TREATISE ONLINE

Number 88

Part V, Second Revision, Chapter 13:
The History of Graptolite Classification

Jörg Maletz

2017

KU PALEONTOLOGICAL INSTITUTE
The University of Kansas

Lawrence, Kansas, USA
ISSN 2153-4012
paleo.ku.edu/treatiseonline

PART V, SECOND REVISION, CHAPTER 13: THE HISTORY OF GRAPTOLITE CLASSIFICATION

Jörg Maletz

[Freie Universität Berlin, Institut für Geologische Wissenschaften, Malteserstrasse 74-100, D-12249 Berlin, Germany, Yorge@zedat.fu-berlin.de]

Graptolite classification has experienced highs and lows during the last more than two hundred and fifty years of research, beginning with a lot of misunderstanding and a trial-and-error method of searching to find a useful taxonomy for the graptolites. Its path has included many wrong directions along the way. From our modern perspective and understanding of fossils, this haphazard search for improvement may seem puzzling, but we need to bear in mind that scientific improvement is a natural development that comes only with the increase of data. Elles and Wood (1902, p. i–xxviii) discussed in detail the history of graptolite research up to the early 20th century, providing important insight into the early beginnings of classification.

THE EARLY YEARS

From the first notice of a possible graptolite published in the 1700s (von Bromell, 1727, as discussed in Tullberg, 1882) until the 1850s, when early monographic works on graptolites began appearing, very little was written on these fossils. Linnaeus (1735) coined the term *Graptolithus* in his first edition of *Systema Naturae*. However, he did not regard *Graptolithus* as a fossil, later stating, "a fossil, properly speaking is not a graptolite" (Linnaeus, 1768, p. 173), but he intended its use for possible inorganic markings on shales. He provided an illustration of a "*Graptolitus*" in *Skånska resa* (Linnaeus, 1751), that can easily be recognized as the depiction of a graptolite (Fig. 1.1). It later became the term for all graptolites and still survives today in the name for the subclass Graptolithina Bronn, 1849, even though the genus names *Graptolithus* Linnaeus, 1758 and *Graptolites* M'Coy, 1850 are now unfamiliar to us. Tullberg (1882, p. 5) discussed the identity of Linnaeus (1751) material and named the locality as a gravel hill near Östra Herrestad in Scania, Sweden. He identified the graptolite specimens as *Climacograptus scalaris* L. and *Monograptus triangulatus* Harkn., based on later records of graptolites from this locality, but the current whereabouts of this material is unknown. *Climacograptus scalaris* L. is recognized as *Normalograptus scalaris* (Hisinger, 1837 in 1837–1841) today (e.g., Loydell & Maletz, 2009) and provides the term for the "scalariform" view (ventral or apertural view) of biserial graptolites (Maletz & others, 2014). *Demirastrites triangulatus* (Harkness, 1851) is an important index fossil for the *Demirastrites triangulatus* Biozone of the basal Aeronian, Llandovery age (Loydell, 2012).

Very little was written on graptolites during the early years of the 1800s, perhaps not surprisingly, until Wahlenberg (1821) realized that some of the Linnaeus material actually represented fossils. However, Wahlenberg accepted the Walch (1771, suppl. IVc) opinion referring the graptolites to the orthoceratites. In the following years, this was a common practice (e.g., Bronn, 1835; Geinitz, 1842). Other authors preferred to identify graptolites as "polyps" in a general sense (Murchison, 1839; Hisinger, 1837–1841; Portlock, 1843). Quenstedt (1840, p. 274–276) discussed the Graptolithi Linn under the heading

Maletz, Jörg. 2017. Part V, Second Revision, Chapter 13: The history of graptolite classification. Treatise Online 88:1–11, 4 fig., 1 table.

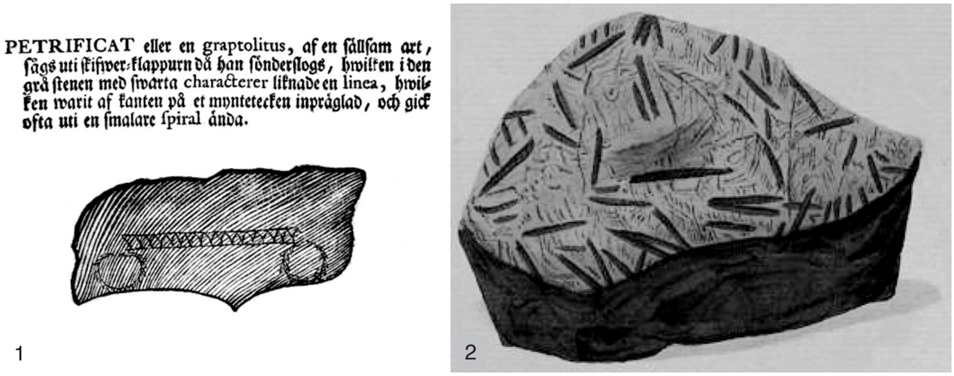

FIG. 1. Early graptolite illustrations. *1,* First illustration of *Graptolitus* (Linnaeus, 1751, p. 147); *2,* possible glacial boulder with graptolites, Stargard, Mecklenburg (Walch, 1771, pl. suppl. 4c,*5*).

"Nautileen," but he suggested including the graptolites with the foraminiferans.

BRONGNIART (1828) described *Fucoides dentatus,* now *Levisograptus dentatus,* (see MALETZ, 2011) and *Fucoides serra*, now *Tetragraptus serra* (see COOPER & FORTEY, 1982) as plants. In general, the research of graptolites was in its infancy, and paleontologists voiced quite diverse opinions on the taxonomical relationships, showing the lack of sufficient data. Graptolites were related to hydroids, corals, even foraminiferans and, not surprisingly, to plants. We can still expect that fossils described as early land plants may turn out to represent pterobranchs, as demonstrated by the example of the Middle Ordovician *Boiophyton* from the Prague Basin (KENRICK, KVACEK, & BENGTSON, 1999).

Some confusion arose over the naming of graptolites with the introduction of the genus name *Priodon,* apparently suggested but not published by S. NILSSON (see TULLBERG, 1882, p. 7; cited also in ELLES & WOOD, 1902, p. vii). The name was used first by BRONN (1835, p. 56), who indicated the homonymy with the genus *Priodon* CUVIER in QUOY & GAIMARD, 1825 and introduced the genus name *Lomatoceras* instead. HISINGER (1837 in 1837–1841) replaced the name *Priodon* with *Prionotus* HISINGER, 1837 in 1837–1841, which unfortunately, is a homonym of *Prionotus* LACÉPÈDE, 1801 (Osteichtyes, Triglidae). The classification confusion finally ended with the suppression of *Lomatoceras* through ICZN Opinion 198 (1954b). In the following years, a number of additional genus name taxa were erected, but no need for an upper-level taxonomy was evident.

1850–1865

Joachim BARRANDE (1850) and James HALL (1847, 1865) laid the scientific foundation of graptolite research by describing their faunas with astonishing detail and insight and developed a first taxonomic system (RUEDEMANN, 1904, p. 469). The mid-19th century was the time during which geologists in many regions of the world began to describe graptolite faunas (e.g., HARKNESS, 1851; SUESS, 1851; GEINITZ, 1852; SALTER, 1852; ROEMER, 1855). Thus, knowledge increased immensely and rapidly, and the graptolites settled into their place within the Anthozoa.

M'COY (1850, p. 270) established the family Graptolitidae of the Silurian Radiata (Zoophyta) as the first family group taxon of the Graptolithina. He differentiated the uniserial taxa under the genus name *Graptolites* from the biserial ones for which he proposed the new name *Diplograpsis,* now *Diplograptus* (see MITCHELL, MALETZ, & GOLDMAN, 2009). This may be seen as the first step in the differentiation of genus level taxa and the starting point of graptolite

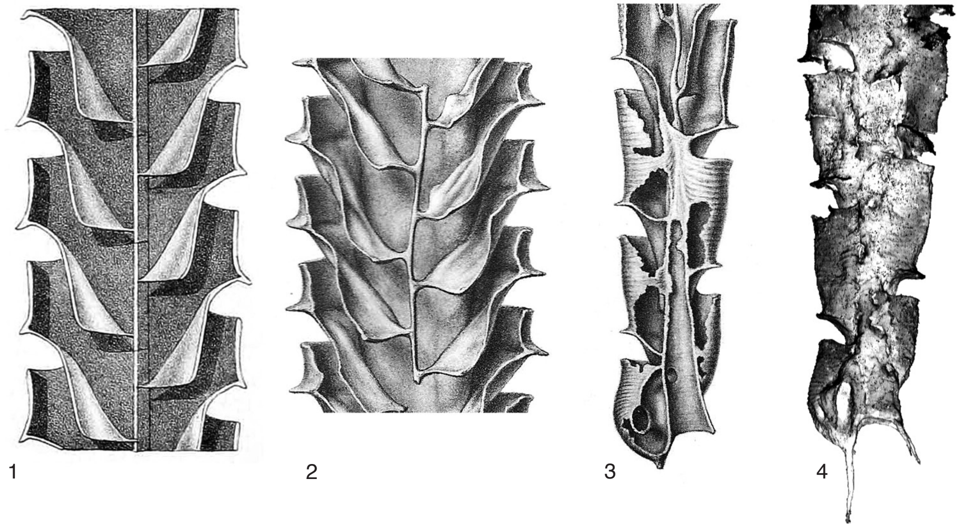

FIG. 2. Comparison of illustrations of *Geniculograptus typicalis* (HALL, 1865). *1,* Reconstruction of internal development (Hall, 1865, pl. A*9*); *2,* internal development, illustration by G. Liljevall for HOLM (Bulman, 1932, pl. 5,*40a*); *3,* proximal end in obverse view showing internal structure (Bulman, 1932, pl. 5,*43*); *4,* proximal end in obverse view, SEM photo, reversed (new). Illustrations not to scale.

taxonomy. It also showed that the differentiation of uni- and biserial taxa and later, the differentiation based on the number of stipes was becoming the basic concept of graptolite classification.

BARRANDE (1850) provided a terminology for the structural features he observed and recognized two subgenera, *Monoprion* and *Diprion*, based on the number of thecal rows. Additional genera were based on the characteristic isolation of the long thecae (*Rastrites* BARRANDE, 1850) and the ancora sleeve meshes of the retiolitids (*Gladiolites* BARRANDE, 1850; *Retiolites* BARRANDE, 1850).

By the 1850S, GEINITZ (1852, p. 19) had already recognized five different genera of graptolites (*Diplograpsus*, *Nereograpsus*, *Cladograpsus*, *Monograpsus*, and *Retiolites*). He suggested abandoning the name *Graptolithus* as it was being used for all graptolites (in the same way that the term trilobite or ammonite was used) as an informal label for a group of organisms, an idea followed by GURLEY (1896). The genus *Graptolithus* was finally suppressed through ICZN Opinion 197 (1954a).

JAMES HALL (e.g., 1847, 1865) was the second of the great observers of graptolite details. His illustrations (largely done by R. P. Whitfield) are highly accurate (Fig. 2.1), as can be seen from the preserved specimens in various museum collections. The illustrations, in part, are comparable to the illustrations of G. Liljevall for HOLM (Fig. 2.2–2.3) and even surpass modern SEM illustrations in clarity (Fig. 2.4). However, not even JAMES HALL was immune to the inclusion of trace fossils as graptolites. For instance, he included *Oldhamia* FORBES, 1848 as a possible graptolite genus (HALL, 1865, p. 51), showing that the scientific understanding of graptolites was not yet settled.

1866–1880

ELLES and WOOD (1902) described the years between 1866 and 1880 as a period in which British workers dominated graptolite research. The interval also saw the beginning of a more comprehensive biostratigraphical use of graptolite faunas. The increasing number of described genera and a better understanding of them led to the addition of higher-level taxa by NICHOLSON (1872a,

Nicholson, 1872	Lapworth, 1873a
Class Hydrozoa	Hydroida
sub-class Graptolitidae	Rhabdophora Allman, 1872
	Section I Graptolitidae
section Monoprionidae	Monoprionidae Hopkinson
	Families
Graptolithus, Didymograpsus, Tetragrapsus, Dichograpsus, Loganograpsus, Pleurograpsus, Coenograpsus (=Helicograpsus), Cyrtograpsus, Rastrites	Monograptidae Nemagraptidae Dichograptidae
	Mono-di-prionidae
	Family
	Dicranograptidae
section Diprionidae	Diprionidae Hopkinson
Diplograpsus, Climacograpsus, Dicranograpsus, Retiolites, Trigonograpsus, Retiograpsus	Family
	Diplograptidae
section Tetraprionidae	Tetraprionidae Hopkinson
	Family
Phyllograpsus	Phyllograptidae
incertae sedis	Section II Retioloidea
Thamnograpsus, Buthograpsus, Inocaulis, Corynoides	Families Glossograptidae Retiolitidae

FIG. 3. Comparison of the graptolite taxonomy of LAPWORTH (1873a, 1873b) and NICHOLSON (1872b) (new).

1872b) and LAPWORTH (1873a, 1873b), but the general structure of the taxonomic tree of the graptolites remained fairly simple (Fig. 3). The construction of the stipes from one, two, or more rows of thecae became the main character used for differentiation of groups within the graptolites. NICHOLSON (1872b, p. 101) used the Graptolitidae at the level of a subclass of the Hydrozoa and differentiated the sections Monoprionidae, Diprionidae, and Tetraprionidae based on the number of back-to-back attached stipes (uniserial, biserial, and quadriserial in modern terms). LAPWORTH (1873a, 1873b) assembled the graptolites under the term Rhabdophora ALLMAN, 1872 and differentiated the Graptolitidae M'COY, 1850 and the Retioloidea LAPWORTH, 1873b as two sections, each with a number of families (Fig. 3). The main difference was LAPWORTH'S addition of the Mono-di-prionidae (family Dicranograptidae) and the section II Retioloidea (which included Glossograptidae and Retiolitidae), taxa not considered by NICHOLSON (1872b). NICHOLSON (1872a) and ALLMAN (1872) discussed the relationships of the graptolites and the extant pterobranchs (known only from *Rhabdopleura* at the time) and came to the conclusion that the graptolites were highly aberrant hydrozoans.

The classifications of LAPWORTH and NICHOLSON are not too different from TULLBERG'S (1883) classification, but TULLBERG (1883, p. 12) introduced a number of new taxa with the Monophyontes, Monoamphiphyontes and Amphiphyontes, which were not accepted by the community and quickly fell into disuse.

The most important aspect of graptolite research in this era became the demonstration of the biostratigraphical use of the graptolite faunas (LAPWORTH, 1878, 1879a, 1879b, 1879c, 1879d, 1880a, 1880b, 1880c, 1880d, 1880e), even though graptolites had been used for biostratigraphic purposes earlier (HALL, 1850; NICHOLSON, 1868). A decade

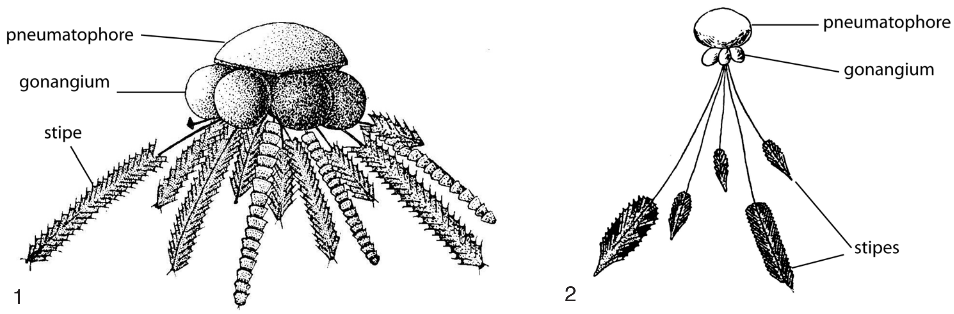

FIG. 4. Historical graptolite reconstructions. *1, Diplograptus pristis* HALL, 1865 (non HISINGER, 1837) (now *Orthograptus quadrimucronatus* (HALL, 1865) (adapted from Ruedemann, 1895, pl. 2); *2, Petalolithus folium* (HISINGER, 1837) (adapted from Frech, 1897, fig. 193). It should be noted that the gonangia and the pneumatophore have never been verified from fossil material and may not exist (Maletz, 2015).

later, LAPWORTH's (1878) demonstration of the use of graptolite faunas in the thick greywacke succession of the Moffat Series was a milestone in stratigraphic and paleontological research (see FORTEY, 1993, fig. 1). During the nearly 150 years since, our biostratigraphic resolution has increased considerably (LOYDELL, 2012), yet the basic succession of LAPWORTH is still recognizable and has changed very little. Today, graptolite biostratigraphy is a standard for working with Paleozoic sedimentary successions and has become an important tool for geological exploration (e.g., PODHALAŃSKA, 2013).

1880–1918

In the years from 1880 to 1918, graptolite research was so dominated by the Scandinavian authors HOLM, MOBERG, TÖRNQUIST, and TULLBERG, that the period may be termed the Scandinavian Period. It is characterized by the detailed taxonomic and biostratigraphic description of very well preserved Ordovician and Silurian graptolite faunas of Scandinavia. The work of HOLM (1895) on chemically isolated, three-dimensionally preserved graptolites is a milestone in graptolite research, even though GÜMBEL (1878) was the first to observe graptolites chemically isolated from the surrounding rocks. This method provided much better information on the tubarium construction than the usual flattened shale material or the strongly tectonized specimens available to most researchers. Much of HOLM's material of chemically isolated Ordovician graptolites from Scandinavian limestones was published posthumously by BULMAN (e.g., 1932, 1933, 1936). The specimens show fine details up to the presence of cortical bandages on the tubarium surface and provide, for the first time, detailed information on the proximal development of the graptolites. HOLM also worked with serial sections to understand the development of material trapped in the sediments.

FRECH (1897) introduced the differentiation into the Axonophora and the Axonolipa, based on whether the graptolite showed development of the nema as a leading rod of the colony or lacked an extended nema. He identified the nema as an axis to which the thecae were attached in the Axonophora. According to FRECH (1897, p. 568), this axis was lacking in the Axonolipa. Even though he misinterpreted part of the graptolite colonies and their development (see Fig. 4.2), following the interpretation of the synrhabdosomes of RUEDEMANN (1895), the Axonophora were reintroduced into the graptolite classification by MALETZ, CARLUCCI, & MITCHELL (2009).

RUEDEMANN (1895) probably wrote the most influential paper of the period. His reconstruction of *Orthograptus quadrimucronatus* (HALL, 1865) under the name *Diplograptus pristis* shows a "supercolony" with basal cyst or pneumatophore, gonangia, and numerous stipes. He also provided a dorsal and lateral view of a similarly reconstructed supercolony of *Diplograptus ruedemanni* (Gurley, 1896). This interpretation (Fig. 4.1) may be regarded as the most discussed and most copied graptolite illustration ever. It is still found in modern paleontology textbooks (e.g., Prothero, 2013), even though the gonangia and pneumatophore have not been verified from fossil material (Maletz, 2015).

THE 20th CENTURY

The 20th century was dominated by detailed research on graptolite taxonomy and biostratigraphy and the recognition of the worldwide distribution of graptolite faunas. Graptolites are now known from all continents, except Antarctica. The use of graptolite biostratigraphy in economical geology often led to increased research. The Bendigo and Castlemain goldfields of Victoria, Australia, are good examples (see Hall, 1895; Phillips & Hughes, 1996), as they are the reason for the detailed Ordovician graptolite biostratigraphy established for the region (Harris & Thomas, 1938; VandenBerg & Cooper, 1992). Research centers developed with a high number of scientists concentrating on graptolite research in Australia (T. S. Hall, Harris, Thomas); China (Hsü, Mu); Europe (Bouček, Bulman, Eisel, Jaeger, Kozłowski, Rickards); North America (Clark, Decker, Ruedemann); Russia (Obut, Sobolevskaya, Tzaj); and many other regions. The increasingly detailed work and mounting data led to two editions on graptolites published by the Treatise on Invertebrate Paleontology (Bulman, 1955, 1970), but taxonomic understanding diverged due to language barriers, lack of communication, and incompatible taxonomic concepts (see Rigby, 1986; Maletz, 2014).

The constructional morphology of the graptolites became important after the recognition of proximal-end development as a key to classification. This was possible with the availability of increasing amounts of chemically isolated graptolites and relief material. Kozłowski (1938, 1949) became one of the leading-edge scientists, describing numerous benthic graptolite taxa from material chemically isolated from cherts. Graptolites were now routinely identified based on their proximal-end construction, and numerous proximal-end development types were established (e.g., Fortey & Cooper, 1986; Mitchell, 1987; Melchin, 1998). Understanding of the distribution patterns of graptolite faunas along with the recognition that not all faunal elements are distributed worldwide, led to the development of the concept of graptolite biogeography (e.g. Skevington, 1969; Goldman & others, 2013).

CLADISTICS

In recent years, graptolite taxonomy and evolution have received a much-needed boost as cladistic methods became increasingly popular (e.g., Fortey & Cooper, 1986; Mitchell, 1987; Lenz & Melchin, 1997; Maletz, Carlucci, & Mitchell, 2009; Melchin & others, 2011; Štorch & others, 2011; Melchin, Lenz, & Kozłowska, 2016). This new method of analyzing graptolite construction and attaining information for a phylogenetic interpretation has dramatically changed our understanding of graptolite taxonomy and evolution. The concept centers around homologous characters and the monophyly of clades (Hennig, 1950, 1965). In the end, it is not really a new concept (see, for instance, Gegenbaur, 1870, p. 78–81), but the idea has never before been promoted so vehemently. Any taxonomic approach searches for homologous characters for classification but does not necessarily state this explicitly. Certainly, even Linnaeus (1758) thought about meaningful characters. Thus, early graptolite taxonomies used easily recognizable characters such as the number of stipes as sorting features. The Monoprionidae and Diprionidae were established as early as the 19th century (Hopkinson, 1869), and even now we use these in a modified sense as the Monograptidae and Diplograptidae. In

TABLE 1. Classification of the Pterobranchia (revised from Maletz, 2014, table 2).

- 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
      - Family Rhabdopleuridae Harmer, 1905, p. 5
      - Family Cysticamaridae Bulman, 1955, p. 42
      - Family Wimanicrustidae Bulman, 1970, p. 52
      - Family Dithecodendridae Obut, 1964, p. 295
      - Family Cyclograptidae Bulman, 1938, p. 22
      - Order Dendroidea Nicholson, 1872b, p. 101
        - Suborder Graptodendroidina Mu & Lin in Lin, 1981, p. 244
          - Family Dendrograptidae Roemer in Frech, 1897, p. 568
          - Family Acanthograptidae Bulman, 1938, p. 20
          - Family Mastigograptidae Bates & Urbanek, 2002, p. 458
      - Order Graptoloidea Lapworth in Hopkinson & Lapworth, 1875, p. 633
        - Suborder Graptodendroidina Mu & Lin in Lin, 1981, p. 244
          - Family Anisograptidae Bulman, 1950, p. 79
        - Suborder Sinograptina Mu, 1957, p. 387
          - 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, 1873b, table 1 facing p. 555
          - Family Didymograptidae Mu, 1950, p. 180
          - Family Pterograptidae Mu, 1950, p. 180
          - Family Phyllograptidae Lapworth, 1873b, table 1 facing p. 555
        - 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 1 facing p. 555
            - Family Lasiograptidae Lapworth, 1880e, p. 188
            - Family Dicranograptidae Lapworth, 1873b, table 1 facing p. 555
              - Subfamily Dicranograptinae Lapworth, 1873b, table 1 facing p. 555
              - Subfamily Nemagraptinae Lapworth, 1873b, p. 556
            - Family Climacograptidae Frech, 1897, p. 607
          - Infraorder Neograptina Štorch & others, 2011, p. 368
            - Family Normalograptidae Štorch & Serpagli, 1993, p. 14
            - Family Glyptograptidae Mitchell, 1987, p. 395
              - Subfamily Glyptograptinae Mitchell, 1987, p. 395
            - Superfamily Retioloidea Lapworth, 1873b, table 1 facing p. 555
              - Family Retiolitidae Lapworth, 1873b, table 1 facing p. 555
                - Subfamily Retiolitinae Lapworth, 1873b, table 1 facing p. 555
                - Subfamily Petalolithinae Bulman, 1955, p. 87
            - Superfamily Monograptoidea Lapworth, 1873b, table 1 facing p. 555
              - Family Dimorphograptidae Elles & Wood, 1908, p. 347
              - Family Monograptidae Lapworth, 1873b, table 1 facing p. 555
                - possibly several subfamilies

general, they were correct and precise at the time and were based on useful characters, but "the devil is in the details," as the saying goes.

Apart from the latest compilations of the Treatise (BULMAN, 1970), a comprehensive modern analysis of all graptolites does not exist. MU and others (2002) provided the latest overview on current graptolite taxonomy in their compilation of all graptolite faunas from China. They modified the taxonomic system slightly by adding and rejecting a number of family-level taxa. The latest classification (Maletz, 2014) provides a combination of cladistic and conservative phenetic taxonomy, keeping up with the established taxonomic groups, but placing them on firmer ground through cladistic analyses when possible, while also accepting analyses from constructional morphology on the graptolite tubaria (Table 1).

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