, 1892; *Dictyodendron* Westergård, 1909; *Dictyograptus* Hopkinson, 1875 *in* Hopkinson & Lapworth (1875); *Dictyograptus* Westergård, 1909; *Diphygraptus* Zhao & Zhang, 1985; *Graptopora* Salter, 1858; *Heterograptus* Zhao & Zhang *in* Lin, 1986; *Holopsigraptus* Zhao & Zhang, 1985; *Hunjiangograptus* Zhao & Zhang, 1985; *Hunnegraptus* Lindholm, 1991; *Kiaerograptus* Spjeldnaes, 1963; *Muenzhigraptus* Zhao & Zhang, 1985; *Neoclonograptus* Zhao & Zhang, 1985; ?*Nephelograptus* Ruedemann, 1947; *Paraclonograptus* Zhao & Zhang, 1985; *Paratemnograptus* Williams & Stevens, 1991; *Phyllograpta* Angelin, 1854; *Psigraptus* Jackson, 1967; *Radiograptus* Bulman, 1950; *Rhabdinopora* Eichwald, 1855 (Fig. 5A, 9A); *Sagenograptus* Obut & Sobolevskaya, 1962 [*non Sagenograptus* Lenz & Kozłowska-Dawidziuk, 2001: see Retiolitidae], *Staurograpsus* Emmons, 1855 (Fig. 9C); ?*Stellatograptus* Erdtmann, 1967; *Toyenograptus* Li, 1984; *Triograptus* Monsen, 1925; *Triramograptus* Erdtmann, 1998 *in* Cooper *et al.* (1998); *Yukonograptus* Lin, 1981.

Discussion. – Anisograptidae is a paraphyletic family at the origin of the Graptoloidea. Mitchell *et al.* (2013) regarded the genera *Rhabdinopora* and *Anisograptus* as basal Graptoloidea, but did not discuss derived graptoloid taxonomy. Maletz *et al.* (2009) identified the Anisograptidae as stem eugraptoloids.

The internal evolutionary structure of the Anisograptidae has never been analysed in detail and the origins of the derived Dichograptina and Sinograpta are uncertain. It is possible that a number of clades originated independently from the Anisograptidae. Mu (1974) named the Anisograptidae informally as the "graptodendroids", but Graptodendroidina Mu & Lin (*in* Lin 1981, pp. 244–245) was introduced as a suborder of Dendroidea. It was used by a number of authors (*e.g.* Erdtman 1988, Wang & Wang 2001, Cho *et al.* 2009).

The proximal development and rhabdosome construction is known from a surprisingly high number of anisograptid taxa. The development of the earliest taxa is quadriradiate (Fig. 9C) with four stipes originating in close succession from the initial theca (th1^1), but tri- (Fig. 9B) and biradiate (Fig. 10A, F) taxa soon take over (Maletz 1992). Anisograptidae generally bear alternate bithecae associated with the autothecae on all stipes, of which the sicular bitheca (Figs 9D, 10B, F) is the earliest and is probably the last bitheca lost through the evolutionary elimination of the bithecae during the late Tremadocian (Lindholm 1991).

Suborder Sinograpta Maletz, Carlucci & Mitchell, 2009 (p. 11) (*ex* Pan-Sinograpta Maletz, Carlucci & Mitchell, 2009)

Definition. – (Maletz *et al.* 2009, p. 11) The crown clade Sinograpta comprises the common ancestor of *Nicholsonograptus fasciculatus* and the first species with a slender sicula and parallel-sided prosicula and all its descendants.

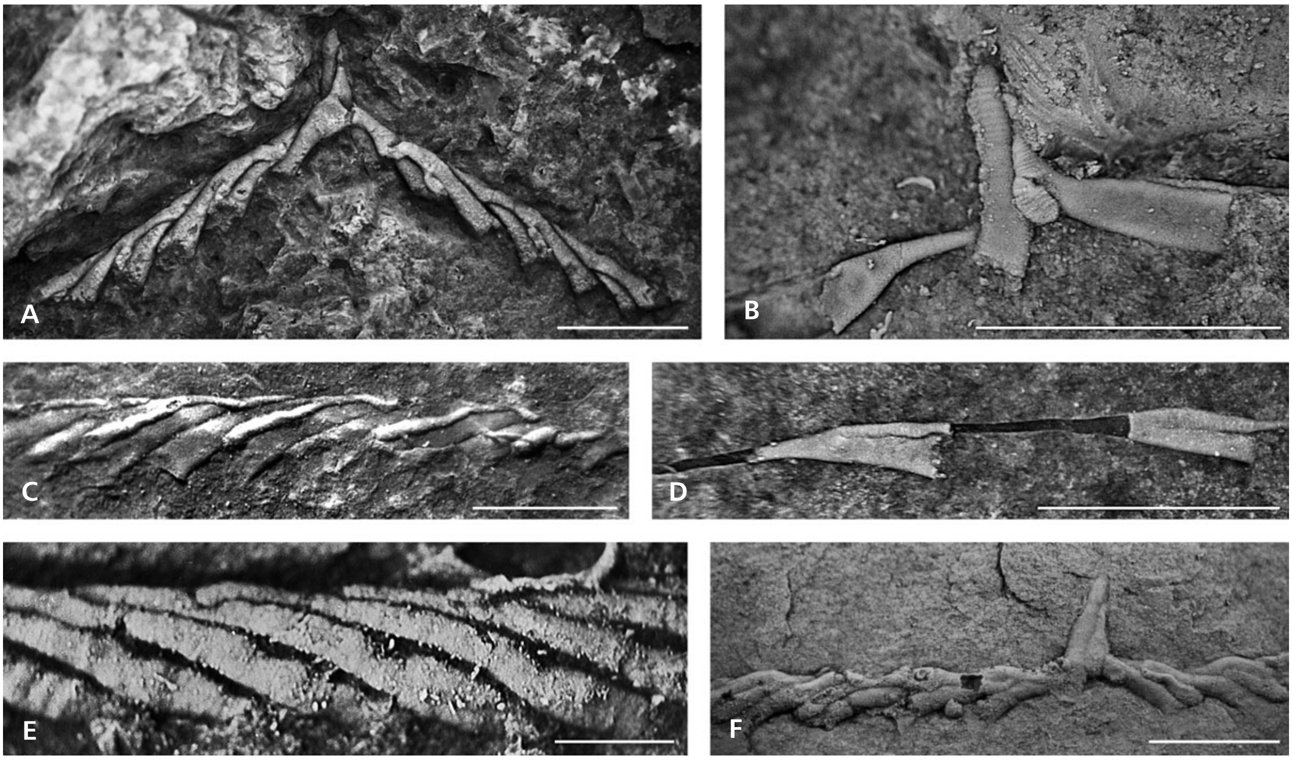

Figure 10. Transitional anisograptids with and without bithecae. • A, F – "*Kiaerograptus*" *supremus* Lindholm, LO 5970T, holotype in reverse view with regular bithecae, (A) and PMO 139.919, specimen in obverse view (F) showing irregularly placed bithecae and more horizontal colony shape. • B, D – *Paradelograptus onubensis* Erdtmann, Maletz & Gutiérrez-Marco, GSC 118739, obverse view, showing large sicular bitheca and helical line in prosicula, (B), GSC 118751, stipe without bithecae (D). • C – *Kiaerograptus kiaeri* Monsen, PMO 72.833, fragment with long, regularly positioned bithecae on stipe. • E – *Paratemnograptus* sp., PMO 108.558, fragment with plaited overlap of thecae (lateral thecal origination), but no bithecae (see Lindholm & Maletz 1989). Scale bar represents 1 mm.

Discussion. – Sinograpta may be characterised by multiramous to two-stiped, horizontal to pendent rhabdosomes. The colony is biradiate with asymmetrical placing of first order stipes, a nearly parallel-sided sicula with parallel-sided prosicula. The origin of the first theca is in the median part of prosicula in early taxa, but in the lower part of the prosicula in younger ones. The thecae are simple or with complex and elaborate apertures, slender and sometimes elongated. At least a sicular bitheca is present in early members (Fig. 10B).

Sinograpta is defined as a monophyletic taxon (Maletz *et al.* 2009), as sister group to the Pan-Reclinata, including a number of family level taxa. Maletz *et al.* (2009) introduced the cohort Pan-Sinograpta for the taxa previously known as the families Sinograptidae and Sigmagraptidae (Fortey & Cooper 1986). Maletz *et al.* (2009) recognized the cohort Pan-Sinograpta as a stem group to the subcohort Sinograpta, but stated that all taxa in their analysis can be referred to the Sinograpta. Early species of *Paradelograptus* show a sicular bitheca (Fig. 10B), but the stipes show simple thecae with dorsal origins (Fig. 10D). Unfortunately, very few graptolites from the upper Tremadocian show details of their rhabdosome development and thus little can be learnt about their evolutionary relationships.

The taxon is here called Sinograpta and differentiated into three families, Sigmagraptidae, the derived Sinograptidae and Abrograptidae of uncertain relationships. The analysis of Maletz *et al.* (2009) provided no resolution within the Pan-Sinograpta, but showed an unresolved polytomy at the base of the unit. A differentiation of Sinograptidae and Sigmagraptidae is possible, based on structural details of the proximal ends (Fig. 11).

The proximal asymmetry (Fig. 11A, C) of the stipe divergence in the Sigmagraptidae is retained as a symplesiomorphic character from the Anisograptidae (Fig. 11B), but the sicula is now positioned vertically to the stipes. The proximal end changed to a symmetrical development in the Sinograptidae (Fig. 11D, E). The stratigraphical distribution of the taxa indicates an origin of Sinograptidae from Sigmagraptidae in the late Dapingian to early Darriwilian.

Family Sigmagraptidae Cooper & Fortey, 1982 (p. 257)
(*ex* Sigmagraptinae Cooper & Fortey, 1982, p. 257)

Diagnosis (emended). – Multiramous to one-stiped, horizontal to pendent rhabdosomes; colony biradiate with asymmetrical placing of first order stipes; sicula

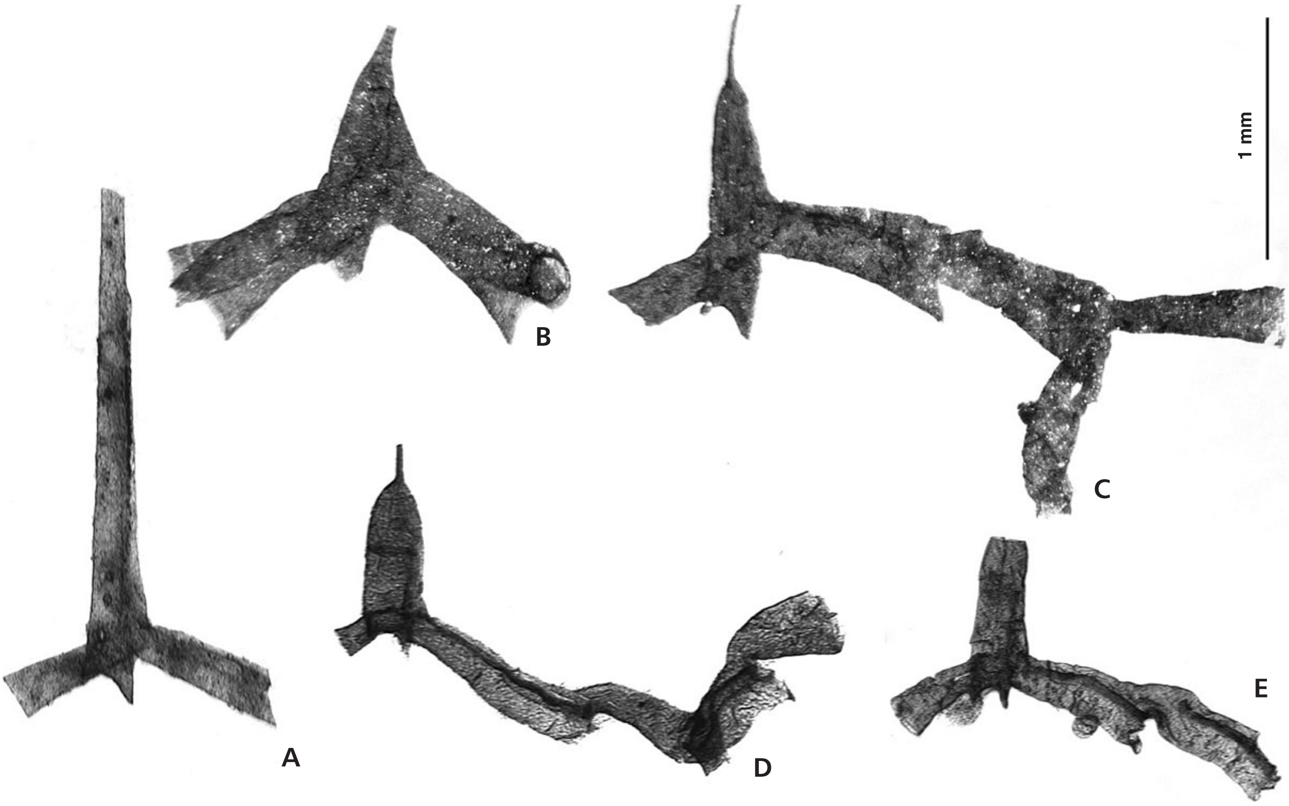

Figure 11. Anisograptidae (B) and Sinograpta (A, C–E), proximal shapes, Sigmagraptidae (A, C) with asymmetrical development and Sinograptidae (D, E) with symmetrical development of stipes. • A – *Sigmagraptus* sp. with elongated, slender sicula, CHN 11.4E. • B – *Anisograptus matanensis* Ruedemann, NGPA 216/07. • C – Sigmagraptine indet., SPI 63. • D – *Anomalograptus reliquus* Clark, WB2.34.42b. • E – *Holmograptus* sp., cf. *Holmograptus lentus* Törnquist, SPSE 4/03c. All specimens flattened, from Cow Head Group, western Newfoundland. Scale bar represents 1 mm.

parallel-sided with parallel-sided prosicula; origin of first theca in median part of prosicula in early taxa, in the lower part of the prosicula in younger ones; thecae simple or with complex and elaborate apertures, slender and sometimes elongated.

Genera included. – *Acrograptus* Tzaj, 1969; *Azygograptus* Nicholson & Lapworth, 1875 *in* Nicholson (1875); *Eoazygograptus* Obut & Sennikov, 1984; *Eotetragraptus* Bouček & Přibyl, 1951; *Etagraptus* Ruedemann, 1904; *Goniograptus* M'Coy, 1876; *Hemigoniograptus* Jin & Wang, 1977; *Jiangnanograptus* Xiao & Chen, 1990; *Jishougraptus* Ge, 1988; *Keblograptus* Riva, 1992; *Kinnegraptus* Skoglund, 1961; *Laxograptus* Cooper & Fortey, 1982; *Maeandrograptus* Moberg, 1892; *Metazygograptus* Obut & Sennikov, 1984; *Oslograptus* Jaanusson, 1965; *Paradelograptus* Erdtmann, Maletz & Gutiérrez-Marco, 1987; *Paraulograptus* Bouček, 1973; *Pendeosalicograptus* Jiao, 1981; *Perissograptus* Williams & Stevens, 1988; *Praegoniograptus* Rickards & Chapman, 1991; *Prokinnegraptus* Mu, 1974; *Sigmagraptus* Ruedemann, 1904 (Fig. 11A); *Taishanograptus* Li & Ge, 1987 *in* Li, Ge & Chen (1987); *Trichograptus* Nicholson, 1876; *Wuninograptus* Ni, 1981; *Yushanograptus* Chen, Sun & Han, 1964.

Discussion. – Sigmagraptidae is a paraphyletic family from which Sinograptidae originated in the late Dapingian to early Darriwilian. Sigmagraptidae is used here at family level, following Fortey & Cooper (1986), as it includes a fairly large group of taxa. Alternatively, Sinograptidae could be kept as a family with the subfamilies Sinograptinae, Sigmagraptinae and Abrograptinae. Sigmagraptidae can be differentiated from Sinograptidae through the presence of an asymmetrical proximal end with the stipes of the first order originating at different levels from the sicula, a plesiomorphic character retained from the Anisograptidae (Fig. 11). Sigmagraptidae have the sicula placed vertically between the stipes (Maletz *et al.* 2009, p. 11: synapomorphy 3) instead of possessing the inclined sicula of the Anisograptidae.

Maletz *et al*. (2009) showed *Maeandrograptus leptograptoides* Monsen as most closely related to *Holmograptus* Kozłowski*, Pseudodichograptus* Chu and *Nicholsonograptus* Bouček & Přibyl, but Maletz (2004) already referred the genus *Maeandrograptus* to the sigmagraptines, based on the proximal development with the asymmetrical development of the crossing canals.

Strangely, *Perissograptus*, closely related to *Maeandrograptus*, is shown as a member of Tetragraptidae in

Maletz *et al.* (2009). *Perissograptus* has a sicula identical in shape and development to *Maeandrograptus*, being typically slender and parallel-sided with slight development of a dorsal and a ventral rutellum. The proximal development differs considerably from the development in the tetragraptids and of *Phyllograptus* Hall, with which it was connected by Maletz *et al.* (2009, fig. 2). The tetragraptids and phyllograptids possess a small prosicula and a distinctly widening metasicula and wide crossing canals. *Phyllograptus* also has a dorsal virgellar spine, not present in *Perissograptus*. A closer relationship of *Perissograptus* to the Tetragraptidae, as suggested by Maletz *et al.* (2009), therefore is unlikely.

The genus *Acrograptus*, referred to the stem reclinatids in a group with taxa identified herein as Pterograptidae by Maletz *et al.* (2009), is identified as a sigmagraptine through the proximal development of *Acrograptus* specimens from the Table Head Group of western Newfoundland (Albani *et al.* 2001). The genus has been used to include slender two-stiped graptoloids often of uncertain relationships. The identity of the species used by Maletz *et al.* (2009) for their analysis is unknown as no further data are provided. The clade including *Acrograptus* in Maletz *et al.* (2009) can be identified as the Pterograptidae, once *Acrograptus* is removed.

The inclusion of the one-stiped genera *Azygograptus* and *Jishougraptus* is based on the development of the sicula with a parallel-sided prosicula and a low prosicular origin of th1^1 in a number of chemically isolated specimens from the Dapingian (Chewtonian in Australasian stratigraphy) of western Newfoundland (Maletz 2004). *Azygograptus* specimens show a dimensionally identical sicula, even though the prosicula cannot be differentiated in any of the known material, as isolated specimens have never been found. "*Azygograptus*" *validus* (*Cymatograptus validus* Törnquist herein) from the Lower Floian of Scandinavia and Britain (Törnquist 1901, Beckly & Maletz 1991) may not be related to *Azygograptus*, but can be interpreted as a one-stiped member of the dichograptid genus *Cymatograptus* Jaanusson. It differs from all other *Azygograptus* species in possessing a long, slowly widening sicula with a high, possibly prosicular origin of the first theca. The development is identical to that of *Cymatograptus undulatus* Törnquist, but the species lacks the second stipe.

Family Sinograptidae Mu, 1957 (p. 387)

Diagnosis (emended). – Multiramous to two-stiped, horizontal to declined rhabdosomes; colony biradiate with symmetrical placing of first order stipes; sicula parallel-sided, often with dorsal and ventral rutellum; parallel-sided prosicula; thecae simple or with complex and elaborate apertures, slender and sometimes elongated, often with prothecal folding.

Genera included. – *Allograptus* Mu, 1957; *Anomalograptus* Clark, 1924 (Fig. 11D); *Atopograptus* Harris, 1926; *Brachiograptus* Harris & Keble, 1932; *Hemiholmograptus* Hsü & Chao, 1976; *Holmograptus* Kozłowski, 1954 (Fig. 11E); *Nicholsonograptus* Bouček & Přibyl, 1951; *Paradidymograptus* Mu, Geh & Yin, 1962 *in* Mu *et al.* (1962); *Pseudodichograptus* Chu, 1965; *Pseudojanograptus* Hsü & Chao, 1976; *Pseudologanograptus* Hsü & Chao, 1976; *Pseudotetragraptus* Hsü & Chao, 1976; *Sinazygograptus* Wang & Wu, 1977 *in* Wang & Jin (1977); *Sinograptus* Mu, 1957; *Tylograptus* Mu, 1957; *Zygograptus* Harris & Thomas, 1941.

Discussion. – Sinograptidae is a monophyletic family including a number of genera united by their proximal development and thecal style. Sinograptidae possess a vertical, parallel-sided sicula with a comparatively large, parallel-sided prosicula (Fig. 11D), a dorsal and a ventral rutellum on the sicula and symmetrically placed stipes. Most sinograptids also have pronounced prothecal folds and further thecal elaborations. They represent a short-lived, but successful group of multiramous to biramous graptoloids in the early Darriwilian. The youngest member occurs in the *Nicholsonograptus fasciculatus* Biozone of mid-Darriwilian age.

Family Abrograptidae Mu, 1958 (p. 261)
(p. 264; English text)

Diagnosis. – Biradiate, multiramous to biserial or uniserial Sinograpta with reduced fusellum and lists showing the thecal outlines; sicula completely sclerotized.

Genera included. – *Abrograptus* Mu, 1958; *Dinemagraptus* Kozłowski, 1951; *Jiangshanites* Mu & Qiao, 1962; *Metabrograptus* Strachan, 1990; *Parabrograptus* Mu & Qiao, 1962.

Discussion. – Little information exists on the constructional details of the family Abrograptidae. The recognition of the members of the family is based on the reduction of the thickness of the fusellum. Isolated material referred to *Jiangshanites* (Maletz 1993) indicates a relationship to Sinograpta. Abrograptids are usually found as poorly preserved flattened specimens in shale. A few chemically isolated proximal ends of *Jiangshanites dubius* (Maletz, 1993) represent the only isolated material available. The specimens show a symmetrical development of the first order stipes of the multiramous colony and a small, parallel-sided sicula with a prominent rutellum and a prosicular origin of th1^1. Finney (1980) included *Reteograptus* Hall in Abrograptidae, but the isolated specimens of that taxon indicate an axonophoran origin due to the presence of a prominent ventral virgellar spine (Finney 1980, fig. 16). It is here preliminarily referred to Climacograptidae based on the lack of proximal spines and the bulbously widened thecae without intrathecal folds. The single isolated specimen of *Dinemagraptus warkae* (Kozłowski 1951) shows a small sicula with a proportionally long prosicula, but little further detail is available. The sicular aperture bears a rutellum or a short virgellar spine. The thecae are outlined by a possibly dorsal list and an apertural ring.

Sinograpta indet. – *Thamnograptus* Hall, 1859.

Discussion. – *Thamnograptus* is a dubious multiramous genus the proximal end of which is unknown. Finney (1980) indicated a biform development of the thecae with spined slender proximal thecae and distal dichograptid thecae, but this is not supported from additional and better-preserved material. The association as fragmented specimens on shale surfaces may be adventitious and a proof of the biform thecal development may only be possible through chemically isolated material. The dichograptid thecal part could also represent remains of the associated *Acrograptus* species. The janograptid fragment (Finney 1980, fig. 4B) may belong to the taxon identified as *Didymograptus* sp. cf. *D. serratulus* Hall, more likely representing an *Acrograptus* species. Similar janograptid specimens are found as chemically isolated material in western Newfoundland (Albani *et al.* 2001). *Thamnograptus* is restricted to the Middle Ordovician (Upper Darriwilian to Sandbian).

Suborder Dichograptina Lapworth, 1873b
(table 1, facing p. 555)
[*ex* Dichograptidae Lapworth, 1873b]
[syn. Didymograptina Lapworth, 1880, p. 192
nom. correct. Jaanusson, 1960, p. 309;
ex Didymograpta Lapworth, 1880]

Diagnosis (emended). – Multiramous to two-stiped graptoloids with biradiate isograptid proximal development and maeandrograptid symmetry; colony shape scandent to reclined, horizontal and even pendent; prosicula small, with widening and much larger metasicula; thecae simple, widening tubes with or without rutellum; branching dichotomous or cladial.

Discussion. – Maletz *et al.* (2009) defined the total clade Pan-Reclinata (Dichograptina plus all derived taxa) to comprise all species that share a more recent common ancestor with *Exigraptus uniformis* Mu *in* Mu *et al.* than with *Nicholsonograptus fasciculatus* Nicholson, easily separated from its sister group, Pan-Sinograpta through the symmetrical proximal end. Their analysis showed only very low resolution within the stem lineage of the group (Fig. 2). Pan-Reclinata is a cladistically valid taxon to describe all dichograptids and derived taxa as a monophyletic clade. It is not used as it would add an unnecessary level in the taxonomic hierarchy used herein.

Dichograptina is a paraphyletic unit with a poor internal resolution (Fig. 2) in need of a more detailed investigation of its members. Dichograptina in this context includes the stem-reclinatids and the Pan-Tetragrapta of Maletz *et al*. (2009, fig. 2) and is largely consistent with the designation of Dichograptina by Lapworth (1873b), except that Sinograpta (Sinograptidae and Sigmagraptidae) were not differentiated at that time and only Fortey & Cooper (1986) recognized the necessity of separating these taxa. The large group of stem reclinatids and the uncertain taxonomic differentiation within the group by Maletz *et al*. (2009) indicates a lack in resolution and understanding of these taxa. Four families are tentatively differentiated in Dichograptina. Based on proximal development and rhabdosome construction, Didymograptidae and Pterograptidae can easily be differentiated, but the basal taxa, the Dichograptidae are less well known. Tetragraptidae is the most diverse group in rhabdosome development, including pendent to reclined and scandent taxa. The proximal development of the Tetragraptidae (Fig. 12B) indicates a most probable origin through a multiramous member of the Dichograptidae that lost its capacity of developing distal dichotomies beyond the first one, as it is basically identical to the development in *Clonograptus* Nicholson (see Lindholm & Maletz 1989).

Family Dichograptidae Lapworth, 1873b (p. 555)
[incl. Schizograptinae Ge *in* Mu *et al.* 2002, p. 201;
Mimograptinae Ge *in* Mu *et al.* 2002, p. 316]

Diagnosis (emended). – Multiramous graptoloids with biradiate proximal development and symmetrically placed crossing canals; colony shape reclined to horizontal and declined; prosicula small, with widening and much larger, conical metasicula; proximal development of the isograptid type; thecae simple, widening tubes without a distinct rutellum; branching dichotomous.

Genera included. – *Anthograptus* Törnquist, 1904; *Calamograptus* Clark, 1924; *Clonograpsus* Nicholson, 1873 (Fig. 12A, C, D, F); *Ctenograptus* Nicholson, 1876; *Dichograpsus* Salter, 1863; *Hermannograptus* Monsen, 1937; *Holograptus* Holm, 1881a; *Kellamograptus* Rickards & Chapman, 1991; *Kstaugraptus* Tzaj, 1973; *Loganograptus* Hall, 1868 (Fig. 12E); *Mimograptus* Harris & Thomas, 1940 (non *Mimograptus* Lapworth *in* Elles & Wood, 1908: see Glossograptidae); *Orthodichograptus* Thomas, 1972; *Rouvilligraptus* Barrois, 1893; *Schizograp-*

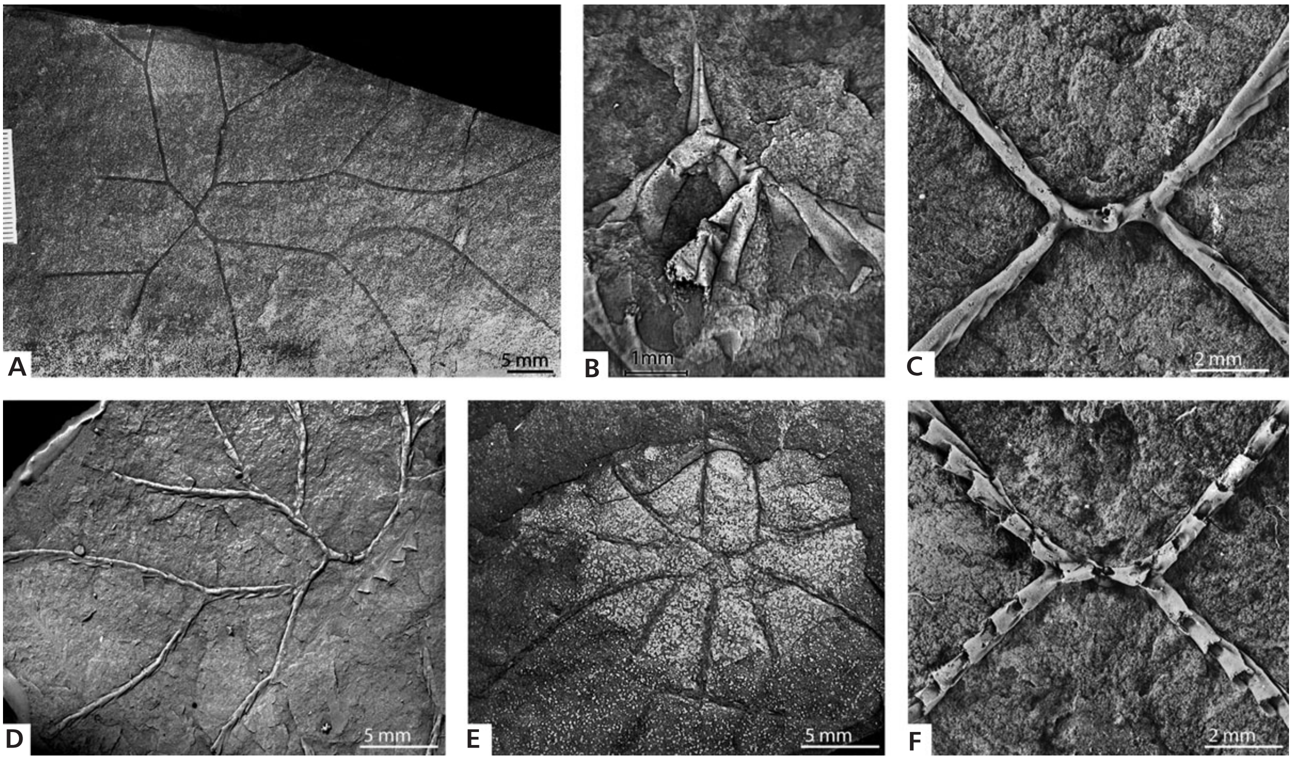

Figure 12. Dichograptina. • A, C, F – *Clonograptus multiplex* (Nicholson), LO 6027t (counterparts), Sweden, Hunneberg. Flattened specimen (A) and proximal ends preserved in relief in dorsal (C) and ventral (F) views, showing thecae and tetragraptid development, sicula visible in centre. • B – *Tetragraptus amii* Elles & Wood, JM Di 7, proximal end in relief showing isograptid proximal development with tetragraptid proximal end (th3^1 and th3^2 dicalycal; only dichotomy one seen) in reverse view. • D – *Clonograptus* sp. cf. *Clonograptus flexilis* (Hall), dorsal view in relief, showing some details of thecae. • E – *Loganograptus logani* Hall, flattened specimen with extensive webbing. Scale bar represents 1 mm.

tus Nicholson, 1876; *Temnograptus* Nicholson, 1876; *Triaenograptus* Hall, 1914; *Tridensigraptus* Zhao, 1964; *Trochograptus* Holm, 1881a.

Discussion. – Dichograptidae is most probably a paraphyletic taxonomic unit, but internal differentiation is impossible due to lack of information on structural details. Tetragraptidae and Didymograptidae may have originated independently from Dichograptidae. Dichograptidae includes all of the multiramous Lower Ordovician taxa (Fig. 12A, C–F) related to *Clonograptus*, *e.g.* multiramous taxa with dichotomous to lateral branching. They are usually based on a tetragraptid proximal end with two first order stipes (Fig. 12C, F) and symmetrically placed crossing canals (Fig. 12B). The proximal end and development are known from isolated and relief specimens of *Clonograptus* (Lindholm & Maletz 1989), but are unknown from all other dichograptids. Isolated material does not exist of most of the taxa and differentiation of genera is based on colony shape and placement/orientation of stipes. Initially two-stiped taxa with distal branchings like *Mimograptus* and *Kstaugraptus* are also included, as their proximal development appears to be identical to that of the remaining Dichograptidae.

Family Didymograptidae Mu, 1950 (p. 180)
(emend. Mu *et al.* 2002, p. 228)

Diagnosis (emended). – Two-stiped, pendent to horizontal, reclined, reflexed and deflexed graptoloids; sicula conical, widening distinctly towards the aperture, with small prosicula; proximal development isograptid or more rarely of *artus* type in derived taxa; thecae simple, widening tubes with or without rutellum; rarely complex or with prothecal folding in derived taxa.

Genera included. – *Aulograptus* Skevington, 1965; *Baltograptus* Maletz, 1994 (Fig. 13B, F); *Cladograpsus* Geinitz, 1852 (*non Cladograpsus* Carruthers, 1858: see Dicranograptinae); *Cymatograptus* Jaanusson, 1965 (Fig. 13D); *Didymograpsus* M'Coy, 1851 *in* Sedgwick & M'Coy (1851) (Fig. 13E); *Expansograptus* Bouček & Přibyl, 1951 (Fig. 13A, C, G, H); *Janograptus* Tullberg, 1880; *Jenkinsograptus* Gutiérrez-Marco, 1986; *Parazygograptus* Kozłowski, 1954; *Trigonograpsus* Nicholson, 1869.

Discussion. – Didymograptidae may turn out to be a monophyletic group of two-stiped graptoloids with a variably developed colony shape and little variation in the proximal end development, but a cladistic analysis of most taxa of the group does not exist. Maletz (1994, fig. 3) used the proximal development with symmetrical position of the crossing canals, the originally isograptid proximal development and the change in the position of the origin of th1^1 from *Baltograptus* to *Didymograptus* and *Aulograptus* to infer an evolutionary relationship of the didymograptids. These taxa with metasicular origin of th1^1 are preceeded by expansograptids with prosicular origin of th1^1, referable to the genus *Cymatograptus* (see range charts in Egenhoff & Maletz, 2007).

Mu (1950) erected the rarely used family Didymograptidae for two-stiped dichograptids. The family originally included two subfamilies: Didymograptinae Mu, 1950 and Pterograptinae Mu, 1950. Ge (*in* Mu *et al.* 2002, p. 316) added the new subfamily Mimograptinae. The genus *Mimograptus* is here referred to the Dichograptidae, however, as it appears to possess dichotomous branchings distally.

Didymograptidae (Fig. 13A–H) represents a small family of two-stiped dichograptids with a fairly symmetrical disposition of the stipes, a large sicula with a relatively small prosicula and simple thecae along the stipes. They certainly originated from a multiramous ancestor, but details are not available. The earliest members appear in the lower Floian *Tetragraptus approximatus* Biozone, but may be preceded by the possibly related, also two-stiped "*Kiaerograptus*" *supremus* Lindholm (Fig. 10A). A number of taxa are known from relief material (Fig. 13) and even from isolated specimens (*e.g.* Holm 1895; Skwarko 1968, 1974; Maletz 1994a; Maletz & Slovacek 2013).

Family Pterograptidae Mu, 1950
(*ex* Pterograptinae Mu, 1950, p. 180)

Diagnosis (emended). – Two-stiped, pendent to deflexed and horizontal graptoloids; sicula conical, widening distinctly towards the aperture, with small prosicula or parallel-sided with comparably large and wide prosicula; sicula with distinct dorsal virgellar spine; thecae simple, widening tubes without or with moderate development of a rutellum; proximal development isograptid or *artus*-type; cladial branching in some taxa.

Genera included. – *Didymograptellus* Cooper & Fortey, 1982 (Fig. 13I, J); *Pseudobryograptus* Mu, 1957; *Pterograptus* Holm, 1881b (Fig. 13K); *Xiphograptus* Cooper & Fortey, 1982 (Fig. 13L); *Yutagraptus* Riva, 1994.

Discussion. – The characteristic dorsal virgellar spine can be seen as the defining synapomorphy and the family might be monophyletic. Maletz *et al.* (2009) indicated a tight group of virgellate taxa among the stem reclinatids, but the internal structure with the genus *Acrograptus* as the most derived taxon is unlikely to be correct. *Acrograptus* bears an asymmetrical proximal end with slender crossing canals, but lacks the dorsal virgellar spine of all other members (*Xiphograptus* to *Didymograptellus*: Maletz *et al.* 2009, fig. 2). The genus is herein referred to the Sigmagraptidae.

Pterograptidae (Fig. 13I–L) is used here to incorporate the virgellate dichograptids, except for the four-stiped, scandent members of the genus *Phyllograptus* (see family Tetragraptidae) in which the virgellar spine evolved independently (Maletz 2010). The proximal end is quite variable with the dimensions of the prosicula changing considerably from the early taxa with a comparably large prosicula (*Didymograptellus*: Fig. 13I, J) to a small one in later taxa (*Xiphograptus*: Fig. 13L). The proximal development originally was of isograptid type, but derived species may show an *artus*-type development (Fig. 13K). The thecae are simple with straight apertures, lacking a distinct rutellum, variably inclined and with constant thecal overlap. All taxa show a two-stiped rhabdosome with a variable orientation of the stipes from pendent to deflexed and horizontal, sometimes also slightly reflexed. The development of a multiramous, pendent colony shape in *Pterograptus* (Maletz 1994b) and *Pseudobryograptus* is based on the formation of thecal cladia at each theca, but on alternating sides of the stipe.

The origin of Pterograptidae can be seen in the Floian (Maletz 2010, fig. 7) with the genus *Didymograptellus*, bearing primitive, symplesiomorphic characters like the high prosicular origin of th1^1, and simple thecae. Characters derived early in the evolution of the group are the large prosicula with a parallel-sided metasicula, adorned with a dorsal virgellar spine (Maletz 2010). A large parallel-sided prosicula and metasicula may, however, be present in the genera *Kiaerograptus*, *Ancoragraptus* and *Psigraptus* (see Spjeldnaes 1963, pl. 18), but in these taxa the metasicula is freely hanging below the stipes. The origin of the dorsal virgellar spine is unknown as no intermediate taxa are available showing its formation.

Based on the rhabdosome shape alone, it might be considered that the Pterograptidae originated from the Didymograptidae, but an independent origin from an anisograptid ancestor is more likely. This is supported by the high prosicular origin of th1^1, found so far only in the Anisograptidae (see Hutt 1974), but it is present also in some early members of the sigmagraptine genus *Paradelograptus* (see Fig. 10B).

Family Tetragraptidae Frech, 1897 (p. 593)
(*ex* subfamily Tetragraptini Frech, 1897, p. 593;
family Tetragraptidae Mu, 1950, p. 180)
(= order Tetragrapta in Maletz *et al.* 2009) (Fig. 14A, B, D)

Definition. – (Modified from Maletz *et al.* 2009, p. 12) The crown-clade Tetragraptidae is the common ancestor of

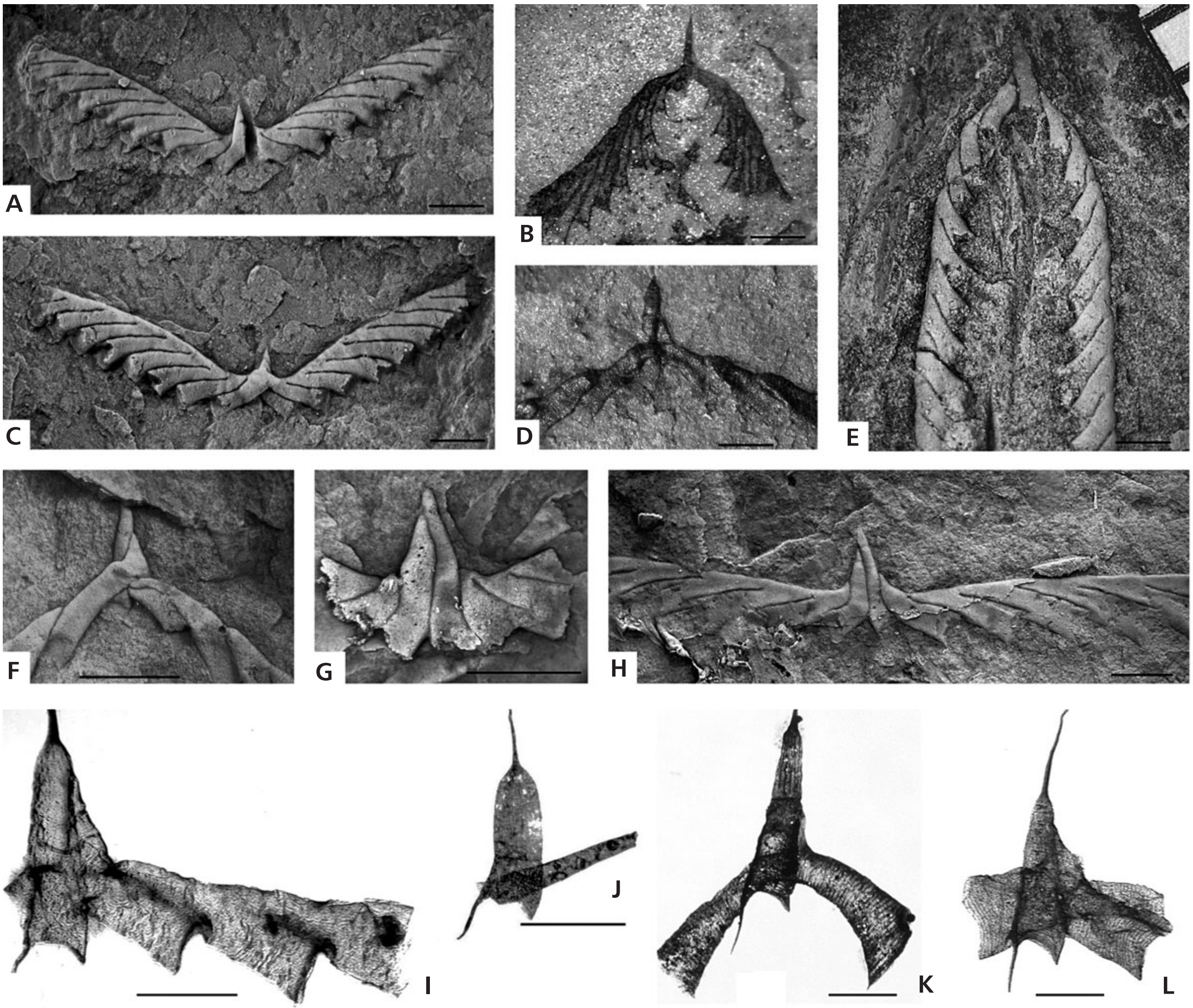

Figure 13. Didymograptidae and Pterograptidae. • A, C – *Expansograptus latus* (Hall) in obverse (A) and reverse (C) views, Di 739, latex. • B – *Baltograptus kunmingensis* (Ni *in* Mu *et al.*), CEGH-UNC 17564. • D – *Cymatograptus bidextro* Toro & Maletz, IANIGLA-PI 1813, reverse view. • E – *Didymograptus artus* Elles & Wood, LO 3266t, obverse view. • F – *Baltograptus vacillans* (Tullberg), Di 839/205, reverse view, latex. • G – *Expansograptus* sp., Di 2, latex, obverse view, showing small prosicula. • H – *Expansograptus grandis* (Monsen), obverse view. • I – *Didymograptellus cowheadensis* Maletz, GSC 133398, reverse view. • J – *Didymograptellus bifidus* (Hall), GSC 133419, juvenile sicula with large, parallel-sided prosicula. • K – *Pterograptus elegans* Holm, GSC 102784, proximal end. • L – *Xiphograptus lofuensis* (Lee), GSC 133389. Latex (A, C, F–H), Infrared photos (I–L). Scale bar represents 1 mm (A–H) and 0.5 mm (I–L).

Tetragraptus serra Brongniart and the first species to have distal dicalycal thecae limited to th3^1 and th3^2, forming a quadriramous rhabdosome.

Genera included. – *Corymbograptus* Obut & Sobolevskaya, 1964; *Paratetragraptus* Obut, 1957; *Pendeograptus* Bouček & Přibyl, 1951; *Phyllograptus* Hall, 1858; *Pseudophyllograptus* Cooper & Fortey, 1982; *Pseudotrigonograptus* Mu & Lee, 1958; *Tetragrapsus* Salter, 1863 (Figs 12B, 14A, B, D); *Tristichograptus* Jackson & Bulman, 1970.

Discussion. – Maletz *et al.* (2009) defined the crown clade Reclinata as the common ancestor of *Tetragraptus serra* and *Exigraptus uniformis* Mu *in* Mu *et al.* and all its descendents, including two monophyletic taxa, the Pan-Tetragrapta (Tetragraptidae herein) and the Pan-Bireclinata (all derived Graptoloidea). Apart from a definition, the authors provided information on a number of synapomorphies for the Reclinata (Fig. 2). These are the presence of a rutellum on the sicula and on the thecae and an elongated or enlarged sicula. Reclinata may be a definable taxon, but appears to be unnecessary, as it adds an unwarranted hierarchical level to the taxonomy. The origin of the subcohort Reclinata from the cohort Pan-Reclinata is unresolved. Maletz

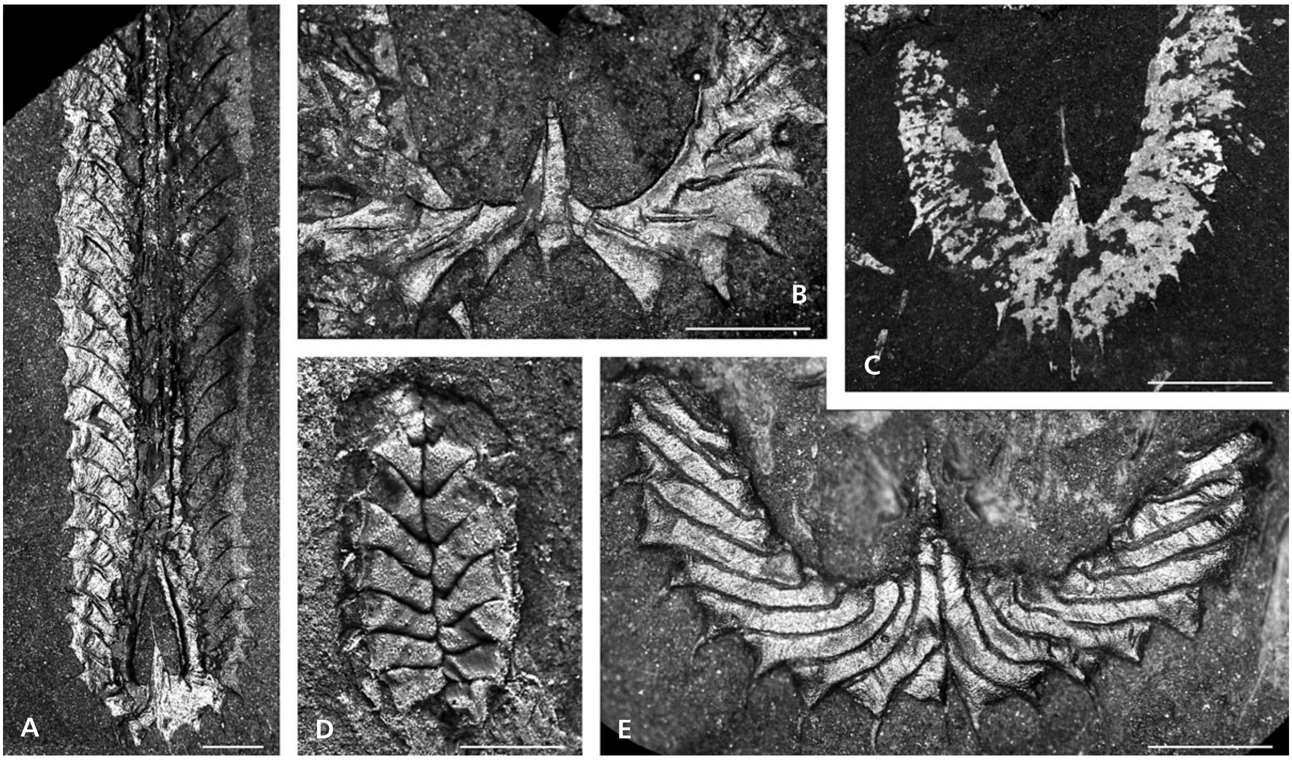

Figure 14. Tetragraptidae and Isograptidae. • A, D – *Tetragraptus cor* (Strandmark) in 1-2 (A) and a-b (D) preservation, Lerhamn drillcore at 19.55 m latex (D). • B – *Tetragraptus reclinatus* Elles & Wood in 1-2 preservation in obverse view, LO 10598t, Lerhamn drillcore. • C – *Isograptus mobergi* Maletz, flattened, SGU 3179 gr04b. • E – *Arienigraptus geniculatus* (Skevington), LO 10601t, relief specimen in reverse view showing manubrium. Scale bar represents 1 mm.

et al. (2009, fig. 2) showed a sister-group relationship to *Aulograptus*, which is highly unlikely as this taxon is a quite derived didymograptid with an isograptid proximal development, low metasicular origin of th1^1 and complex, geniculate thecae. Reclinata, however, includes four-stiped taxa with a prosicular origin of th1^1 on the sicula and their descendents, most probably derived from a multiramous dichograptid ancestor.

Tetragraptidae can be characterised by a four- to two-stiped, pendent to horizontal, reclined, reflexed and scandent, biradiate rhabdosome. The sicula is conical, widening distinctly towards the aperture, with a relatively small prosicula. The thecae are simple, widening tubes often with distinct rutellum. Tetragraptidae is defined as a monophyletic taxon (Maletz *et al.* 2009, fig. 2), which contradicts the notion of Maletz & Mitchell (1996) that the isograptids originate from a reclined tetragraptid ancestor.

Tetragraptidae was erected as a family by Mu (1950) as a form taxon including four-stiped dichograptids, but Frech (1897) had already used the term Tetragraptini for a subfamily of the Dichograptidae and the term Tetragraptidae is, therefore, attributed to him. The phylogenetic relationships of some of the original members exclude them from the taxon, but a clearly defined group of generally four-stiped dichograptids can be referred to the Tetragraptidae (see Maletz *et al.* 2009: superorder Pan-Tetragrapta). There is little doubt, that the scandent tetragraptids (phyllograptids) can be included in Tetragraptidae as derived members (Maletz *et al.* 2009), as they are connected through a number of intermediate taxa [*e.g. Tetragraptus cor* Strandmark, often identified as *Pseudophyllograptus cor* (Fig. 14A, D), *Tetragraptus phyllograptoides*: Cooper & Lindholm 1985].

Maletz *et al.* (2009) included *Perissograptus pygmaeus* Ruedemann as a derived member of Tetragraptidae. The proximal development with the long free hanging apertural part of the sicula and the thecal style, however, suggest a relationship to the sigmagraptines and especially the genus *Maeandrograptus*.

Suborder Glossograptina Jaanusson, 1960 (p. 319)

Definition. – The paraphyletic taxon Glossograptina includes the partial clade identified by the isograptid symmetry of the colony as the defining synapomorphy (see Maletz & Mitchell 1996, fig. 8; Maletz *et al.* 2009, fig. 2: Pan-Bireclinata), but excludes the Axonophora (biserial, dipleural graptoloids).

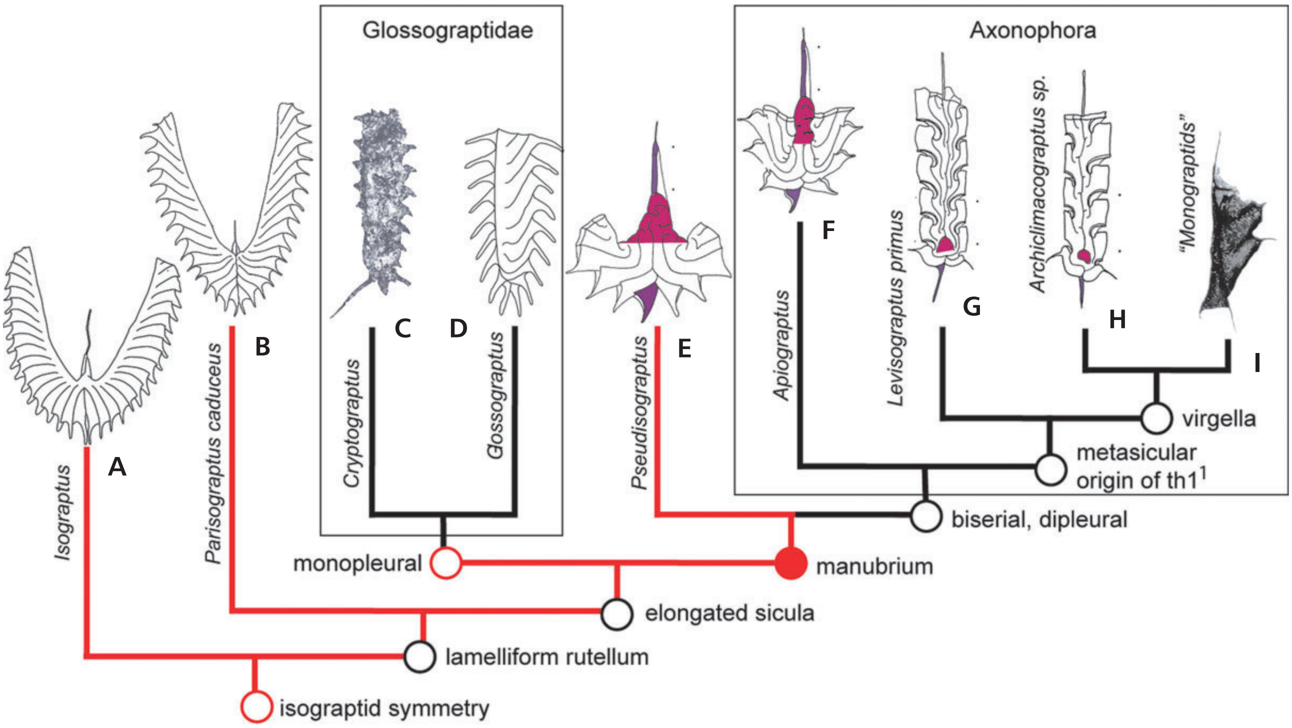

Figure 15. The Isograptidae and the expression of the manubrium in their descendants, based on data in Maletz (2010, fig. 4). A number of photos of axonophorans have been changed to line drawings to show the remains of the manubrium more clearly. This diagram is not compatible with the interpretation of Maletz & Mitchell (1996, fig. 8) and both show only part of the complex history of the groups. Manubrium and remains of it shown in red (E–H). Red lines in diagram indicate taxa belonging to the Isograptidae.

Discussion. – Glossograptina are two-stiped, reclined to scandent, biradiate graptoloids with isograptid symmetry. Scandent taxa have a monopleural or dipleural arrangement of the stipes. The sicula is conical, widening distinctly towards the aperture and possesses a small prosicula. The proximal development is isograptid, dextral with prosicular origin of th1^1 or derived pattern. The thecae are simple, slowly widening tubes, often with distinct rutellum. Lateral apertural thecal spines and a lacinia are present in derived taxa and attenuation of the fusellum (periderm in earlier papers) is common.

Glossograptina (Fig. 2) includes the suborder Pan-Glossograpta and the "stem-isograptids" of the Pan-Bireclinata of Maletz *et al.* (2009). The taxon Pan-Bireclinata is not used herein as it would add another unnecessary level in the taxonomic hierarchy. Pan-Bireclinata is a cladistically defined monophyletic taxon, including all two-stiped taxa with an isograptid symmetry and their descendants, starting with the genus *Isograptus* Moberg. The order Bireclinata of Maletz *et al.* (2009) includes all Glossograptidae as discussed herein and the derived Pan-Axonophora (biserial graptolites and derived taxa). The only detailed cladistic analysis of the Isograptidae and Glossograptidae by Maletz & Mitchell (1996, fig. 8) indicates that the Glossograptidae (monopleural taxa) and the Axonophora (dipleural taxa) originate independently from different isograptid ancestors. The result in Maletz *et al.* (2009), thus, may have to be explained as an artefact of low resolution of the analysis as only a single species of the genus *Isograptus* was included.

Maletz & Mitchell (1996, p. 651) included the isograptids in an expanded family Glossograptidae to show their close phylogenetic relationships. The authors (Maletz & Mitchell 1996, p. 651) stated that it is not possible to define a taxon as a monophyletic unit without including both, the traditional glossograptids and the isograptids. Glossograptina, including the stem group, is defined by the reclined two-stiped rhabdosome with an isograptid symmetry (defining synapomorphy) as a paraphyletic group, excluding Axonophora as biserial, dipleural graptoloids.

Family Isograptidae Harris, 1933 (p. 85)
(incl. family Arienigraptidae Yu & Fang, 1981, p. 29;
emend. Maletz & Mitchell, 1996, p. 653;
ex Arienigraptinae Yu & Fang, 1981
[= Pseudisograptidae Cooper & Ni, 1986])

Definition. – The family Isograptidae is the paraphyletic partial clade based on the reclined, two-stiped colony with the isograptid symmetry as the defining synapomorphy (see

Maletz & Mitchell 1996), but excluding the monophyletic Glossograptidae with a monopleural colony shape and the virgellate Axonophora with the biserial, dipleural development of the colonies.

Genera included. – *Arienigraptus* Yu & Fang, 1981 (Fig. 14E); *Cardiograptus* Harris & Keble, 1916 *in* Harris (1916); *Isograptus* Moberg, 1892 (Fig. 14C); *Oncograptus* Hall, 1914; *Paracardiograptus* Mu & Lee, 1958; *Parisograptus* Chen & Zhang, 1996 (Fig. 15B); *Procardiograptus* Xiao, Xia & Wang 1985; *Proncograptus* Xiao, Xia & Wang, 1985; *Pseudisograptus* Beavis, 1972 (Fig. 15E); *Xiushuigraptus* Yu & Fang, 1983.

Discussion. – Isograptidae is a paraphyletic taxon from which two clades of scandent, biserial graptolites originated independently, the small clade of the family Glossograptidae and the axonophorans, as was shown by Maletz & Mitchell (1996, fig. 8). Isograptidae was not discussed by Maletz *et al.* (2009, fig. 2), who identified the genera *Isograptus* and *Parisograptus* as "stem isograptids", but did not define this group.

Isograptidae includes two-stiped, reclined to scandent, biradiate graptoloids with isograptid or derived maeandrograptid symmetry, with or without manubrium. The scandent taxa of the family (*Cardiograptus, Procardiograptus*) are dipleural. The sicula is conical, often elongated and widens slowly towards the aperture. The prosicula is relatively small, less than one-fourth of the length of the metasicula. The origin of th1^1 is in the lower part of the prosicula. The proximal development is isograptid, dextral. The thecae are simple, widening tubes, often with distinct rutellum.

Isograptidae includes the group of manubriate isograptids (*e.g.* Cooper 1973). The origin of the Isograptidae lies within the reclined tetragraptids of the genus *Tetragraptus* (Maletz & Mitchell 1996, Maletz *et al.* 2009, Maletz 2010). The Isograptidae led to the scandent monopleural Glossograptidae through a taxon similar to the partial monopleural *Bergstroemograptus* (Maletz & Mitchell 1996), but the differentiation of the two groups is difficult as the synapomorphies are hard to identify from flattened material. A second independent lineage led from the derived arienigraptids to the axonophoran graptolites (Fig. 15). Isograptids provide a number of quite important biostratigraphical marker species for the Dapingian to Darriwilian (Middle Ordovician) (Harris 1933, Cooper 1973).

Yu & Fang (1981) originally defined Arienigraptinae as a subfamily of Kalpinograptidae Jiao, 1977 (Qiao *in* Mu *et al.* 2002, p. 369). Maletz & Mitchell (1996) elevated the subfamily to family rank and recognized the genus *Arienigraptus* (Fig. 14E) as a pseudisograptid, while *Kalpinograptus* Jiao is now regarded as a secondarily two-stiped glossograptid (Maletz & Mitchell 1996). The arienigraptids are here included in Isograptidae as was done by Harris (1933) and are interpreted as a paraphyletic group, from which the Axonophora, the biserial, dipleural graptolites originated (Mitchell *et al.* 1995, Fortey *et al*. 2005, Maletz 2010). The definition of the precise boundary between Isograptidae and Axonophora remains problematical and is difficult to establish because of the need for well-preserved and isolated specimens to observe the important synapomorphic characters in this transition (see discussion under Axonophora).

Family Glossograptidae Lapworth, 1873b (p. 555)
(incl. Kalpinograptidae Jiao, 1977)

Definition. – (Maletz *et al.* 2009, p. 14) The crown clade Glossograptidae is the common ancestor of *Glossograptus acanthus* Elles & Wood and the first species to have a monopleural arrangement of the stipes.

Genera included. – *Apoglossograptus* Finney, 1978; *Bergstroemograptus* Finney & Chen, 1984; *Corynites* Kozłowski, 1956; *Corynograptus* Hopkinson & Lapworth, 1875; *Corynoides* Nicholson, 1867; *Cryptograptus* Lapworth, 1880f (Fig. 15C); *Glossograpsus* Emmons, 1855 (Fig. 15D); *Kalpinograptus* Jiao, 1977; *Lonchograptus* Tullberg, 1880; *Mimograptus* Lapworth, 1908 *in* Elles & Wood (1908) (*non Mimograptus* Harris & Thomas, 1940: see Dichograptidae); *Nanograptus* Hadding, 1915; *Paraglossograptus* Mu *in* Hsü, 1959; *Rogercooperia* Sherwin & Rickards, 2000; *Sinoretiograptus* Mu *et al*., 1974; *Skiagraptus* Harris, 1933; *Tonograptus* Williams, 1992.

Discussion. – Glossograptidae includes two-stiped, scandent, biradiate graptoloids with isograptid symmetry and monopleural development. The sicula is conical, widening distinctly towards the aperture and possesses a relatively small prosicula. The thecae are simple, widening tubes with distinct rutellum. Apertural thecal spines are common and are connected by a lacinia in a few taxa. A number of taxa show a reduction of the fusellum or a reduction of the number of thecae.

The monophyletic Glossograptidae is a group of biserial, monopleural taxa (Fig. 15D) with a simple isograptid proximal development covered by the later growth of the colony. Thus, proximal end development is hard to verify and has been a matter of debate for many years (Bulman 1945, Strachan 1985, Maletz & Mitchell 1996). Some of the younger members are included even though their colony development is so reduced that important characteristics for an analysis are not recognizable (*e.g.* *Corynoides*, *Corynites*).

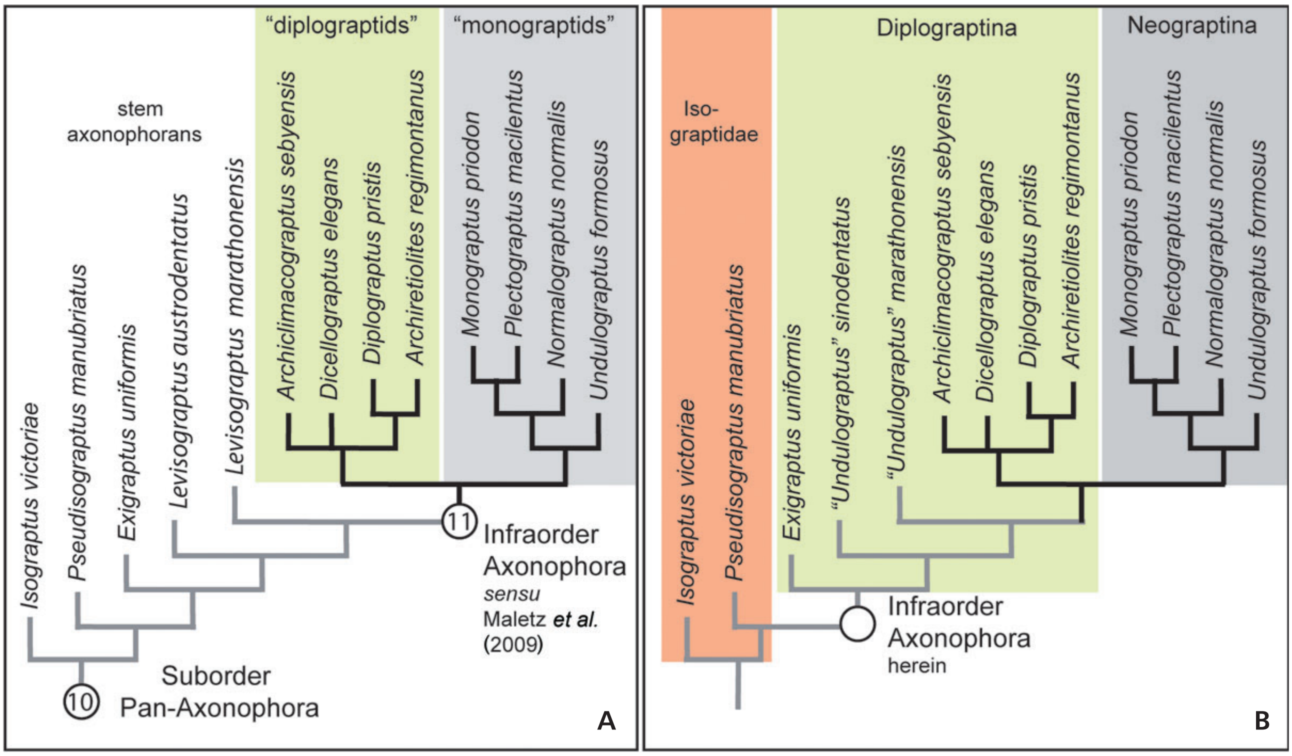

Figure 16. The Axonophora. • A – modified from Maletz *et al.* (2009, fig. 6). • B – revised interpretation showing concept of the Axonophora used herein. *Undulograptus formosus* may be in wrong position in B; see discussion in text.

Suborder Axonophora Frech, 1897 (p. 607)
[= Virgellina Fortey & Cooper, 1986, p. 639;
Fortey *et al.* 2005, p. 1255
(*pars*; see Maletz 2010 for the exclusion of xiphograptids and phyllograptids); = Diplograptacea *in* Mitchell, 1987;
= Diplograptoidea in Mitchell *et al.* 2007]

Definition. – (Revised from Maletz *et al.* 2009, p. 14) The crown clade Axonophora is the first species to acquire a biserial, dipleural rhabdosome and all its descendants.

Discussion. – Axonophora can be described as graptoloids with a nema as the leading rod followed by or engulfed in the growth of the thecal rows. The rhabdosomes are either biserial or uniserial. The proximal development is complex, with prosicular or more commonly metasicular origin of th1^{1} and delayed dicalycal theca.

Maletz *et al.* (2009) defined the total clade Pan-Axonophora by two synapomorphies: presence of a manubrium and the left-handed origin of th1^{2} from the obverse side of th1^{1} (Maletz *et al.* 2009, p. 14). However, the left-handed origin of th1^{2} from th1^{1} would exclude the genus *Arienigraptus* from Pan-Axonophora and, thus, disrupt a small and precisely defined group, the arienigraptids or pseudisograptids *sensu* Maletz & Mitchell (1996). The taxon is, therefore not used and it is suggested to examine more details of early axonophoran evolution, of which little is known so far (see Maletz 2011c) and phylogenetic interpretations are controversial.

Maletz & Mitchell (1996, fig. 8) indicated the origin of Arienigraptidae [Isograptidae herein], and with it Axonophora, from an early isograptid ancestor, prior to the separation of the *Parisograptus* lineage leading to Glossograptina. Thus, Glossograptidae and the Axonophora originate separately from an isograptid ancestor (Fig. 15). In the less well resolved analysis of Maletz *et al.* (2009), the order Bireclinata (Pan-Glossograpta and Pan-Axonophora) is shown to originate as a sister group to the genus *Parisograptus*.

Axonophora as used here is a monophyletic clade. The name should be used in the sense of Frech (1897), including all dipleural biserials with a nema included in the biserial rhabdosome and the monograptids with the nema leading the growth of the stipe (Fig. 16B). Frech (1897), however, largely misinterpreted the colony development, following Ruedemann's (1895) reconstructions of synrhabdosomes in his understanding, but recognized the importance of the nema for the growth of the colonies and for the evolutionary relationships it indicates. As he did not know details of the proximal development of graptolites, he did not consider the characters that are so important for our modern interpretation of graptolites. Fortey *et al.* (2005, p. 1255) discussed the early evolution of the axonophorans, but preferred the name Virgellina for this clade, called the Diplograptoidea by Mitchell *et al.* (2007).

Maletz *et al.* (2009) used a slightly different concept, excluding the early biserials of the "*Undulograptus*" (now: *Levisograptus*) *austrodentatus* group (see Maletz 2011a) with the aim of creating an infraorder Axonophora with two monophyletic sister groups (Fig. 17A). The authors separated the *Levisograptus austrodentatus* group as stem axonophorans and added Arienigraptidae *sensu* Maletz & Mitchell (1996) to the stem. Their definition modifies the Axonophora in a way that excludes the *austrodentatus* group, which have generally been accepted as earliest biserials or axonophorans in the past. It is here advocated to include all biserial, dipleural taxa derived from the two-stiped genus *Pseudisograptus*, thus including even the early biserial, dipleural genera *Exigraptus* Mu in Mu *et al.* and *Apiograptus* Cooper & McLaurin as axonophorans.

A major problem in the understanding of the axonophorans is the lack of knowledge of proximal development types (Fig. 18) and rhabdosome construction of the early transitional taxa. The general transition of Isograptidae to Axonophora has been established (see Mitchell *et al.* 1995, Fortey *et al.* 2005, Maletz 2010), but important details are not available. Maletz (2010, fig. 4) discussed the evolutionary origin and modification of the ventral virgellar spine of the Axonophora, but did not provide information on other details of the proximal development. A change from a prosicular origin of th1^1 (Isograptidae) to the metasicular origin (Axonophora) is known, but it is uncertain how and when the transition took place. The earliest known taxon with a metasicular origin of th1^1 is *Levisograptus sinodentatus* Mu & Lee (see Mitchell 1994, fig. 1C). The biserial, dipleural *Exigraptus uniformis* Mu in Mu *et al.* still shows a high, possibly prosicular origin of th1^1 (Mitchell & Maletz 1995) as is found in typical pseudisograptids (see Cooper & Ni 1986), but bears a pattern U astogeny (Fortey *et al.* 2005).

As any solution would mean an artificial break within a lineage, I would prefer to make one that can be followed easily even in poorly preserved material. Thus, I would advocate identifying the genera *Exigraptus* and *Apiograptus* with a manubrium and a prosicular origin of th1^1, indicating a close relationship to the Isograptidae, as the earliest (known) axonophorans. The defining synapomorphy then will be the biserial, dipleural rhabdosome (Fig. 16B) following the concept of Frech (1897). The manubrium or remains of it in the early axonophorans *Exigraptus*, *Apiograptus* and *Levisograptus* Maletz (Fig. 15) represents a symplesiomorphic character shared with the Isograptidae. The lamelliform rutellum evolved into a virgella during the evolution of the early axonophorans, but is not characteristic of the earliest taxa as the genus *Levisograptus* retains a lanceolate virgella (Maletz 2010). The development of the virgella in *Exigraptus* and *Apiograptus* remains unknown.

Infraorder Diplograptina Lapworth, 1880e (p. 19)
[*ex* Diplograpta Lapworth, 1880e, p. 191;
transl. Obut, 1957, p. 17]
(= suborder Diplograptacea Lapworth *in* Mitchell, 1987, p. 367;
= order Diplograptoidea in Mitchell *et al.* 2007;
non superfamily Diplograptoidea in Štorch *et al.* 2011, fig. 6)

Diagnosis (emended). – Biserial, dipleural axonophorans, secondarily two-stiped or partly two-stiped or with cladial branching; proximal end with or without a manubrium, initially with prosicular origin of th1^1, but metasicular origin of th1^1 in derived taxa; proximal end square to highly asymmetrical, generally provided with a virgellar spine and additional apertural spines on the first thecal pair at least; proximal development type progressively more simple, losing the manubrium; thecae variable, often with complex apertural or genicular additions; intrathecal folds and complete median septum in earlier taxa; rhabdosome with attenuated fusellum in some taxa.

Discussion. – Diplograptina as used herein is not identical to the Diplograptina of Štorch *et al.* (2011, p. 315), as it includes also the stem group taxa starting with the first biserial, dipleural taxon. Diplograptina as used herein is a paraphyletic unit from which Neograptina originated. Maletz *et al.* (2009, fig. 6) decided to exclude the early axonophorans as stem group axonophorans in order to create two monophyletic clades, Diplograptina ("diplograptids") and Neograptina ("monograptids"), an argument that is not followed here. Štorch *et al.* (2011) also differentiated two major clades in the Axonophora (Fig. 17). The detailed relationships of both taxa are still uncertain, as the early evolution of the axonophorans is poorly known (Maletz 2011c). Štorch *et al.* (2011, p. 368) recognized the earliest taxon of the Neograptina as *Undulograptus formosus* Mu & Lee, a typical axonophoran with a pattern C astogeny (Mitchell *et al.* 2007, fig. 1), most probably derived from a diplograptine ancestor as is indicated by its derived proximal development pattern (see Fig. 18). This leads to the interpretation of the Diplograptina as a paraphyletic taxon from which the Neograptina originated in the early Darriwilian (see also Fig. 16). The concept used here for the Diplograptina differs from that of Mitchell *et al.* (2007, fig. 1A) mainly through the inclusion of the stem group of earliest biserials and is identical to their order Diplograptoidea.

Štorch *et al.* (2011) included the superfamilies Dicranograptoidea, Diplograptoidea and Climacograptoidea in the Diplograptina (Fig. 17A) and showed the origin of these in a unresolved trichotomy. It is here suggested to keep these units as family level taxa (Fig. 17B) and regard the superfamilies as an unnecessary rank within the Diplograptina.

The proximal development types of the Diplograptina (*e.g.* Mitchell 1987, Melchin 1998, Melchin *et al.* 2011)

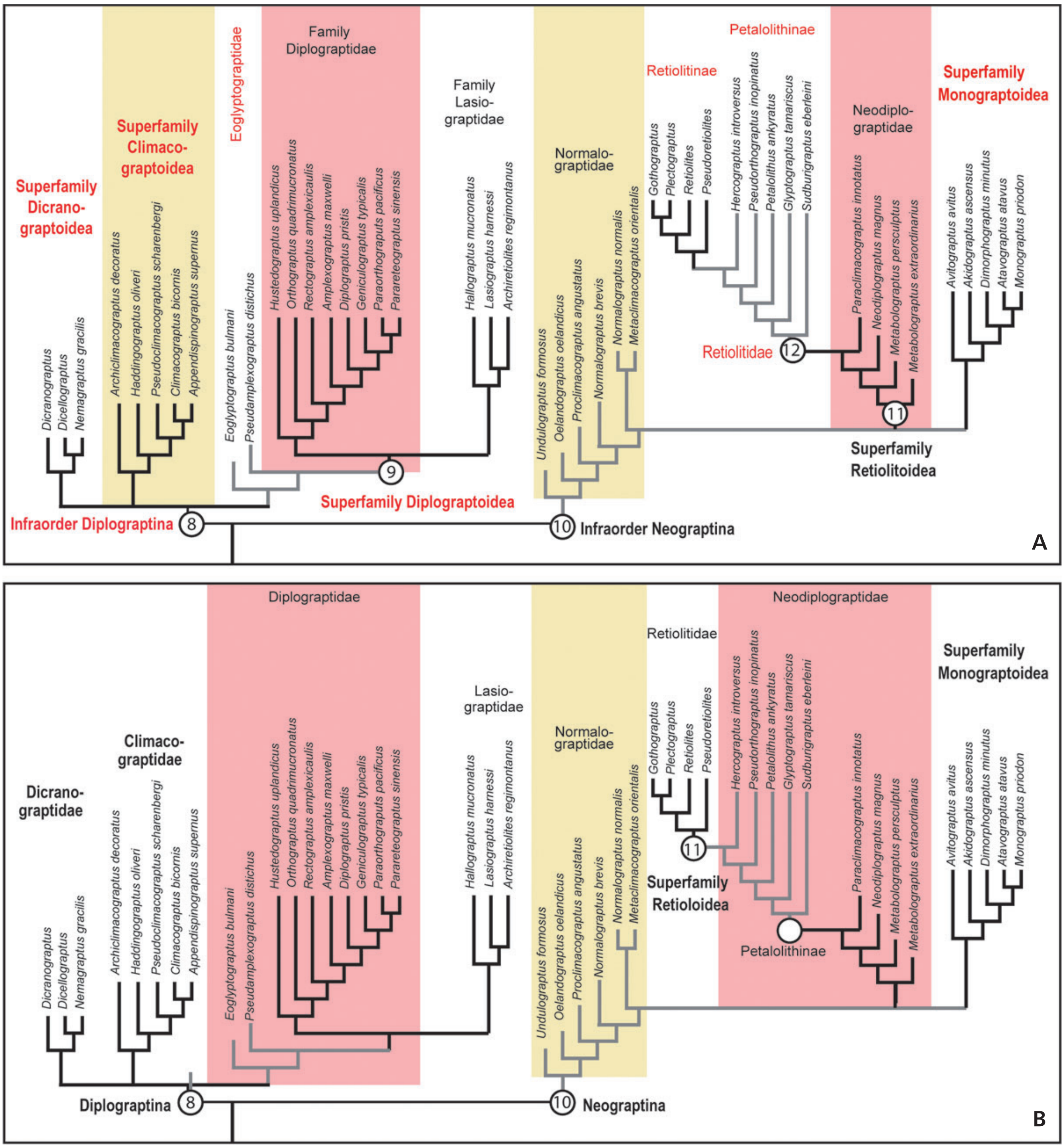

Figure 17. A – the differentiation of the Axonophora (diagram based on Mitchell *et al.* 2007, Melchin *et al.* 2011, Štorch *et al.* 2011 as compiled by Mitchell & Melchin 2011). Taxa not used or used in a different context indicated in red. • B – the alternative interpretation preferred here. The diagram does not show the earliest Axonophora (*Exigraptus*, *Apiograptus*, *Levisograptus*: see text). *Undulograptus*, *Oelandograptus* and *Proclimacograptus* should be removed from the Neograptina and transferred to the Climacograptidae.

have been proven useful for an understanding of the taxonomy and evolution of biserial graptolites. They show the complex origins and growth directions of the proximal thecae of the biserial colonies (Fig. 18), but are difficult to understand without isolated growth series of the taxa. The earliest known development is the pattern U astogeny of *Levisograptus* (Fig. 18U), derived from the manubriate genera *Pseudisograptus* and *Apiograptus* (see Fig. 15). Simplification led to the derived patterns and eventually through the loss of the dicalycal theca and the second stipe

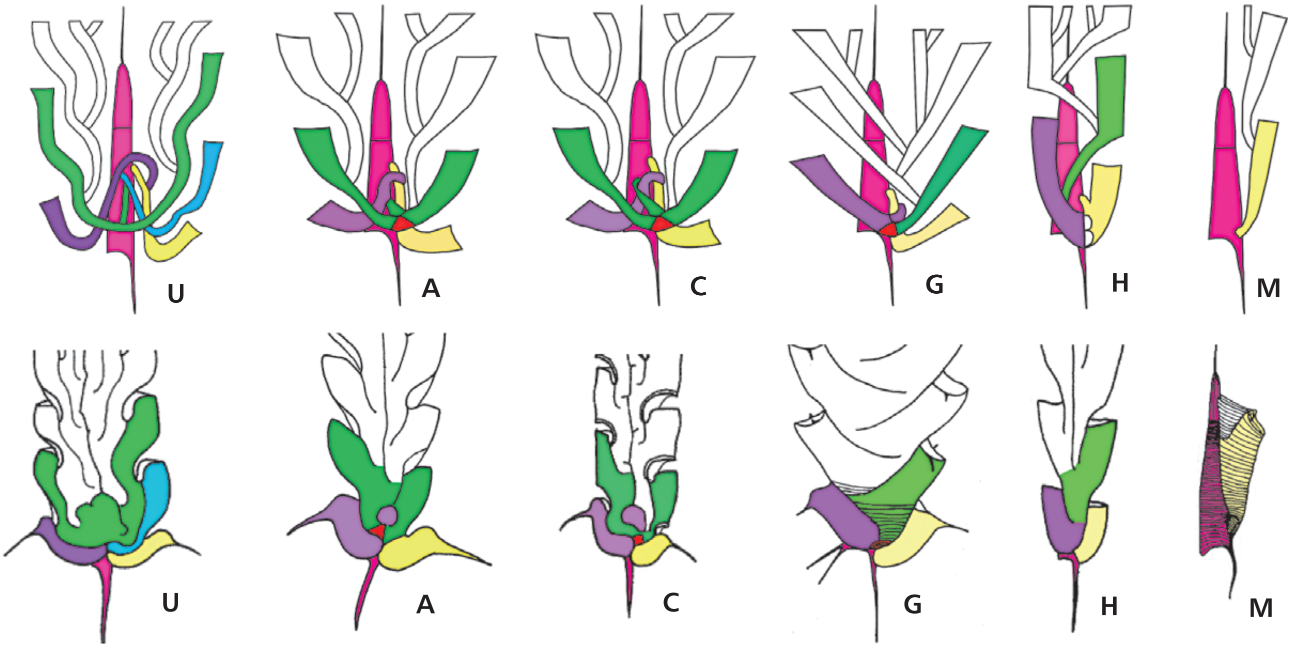

Figure 18. Important proximal development types in the Axonophora. The upper row shows the development types discussed in the text. The lower row shows corresponding illustrations of proximal ends of representative specimens in reverse view. • Pattern U astogeny, *Levisograptus austrodentatus* Harris & Keble. • Pattern A astogeny, *Hustedograptus teretisuculus* (Hisinger). • Pattern C astogeny, *Archiclimacograptus angulatus* (Bulman). • Pattern G astogeny, *Orthograptus quadrimucronatus* (Hall). • Pattern H astogeny, *Normalograptus antiquus* (Ge). • Pattern M astogeny, *Pristiograptus dubius* (Suess).

to the pattern M astogeny (Fig. 18M) of the Monograptidae. The evolutionary transitions between most of these development patterns are poorly known, however.

Family Diplograptidae Lapworth, 1873b
(table 1 facing p. 555)
(incl. Orthograptidae Mitchell, 1987, p. 377;
Peiragraptidae Jaanusson, 1960)

Diagnosis (emended). – Biserial, dipleural axonophorans; proximal end with or without a manubrium, initially with prosicular origin of th1^1, but metasicular origin of th1^1 in derived taxa; proximal end square to highly asymmetrical, generally provided with a virgellar spine and additional apertural spines on the first thecal pair; proximal development type progressively more simple, losing the manubrium; thecae variable, often with complex apertural or genicular additions; intrathecal folds and complete median septum in earlier taxa; rhabdosome with attenuated fusellum in some derived taxa.

Subfamily Diplograptinae Lapworth, 1873b
(table 1 facing p. 555)

Diagnosis. – Biserial, dipleural axonophorans; proximal end with or without a manubrium, initially with prosicular origin of th1^1, but metasicular origin of th1^1 in derived taxa; proximal end square to highly asymmetrical, generally provided with a virgellar spine and additional apertural spines on the first thecal pair; proximal development type progressively more simple, losing the manubrium; thecae variable, often with complex apertural or genicular additions; intrathecal folds and complete median septum in earlier taxa; rhabdosome with attenuated fusellum in some derived taxa; excluding aseptate to septate taxa with paired antivirgellar spines and a pattern A or G astogeny (Orthograptinae, Lasiograptidae).

Genera included. – *Apiograptus* Cooper & McLaurin, 1974; *Archiclimacograptus* Mitchell, 1987 (Figs 18C, 19F, G); *Diplograpsis* M'Coy, 1850 (Fig. 19N); *Eoglyptograptus* Mitchell, 1987 (Fig. 19H); *Exigraptus* Mu, 1979 *in* Mu *et al.* (1979); *Fenhshiangograptus* Hong, 1957; *Levisograptus* Maletz 2011 (Figs 18U, 19C–E); *Mesograptus* Elles & Wood, 1907; *Oepikograptus* Obut, 1987 (Fig. 19K); *Prorectograptus* Li, 1994; *Pseudamplexograptus* Mitchell, 1987 (Fig. 19I, J); *Urbanekograptus* Mitchell, 1987.

Discussion. – Diplograptinae as used herein is a paraphyletic taxon from which Lasiograptidae originated as a monophyletic clade (Fig. 17B). The early biserials *Apiograptus* and *Exigraptus* (Fig. 19A, B) are here included in Diplograptidae, even though they are not shown in the cladistic analysis (Fig. 17). Thus, Diplograptidae include the earliest axonophorans. The precise differentiation of Climacograptidae (discussion in Maletz 2011b) and Dicranograptidae (see Maletz 1998) is unclear and more work on early

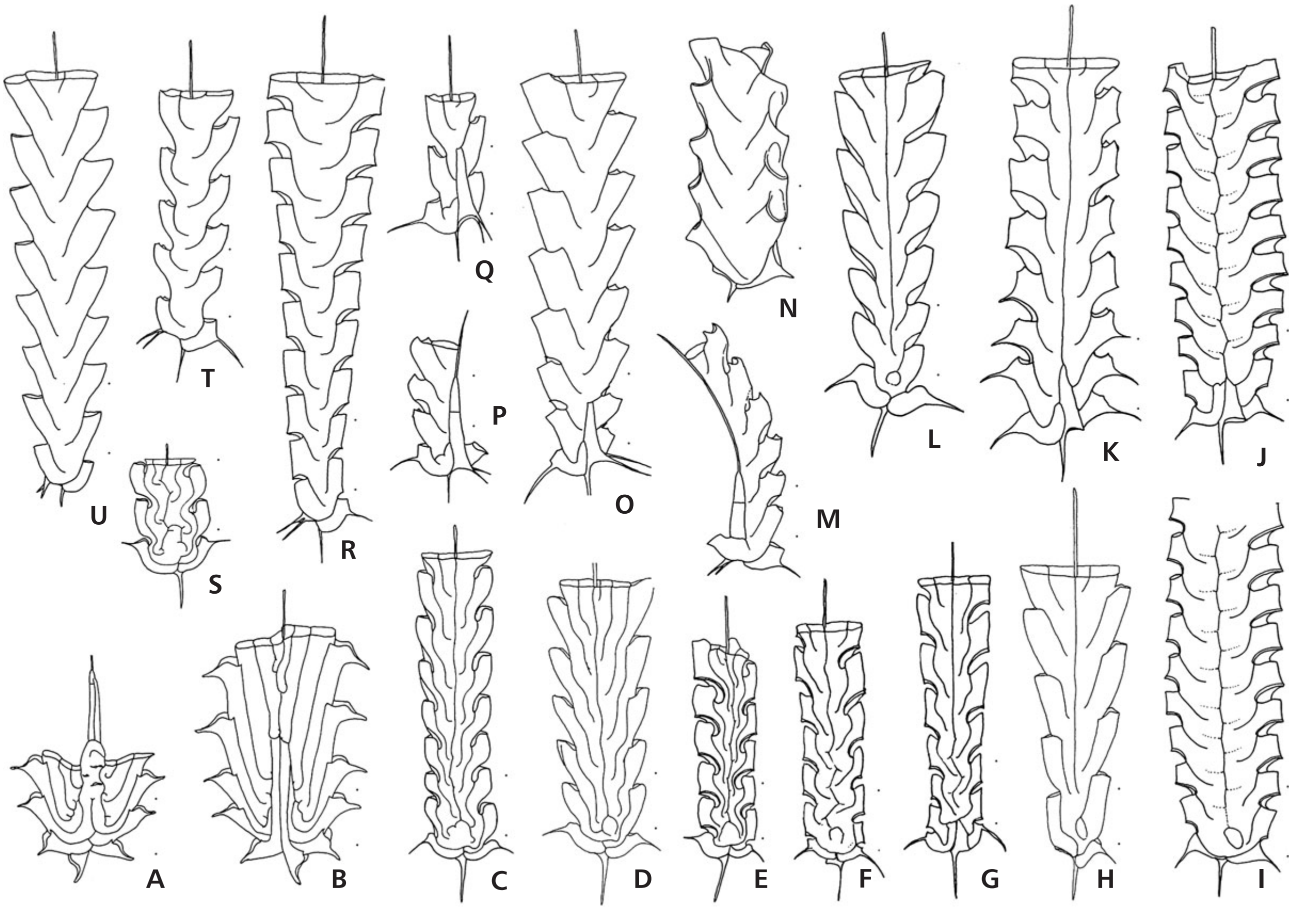

Figure 19. Examples of Diplograptidae. • A, B – *Apiograptus* sp. • C, S – *Levisograptus austrodentatus* (Harris & Keble). • D – *Levisograptus dentatus* (Brongniart). • E – *Levisograptus primus* (Legg). • F, G – *Archiclimacograptus* sp. • H – *Eoglyptograptus gerhardi* Maletz. • I, J – *Pseudamplexograptus distichus* (Eichwald). • K – *Oepikograptus bekkeri* (Öpik). • L – *Hustedograptus* sp. • M, P – *Peiragraptus fallax* Strachan. • N – *Diplograptus pristis* (Hisinger). • O – *Rectograptus* sp. • Q, T – *Anticostia* sp. • R – *Amplexograptus praetypicalis* Riva. • U – *Arnheimograptus anacanthus* (Mitchell & Bergström). A, C–F, H, I, L–N, R–U in reverse view, rest obverse view. Reconstructions (JM) based on various sources. The scale is shown by two dots at a distance of 1 mm close to each specimen.

biserial taxa might be necessary to find a solution. Diplograptidae is a paraphyletic family from which Lasiograptidae, Dicranograptidae and possibly the Climacograptidae originated independently (Fig. 17).

The concept of the family Diplograptidae has changed considerably during the time of its use. Lapworth (1873b) introduced the taxon for biserial, dipleural graptolites, but the author stated that this arrangement was provisionally and essentially artificial. As used by Mitchell *et al.* (2007), it includes most of the Orthograptidae of Mitchell (1987), except for the Lasiograptinae, now recognized as the family Lasiograptidae (Mitchell *et al.* 2007). Even though a number of taxa are well known from isolated material, many questions still remain regarding the internal structure of Diplograptidae.

Mitchell *et al.* (2009) revised the genus *Diplograptus* M'Coy (Fig. 19N), the name giver to Diplograptidae and showed it to nest among the main plexus of the Orthograptidae of Mitchell (1987), a clade of biserials with a pattern G astogeny (Fig. 18G) or one derived from a pattern G astogeny and possessing distinct paired antivirgellar spines. Except for the proximal end pattern, the genus might better be placed with the archiclimacograptids as was stated by the authors. The inclusion among the derived orthograptids in their analysis may be seen as a result of the simplified proximal development type leading to wrong conclusions due to the lack of sufficient characters for a proper taxonomic resolution. It is here suggested to interpret *Diplograptus* as a derived diplograptid with its ancestry among the archiclimacograptids due to the lack of antivirgellar spines, the relatively short sicula and the simple thecal style.

Subfamily *Orthograptinae* Mitchell, 1987 (p. 380)
(incl. Peiragraptinae Jaanusson, 1960, p. 322)

Diagnosis. – (Mitchell, 1987, p. 380) Aseptate to septate species with straight median septum; pattern A or pattern G astogeny; strongly asymmetrical proximal end with sicula extensively exposed on obverse side; sicula commonly bearing paired antivirgellar spines.

Genera included. – *Amplexograptus* Elles & Wood, 1907 (Fig. 19R); *Anticostia* Stewart & Mitchell, 1997 (Fig. 19Q, T); *Arnheimograptus* Mitchell, 1987 (Fig. 19U); *Ceramograptus* Hudson, 1915; *Geniculograptus* Mitchell, 1987; *Hustedograptus* Mitchell, 1987 (Figs 18A, 19L); *Orthograptus* Lapworth, 1873 (Fig. 18G); *Orthoretiograptus* Mu, 1977 *in* Wang & Jin (1977); *Pacificograptus* Koren', 1979; *Paraorthograptus* Mu *et al*., 1974; *Pararetiograptus* Mu *et al*., 1974; *Peiragraptus* Strachan, 1954 (Fig. 19M, P); *Pseudoreteograptus* Mu, 1993 *in* Mu *et al*. (1993); *Rectograptus* Přibyl, 1949 (Fig. 19O); *Uticagraptus* Riva, 1987.

Discussion. – Mitchell (1987) introduced the Orthograptidae with three subfamilies, Orthograptinae Mitchell, 1987, Peiragraptinae Jaanusson, 1960 and Lasiograptinae Lapworth, 1879. He included only the genera *Orthograptus* and *Hustedograptus* in the subfamily Orthograptinae.

Family Lasiograptidae Lapworth, 1880e (p. 188)
(incl. Archiretiolitinae Bulman, 1955, p. 88)

Diagnosis (emended). – Biserial, dipleural axonophorans; metasicular origin of th1[1]; proximal end square to highly asymmetrical, generally provided with a virgellar spine and paired antivirgellar spines; proximal development type poorly known due to attenuation of fusellum in most taxa, but assumed to be of derived pattern G astogeny (Mitchell 1987, Mitchell *et al*. 2007); simple to progressively more complex development of lacinia.

Genera included. – *Arachniograptus* Ross & Berry, 1963; *Archiretiolites* Eisenack, 1935; *Brevigraptus* Mitchell, 1988; *Hallograptus* Lapworth, 1876a; *Lasiograptus* Lapworth, 1873; *Neurograptus* Elles & Wood, 1908; *Nymphograptus* Elles & Wood, 1908; *Orthoretiolites* Whittington, 1954; *Paraplegmatograptus* Mu & Lin, 1984; *Phormograptus* Whittington, 1955; *Pipiograptus* Whittington, 1955; *Plegmatograptus* Elles & Wood, 1908; *Sunigraptus* Mu, 1993 *in* Mu *et al*. (1993); *Tysanograptus* Elles & Wood, 1908; *Yangzigraptus* Mu, 1983 *in* Yang *et al*. (1983); *Yinograptus* Mu, 1962 *in* Mu & Chen (1962).

Discussion. – Lasiograptidae appears to be a monophyletic clade originating from a diplograptid ancestor. Mitchell *et al*. (2007, p. 336) recognized Lasiograptidae as a well-supported clade in their analysis. The group includes also Archiretiolitinae, referred to the Retiolitidae by Bulman (1955, 1970). The authors (Mitchell *et al*. 2007, p. 337) referred to *Hallograptus mucronatus* Hall as the earliest taxon of the Lasiograptidae. It has a pattern A astogeny (Fig. 18A) and not the derived pattern G astogeny (Fig. 18G) of later lasiograptids, including *Lasiograptus*. The clade is not well supported by structural data as the proximal development of many of the highly reticulate taxa is virtually unknown and cannot be compared with that of the *Hallograptus*/*Lasiograptus* group of taxa. Mitchell *et al*. (2007, text-fig. 1B) labeled the proximal development pattern as pattern L, but did not describe it.

Family Climacograptidae Frech, 1897 (p. 607)
(*ex* Familie Climacograptidi Frech, 1897)
(= Superfamily Climacograptoidea Frech
sensu Štorch *et al*. 2011, p. 353)

Diagnosis. – Biserial, dipleural axonophorans; metasicular origin of th1[1]; proximal end square to highly asymmetrical, generally provided with a virgellar spine as the only proximal spine, but secondarily there is development of thecal spines on the first thecal pair; proximal development type of pattern C astogeny (Mitchell *et al.* 2007) and progressively more simple; thecae with distinct geniculum; intrathecal folds and complete, often strongly zigzag shaped median septum in earlier taxa, parasiculae and parathecae common.

Genera included. – *Appendispinograptus* Li & Li, 1985; *Clathrograptus* Lapworth, 1873; *Climacograptus* Hall, 1865; *Diplacanthograptus* Mitchell, 1987 (Fig. 20K–N), *Ensigraptus* Riva, 1989 *in* Riva & Ketner (1989); *Euclimacograptus* Riva, 1989 *in* Riva & Ketner (1989); *Gymnograptus* Bulman, 1953; *Haddingograptus* Maletz, 1997 (Fig. 20C–F), *Idiograptus* Lapworth, 1880; *Leptothecalograptus* Li, 2002 *in* Mu *et al*. (2002); *Mendograptus* Rusconi 1948; *Notograptus* Rusconi 1948; *Oelandograptus* Mitchell, 1987 (Fig. 20A); *Proclimacograptus* Maletz, 1997 (Fig. 20G, H); *Prolasiograptus* Lee, 1963 (Fig. 20I, P); *Pseudoclimacograptus* Přibyl, 1947 (Fig. 20O, Q); *Reteograptus* Hall, 1859 (= *Retiograptus* Hall, 1865); *Styracograptus* Štorch *et al*., 2011 (Fig. 20J); *Undulograptus* Bouček, 1973 (Fig. 20B).

Discussion. – The derived members of Climacograptidae may represent a monophyletic clade, as discussed by Štorch *et al.* (2011), who referred to the unpublished analysis of Cone (2004) to support their claim. Details of the origin and early taxa of the group are difficult to obtain and Mitchell *et al.* (2007) identified early biserials (*e.g. Undulograptus*, *Archiclimacograptus*) as stem group Diplograptoidea. The authors identified the archiclimacograptids as clearly paraphyletic. Maletz (2011b, figs 2, 3) without

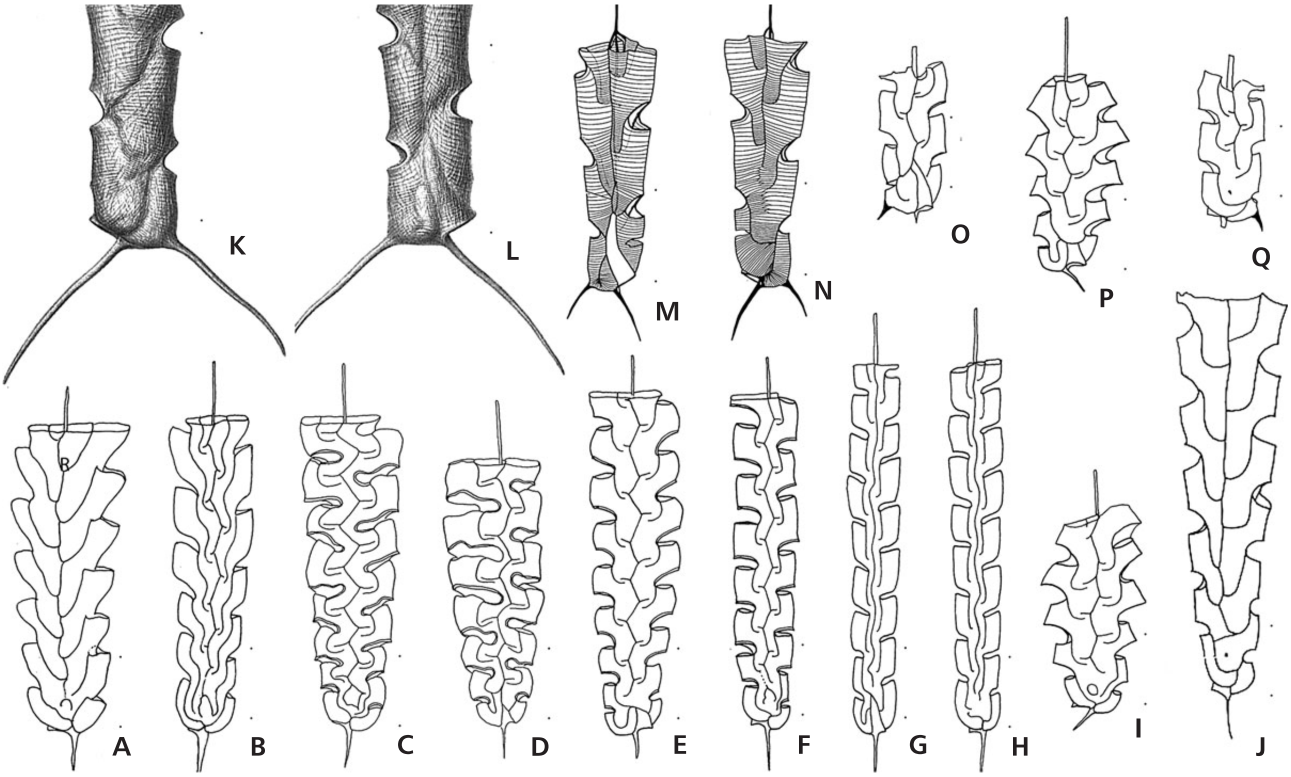

Figure 20. Climacograptidae. • A – *Oelandograptus oelandicus* (Bulman). • B – *Undulograptus formosus* (Mu & Lee). • C, D – *Haddingograptus oliveri* (Bouček). • E, F – *Haddingograptus intermedius* (Berry). • G, H – *Proclimacograptus angustatus* (Ekström). • I, P – *Prolasiograptus haplus* (Jaanusson). • J – *Styracograptus tubuliferus* (Lapworth). • K–N – *Diplacanthograptus spiniferus* (Ruedemann) (K, L from Bulman 1932, showing cortical bandages). • O, Q – *Pseudoclimacograptus scharenbergi* (Lapworth). A–C, F, H–K, N, Q in reverse view, rest obverse view. Reconstructions (JM) based on various sources. The scale is shown by two dots at a distance of 1 mm close to each specimen.

re-analyzing the climacograptids, provided two alternatives for the interpretation of early climacograptids (archiclimacograptids), but was unable to resolve the problems of early climacograptid evolution. His alternate interpretation (Maletz 2011b, fig. 3) suggested an early differentiation of the climacograptids from *Undulograptus* and a separate and independent evolution of the archiclimacograptids.

Climacograptidae originally included *Climacograptus*, Dicranograptidae and Glossograptidae, and also the genus *Monoclimacis* and was based entirely on the "climacograptid" (geniculate) thecal outline (Frech 1897). Bulman (1955, 1970) included *Climacograptus* in Diplograptidae, while Štorch *et al.* (2011) in the latest revision referred the "climacograptids" (now split into a number of genera) to the superfamily Climacograptoidea. The origin and early evolution of the climacograptids is still speculative (*cf.* Fig. 21) and uncertain as is seen from the interpretation in Maletz (2011b, fig. 3) deriving *Pseudoclimacograptus* and its descendants from an ancestor such as *Haddingograptus*, a genus without the typical proximal spines of *Archiclimacograptus* and derived taxa.

Štorch *et al.* (2011, fig. 6) discussed *Undulograptus formosus* Mu & Lee as the earliest member of the Neograptina, and, thus, Normalograptidae. The early taxa *Undulograptus*, *Oelandograptus* and *Proclimacograptus* are here regarded as early members of Climacograptidae, however (see discussion under Neograptina) and may have to be removed from the Neograptina as shown in Fig. 17.

Family Dicranograptidae Lapworth, 1873b
(table facing p. 555)
(= Superfamily Dicranograptacea Lapworth, 2007
in Mitchell *et al.* 2007
[misspelled Dicranograptacae in fig. 1];
= Superfamily Dicranograptoidea Lapworth, 1873
in Štorch *et al.* 2011)

Diagnosis. – Biserial, dipleural axonophorans, secondarily two-stiped or partly two-stiped, uniserial, or with cladial branching; proximal end with metasicular origin of th1^1; proximal end provided with a virgellar spine and additional apertural spines on the first thecal pair at least; proximal development type of derived pattern A astogeny (see Mitchell 1987); thecae variable, often geniculate and with isolated, introverted apertures; intrathecal folds and complete median septum in biserial taxa, lost in some younger taxa with shortened thecal overlap and thecal simplification.

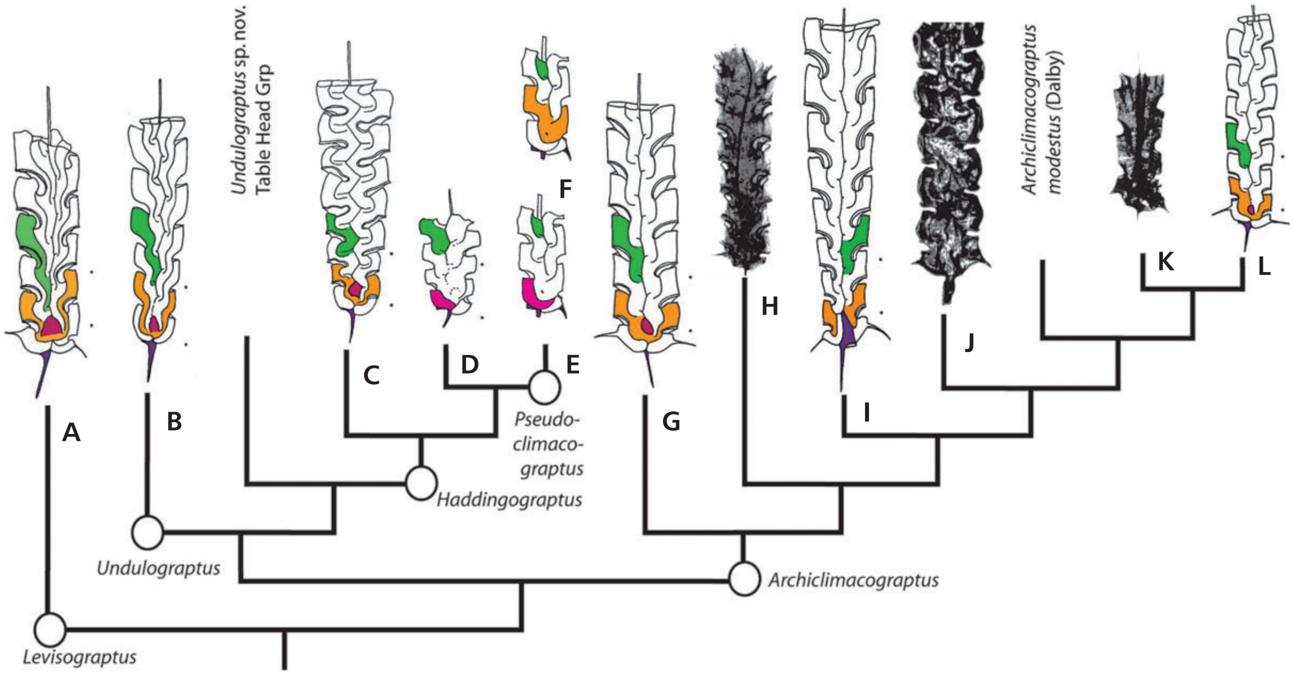

Figure 21. Origin of Climacograptidae, alternative interpretation of Maletz (2011b, fig. 3). • A – *Levisograptus primus*. • B – *Undulograptus formosus*. • C – *Haddingograptus oliveri*. • D – *Haddingograptus eurystoma* (Jaanusson). • E, F – *Pseudoclimacograptus scharenbergi*. • G – *Archiclimacograptus modicellus* (Harris & Thomas). • H – *Archiclimacograptus decoratus* (Harris & Thomas). • I – *Archiclimacograptus sebyensis* (Jaanusson). • J – *Archiclimacograptus* sp. • K – *Archiclimacograptus skagensis* (Jaanusson & Skoglund). • L – *Archiclimacograptus meridionalis* (Ruedemann).

Discussion. – Dicranograptidae is considered to be a monophyletic clade with its members showing a quite variable colony shape from multiramous to one-stiped (Fig. 22). A number of taxa even show a secondarily multiramous colony with cladial distal branchings. They are all related through a number of proximal end characters or homologies on the sicula and the first thecal pairs (see Mitchell 1987, Mitchell *et al.* 2007). The precise origin and early evolution of the group is uncertain. Mitchell *et al.* (2007) included the biserial, dipleural *Dicaulograptus hystrix* as a basal member of Dicranograptidae. Maletz (1998, p. 114) suggested a possible origin of the dicranograptids through *Undulograptus sinicus* Mu & Lee (*Levisograptus sinicus* in Maletz 2011a), as indicated by the presence of the earliest two-stiped dicellograptids such as *Levisograptus dicellograptoides* Maletz (Maletz 1998) and *Undulograptus* sp. nov. (Kraft & Kraft 2003) in the lower Darriwilian.

Subfamily Dicranograptinae Lapworth, 1873b
(table 1, facing p. 555)

Diagnosis (revised). – Biserial, dipleural axonophorans, secondarily two-stiped or partly two-stiped, uniserial, or with cladial branching; proximal end with metasicular origin of th1^1; proximal end provided with a virgellar spine and additional apertural spines on the first thecal pair at least; proximal development type of derived pattern A astogeny (see Mitchell 1987); thecae variable, often geniculate and with isolated introverted apertures; intrathecal folds and complete median septum in biserial taxa.

Genera included. – *Aclistograptus* Ge, 2002 *in* Mu *et al.* (2002); *Amphigraptus* Lapworth, 1873 (Fig. 22D); *Cladograpsus* Emmons, 1855; *Cladograpsus* Carruthers, 1858 (*non Cladograpsus* Geinitz, 1852: syn. of *Didymograptus*); *Clematograptus* Hopkinson, 1875 *in* Hopkinson & Lapworth (1875); *Deflexigraptus* Mu, 2002 *in* Mu *et al.* (2002); *Dicaulograptus* Rickards & Bulman, 1965; *Dicellograpsus* Hopkinson, 1871 (Fig. 22C); *Diceratograptus* Mu, 1963; *Dicranograptus* Hall, 1865 (Fig. 22A, B, E); *Incumbograptus* Ge, 2002 *in* Mu *et al.* (2002); *Jiangxigraptus* Yu & Fang, 1966; *Leptograptus* Lapworth, 1873; *Ningxiagraptus* Ge, 2002 *in* Mu *et al.* (2002); *Pseudazygograptus* Mu, Lee & Geh, 1960; *Syndyograptus* Ruedemann, 1908; *Tangyagraptus* Mu, 1963.

Discussion. – Dicranograptinae is a paraphyletic group of taxa from which the Nemagraptinae originated through a number of changes in the proximal end of the colony. Several dicranograptine genera developed single (*Tangyagraptus*) or even paired (*Amphigraptus*) cladia along the stipes as a secondary branching style independently from the cladial evolution in the genus *Nemagraptus*. The biserial-uniserial rhabdosome shape of *Dicranograptus* appears to be a secondary development, originating through a di-

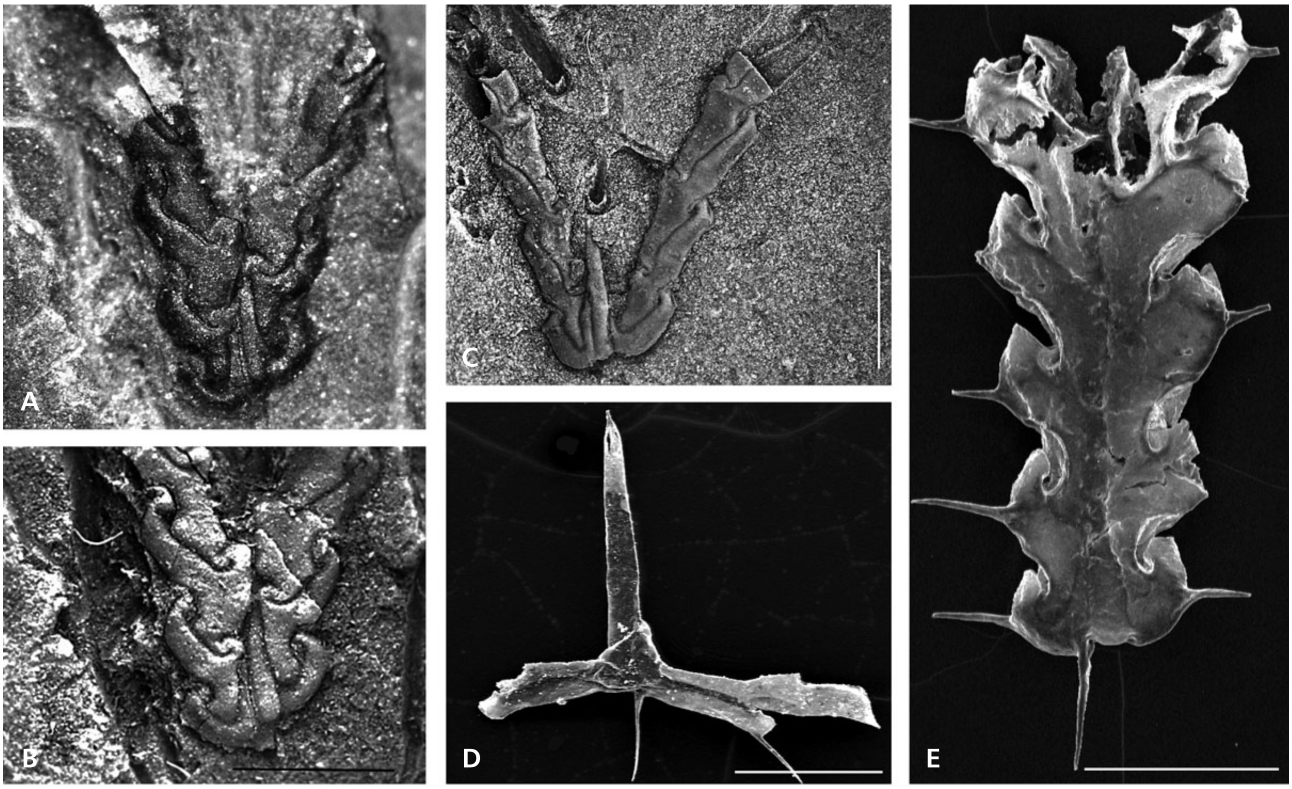

Figure 22. Examples of Dicranograptidae. • A, B – *Dicranograptus irregularis* Hadding, syntype LO 2432t. • C – *Dicellograptus vagus* Hadding, LO 2439t. • D – *Amphigraptus* sp., JM 94/01, early growth stage, Viola Limestone. • E – *Dicranograptus* sp., JM 26/17, Viola Limestone. All specimens in obverse view except for D (reverse view). Scale bar represents 1 mm.

cellograptid ancestor. This change from uniserial to biserial-uniserial rhabdosomes and vice versa could also be interpreted as an inter-taxon variability without major taxonomic importance.

Subfamily Nemagraptinae Lapworth, 1873b (p. 556)
(*ex* Nemagraptidae Lapworth, 1873b)

Diagnosis (revised). – Secondarily two-stiped dicranograptids with or without cladial branching; proximal end with metasicular origin of th1^1; proximal end provided with a virgellar spine and additional apertural spines on the first thecal pair at least; proximal development type of pattern N astogeny (see Mitchell 1987); thecae variable, often geniculate and with isolated introverted apertures; intrathecal folds in some taxa.

Genera included. – *Coenograptus* Hall, 1868; *Geitonograptus* Obut & Zubtzov, 1964; *Helicograpsus* Nicholson, 1868; *Nemagrapsus* Emmons, 1855; *Ordosograptus* Lin, 1980; *Pleurograpsus* Nicholson, 1867; *Stephanograptus* Geinitz, 1866.

Discussion. – Nemagraptidae has commonly been used as a taxonomic unit of the family level (*e.g.* Bulman 1970, Mu *et al.* 2002), but is here used as a subfamily to indicate its proper relationships to the dicranograptids. The Nemagraptinae originate from a dicellograptid ancestor in the late Darriwilian (see Mitchell 1987, figs 13, 17; Mitchell *et al.* 2007), but the transition is poorly documented. *Nemagraptus linmassiae* Finney, 1985 still possesses the intrathecal folds (recognized as prothecal folds in Finney 1985) as a symplesiomorphic character retained from the dicellograptids, but already shows the isolated metasicula as the main synapomorphy of the nemagraptids (Finney 1985, fig. 23). Unfortunately, this taxon is found only at a single locality and its biostratigraphical range is unknown.

Infraorder Neograptina Štorch, Mitchell, Finney & Melchin, 2011 (p. 368)
(= Monograptidae *sensu* Mitchell 1987)

Definition. – (Štorch *et al.* 2011, p. 368) Neograptina is the total clade comprising all species sharing a more recent common ancestor with *Monograptus priodon* than with *Diplograptus pristis* (*i.e.*, the species on the branches arising from the right side of node 1 in Fig. 6 [of Štorch *et al.* 2011] and all their descendants).

Discussion. – Štorch *et al.* (2011) erected the monophyletic taxon Neograptina (Figs 16, 17) as a sister taxon to Diplograptina and identified *Undulograptus formosus* as the earliest member of the clade. The authors (Štorch *et al.* 2011, p. 368) provided a cladistic definition for the Neograptina, even though they called it a diagnosis.

Undulograptus is here referred to the Climacograptidae, but its precise phylogenetic relationship at the roots of Climacograptidae and Normalograptidae is uncertain (see Maletz 2011b). The origin and early evolution of proximally spineless (except for the virgella) axonophorans is completely unresolved and Maletz (2011b) suggested an origin of the climacograptids (*Pseudoclimacograptus* and descendants) from a proximally spineless ancestor (Fig. 21). The proximal end spines of derived climacograptids then would be secondarily derived, a suggestion that may be supported by the highly variable presence and/or position of proximal spines in derived climacograptids (see Štorch *et al.* 2011). If this turned out to be correct, Climacograptidae may actually be part of the Neograptina.

Neograptina, as understood here, possess a relatively narrow proximal end without spines, except for the virgella and a pattern C astogeny of the early members. The concept of Neograptina follows largely the ideas of Mitchell (1987) and Mitchell *et al.* (2007), who extended the name Monograptina to include the stem group of biserials, the normalograptids. The resulting confusion led Štorch *et al.* (2011, p. 314) to reverse this move and use the term Neograptina for the same clade. Neograptina includes here the two superfamilies Retioloidea and Monograptoidea, but Normalograptidae as a stem group have not been assigned to a superfamily.

Family Normalograptidae Štorch & Serpagli, 1993 (p. 14)
(= Normalograptoidea Mitchell *et al.* 2007)

Definition. – (Emended from Melchin *et al*. 2011, p. 293) Paraphyletic taxon that includes all members of the clade Infraorder Neograptina excluding those included herein within the clades family Neodiplograptidae, superfamily Monograptoidea and superfamily Retiolitoidea.

Genera included. – *Clinoclimacograptus* Bulman & Rickards, 1968; *Cystograptus* Hundt, 1942; *Hedrograptus* Obut, 1949; ?*Hirsutograptus* Koren' & Rickards, 1996; ?*Limpidograptus* Khaletskaya, 1962; *Lithuanograptus* Paskevicius, 1976; *Metaclimacograptus* Bulman & Rickards, 1968; *Neodicellograptus* Mu & Wang, 1977 *in* Wang & Jin (1977); *Neoglyptograptus* Rickards *et al.* 1995; *Normalograptus* Legrand, 1987 (Fig. 23A, C, D, F); *Pseudoglyptograptus* Bulman & Rickards, 1968; *Retioclimacis* Mu *et al*., 1974; *Rhaphidograptus* Bulman, 1936; *Scalarigraptus* Riva, 1988; *Sichuanograptus* Zhao, 1976; *Skanegraptus* Maletz, 2011c (Fig. 23B); *Talacastograptus* Cuerda, Rickards & Cingolani, 1988.

Discussion. – Štorch *et al.* (2011, p. 368) discussed the family as a paraphyletic taxon and extended it to include the basal Neograptina, but did not provide a revised diagnosis or definition. The authors erroneously included all "post-Hirnantian graptolites" in Normalograptidae in their cladogram (Štorch *et al.* 2011, fig. 6), even though they explicitly excluded some of them in the acompanying text. Melchin *et al.* (2011) provided a definition based on a cladistic analysis and stated (Melchin *et al.* 2011, p. 293): "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."

Normalograptidae represents a paraphyletic family with roots in the early Darriwilian (Middle Ordovician). The precise origin and evolution of the early Normalograptidae and the differentiation from Climacograptidae is unclear (Maletz 2011c). The first taxon with a proximal end pattern similar to proximal development type H is *Skanegraptus* (Fig. 23B), but this still has a number of characters similar to those of a pattern C astogeny and its evolutionary origin is uncertain (Maletz 2011c). As Maletz (2011b) provided an alternative for the evolutionary relationships of the early Climacograptidae (Fig. 21), the origin of Normalograptidae may have to be re-evaluated and it is preferred here to base them on the origin of a pattern H astogeny for the moment, instead of including taxa with a pattern C astogeny and without proximal spines except for the virgella (*e.g. Haddingograptus*, *Oelandograptus*, *Proclimacograptus*, *Undulograptus*). The evolutionary relationships of these are uncertain and pattern H astogeny may have evolved several times independently (see Maletz 2011c). The origin of Neograptina from within a paraphyletic Diplograptina, however, is quite likely.

Family Neodiplograptidae Melchin, Mitchell, Naczk-Cameron, Fan & Loxton, 2011 (p. 296)

Definition. – (Melchin *et al.* 2011, p. 296) The partial clade that includes the most recent common ancestor of *Metabolograptus ojsuensis* (Koren' & Mikhaylova) and *Retiolites geinitzianus* (Barrande) but excluding those taxa included in the Family Retiolitidae.

Subfamily Neodiplograptinae Melchin, Mitchell, Naczk-Cameron, Fan & Loxton, 2011 (p. 296)

Definition. – The partial clade that includes the most recent common ancestor of *Metabolograptus ojsuensis* and *Retio-*

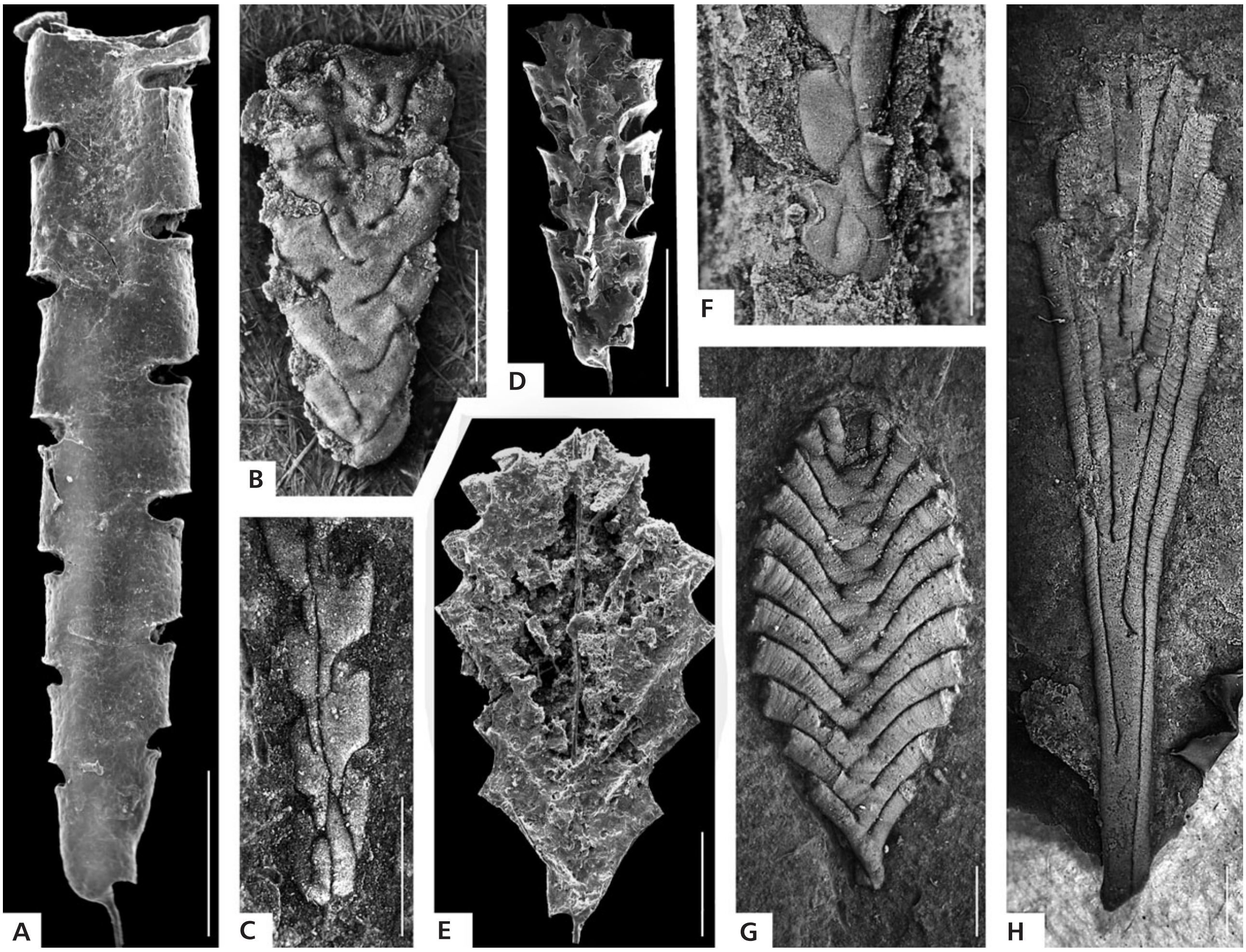

Figure 23. Examples of biserial Neograptina. • A – *Normalograptus scalaris* (Hisinger), NMW 2002/19G.4C. • B – *Skanegraptus janus* Maletz, LO 11196T. • C – *Normalograptus brevis* (Elles & Wood), LO 2407t. • D – *Normalograptus* sp., JM 05/1. • E – *Parapetalolithus* sp. OSM-4-1-07. • F – *Normalograptus antiquus* (Ge), PMO 138.625. • G – *Petalolithus minor*, LO 1115t. • H – *Cephalograptus cometa* (Geinitz), LO 1120t, latex cast. Scale bar represents 1 mm.

lites geinitzianus but excluding those taxa included in the Family Retiolitidae and the subfamily Petalolithinae.

Genera included. – *Korenograptus* Melchin *et al*., 2011; *Metabolograptus* Obut & Sennikov, 1985; *Neodiplograptus* Legrand, 1987; *Paraclimacograptus* Přibyl, 1948b; *Persculptograptus* Koren’ & Rickards, 1996; *Rickardsograptus* Melchin *et al*., 2011.

Discussion. – The taxon is paraphyletic (Fig. 17), based on the definition by Melchin *et al.* (2011, p. 296). It is suggested here to keep Petalolithinae as a separate subfamily in the Neodiplograptidae, from which they undoubtedly originated (see Melchin *et al.* 2011) and not include them in Retiolitidae. Therefore, a subfamily Neodiplograptinae has been established. Neodiplograptidae then should be excluded from the Retioloidea and referred as a family rank taxon of the Neograptina.

Subfamily Petalolithinae Bulman, 1955 (p. 87)
(*nom. correct*. Melchin *et al.* 2011, p. 298
from Petalograptinae Bulman, 1955)

Definition. – (Emended from Melchin *et al.* 2011, p. 298) The partial clade that includes the first species that acquired a unistipular (aseptate) biserial rhabdosome in the clade that contains *Paramplexograptus madernii* (Koren’ & Mikhaylova) and *Retiolites geinitzianus* and its descendants, but excluding the taxa included in the Family Retiolitidae.

Genera included. – *Agetograptus* Obut & Sobolevskaya *in* Obut *et al*., 1968; *Cephalograpsus* Hopkinson, 1869 (Fig. 23H); *Comograptus* Obut & Sobolevskaya, 1968 *in* Obut *et al*. (1968); *Corbograptus* Koren’ & Rickards, 1996; *Demicystifer* Hundt, 1959; ?*Demicystograptus* Hundt, 1950; *Dimorphograptoides* Koren’ & Rickards, 1996; *Diprion* Barrande, 1850 (non *Diprion* Schrank, 1802 [Hymenoptera]); *Dittograptus* Obut & Sobolevskaya, 1968 *in* Obut *et al*. (1968); *Glyptograptus* Lapworth, 1873; *Hercograptus* Melchin, 1999; *Paramplexograptus* Melchin *et al*., 2011; *Parapetalolithus* Koren' & Rickards, 1996 (Fig. 23E); *Petalograptus* Suess, 1851; *Petalolithus* Suess, 1851 (Fig. 23, G), *Pseudorthograptus* Legrand, 1987 (?Fig. 24C); *Rivagraptus* Koren' & Rickards, 1996; *Songxigraptus* Fang, Liang & Yu, 1990; *Spinadiplograptus* Hundt, 1965; *Sudburigraptus* Koren' & Rickards, 1996; *Victorograptus* Koren' & Rickards, 1996.

Discussion. – Melchin *et al*. (2011) defined Petalolithinae as a paraphyletic taxon and revised the name of the subfamily, referring to the genus *Petalolithus*, one of the few genera without the typical graptolite genus ending -*graptus*. Bulman (1970) did not refer to the Petalolithinae, but included *Petalograptus* (now *Petalolithus*: see Loydell 1993, p. 36) in Diplograptidae.

A number of species of the genera included here in Petalolithinae (ancorate petalolithids in Kozłowska-Dawidziuk *et al*. 2003) bear a four-pronged ancora, typical of the Retiolitidae, and *Hercograptus* even has a special development of an ancora sleeve. Thus, these taxa may have to be included in Retiolitidae as done by Kozłowska-Dawidziuk *et al*. (2003), cutting down on the taxa included in Neodiplograptidae (Petalolithinae) as used herein (Fig. 17B).

Superfamily Retiolitoidea Lapworth, 1873b
(table 1 facing p. 555) (emend. Melchin *et al.* 2011, p. 296)
(*non* Retiolitoidea Kozłowska-Dawidziuk,
Lenz & Bates, 2003, p. 565)

Diagnosis (emended). – Axonophorans (Neograptina) with scandent, biserial, dipleural rhabdosome; normally preserved as a framework of lists formed of cortical bandages; a combination of the thecal framework lists joined with the ancora sleeve, a distal development of the ancora umbrella; fusellum rarely preserved, but fragments of fuselli generally preserved along list seams; sicula preserved in earlier taxa, but reduced and lacking in younger forms; list surfaces seamed inside; smooth, longitudinally striated, or pustulose.

Discussion. – The taxon was originally spelled Retioloidea by Lapworth (1873b). Kozłowska-Dawidziuk *et al.* (2003) named the presence of the ancora umbrella as the defining synapomorphy of their superfamily Retiolitoidea, which included also the ancorate petalolithids. Melchin *et al.* (2011, p. 296) provided a cladistic definition for the emended taxon Retiolitoidea including the Neodiplograptidae and Petalolithinae, extending considerably the concept of the Retiolitoidea Lapworth (Fig. 17A). Melchin *et al.* (2011) stated the presence of several synapomorphies appearing near the base of the Retiolitoidea, with the "presence of inclined distal thecal subapertural walls and interthecal septa", a character difficult to observe in most flattened material and likely to be modified by compaction of specimens on shale surfaces. The concept of the Retiolitoidea has been changed considerably from what is generally understood as a retiolitid and their relatives by adding a number of taxa that do not even bear indications of an ancora. It thus differs even from the concept of Kozłowska-Dawidziuk *et al*. (2003) in which only ancorate taxa are included and a number of new subfamilies are introduced for the Retiolitidae. It might actually be better to include in the Retiolitoidea only taxa with an ancora and a reduction of the fusellum as the inclusion of non-ancorate "typical" axonophorans is misleading in a similar way as the extended Monograptidae of Mitchell (1987).

Family Retiolitidae Lapworth, 1873b
(table 1 facing p. 555) (*non* Melchin *et al.* 2011)

Diagnosis (emended). – Axonophorans (Neograptina) with scandent, biserial, dipleural rhabdosome; normally preserved as a framework of lists formed of cortical bandages; a combination of the thecal framework lists joined with the ancora sleeve, a distal development of the ancora umbrella; fusellum rarely preserved, but fragments of fuselli generally preserved along list seams; sicula preserved in earlier taxa, but reduced and lacking in younger forms; list surfaces seamed inside; smooth, longitudinally striated, or pustulose.

Discussion. – Melchin *et al.* (2011, p. 300) defined the clade (named Retiolitinae) as "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 descendants" as a monophyletic clade. The authors included Petalolithinae in Retiolitidae, but it is here preferred to keep them in Neodiplograptidae as a subfamily and use Retiolitidae in the established way following Bulman (1955, 1970) and Bates *et al.* (2005). The precise definition of Retiolitidae has become rather blurred in recent literature as early ancorate and even ancora sleeve bearing taxa are excluded or included and the family extended in some cases (*cf.* Kozłowska-Dawidziuk *et al.* 2003, Kozłowska-Dawidziuk 2004, Bates *et al.* 2005, Melchin *et al*. 2011). The preliminary solution proposed here (Fig. 21B) might have to be revised in the light of the interpretation of characteristic homologous features in some Petalolithinae.

Lenz & Melchin (1987) found the surface sculptures on the retiolitid lists to be diagnostic for the subfamilies

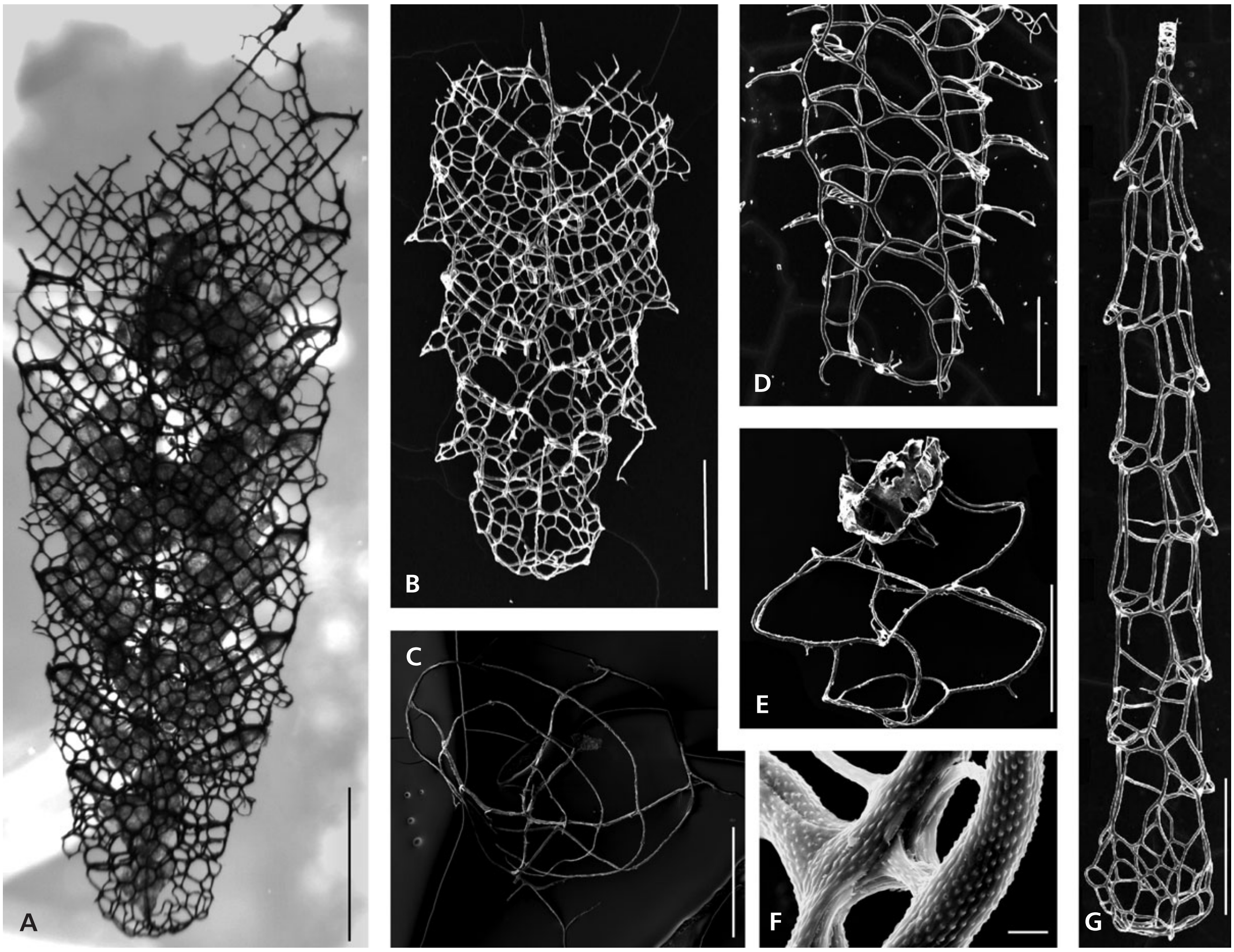

Figure 24. Examples of ancorate Petalolithinae and Retiolitidae. • A, B – *Retiolites geinitzianus* Barrande, SMF.XXIV450, JM 85/04, A showing preservation of thecae. • C – ?*Pseudorthograptus* sp., Kal11-1-10, ancora umbrella from the outside. • D – *Plectograptus macilentus* (Törnquist), MB.G.1081. E. *Rotaretiolites* sp., Osm12-1-1a. • F – pustulose surface of bandages in plectograptines. • G – *Neogothograptus balticus* (Eisenack), MB.G.1082. All are chemically isolated specimens.

Retiolitinae and Plectograptinae. An earlier cladistic interpretation of the Retiolitidae by Lenz & Melchin (1997) recognized the Retiolitinae and Plectograptinae as monophyletic taxa and a stem-group taxon *Pseudoretiolites*, but included "*Rotaretiolites*" and *Rotaretiolites* as basal members in the Plectograptinae. In the accompanying diagram (Lenz & Melchin 1997, fig. 4), however, the retiolitines (in black) are shown as a paraphyletic group from which the monophyletic plectograptines originate.

Subfamily Retiolitinae Lapworth, 1873b
(table 1 facing p. 555) (*non* Melchin *et al.* 2011, p. 300)

Diagnosis (emended). – Retiolitids with smooth or longitudinally striated lists.

Genera included. – *Dabashanograptus* Ge, 1990; *Dimykterograptus* Haberfelner, 1936; *Eiseligraptus* Hundt, 1965; *Eorograptus* Sennikov, 1984; *Gladiograptus* Lapworth, 1875 *in* Hopkinson & Lapworth (1875); *Gladiolites* Barrande, 1850 [suppressed ICZN 1954c]; *Pileograptus* Lenz & Kozłowska, 2007; *Pseudoplegmatograptus* Přibyl, 1948b; *Pseudoretiolites* Bouček & Münch, 1944; *Retiolites* Barrande, 1850 (Fig. 24A, B); *Rotaretiolites* Bates & Kirk, 1992 (Fig. 24E); *Sinostomatograptus* Huo, 1957; *Stomatograptus* Tullberg, 1883; *Tscharyschograptus* Sennikov, 1984.

Discussion. – Melchin *et al.* (2011) referred all retiolitids to Retiolitinae and did not differentiate Retiolitinae and Plectograptinae of previous authors (*e.g.* Bouček & Münch 1952, Bates *et al.* 2005). Thus, the concept is identical to the Retiolitidae of other authors. Retiolitinae as used herein is a paraphyletic taxon from which the Plectograptinae were derived.

Subfamily Plectograptinae Bouček & Münch, 1952 (p. 10) [p. 110, English text] (Fig. 24D, F, G)

Diagnosis (emended). – Retiolitids with pustulose lists.

Genera included. – *Agastograptus* Obut & Zaslavskaya, 1983; *Baculograptus* Lenz & Kozłowska-Dawidziuk, 2002; *Balticograptus* Bouček & Münch, 1952; *Cometograptus* Kozłowska-Dawidziuk, 2001; *Doliograptus* Lenz & Kozłowska-Dawidziuk, 2002; *Eisenackograptus* Kozłowska-Dawidziuk, 1990; *Giganteograptus* Lenz & Kozłowska, 2007; *Gothograptus* Frech, 1897; *Holoretiolites* Eisenack, 1951; *Kirkigraptus* Kozłowska & Bates, 2008; *Mirorgraptus* Lenz & Kozłowska, 2007; *Neogothograptus* Kozłowska-Dawidziuk, 1995 (Fig. 24F, G); *Papiliograptus* Lenz & Kozłowska, 2002; *Paraplectograptus* Přibyl, 1948a; *Plectodinemagraptus* Kozłowska-Dawidziuk, 1995; *Plectograptus* Moberg & Törnquist, 1909 (Fig. 24D); *Pseudoplectograptus* Obut & Zaslavskaya, 1983; *Quattuorgraptus* Dobrowolska, 2013; *Reticuloplectograptus* Kozłowska, Bates & Piras, 2010; *Sagenograptoides* Lenz & Kozłowska, 2010; *Sagenograptus* Lenz & Kozłowska-Dawidziuk, 2001 (*non Sagenograptus* Obut & Sobolevskaya, 1962: see Anisograptidae)*,* *Semiplectograptus* Kozłowska-Dawidziuk, 1995; *Sokolovograptus* Obut & Zaslavskaya, 1976; *Spinograptus* Bouček & Münch, 1952; *Valentinagraptus* Piras, 2006.

Discussion. – Bouček & Münch (1952) separated the Plectograptinae mainly through their biostratigraphical appearance (see Bouček & Münch 1952, diagram on p. 8), recognizing an interval without the occurrence of retiolitids in the *Monograptus firmus/Monograptus riccartonensis* biozones. They also recognized a few novel characters like the lack of the reticulum in most Plectograptinae and the small size of most colonies among others, but the authors did not use isolated material to work on that later workers used for their analyses (*e.g.* Lenz & Melchin 1997, Bates *et al.* 2005, Kozłowska-Dawidziuk *et al.* 2003). Plectograptinae has more recently been based on the presence of pustulose bandages with smooth to striated bandages present in Retiolitinae (Lenz & Melchin 1997). However, Lenz & Melchin (1997) included *Rotaretiolites* with striated bandages in the Plectograptinae. The consensus tree in Bates *et al.* (2005, fig. 8) showed *Rotaretiolites* in a basal position, while the McClade default tree indicated a more derived position for the taxon. The ambiguity of the position of *Rotaretiolites* with its characteristic striated bandages in the analysis may indicate incomplete knowledge of retiolitid faunas from the mid-Telychian time interval. The strict separation of the Retiolitinae and Plectograptinae in Lenz & Melchin (1987) may be an artefact of the poor fossil record and intermediate taxa may show a more complex picture when found.

Superfamily Monograptoidea Lapworth, 1880e (p. 191)
(*ex* Monograpta (Monoprionida) Lapworth, 1880e, p. 191)

Definition. – (Melchin *et al.* 2011, p. 294) The most recent common ancestor of *Avitograptus avitus* and *Monograptus priodon* and all of its descendants (Node 1, Figs 2, 3 [in Melchin *et al.* 2011]).

Discussion. – Graptoloids with a pattern J or pattern M astogeny and a biserial, uni-biserial or uniserial colony are included in the taxon. Cladial branching is present in some derived taxa and may appear independently in a number of groups. The thecal style is highly variable and needs a detailed analysis.

Lapworth (1880e) included only the family Monograptidae with the three genera *Rastrites*, *Cyrtograptus* and *Monograptus* in the Monograpta or Monoprionida. The dimophograptids (genus *Dimorphograptus*) he included as a subgenus in the genus *Diplograptus*. Melchin *et al.* (2011) emended Monograptoidea and included Dimorphograptidae as a stem group. The defining synapomorphies include the pattern J astogeny with a slender, elongate, U-shaped proximal thecal pair and an abrupt lateral differentiation of th1^2 from the upward growing portion of th1^1 (Melchin *et al.* 2011, pp. 294–295).

Mitchell (1987) suggested including Glyptograptinae, Dimorphograptinae and Retiolitinae as subfamilies in Monograptidae, expanding the concept of the Monograptidae considerably. This concept is essentially the concept of the Neograptina as proposed by Štorch *et al.* (2011) and was difficult to accept for most specialists, even though from a cladistic point of view it made sense showing the large-scale phylogenetic relationships.

Family Dimorphograptidae Elles & Wood, 1908 (p. 347)
(= Heteroprionidae Tullberg, 1883, p. 14)
(incl. Akidograptinae Li & Ge 1981, p. 227)

Definition. – (Melchin *et al.* 2011, p. 295) 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).

Genera included. – *Akidograptus* Davies, 1929; *Avitograptus* Melchin *et al.*, 2011; *Bulmanograptus* Přibyl, 1948b; *Cardograptus* Hundt, 1965; *Dimorphograptus* Lapworth, 1876b; *Metadimorphograptus* Přibyl, 1948b; *Parakidograptus* Li & Ge, 1981.

Discussion. – Dimorphograptidae includes graptolites with a pattern J astogeny, which may be uni-biserial or fully biserial. The sicula is relatively long (usually 1.7–2.0 mm) and is fully exposed on its dorsal side. The downward growing portion of th1^1 is strongly reduced and does not reach down to sicular aperture, leaving a portion of sicula exposed for its full circumfence. Obverse and reverse walls of th1^1 both grow straight upward for all or much of their length. The rhabdosome is fully or partly septate. The thecae are commonly orthograptid to climacograptid but may be partly isolate or slightly hooked, especially in uniserial portions (Melchin 1989, p. 301).

Elles & Wood (1908) erected Dimorphograptidae for the single genus *Dimorphograptus* as a substitute for the family Heteroprionidae Tullberg (1883) in order to "bring it into harmony with the names of the other families of the Graptoloidea" (Elles & Wood 1908, p. 348). A number of genera was subsequently referred to the family and its content redefined by Melchin (1998) and especially by Melchin *et al.* (2011) as a paraphyletic taxon. The differentiation of Akidograptidae and Dimorphograptidae by Koren' & Rickards (1996) is not followed here, as most taxa are known only from flattened shale material and constructional details are not available for a precise differentiation.

Family Monograptidae Lapworth, 1873b
(table facing p. 555) (emend. Melchin *et al.* 2011, p. 295)
(= Monoprionidae Tullberg, 1883, p. 14
[misspelt Mono-Diprionidae in Latin version, p. 12])
(non Monograptidae of Mitchell 1987
[= Neograptina: Melchin *et al.* 2011])

Definition. – (Melchin *et al.* 2011, p. 295) The first species within the clade that contains *Monograptus priodon* to develop a scandent, uniserial rhabdosome and all its descendants (Node 2, figs 2, 3 in Melchin *et al.* 2011).

Genera included. – *Abiesgraptus* Hundt, 1935; *Acanthograptus* Tsegelniuk, 1976; *Alexandrograptus* Přibyl, 1981; *Atavograptus* Rickards, 1974; *Averianowograptus* Obut, 1949; *Awarograptus* Zalasiewicz & Howe, 2003; *Barrandeograptus* Bouček, 1933; *Bohemograptus* Přibyl, 1967a; *Bugograptus* Tsegelniuk, 1976; *Campograptus* Obut, 1949; *Cochlograptus* Obut, 1987; *Colonograptus* Přibyl, 1942; *Coronograptus* Obut & Sobolevskaya, 1968 *in* Obut *et al.* (1968); *Corymbites* Obut & Sobolevskaya, 1967 *in* Obut *et al.* (1967); *Crinitograptus* Rickards, 1995; *Cucullograptus* Urbanek, 1954; *Cultellograptus* Loydell & Nestor, 2006; *Cyrtograpsus* Carruthers, 1867 *in* Murchison (1867); *Damosiograptus* Obut, 1950; *Demirastrites* Eisel, 1912; *Dibranchiograptus* Hundt, 1949; *Didymograptoides* Hundt, 1951; *Diversograptus* Manck, 1923; *Dulebograptus* Tsegelniuk, 1976; *Egregiograptus* Rickards & Wright, 1997; *Enigmagraptus* Rickards & Wright, 2004; *Euroclimacis* Štorch, 1998a; *Falcatograptus* Hundt, 1965; *Formosograptus* Bouček *et al.*, 1976; *Fterograptus* Tsegelniuk, 1976; *Gangliograptus* Hundt, 1939; *Globosograptus* Bouček & Přibyl, 1948 *in* Přibyl (1948a); *Heisograptus* Tsegelniuk, 1976; *Hemimonograptus* Zhao 1984; *Hubeigraptus* Li, 1995; *Huttagraptus* Koren' & Bjerreskov, 1997; *Istrograptus* Tsegelniuk, 1976; *Korenea* Rickards *et al.*, 1995; *Kurganakograptus* Golikov, 1969; *Lagarograptus* Obut & Sobolevskaya, 1968 *in* Obut *et al.* (1968); *Lapworthograptus* Bouček & Přibyl, 1952; *Lenzia* Rickards & Wright, 1999; *Linograptus* Frech, 1897; *Lituigraptus* Ni, 1978; *Lobograptus* Urbanek, 1958; *Lomatoceras* Bronn, 1835; *Mediograptus* Bouček & Přibyl, 1948 *in* Přibyl (1948a); *Metamonograptus* Wang, 1977; *Monoclimacis* Frech, 1897; *Monograpsus* Geinitz, 1852; *Monoprion* Barrande, 1850; *Mystiograptus* Hundt, 1965; *Neocolonograptus* Urbanek, 1997; *Neocucullograptus* Urbanek, 1970; *Neodiversograptus* Urbanek, 1963; *Neolagarograptus* Štorch, 1998b; *Neolobograptus* Urbanek, 1970; *Neomonograptus* Mu & Ni, 1973; *Obutograptus* Mu, 1955; *Oktavites* Levina, 1928; *Paradiversograptus* Sennikov, 1976; *Paragraptus* Hundt, 1965; *Paramonoclimacis* Wang & Ma, 1977 *in* Wang & Jin (1977); *Pernerograptus* Přibyl, 1941; *Polonograptus* Tsegelniuk, 1976; *Pomatograptus* Jaekel, 1889; *Přibylograptus* Obut & Sobolevskaya, 1966 (Fig. 25B); *Pristiograptus* Jaekel, 1889; *Prochnygraptus* Přibyl & Štorch, 1985; *Procyrtograptus* Poulsen, 1943; *Prolinograptus* Rickards & Wright, 1997; *Proteograptus* Lenz *et al.*, 2012; *Pseudomonoclimacis* Mikhailova, 1975; *Pseudostreptograptus* Loydell, 1991a; *Quasipernerograptus* Zhao, 1984; *Rastrites* Barrande, 1850 (Fig. 25A); *Rastrograptus* Hopkinson & Lapworth, 1875; *Saetograptus* Přibyl, 1942; *Sinodiversograptus* Mu & Chen, 1962; *Skalograptus* Tsegelniuk, 1976; *Slovinograptus* Urbanek, 1997; *Spirograptus* Gürich, 1908 (Fig. 25C), *Stavrites* Obut & Sobolevskaya, 1968 *in* Obut *et al.* (1968); *Stimulograptus* Přibyl & Štorch, 1983; *Streptograptus* Yin, 1937 (Fig. 25E–G), *Tamplograptus* Tsegelniuk, 1976; *Testograptus* Přibyl, 1967b; *Thuringiograptus* Hundt, 1935; *Tirassograptus* Tsegelniuk, 1976; *Torquigraptus* Loydell, 1993; *Trimorphograptus* Zhao, 1984; *Tyrsograptus* Obut, 1949; *Uncinatograptus* Tsegelniuk, 1976; *Uralograptus* Koren', 1962; *Urbanekia* Rickards & Wright, 1999; ?*Vietnamograptus* van Phuc, 1998; *Wandograptus* Rickards & Jell, 2002; *Wolynograptus* Tsegelniuk, 1976.

Discussion. – The Monograptidae includes single-stiped axonophorans with the stipe growing in opposite direction of the sicular aperture (Fig. 25A, C–E) and along the nema. The rhabdosome shapes and thecal styles are highly variable and the secondary development of multiramous colonies through cladial branching is common.

Melchin *et al.* (2011) redefined Monograptidae as a monophyletic taxon, stating the defining synapomorphies to be the loss of the dicalycal theca and the loss of the initial downward growth of the first theca. The content of the

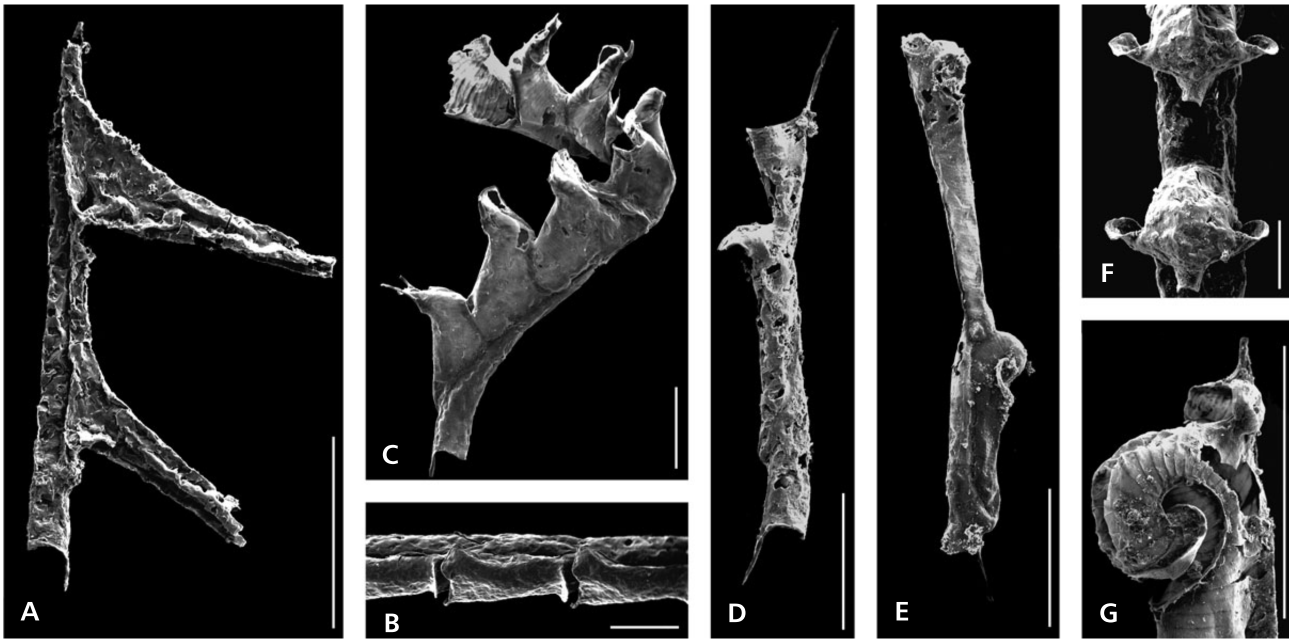

Figure 25. Examples of Monograptidae, based on isolated material, showing siculae and complex thecal development. • A – *Rastrites* sp., JM14-3a, thecal apertures missing. • B – *Pribylograptus argutus* (Lapworth), NMW 2002/19G.29A, stipe fragment. • C – *Spirograptus turriculatus* (Barrande), SOL 1-97-1-4a, small specimen with proximal end showing curved sicula. • D – *Monograptus* sp., JM07-2a. • E, G – *Streptograptus sartorius* (Törnquist), small sicula with two thecae and an isolated metatheca with cupulae at the growing end, NMW 2002/19G.13C, NMW 2002/19G.15C. • F – *Streptograptus dalecarlicus* Loydell & Maletz, NMW 2002/19G.8E, fragment, showing thecae in ventral view. Scale bar represents 1 mm.

family was not changed from the original intent of Lapworth (1873b), however. Monograptidae includes at least 95 genera, of which a considerable number may represent synonyms of other taxa. This is the highest number of genera in any graptolite family.

The pattern M astogeny (Fig. 18) is generally considered the development in all monograptids (Mitchell 1987, Melchin 1998), but considerable variation was found more recently in the development of the porus type and a number of slightly divergent development types have been noted (*e.g.* Lukasik & Melchin 1994, 1997; Dawson & Melchin 2007).

A number of subfamilies have been described subsequently [*e.g.* Cucullograptinae Urbanek, 1958; Linograptinae Obut, 1957; Monograptinae Lapworth (Urbanek 1958, p. 43); Neocucullograptinae Urbanek, 1970; Pristiograptini Gürich, 1908; Saetograptinae Urbanek, 1958], but these are not discussed by Bulman (1955, 1970) or Melchin *et al.* (2011). A modern assessment of the included genera does not exist.

A number of phylogenetic analyses has been proposed recently for the genus *Pristiograptus* and its descendants, showing the genus to be extremely long-ranging and producing a number of "off-shoots" that radiated into new monograptid taxa (Radzevičius 2007, Urbanek *et al.* 2012), but a cladistic analysis for the whole group does not exist and the monograptids, despite their important use in biostratigraphy, are one of the least known graptolite taxa when it comes to their phylogeny. Except for detailed studies of smaller groups within the Monograptidae, Rickards *et al.* (1977) provided the last comprehensive overview of evolutionary relationships among the monograptids.

Genera of uncertain relationships and non-graptolitic taxa

Many genera have been assigned to the graptolites, the relationships of which are uncertain or doubtful. Some of these have been referred to a number of non-graptolitic fossil groups (*e.g. Megalograptus* to the eurypterids), but others clearly belong to the Graptolithina. All of these genera are listed here for convenience. Most of the taxa have not been revised in recent years and often further information is not available. Bulman (1955, 1970) listed several "unrecognizable genera" in the two available editions of the *Treatise*.

Algae. – *Boučekocaulis* Obut, 1960; *Calyptograpsus* Spencer, 1878; *Crinocaulis* Obut, 1960; *Diplospirograptus* Ruedemann, 1925; *Estoniocaulis* Obut & Rytsk, 1958; *Inocaulis* Hall, 1852, *Leveillites* Foerste, 1923; *Medusaegraptus* Ruedemann, 1925; *Palmatophycus* Bouček, 1941; *Rhadinograptus* Obut, 1960; *Thallograptus* Ruedemann, 1925.

Discussion. – LoDuca (1990), Mierzejewski (1991) and Tinn *et al.* (2009) are among the authors who have re-identified a number of supposed graptolites as noncalcified dasycladacean and thallophytic algae. The genera *Medusaegraptus*, *Diplospirograptus*, *Palmatophycus* and *Leveillites* can safely be referred to various groups of algae. Many additional taxa have not yet been investigated, but may also turn out to represent algae and, thus, are listed here.

Phyllocarids. – *Coronagraptus* Hundt, 1951; *Dawsonia* Nicholson, 1873 [*non Dawsonia* Hartt *in* Dawson, 1868: Trilobita, Eodiscidae]

Discussion. – The genus *Coronagraptus* may be identified as the phyllocarid *Peltocaris* Salter, 1862. The only available specimen from the Silurian of Thuringia (Hundt 1951a, fig. 16) clearly shows a bivalved imprint in black shale. Gürich (1928) recognized the similarity of *Dawsonia* to *Peltocaris*. Page *et al*. (2009) discussed the problematical origin and interpretation of the genus *Dawsonia*. The authors recognized a part of the material described initially by Nicholson (1873) as *Dawsonia* and interpreted by him as "ovarian vesicles" of graptolites as tail-pieces of phyllocarids and phosphatic brachiopods, but included also some unidentified fossil remains.

Trace fossils. – *Nereograpsus* Geinitz, 1852; *Protovirgularia* M'Coy, 1850; *Triplograptus* Richter, 1871; *Triplograptus* Hundt, 1965.

Discussion. – A number of trace fossils have been identified as graptolites in earlier publications, as the concept of the "graptolites" was still emerging and details were unexplored. Even the trace fossil *Oldhamia* has been identified as a graptolite in the past (see Grant 1893). Thus, it is no surprise that M'Coy (1850) and Geinitz (1852) among others referred fossils now recognized as trace fossils to the graptolites. The genus *Protovirgularia* is now considered to be the trace of a bivalve (Seilacher & Seilacher 1994) for example. In the case of *Nereograpsus*, Geinitz (1866) himself corrected his earlier (Geinitz 1852) opinion.

Hydroids. – *Archaeodendrum* Obut, 1974; *Chaunograptus* Hall, 1879; *Dyadodendrum* Sennikov, 1998; *Plumalina* Hall, 1858; *Protohalecium* Chapman & Thomas, 1936.

Discussion. – Especially Mierzejewski (1986a) discussed a number of taxa initially referred to the graptolites as hydroids and scyphozoans. The author discussed the Chaunograptidae Bulman, 1955 (Mierzejewski 1986a, p. 162) in some details and referred them to the hydroid suborder Thecaphora. The author also included the Inocaulidae as a family in the Hydroidea and treated the Cambrian Dithecoidea as possible colonial scyphozoans. Some of the latter taxa are, however, now recognized as genuine graptolites through the recognition of fusellar structures (Maletz *et al*. 2005).

Uncertain taxa. – *Acanthastus* Kozłowski, 1949; *Ascograptus* Ruedemann, 1925; *Birastrites* Geinitz, 1866; *Buthograptus* Hall, 1861; *Cameragraptus* Hundt, 1953b; *Coelograptus* Ruedemann, 1947; *Conograptus* Ruedemann, 1947; *Cystoturriculagraptus* Hundt, 1953a; *Demicystifer* Hundt, 1959; *Discophyllum* Hall, 1847; *Furkagraptus* Hundt, 1959; *Geminograptus* Hundt, 1951; *Halograptus* Hundt, 1936a; *Humiligraptus* Hundt, 1940; *Hunanodendrum* Mu *et al*., 1974; *Labrumograptus* Hundt, 1953a; *Nereitograptus* Hundt, 1951; *Nodosugraptus* or *Nodosograptus* Hundt, 1951; *Parademicystograptus* Hundt, 1950; *Paradimorphograptus* Hundt, 1951; *Phycograptus* Gurley, 1896; *Planktograptus* Yakovlev, 1933; *Pleurograptoides* Averianow, 1931; *Polygonograptus* Bouček, 1957; *Protabrograptus* Ni, 1981; *Protistograptus* McLearn, 1915; *Protograptus* Matthew, 1886; *Ramulograptus* Ross & Berry, 1963; *Sinograptus* Shrubsole, 1880 (cited in Münch 1931, p. 42); *Spinosudiplograptus* Hundt, 1951; *Stelechograptus* Ruedemann, 1947; *Stolonofolliculus* Zessin & Puttkamer, 1994; *Strophograptus* Ruedemann, 1947; *Thecocystograptus* Hundt, 1950; *Undagraptus* Hemmann, 1951; *Undograptus* Hundt, 1949 *in* Nindel (1949).

Discussion. – The genera listed here have been included in the list for various reasons. They were originally described as graptolitic, but are either too poorly preserved for a positive identification or are clearly not graptolitic. In a number of taxa, the identification may be established in the future, but for others it may never be possible to recognize their identity. The type material for *Humiligraptus*, for example, has never been identified in a collection and judging from the photos, the specimens are not to be attributed to the graptolites, but may represent trace fossils or inorganic markings on the rock surfaces. A number of taxa named by Hundt in various publications have generally been considered unrecognizable (see Bulman 1970), but these are not the only described genera, that are only questionably referred to the graptolites. Specimens identified under the name *Cameragraptus* can be identified as biserial graptolites in scalarifrom view only. Others are too poorly characterized and the type material is very incomplete. Thus, an unambiguous identification is impossible. A re-investigation of the types of the genus *Protabrograptus*, for example, did not provide convincing evidence of a graptolitic nature of the material. A careful re-examination of the material referred to the above listed genera may be necessary to establish their taxonomic relationships.

Names not used any more. – *Graptolithus* Linnæus, 1758 [suppressed ICZN 1954a]; *Lomatoceras* [suppressed ICZN 1954b]; *Monoprion* [suppressed ICZN 1954b]; *Prionotus* Hisinger, 1837 [syn. of *Graptolithus*; homonym of *Prionotus* Lacépède, 1801: Actinopterygii, family Triglidae].

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