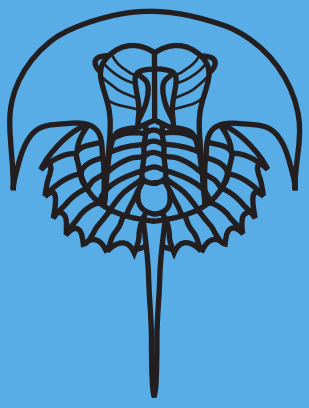

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PART V, SECOND REVISION, CHAPTER 29: UNCERTAIN GENERA

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The history of research on graptolites includes quite a number of genus-level taxa that have later been identified as belonging to other groups of organisms, even to trace fossils. Some genera have been described that cannot be identified at all. Bulman (1955, 1970) provided a list of unrecognizable taxa. That list is updated here with additional information to provide a better understanding of the current status of these genus-level names. In the future, some of these taxa will be properly identified and referred to other fossil groups or recognized as genuine graptolite taxa. Organic macrofossils can be very similar in fossil preservation to some graptolites, and differentiation is often difficult or impossible in poorly preserved material. Thus, some Neoproterozoic taxa identified as worms, algae, or other organisms, have features that are strongly reminiscent of early graptolites and graptolitic tubaria. The organic-walled taxa of the Sabelliditidae may have distinct tubular structures with wrinkled surface ornamentation (Urbanek & Mierzejewska, 1977) similar to the fusellar construction of the graptolite tubaria. Maletz and Beli (2018) and Maletz (2019) identified material of the presumed sabelliditid *Sokoloviina costata* Kirjanov, 1968 as remains of early pterobranchs and referred them preliminarily to the Rhabdopleuridae.

GRAPTOLITIC (PTEROBRANCH) REMAINS OF UNCERTAIN VALUE

A number of genus-level taxa have been mentioned but never described or are based on inadequate material. These taxa are listed here if a graptolitic identity can be suggested. This possible graptolite identity is generally based on the preservation of organic material in the fossil specimens or in the concept of the described genus. In some cases, it may be that the publications with descriptions of those taxa have not been traced or are not currently identifiable. For example, many of the several hundred publications of Rudolf Hundt were in newspapers or in obscure or difficult-to-obtain local journals and are impossible to trace, especially if references to these are not correct. Other genera listed here have been referred to a number of fossil groups but can be recognized as graptolitic in nature.

Alexandrograptus Přibyl, 1981, p. 373 (*nom. dub.,* Urbanek & Teller, 1997, p. 43; rejected and invalid name, ICZN, 2003, p. 74) [*Monograptus butovicensis* Bouček, 1936, p. 4; OD]. Přibyl (1981, p. 375) recognized *Alexandrograptus* as a synonym of *Polonograptus,* based on the same types species in a postscript to his paper. Urbanek and Teller (1997) identified the type species *Monograptus butovicensis* as a *nomen dubium* and Riva, Koren', and Rickards (2001) applied to ICZN to replace *Monograptus butovicensis* with *Polonograptus podoliensis* Přibyl, 1983 as the type species of *Polonograptus*.

Amansites Brongniart, 1828, p. 70, *nom. dub.,* herein, *ex Fucoides*, section *Amansites,* Brongniart, 1828, p. 70. The author of the genus *Amansites* is usually listed as Brongniart in d'Orbigny (1849), but it was introduced earlier by Brongniart (1828). The genus was listed as algal remains in d'Orbigny (1849, p. 145), based on the two species: *Amansites serra* Brongniart, 1828 (=*Tetragraptus serra*) and *Amansites dentata* Brongniart, 1828 (=*Levisograptus dentatus*). It was listed in Andrews (1970, p. 16), Burkhardt (2018), and most recently in the Guiry and Guiry (2020) algae database. A type species has never been designated for the genus,

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and it has never been discussed or revised. If these remains are not plant fossils, the genus *Amansites* would be a senior synonym of *Tetragraptus* Salter, 1863a or *Levisograptus* Maletz, 2011. [The history of this taxon can be regarded as a good example of an unwarranted resurrection of a long-unused taxon name for recent interpretations (see Guiry & Guiry, 2020) and also the difficulty of identifying organically preserved fossils.]

Ascograptus Ruedemann, 1925, p. 18, *nom. dub.,* herein [**A. similis;* OD]. Small, conical thecae, arranged spirally along an unbranched axis. *Silurian, Ludlow (Gorstian):* North America. [This taxon could represent a juvenile dendroid graptolite; herein].——Fig. 1,*1a–b*. **A. similis; 1a*, holotype; *1b*, reconstruction (Ruedemann, 1925, pl. 6,*6* and 6,*8*). Scale bars, 1 mm.

Birastrites Geinitz, 1866, p. 125, *nom. dub.,* herein. Remarks of Geinitz (1866) suggest, that he intended to include biserial forms with isolated thecal tubes in the genus, based on a theoretical concept, not on actual material.

Ceramograptus Hudson, 1915, p. 129, *nom. dub.*, herein [**C. ruedemanni;* OD]. *Upper Ordovician:* Canada. The type specimen is preserved on the slab with the holotype of *Urasterella pulchella* (Billings, 1857) as stated by Hudson (1915, p. 129). The specimen is at the GSC, Ottawa, Canada. It is clearly an indeterminable biserial graptolite fragment.——Fig. 1,*2*. **C. ruedemanni,* magnification unclear (Hudson, 1915, pl. 2).

Changyangograptus Shao, Jia, Liu, Fu, Zhang, Qin, Jiang, Tang, Wang, & Hu, 2018, p. 422, *nom. nud.*, herein [**Monograptus changyangensis* Sun, 1933, p. 43; OD]. The taxon was listed in a range chart with a single species from the Aeronian (Lower Silurian), here regarded as the type species, but there is no description available. Chen and Lin (1978) described and illustrated the Llandovery (lower Silurian) *Monograptus changyangensis* on which the genus may be based.

Coelograptus Ruedemann, 1947, p. 266, *nom. dub.,* herein [**Inocaulis problematicus* Spencer, 1878; OD]. Multiramously branching, encrusting colony; thecal style and development unknown. *Silurian, Ludlow (Gorstian):* Canada. [This might be a benthic, encrusting graptolite].——Fig. 1,*3a–b*. **C. problematica* (Spencer), Niagara Dolomite, Hamilton, Ontario, Canada. *3a,* holotype, scale bar, 10 mm (Ruedemann, 1947, pl. 91,*3*); *3b,* plesiotype, scale bar, 5 mm (Ruedemann, 1947, pl. 39,*12*).

Cystoturriculagraptus Hundt, 1953, p. 40, *nom. nud.,* herein. It was cited as *Cystoturriculagraptus* Hundt, 1952, but a 1952 paper with such a citation has not been identified. The genus was listed under the heading Monograptidae without a description or illustration.

Demicystifer Hundt, 1959, p. 27, *nom. dub.,* herein [**Demicystifer cavernalis;* OD]. *Silurian, Llandovery (Rhuddanian,* Parakidograptus acuminatus–Cystograptus vesiculosus *Biozone):* Germany. No description is included, but there is a single illustration of an unidentifiable distal fragment of a biserial graptolite bearing a nematularium. This is not a misspelling of the petalolithid *Demicystograptus* Hundt, 1950; see Lenz & others (2018).—— Fig. 1,*4*. **D. cavernalis,* holotype, Hohenleuben, Thuringia, Germany (Hundt, 1959, pl. 6.*1;* specimen not identified). Scale unclear.

Furkagraptus Hundt, 1959, p. 18, *nom. nud.,* herein [**F. furkatus;* OD]. *Silurian, Llandovery (Telychian,* Spirograptus turriculatus *Biozone):* Germany. The taxon was listed but neither described nor illustrated by Hundt, 1959.

Geminograptus Hundt, 1953, p. 40, *nom. nud.,* herein). The taxon was listed in Hundt (1953) as having been published in Hundt (1951), but a paper describing the taxon has not been identified. There is no illustration or description available. Hundt (1953) also listed a family Geminograptidae.

Graptolites M'Coy, 1850, p. 270. M'Coy (1850) introduced the name as a genus name for monograptids and compared it to '*Diplograpsis*' (now *Diplograptus*) introduced for biserial graptolites. Nicholson (1868) used the genus name, but it survives only as the common name for the group, as it was already used by Barrande (1850) and has never been accepted as a valid genus name.

Graptolithus Linnaeus, 1768, p. 173. Linnaeus (1768) listed the genus *Graptolithus* with a number of taxa that may have included plants (algae), dendrites, and other inorganic objects (In a note on the bottom of page 173: "Petrificatum, proprie dictum, non est Graptolithus, licet petrificaris communiter annumeretur"). The genus name was originally applied to inorganic marks simulating fossils (Linnaeus, 1735). Linnaeus (1751, p. 147) for the first time illustrated a *Graptolitus* (sic) in his account of his Scania visit. This illustration has often been copied and may remain the earliest illustration of a graptolite (see Maletz, 2017, fig. 15,*1*), but a specific identification of the taxon is impossible and the original material is not preserved. Linnaeus (1768) listed among others *Graptolithus sagittarius* and *Graptolithus scalaris*. ICZN Opinion 197 (1954) finally suppressed the genus name *Graptolithus* Linnaeus, 1768 and the species *Graptolithus scalaris* Linnaeus, 1768.

Halograptus Hundt, 1936, p. 36, *nom. nud.,* herein. Hundt (1936) stated that *Halograptus* can be compared to *Abiesgraptus* (Lower Devonian), but is from the Ordovician (Lower Sulurian) at that time in Germany). It may be a misspelling of *Holograptus,* but Hundt never illustrated a specimen under this name in any of his papers.

Janograptus Tullberg, 1880, p. 314, *nom. dub.,* herein [**J. laxatus;* M]. *Lower Ordovician (Floian)–Middle Ordovician (Darriwilian):* worldwide. Regenerated stipe fragments of expansograptid or acrograptid origin; see Albani & others, 2001, p. 390.—— Fig. 1,*5a*. **J. laxatus*, LO 413t, syntype, Scania, Sweden, scale bar, 1 mm (Tullberg, 1880, fig. 5).——Fig. 1,*5b*. Janograptid specimen, GSC 119829, *Pterograptus elegans* Biozone, Mainland,

western Newfoundland, Canada, scale bars, 1 mm (Albani & others, 2001, fig. 5D).

Labrumograptus Hundt, 1953, fig. 122, *nom. dub.,* herein [**L. primigenius;* M]. *Silurian, Ludlow* (Zone 20): Germany. The illustration shows a robust monograptid fragment preserved as an internal cast in pyrite. It is specifically indeterminable.——Fig. 1,*6*. **L. primigenius* Hundt, Ronneburg-Raitzhain, Thuringia, Germany, scale bar, 1 mm (Hundt, 1953, fig. 122; specimen is not identified).

Lunatograptus Shao, Jia, Liu, Fu, Zhang, Qin, Jiang, Tang, Wang & Hu, 2018, p. 422, *nom. nud.,* herein. Three species from the Aeronian (lower Silurian) were listed under this genus name in a range chart, but there is no description available. The species are *Lunatograptus lunata* (Chen & Lin, 1978), *Lunatograptus variabilis* (Ni, 1978), and *Lunatograptus falcata* (Chen & Lin, 1978).

Mystiograptus Hundt, 1965, p. 45, *nom. dub.,* herein [**M. primus;* OD]. Proximally uniserial and distally biserial colony with triangular to hook-shaped thecae. *Silurian, Llandovery (Telychian,* Spirograptus turriculatus *Biozone):* Germany. [The holotype BAF 186/299 (Hundt, 1965, fig. 36.1) is based on an indeterminate tectonically deformed curved uniserial graptolite fragment. The locality is Arnsbach near Gräfenthal, Thuringia, Germany.]

Nereitograptus Hundt, 1953, p. 40, *nom. dub.*, herein [type not selected; ?*N. linearis* Hundt, 1965; M]. The taxon was listed in Hundt (1953) as having been published in Hundt (1951), but a paper describing the taxon has not been identified. Hundt (1965, fig. 36,*2*) illustrated a single specimen as *N. linearis* Hundt, 1965 (BAF H225?). This is a non-identifiable graptolite fragment. Hundt (1953) also used the family name Nereitograptidae.

Nodosograptus Hundt, 1965, p. 46, *nom. dub.,* herein) [**N. pensilis* Hundt, 1965; M]. The genus was spelled *Nodosugraptus* in Hundt, 1953, p. 40. The taxon was already listed in Hundt (1953) as having been published in Hundt (1951), but this paper has not been identified and may not exist. The illustration of *N. pensilis* in Hundt (1965, fig. 38) may be a dorsoventrally preserved fragment of a *Campograptus* or *Monograptus* specimen from the *Stimulograptus sedgwickii* to *Spirograptus turriculatus* Biozone interval at Steinpöhl, Vogtland, Thuringia, Germany.

Paradimorphograptus Hundt, 1953, p. 40, *nom. nud.,* herein). The taxon was listed in Hundt (1953) as having been published in Hundt (1951), but a paper describing the taxon has not been identified.

Phycograptus Gurley, 1896, p. 89, *nom. dub.,* herein [**P. brachymera;* OD]. Ruedemann (1908, p. 245) considered *P. brachymera* Gurley, 1896 from the Lower *Dicellograptus* Zone at Stockport, New York as a frontal view (ventral view) of a *Dicellograptus* stipe, based on his material, but he was unable to find the type specimen in the Gurley collection. Ruedemann (1908, p. 246) discussed *P. laevis* (Hall, 1847) as an undescribed sponge taxon. The type is from the Utica Shale of Turin, Lewis County, New York, USA, and is preserved at the AMNH.

Polygonograptus Bouček, 1957, p. 151, *nom. dub.,* herein [**Palaeodictyota sokolovi* Obut, 1953, p. 54; OD]. Irregular network of mainly pentagonal or hexagonal meshes; thecal structure completely unknown. *Upper Ordovician–Silurian, Wenlock* (Testograptus testis *Biozone*): Czech Republic, Russia. [The genus is unrecognizable and may represent a fragment of a callograptid or dendrograptid graptolite].——Fig. 1,*7a*. **P. sokolovi* (Obut), holotype, Leningrad area, Russia, scale bar, 1 mm (Obut, 1953, pl. 11,*4a*).——Fig. 1,*7b*. *P. boncevi* Bouček, 1957, holotype, Czech Republic, scale bar, 10 mm (Bouček, 1957, pl. 38,*1*).

Praerhynia Hundt, 1949, p. 45, *nom. dub.,* herein. Hundt (1949) introduced the genus without diagnosis and illustrated two specimens. These can probably be recognized as *Cephalograptus cometa* juveniles (Hundt, 1949, fig. 31; *Praerhynia*) and an unidentifiable biserial, most likely a *Normalograptus* fragment (Hundt, 1949, fig. 30, identified as "Sporangien von *Praerhynia*"). The material originated from the Llandovery of Thuringia, probably from the *Lituigraptus convolutus* Biozone, but different biostratigraphic levels were given in Hundt (1949, 1965) for the same specimen. The specimen initially identified as a sporangium of *Praerhynia* was later re-illustrated under the name *Triplograptus triangulatus* (Hundt, 1965, fig. 120; BAF 186/2296, Heinrichsruh/Schleiz, Zone 11/12).

Priodon Nilsson cited in Hisinger, 1831, p. 29, 37; homonym of *Priodon* (attributed to Cuvier) Quoy & Gaimard, 1825, p. 377 [**P. annulatus* Quoy & Gaimard; OD; =*Naso annulatus* (Actinopterygii, Acanthuridae)]. Some confusion arose over the naming of graptolites with the introduction of the genus name *Priodon*, apparently suggested but not published by Sven Nilsson (see Tullberg, 1882, p. 7; cited also in Elles & Wood, 1902, p. vii) and used first by Bronn (1835, p. 56), who indicated the homonymy with the genus *Priodon* Quoy & Gaimard, 1825.

Prionotus Nilsson, cited in Hisinger, 1837, p. 113; homonym of *Prionotus* Lacepède, 1801, p. 20 (a fish genus of the family Triglidae, searobins). A note to the preoccupation of the name *Prionotus* can be found in Tullberg (1882) and Bulman (1929). Regnéll (1991) discussed the influence of the Swedish scientist Sven Nilsson on graptolite research in Sweden and explained the reason for the reference of the genus names *Priodon* and *Prionotus* to Nilsson, even though Nilsson never published a single paper on graptolites.

Procyrtograptus Poulsen, 1943, p. 304, (*nom. dub.,* Bjerreskov, 1975, p. 46) [**P. garboei;* OD]. Bjerreskov demonstrated that this genus consists of a combination of specimens of *Coronograptus gregarius* and *Pernerograptus sudburiae* and is therefore not a valid genus.——Fig. 1,*8*. **P. garboei,* 2943, Bornholm, Denmark, scale bar, 1 mm (Poulsen, 1943, fig. 2).

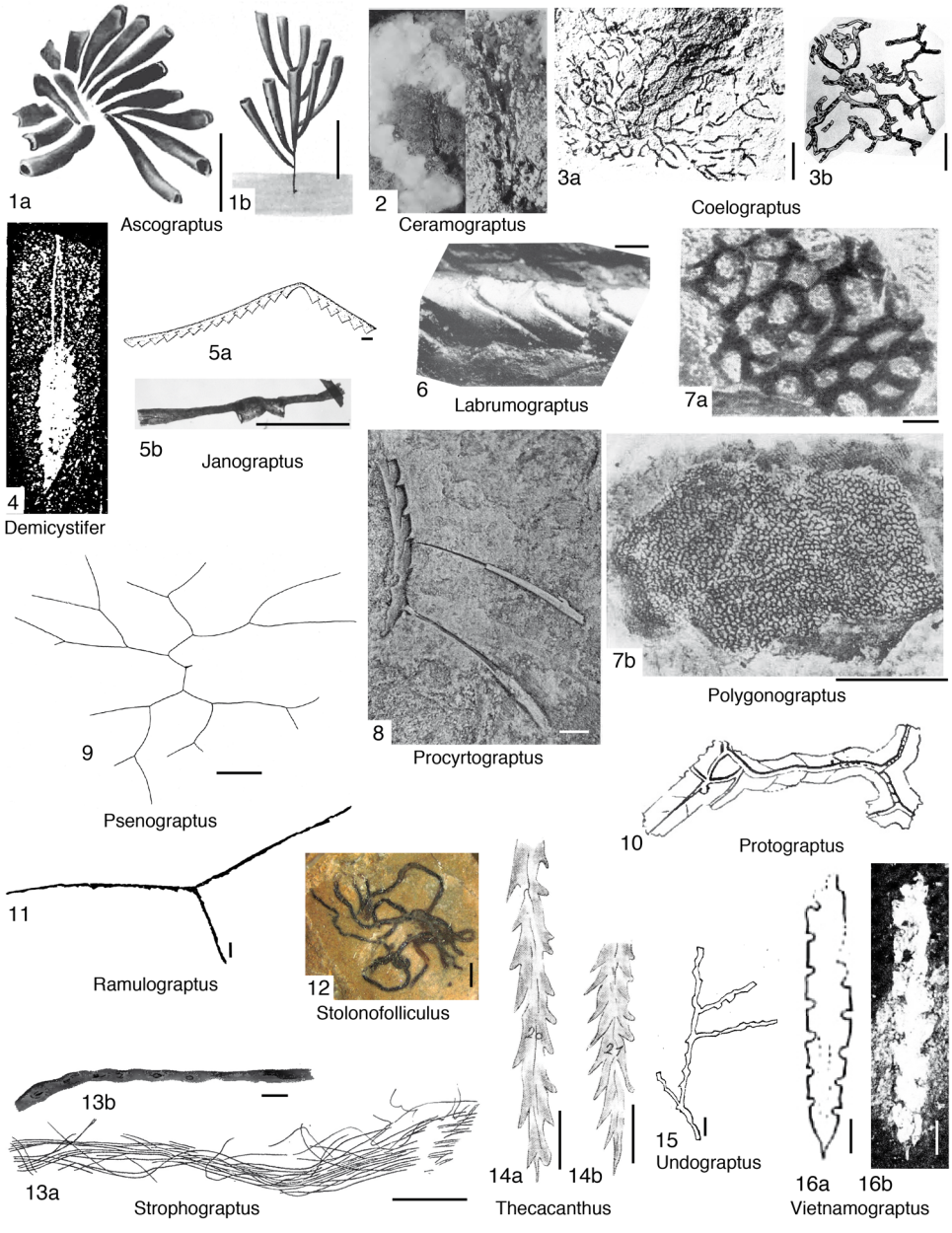

FIG. 1. Uncertain graptolitic remains (p. 2–6).

Protograptus MATTHEW, 1886, p. 31 *nom. correct. pro Protograpsus* MATTHEW, 1886, p. 31, ICZN, Opinion 650, 1963, *nom. dub.,* herein [**P. alatus;* M]. Peculiar in its alation which extends along the axis of the stipe, without apparently bearing cells at the margin. ?*Middle Cambrian:* Canada. [This fragment looks like a late Tremadocian to Floian adelograptid or clonograptid but is specifically indeterminable. It is associated with *Dendrograptus*(?) *primordialis* MATTHEW, 1886. The material is supposed to come from the "highest *Paradoxides* horizon of the St. John Group" (MATTHEW, 1893a, p. 4), thus the middle Cambrian.]——FIG. 1,*10. *P. alatus,* Porter's Brook, St. Martin's, New Brunswick, Canada (Matthew, 1886, pl. 5,*6*).

Psenograptus VandenBerg, 2019, p. 47, *nom. dub.,* herein [* *P. costermansi;* OD]. Multiramous taxa with horizontal funicle, lacking visible thecae. *Lower Ordovician (Floian,* Paratetragraptus approximatus *Biozone):* Australia. [The material is poorly preserved, does not show thecae and therefore is unidentifiable even at the genus level. However, it may represent a multiramous sigmagraptine or dichograptine from the Floian Stage of Australia and is similar to *Clonograptus subtilis* Törnquist (1904) from the Floian of Sweden, in which low-inclined thecae are visible.]——Fig. 1,*9. *P. costermani,* holotype, NMV P 327560, Campbelltown, Victoria, Australia, scale bar, 10 mm (new; drawing based on VandenBerg, 2019, fig. 48).

Ramulograptus Ross & Berry, 1963, p. 84, *nom. dub.,* herein [**R. surcularis;* OD]. *Middle Ordovician (Dapingian–Darriwilian,* Isograptus *Zone):* USA. The specimen appears to be an indeterminable graptolite fragment of dichograptid or sigmagraptid origin.——Fig. 1,*11. *R. surcularis*, holotype, USNM 138492, Vinini Formation, Nevada, USA, scale bar, 1 mm (Ross & Berry, 1963, pl. 5,*6*).

Sinograptus Shrubsole, 1880 (?), *nom. nud.,* herein. Münch (1931, p. 42) discussed the name, but a paper providing a description or illustration is not currently available. According to Münch (1931), "Mr. Korn initially compared the new species with a graptolite described in American literature under the name *Sinograptus* by Shrubsole (1880), but did not find a match" (Münch, 1931, p. 42, translated by J. Maletz). It appears that the name *Sinograptus* Shrubsole, 1880 was used to describe a retiolitid graptolite (see discussion in Münch, 1931, p. 42), but it might not have been published officially and has not been found in an unpublished manuscript. The genus cannot be identified with *Sinograptus* Mu, 1957 (see Maletz, Zhang, & VandenBerg, 2018, Treatise Online, Part V, Chapter 19: Sinograptina).

Spinosudiplograptus Hundt, 1953, p. 40, *nom. nud.,* herein). The taxon was listed in Hundt (1953) as published in Hundt (1951), but a paper describing the taxon has not been identified. Hundt (1953) included the genus in the Diplograptidae, but did not provide a diagnosis, description, or illustration.

Stenograptus Gurley, 1896, p. 296, *nom. nud.*, herein. *Lower Ordovician (Floian–Dapingian?):* Canada. The name was used in a manuscript sent from Charles Lapworth to R. R. Gurley (see Gurley, 1896, p. 303) but appears not to have been published by Lapworth subsequently. The only record is in a list in Gurley (1896, p. 296), in which the species *Stenograptus speciosus* "Lapworth, MS" is included.

Stolonofolliculus Zessin & Puttkamer, 1994, p. 570 (*nom. dub.*, Mierzejewski & Urbanek, 2004, p. 521–522) [**Melanostrophus signum* Öpik, 1930; OD]. Zessin & Puttkamer (1994) even erected a new family, Stolonofolliculidae, for the genus. Mierzejewski (1988) stated that the type material of *M. signum* was lost but referred the taxon to *Graptovermis intestinalis* Kozłowski, 1949.——Fig. 1,*12. **S. signum* (Öpik), holotype, TUG 1053-17, Kukruse Stage, Kohtla, Estonia, scale bar, 1 mm (new; provided by Ursula Toom).

Strophograptus Ruedemann, 1904, p. 716, *nom. dub.,* herein [* *S. trichomanes;* OD]. Bundles of long thin flexuous carbonaceous fibers, subparallel and not bifurcating; thecae indistinct, perhaps represented by minute pores along the stipes. *Middle Ordovician* (*lower Darriwilian,* Levisograptus dentatus *Biozone*): USA. [The genus has to be regarded as graptolite indet. at the moment. It is not even clear whether the material represents graptolite remains. The few known specimens were collected from graptolitic shales and are apparently comprised of organic material.]——Fig. 1,*13a–b*. **S. trichomanes,* holotype (*a*) and enlargement (*b*) of single stipe; scale bar, 10 mm (*a*); 1 mm (*b*) (Ruedemann, 1904, pl. 4,*17,20*).

Thecacanthus Hernández Sempelayo, 1960, p. 35, *nom. dub.*, herein, *ex Glossograptus* (*Thecacanthus*) Hernández Sempelayo, 1960, p. 35 [**Glossograptus (Thecacanthus) loxos;* OD]. *Silurian:* Spain. This taxon was introduced for biserial forms where the interthecal septa "are not precisely marked inside the fossil" and whose "thecae are individualized and prolongate to end in spines with proximal inclination" (Hernández Sempelayo, 1960, p. 35). The material originated from the Almadén syncline and the Almadén mine and may instead represent distal fragments of *Parapetalolithus* or *Glyptograptus*. (information and translation, J. C. Gutiérrez-Marco, May, 2020)].——Fig. 1,*14a–b*. **T. loxos,* two examples, scale bars, 1 mm (Hernández Sampelayo, 1960, pl. 16,*20–21*).

Triplograptus Hundt, 1965 (listed in Hundt, 1959, p. 19) *nom. dub.*, herein [*non Triplograptus* Richter, 1871, p. 251 (type, *T. nereitarum,* OD, trace fossil *Protovirgularia*, see p. 9)]. Tubaria with three rows of thecae. *Silurian, Llandovery (Aeronian):* Germany. [Hundt (1965, in explanation to fig. 39,*1–3*) listed a family Triplograptidae. Hundt (1965) listed a number of species that may belong to the genera *Cystograptus*, *Petalolithus,* and *Normalograptus*.]

Undograptus Nindel, 1949, p. 24, *nom. dub.,* herein [**U. nodosus;* OD]. Undulating stipes with ?alternate thecae, branching observable. [This is certainly a strongly tectonized monograptid graptolite, but too poorly preserved for identification. Nindel (1949, p. 24) indicated that the genus was already described by Hundt (1946), but this paper is unknown].——Fig. 1,*15. **U. nodosus,* Raitzhain, Ronneburg, Thuringia, Germany, Zone 15 (*Monograptus exiguus* Zone of Eisel, 1903; =*crispus/griestoniensis* Zone), scale bar, 1 mm (Nindel, 1949, fig. 21,*4*).

Vietnamograptus van Phuc, 1998, p. 286, *nom. dub.*, herein [**V. thamhocensis;* OD]. According to the author, the new genus is small and short, slender and undulated. The rhabdosome has two types of thecae: monograptid type on one side, but glyptograptid type with the star thecal apertures on the other side (van Phuc, 1998). *Lower Devonian,*

Lochkovian (Uncinatograptus hercynicus *Biozone*): Austria, Vietnam. [No illustrations of Vietnam material are available, but JAEGER (1988) illustrated a single specimen, which is not mentioned in the abstract in which the genus was introduced. It appears to be a secondarily? biserial taxon, originating from a monograptid ancestor (comparable to the abnormal, partly biserial specimen of *Slovinograptus balticus* in URBANEK, 1997, fig. 10)].——FIG.1,*16a–b*. **V. thamocensis,* Obere Bischoffsalm, Carnic Alps, Austria; *16a,* drawing (Jaeger, 1988, fig. 1K); *16b,* photo (Flügel, Mostler, & Schönlaub, 1993). Scale bars, 1 mm.

TAXA OF UNCERTAIN ORIGIN

The genera listed here do not represent graptolitic remains, but cannot currently be assigned to any fossil group. They were initially described as graptolites.

Acanthastus KOZŁOWSKI, 1949, p. 226 [**A. luniewskii;* OD]. *Lower Ordovician (Tremadoc):* Poland. BULMAN (1970) included the order Acanthastida KOZŁOWSKI, 1949 with its single genus *Acanthastus* under the heading Graptolithina *incertae sedis*. KOZŁOWSKI (1949) suggested a chitinous composition and a possible secretion of the features as evidence of a possible graptolite relationship, which has not been verified. The complex development of the specimens and the lack of any recognizable pterobranch features may render doubtful the assignment to the Pterobranchia.——FIG. 2,*1a–c*. **A. luniewskii,* holotype, dorsal (*a*), ventral (*b*), and lateral (*c*) views; scale bars, 1 mm (Kozłowski, 1949, pl. 40,*2*).

Conograptus RUEDEMANN, 1947, p. 267 [**C. simplex;* OD]. Simple, conical tube that contains bundles of filiform thecae within the outer periderm; thecal apertures circular, scattered on surface of rhabdosome. *Cambrian:* USA (Colorado).——FIG. 2,*2a–b*. **C. simplex,* drawings of two fragmented specimens; scale bars, 1 mm (Ruedemann, 1947, pl. 40,*26–27*).

Crinisdendrum DZIK, BALIŃSKI, & SUN, 2016, p. 327 [**C. sinicum;* M]. Mature colony with lateral branches (thecae?) distributed along axis. *Lower Ordovician (Floian,* ?Tetragraptus approximatus *Biozone):* China (Hubei Province). [DZIK, BALIŃSKI, and SUN (2016) erected the family Crinisdendridae for the genera *Crinisdendrum* and *Webbyites* KRAFT, KRAFT, & PROKOP, 2001 and suggested a pterobranch affinity as the most likely hypothesis. There is no evidence of fusellar construction in these taxa to support a pterobranch affinity].——FIG. 2,*10a–b*. **C. sinicum,* Fenxiang Formation, Hubei Province, China; *10a*, juvenile colony, scale bar, 0.5 mm; *10b*, part of mature colony; scale bars 5 mm (DZIK, BALIŃSKI, & SUN, 2016, fig. 5).

Hunanodendrum MU, LI, GE, CHEN, NI, LIN & MU, 1974, p. 220 [**H. typicum;* OD]. *Silurian, Llandovery (Telychian):* China. It is impossible to relate the material to any known graptolite taxon.——FIG. 2,*3a*. **H. typicum,* syntype, scale bar, 10 mm (Mu & others, 2002, pl. 33,*5*).——FIG. 2,*3b*. *H. irregulare* NI, in LI & NI, 1979, holotype, scale bar, 10 mm (Mu & others, 2002, pl. 33,*9*).

Protistograptus MCLEARN, 1915, p. 55 [**Creseis corrugata* MATTHEW, 1892, p. xviii & Errata (listed as *Cyrtotheca* on p. xviii, revised in Errata; no page number); OD; see BULMAN, 1929, p. 181 (referred to *Styliola* by BASSLER, 1915, p. 1242)]. Arched or straight cone, formed from carbonaceous material; probably representing a sicula comparable to the genus *Corynoides*. *Lower Ordovician (?Floian)–Upper Ordovician (Sandbian):* ?Australia (Tasmania), Canada, USA. [The graptolitic assignment is based on the presence of carbonaceous material and the interpretation as a large sicula, but the identification is uncertain. MATTHEW (1893b, p. 105) described it as "a horny consistency, or of thick chitenous substance." The specimens may be comparable with carbonaceous problematica from the Martinsburg Formation of Pennsylvania (MEYER & others, 2018) (see Fig. 2,*5b*)].——FIG. 2,*5a*. **P. corrugata* (MATTHEW), St. John, New Brunswick, Canada, scale bar, 1 mm (McLearn, 1915, fig. 2).——FIG. 2,*5b*. Carbonaceous problematica, Martinsburg Formation, USA, scale bar, 1 mm (Meyer & others, 2018, fig. 5D).

Quadruplograptus HAUPT, 1878, p. 51 [**Q. rhomboidalis;* M]. The identity of this material is uncertain and it might not have been a graptolite. Haupt's paleontological collection may be at the University of Wrocław, Poland (formerly Breslau) (SCHÖNWÄLDER, 1882), but the specimen has not been identified.

Undagraptus HEMMANN, 1951, p. 75 [**U. stolzenbergensis;* OD]. The identification is based on the undulating shape of the specimen. The original was said to be in the collection of the author. The counterpart is at Paläontologisches Institut, Martin Luther Universität Halle, Germany (Nr. 48015). The available photo is too poor for an identification or re-illustration.

ARTHROPODS

A few taxa were described initially as graptolites but can be recognized as arthropods. Pieces of phyllocarids, in particular, have been identified as graptolites in the past, either as colonies (rhabdosomes; tubaria), floats, or ovarian capsules due to their representing organically preserved material in graptolitic shales. MANCK (1927) described a number of examples as gonothecae and float structures of graptolites from the Silurian of Germany. GÜRICH (1928) strongly opposed this view and recognized some of the specimens as phyllocarid remains. The most prominent example may be *Megalograptus* MILLER,

1874, now recognized as fragments of an eurypterid.

Coronagraptus Hundt, 1951, p. 60 [**C. singularis;* OD]. *Silurian, Llandovery (Telychian,* Spirograptus turriculatus *Biozone):* Germany. Bulman (1970) considered the genus as unrecognizable. It is clearly a phyllocarid fragment, possibly belonging to the genus *Peltocaris* Salter, 1862 as described by Salter (1863b). The species may be common in the Unterer Graptolithenschiefer in Germany. The genus should not be confused with *Coronograptus* Obut & Sobolevskaya in Obut, Sobolevskaya, & Merkureva, 1968, a Silurian monograptid.——Fig. 2,*6*. **C. singularis*, holotype, not identified, Hässlich near Weckersdorf, Thuringia, Germany, scale bar, 5 mm (Hundt, 1951, fig. 16).

Dawsonia Nicholson, 1873, p. 139 [**D. campanulata;* SD Miller, 1889, p. 184] [*non Dawsonia* Hartt in Dawson, 1868 (Trilobita, Eodiscina); Axheimer, 2006]. The genus is a junior homonym to *Dawsonia* Hartt in Dawson, 1868, thus invalid. Rolfe (1969, p. 316) stated that *Dawsonia* Nicholson, 1873 is a junior synonym of *Caryocaris* Salter, 1863a, but Page and others (2009) discussed *D. campanulata* as a fossil of uncertain origin, a flat problematicum, but recognized that a number of unrelated fossil remains were described under this name, including linguliform brachiopods and crustacean tail pieces.——Fig. 2,*7*. **D. campanulata,* lectotype NHMUK Q253, Silurian, Llandovery, Dob's Linn, Scotland, scale bar, 1 mm (Page & others, 2009, fig. 1a).

Megalograptus Miller, 1874, p. 343 [**M. Welchi;* OD]. Ruedemann (1908, p. 247) discussed the genus as "fragments of a crustacean" and compared it with *Echinognathus clevelandi* Walcott, 1882. Clarke and Ruedemann (1912a, 1912b) referred the material to the Eurypterida. Lamsdell and others (2015) included it in the family Megalograptidae (see Størmer, 1955, p. 36) and recognized the members of the family as the oldest known eurypterids. Tollerton (1989) elevated the family to the superfamily Megalograptoidea.

HYDROIDS

Quite a number of dendroid graptolites have been identified as hydroids in the past (see Maletz & Beli, 2018). Due to their poor preservation, it is often difficult or impossible to determine the true affinity of such taxa. Muscente, Allmon, and Xiao (2016), for example, recognized the hydroid genus *Archaeoantennularia* Decker, 1952 as a benthic graptolite, and there might be more such taxa that could be identified as graptolites in the fossil record. Other taxa have been regarded as graptolites but may belong to the hydroids, as was verified for the genus *Plumalina* (see Muscente & Allmon, 2013).

Archaeodendrum Obut, 1974, p. 9 [* *A. bulmani;* OD] Colony slender, flexuous, shape unknown; thecae tubular, elongate, isolated distally, slightly widening toward the aperture, arranged in triad groups on alternate sides of stem. *Cambrian, Miaolingian (upper Drumian,* Anomocaroides *Zone):* Russia (Siberian Platform). [According to Rickards & Durman (2006, p. 58), this taxon belongs to the Hydroida. It does show an unusual grouping of the thecae and a flexing of the axis. No fusellar features or stolons are known.]——Fig. 2,*8a–b*. **A. bulmani,* holotype (*a*) and paratype (*b*), scale bars, 1 mm (Rickards & Durman, 2006, fig. 47).

Dyadodendrum Sennikov, 1998, p. 18., *ex Archaeodendrum* (*Dyadodendrum*) Sennikov, 1998, p. 18, herein [**A.* (*D.*) *obuti;* OD]. According to Rickards and Durman (2006, p. 58), this taxon belongs to the Hydroida. The authors did not recognize much difference from *Archaeodendrum,* but did not synonymize the two taxa, which they regarded as subgenera.

Plumalina Hall, 1858, p. 143 [**P. plumaria;* OD]. Hall (1858) included the taxon in his family Graptolitidae. Ruedemann (1916) and Bayer (1956) referred *Plumalina* to the Gorgoniidae (Alcyonaria). Sass and Rock (1975) suggested a possible inclusion in the Hydrozoa but were uncertain. Muscente and Allmon (2013) identified the genus *Plumalina* as a hydroid of the superfamily Plumularioidea McCrady, 1859. Dzik, Baliński, and Sun (2016) rejected the hydrozoan affinity of *Plumalina* and suggested an algal relationship.

Protohalecium Chapman & Thomas, 1936, p. 203 [**P. hallianum;* M]. Erect, multiramous tubarium, with isolated tubular thecae, formed in bundles. *Cambrian, Furongian (Paibian,* Olenus *Zone);* Australia. [Rickards and Durman (2006) regarded the genus *Protohalecium* from the Middle Cambrian of Australia as a hydroid. However, there is a chance that the taxon belongs to the Dithecodendridae if the presence of fusellar construction can be proven.]——Fig. 2,*9a–c*. **P. hallianum; 9a*, holotype, Victoria, Australia (Rickards & Durman, 2006, fig. 50a); *9b–c*, counterpart specimens from Que River, Tasmania (Rickards & Durman, 2006, fig. 50). Scale bars, 1 mm.

ECHINODERMS?

Planctograptus Yakovlev, 1933, p. 979 (misspelled as *Planktograptus* in Bulman, 1955, 1970) [**P. rastritoides;* M]. Hexagonal central body (also identified as a central disk, 7.3 × 10 mm) and cirrus rays emanating from its corners. *Upper Silurian?* [Based on the original illustration, the genus may represent an unusual echinoderm but needs to be re-investigated. It is certainly not a graptolite.]——

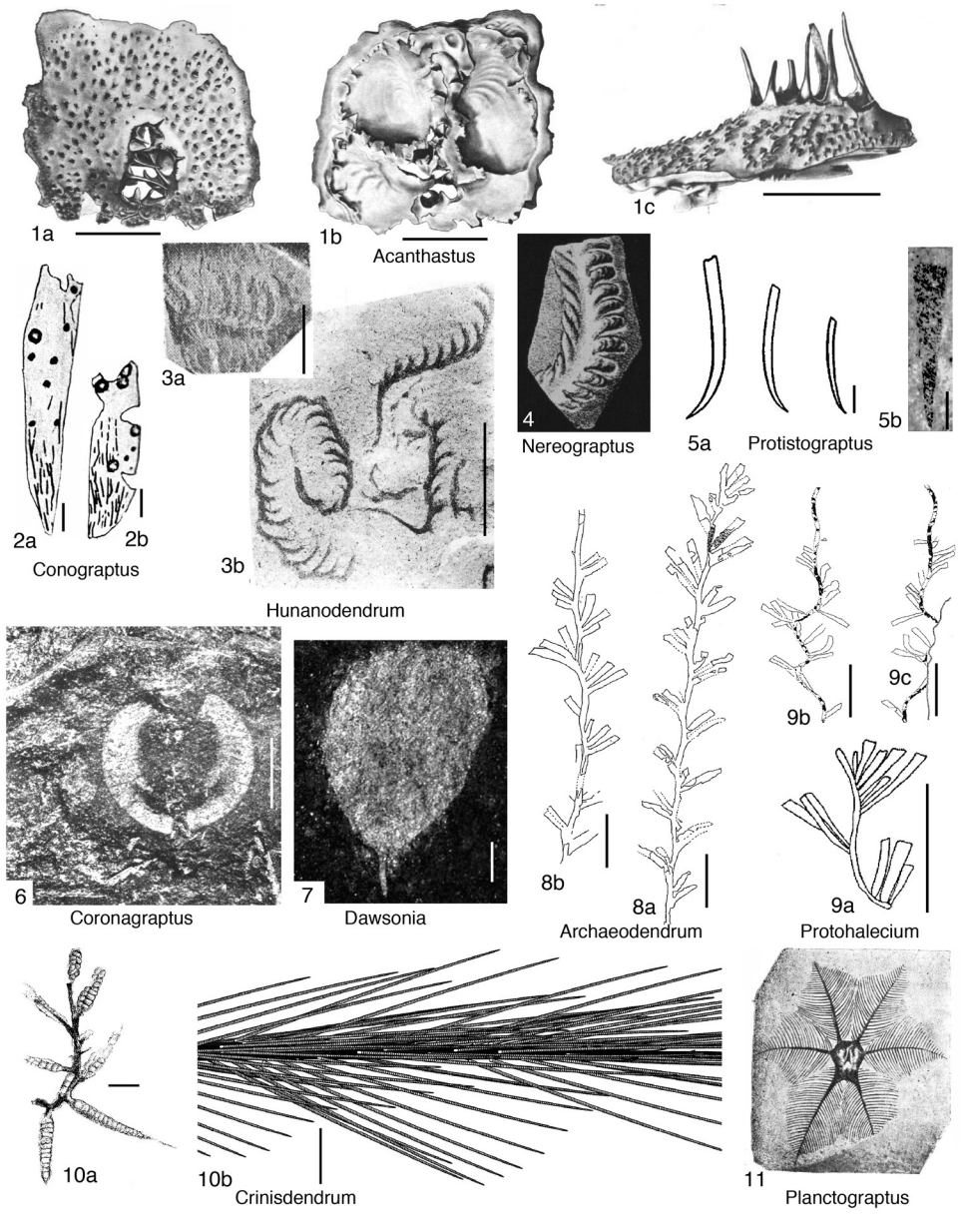

FIG. 2. Genera of uncertain affinity and genera possibly assignable to arthropods, hydroids, echinoderms, or trace fossils (p. 6–9).

FIG. 2,*11*. **P. rastritoides*, holotype, Kazakhstan, scale unknown (Yakovlev, 1933, pl. 2,*2b*).

TRACE FOSSILS

Due to an incomplete understanding of graptolites, early researchers often included unrelated fossils in the group. Thus, a number of genera were initially described as graptolite remains but later recognized as trace fossils. HALL (1865, p. 51) included—with a question mark—the genus *Oldhamia* FORBES, 1849 in his Graptolitidae and listed

the species *Oldhamia fruticosa* HALL 1865 but did not describe or illustrate the species. WHITFIELD (1894) described fossil material as the marine alga *Callithamnopsis fruticosa* (HALL, 1865). The taxon was regarded as a noncalcified dasycladacean alga by LODUCA, KLUESSENDORF, and MIKULIC (2003), who referred to WHITFIELD (1894) as the author of the species. This example illuminates the difficulty of understanding graptolite remains during the early stages of investigation.

Humiligraptus HUNDT, 1940, p. 244 [**H. attenuatus;* SD herein]. *Ordovician (late Tremadocian–Floian):* Thuringia, Germany. HUNDT (1940) referred three species from the Phycodes Group (late Tremadocian–Floian) of Thuringia to this new genus. *H. attenuatus* may represent a poorly preserved trace fossil. There are no good illustrations of the specimens referred to this genus available, and the material has never been revised and was not identified in the Hundt collection at FU Bergakademie Freiberg Thuringia, Germany.

Nereograptus GEINITZ, 1852, p. 27, *nom. correct. pro Nereograpsus* GEINITZ, 1852, p. 27; GEINITZ, 1866, p. 123 [**Nereites cambrensis* MURCHISON, 1839; OD]. GEINITZ (1852) clearly identified *Nereograptus* as giant graptolites (zum Teil gigantische Graptolithinen) from the Ordovician (lower Silurian at the time) of Thuringia, Germany. It seems he wanted to introduce the name *Nereograptus* to demonstrate his interpretation of these fossils as graptolites, because he synonymized the genus *Nereites* with his *Nereograptus*. RICHTER (1849) had previously described *Nereites cambriensis* from Thuringia, even though at the time he did not identify it as a trace fossil but as a kind of fossil worm. There is no doubt that *Nereograptus* GEINITZ, 1852 is a trace fossil and the name is a synonym of *Nereites* MACLEAY, 1839.—— FIG. 2,*4*. **Neoreograptus cambrensis* (MURCHISON), Ordovician, Saalfeld, Thuringia, Germany, scale uncertain (Geinitz, 1852, pl. 5,*20*).

Protovirgularia M'COY, 1850, p. 272 [**P. dichotoma;* M] [=*Triplograptus* RICHTER, 1871, p. 251 (type, *Cladograpsus Nereitarum* RICHTER, 1853, p. 450; M); HAN & PICKERILL, 1994, p. 203]. M'COY (1850) referred the genus *Protovirgularia* to the family Gorgonidae and compared it with some biserial graptolites. HAN and PICKERILL (1994) revised the genus, and SEILACHER and SEILACHER (1994) identified it as a bivalve trace fossil.

MACROALGAE

The identification of fossil algae as graptolites has been common in the past. The reasons for this may be (1) the preservation as organic remains and (2) the general similarity of algal shapes to the shapes of dendroid graptolite tubaria. The taxonomy of fossil noncalcified macroalgae is very difficult due to the typically poor preservation as thin films of carbonaceous material in shales, siltstones, and limestones. They have often been transported and, thus, fragmented and are rarely preserved as complete specimens in their original growth position (see LODUCA & BRETT, 1997; LODUCA, MELCHIN, & VERBRUGGEN, 2011). In a number of genera, the phylogenetic relationships to other macroalgae have been proposed in the literature, but for many forms, an algal origin can only be inferred from the shape of the fossil. The material invariably does not have the typical fusellar structure of the Pterobranchia (graptolites) but is preserved as structureless, dark carbonaceous material. MALETZ and CAMERON (2016) identified the Cambrian alga *Yuknessia* WALCOTT, 1919 as a pterobranch, based on the presence of fusellar construction (LODUCA & others, 2015). MALETZ and BELI (2018) listed the Cambrian algae *Dalyia* WALCOTT, 1919 and *Malongitubus* HU, 2005 as Graptolithina *incertae sedis* and recognized the presumed hydroids *Archaeolafoea* CHAPMAN, 1919 and *Sphenoecium* CHAPMAN & THOMAS, 1936 as rhabdopleurid pterobranchs.

LODUCA, MELCHIN, and VERBRUGGEN (2011) provided the description of a number of dasycladacean algae associated with graptolites from Cornwallis Island in the Canadian Arctic, showing the usual preservation of these floras. LODUCA (1990) identified the genus *Medusaegraptus* RUEDEMANN, 1925 from the Silurian of New York State as a noncalcified dasycladacean, based on the type material and additional specimens from a variety of localities in New York State, USA, and Ontario, Canada. This may have been the start of a more cautious approach to some so-called dendroid graptolite remains and the recognition that some genera may better be referred to as algal remains of various types.

LODUCA and BRETT (1997) described the so-called *Medusaegraptus* epibole of the

Lockport Group (Silurian) of western New York and southern Ontario, in which thallophytic algae and dendroid, benthic graptolites were a common constituent of the fauna and flora. Many specimens of these were found *in situ* because they had grown on the sea floor, associated with other algae, brachiopods, conularids, corals, mollusks, annelids, and arthropods. The authors suggested a water depth of ~10–15 m for the environment in which the *Medusaegraptus* epibole flourished.

No attempt is made to differentiate the discussed genera and refer them to any taxonomic units within the Dasycladales here; therefore the genera are listed in alphabetical order. Only taxa with uncertain, but possible, algal affinity are illustrated through their type material (Fig. 3). Otherwise, the most current revisions of the taxa are referenced below.

Boucekocaulis Obut, 1960, p. 148 [**Acanthograptus jubatus* Obut, 1953, p. 53; OD]. This taxon may represent an alga but needs to be re-investigated.——Fig. 3,*1*. **B. jubatus* (Obut, 1953), fragment, Russia, scale unclear (Obut, 1953, pl. 12,*5a*).

Buthograptus Hall, 1861, p. 18 [**B. laxus;* M]. *Upper Ordovician:* USA. Hall (1861) described *Buthograptus* as a benthic graptolite from the Upper Ordovician of Wisconsin, but Whitfield (1894, p. 352) first identified the taxon as an alga and LoDuca (2019) more recently revised the genus and referred it to the green algal order Bryopsidales.

Calyptograptus Spencer, 1878, p. 459, *nom. correct. pro Calyptograpsus* Spencer, 1878, p. 459, ICZN, Opinion 650, 1963 [**C. cyathiformis;* OD]. The genus is herein identified as a possible alga. The type may, however, represent a poorly preserved callograptid or dendrograptid, but there is no evidence of thecae or fusellar construction.——Fig. 3,*2*. **C. cyathiformis,* 1878), holotype, scale bar, 10 mm (Bassler, 1909, fig. 48).

Crinocaulis Obut, 1960, p. 148 [**C. flosculus;* OD]. The identity of this strange taxon is uncertain, but an algal relationship cannot be excluded.——Fig. 3,*3*. **C. flosculus,* scale unclear (Obut, 1960, pl. 3, fig. 1A).

Diplospirograptus Ruedemann, 1925, p. 34 [**D. goldringae;* OD]. Bulman (1938) expressed doubts about the graptolitic nature of this taxon and suggested an algal affinity. Mierzejewski (1986) discussed *D. goldringae* as a possible alga of the class Chlorophyceae, essentially rejecting an inclusion in the graptolites. This interpretation is supported by the assignment of LoDuca (1990) and LoDuca, Kluessendorf, and Mikulic (2003).

Estoniocaulis Obut & Rotsk, 1958, p. 137 [**E. jaervensis*; OD]. Mierzejewski (1991) investigated the type material and recognized solid, roller-like elements that he compared with the melanosclerites and preliminarily referred the taxon to the order Melanoskleritoidea, a clade of possible algae from the lower Silurian.

Inocaulis Hall, 1852, p. 176 [**I. plumulosa;* M] ?*Ordovician–Silurian:* worldwide. The genus has long been identified as a dendroid graptolite and in the family Inocaulidae, established by Ruedemann (1947). Furthermore, Bouček (1957) referred to the group as the order Inocaulida Bouček, 1957. Mierzejewski (1986, p. 166) doubted the graptolitic nature of *Inocaulis* and discussed the genus as a hydroid. Maletz (2014) suggested that *Inocaulis plumulosa* is an alga, but LoDuca and others (2017, p. 599) illustrated *I. plumulosus* as a "hemichordate with an alga-like tubarium." Because fusellar construction has not been identified in the type species of the genus, its inclusion in the graptolites is uncertain, and the preference here is to keep it as an alga. However, most species referred to *Inocaulis* may represent species of the Callograptidae and should be referred to a number of other genera. Muir, Zhang, and Lin (2013) discussed a single fragment as *Inocaulis* sp., in which fusellar construction was detected.——Fig. 3,*4a–b*. **I. plumulosa; 4a*, illustration of type (Hall, 1865, fig. 26); *4b–c*, commonly illustrated typical specimens; scale bars, 10 mm (Bassler, 1909, fig. 59, 61).

Leveilleites Foerste, 1923, p. 62 [**L. hartnageli;* M]. The taxon was originally described as a possible alga but referred to the graptolites by Ruedemann (1947). An alga with similar form has been illustrated in Tinn and others (2009) from the Llandovery (Aeronian) of Estonia, suggesting an algal relationship of *Leveilleites*.

Medusaegraptus Ruedemann, 1925, p. 29 [**M. mirabilis;* OD]. Bulman (1938) already expressed his doubts on this taxon and suggested an algal affinity. Mierzejewski (1991) discussed *Medusaegraptus* as an alga, and LoDuca (1990) referred the taxon to the noncalcified dasycladacean algae.

Palmatophycus Bouček, 1941, p. 3 [**P. kettneri;* OD]. *P. kettneri* was originally described as a dendroid graptolite from the Silurian (Wenlock/Ludlow) of the Czech Republic. LoDuca and others (2017) illustrated the taxon from the Eramosa Formation of Canada as a non-calcified marine alga.

Rhadinograptus Obut, 1960, p. 151 [**R. jurgensonae;* OD]. Mierzejewski (1991) did not find evidence of a graptolitic relationship and suggested that the taxon should be regarded as a fossil alga.

Thallograptus Ruedemann, 1925, p. 35 [**Dendrograptus? succulentus* Ruedemann, 1904; OD] [*non Thallograptus* Öpik, 1928, p. 35 (type, *T. sphaericola,* OD [Wimanicrustidae, Graptolithina]); =*Hormograptus* Öpik, 1930 (Wimanicrustidae)]. Ruedemann (1925) discussed a close similarity in shape to marine algae and reported that the thecal apertures appear as pores on the surface. Hewitt

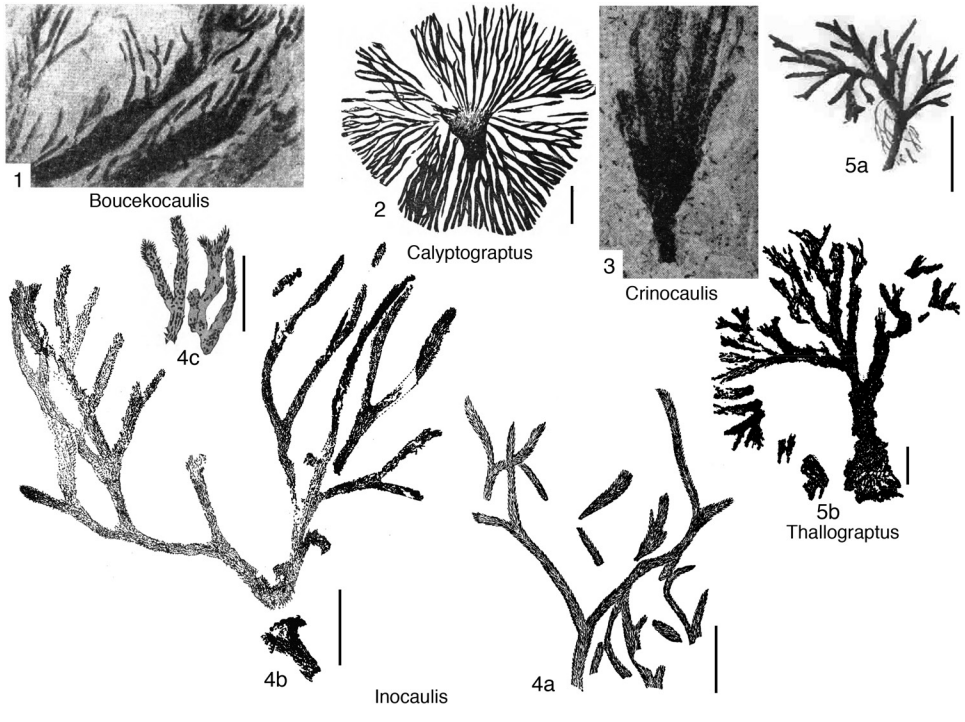

FIG. 3. Possible algae identified as graptolites (p. 10–11).

and BIRKER (1986) discussed the type specimens of *Buthotrephis grantii* DAWSON, 1890 and *Inocaulis vegetabilis* GURLEY in BASSLER, 1909) from the Silurian Eramosa Member of the Lockport Dolomite of Ontario, Canada. Both types represent fragments of a single specimen referred now to *Thallograptus grantii* (DAWSON, 1890) and interpreted as a possible alga, supporting the algal origin of some but not all taxa referred to the genus *Thallograptus* in the past. BULMAN (1970) interpreted *Thallograptus* as a member of the Acanthograptidae (now Callograptidae). Many taxa assigned to the genus in the past may need to be re-evaluated and referred to other genera of the Callograptidae.——Fig. 3,*5a*. **T. succulentus* (RUEDEMANN), syntype, scale bar, 10 mm (Ruedemann, 1904, pl. 4,*4*).——FIG. 3,*5b*. *T. phycoides* (SPENCER, 1884), specimen illustrated as *Thallograptus cervicornis* in BULMAN (1970, fig. 22,*2*). RUEDEMANN (1925, fig. 23) illustrated the specimen as characteristic of the genus *Thallograptus*, scale bar, 10 mm.

LAND PLANTS

It should not be forgotten, that Rudolf HUNDT identified graptolite remains as early land plants. HUNDT (1949, fig. 29) illustrated fragments of a biserial graptolite as "*Praerhynia* spec. Sporangien" and re-illustrated the specimen as *Triplograptus triangulatus* HUNDT in HUNDT (1965). Also, material he identified as *Baragwanathia oelheyi* HUNDT, 1952a (HUNDT, 1952a, fig. 30) might represent graptolite fragments. Uncertain fossils are also the "Praepsilophyten mit Sporangien" (HUNDT, 1952b). Unfortunately, the material illustrated by HUNDT in these papers has not been identified in his collection.

ABBREVIATIONS FOR MUSEUM REPOSITORIES

BAF: Palaeontological collection, Department of Geology, TU Bergakademie Freiberg, Germany

GSC: Geological Survey of Canada, Ottawa, Canada

LO: Lunds Originale, Department of Geology, Lund University, Sweden

NHMUK: The Natural History Museum, London, UK

TUG: Geological collections at the Institute of Geology at Tallinn University of Technology, Tallinn, Estonia

USNM: US National Museum of Natural History, Washington DC, USA

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