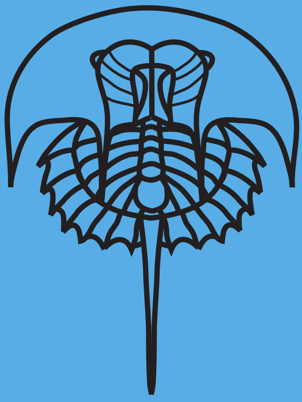

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PART V, SECOND REVISION, CHAPTER 5: HEMICHORDATE TAPHONOMY

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The investigation of taphonomy has long been neglected in the study of fossil Hemichordata, and the results of taphonomic processes are often underestimated. Therefore, misidentifications of pterobranch or graptolite specimens are common, as taphonomic features are often regarded as genuine taxonomic characters. The extremely poor fossil record of the Enteropneusta (see Maletz, 2014a) indicates that preservation is even more difficult in soft-bodied organisms. The taphonomical changes of a specimen start with the death of the organism and the beginning of the decay of its body. Nanglu, Caron, and Cameron (2015) investigated the decay of extant enteropneusts to understand the morphology and early evolution of this group and found some consistent patterns. Cameron (2016) used this information to interpret the early evolution of enteropneusts and to identify characters previously not recognized in fossil taxa (also see Cameron, 2018). Preservational aspects of the few fossil enteropneusts are largely unknown and details have not been investigated. The Burgess Shale species *Spartobranchus tenuis* (Walcott, 1911) as described by Caron, Conway Morris, and Cameron (2013), representing the oldest known enteropneust taxon, is based on flattened carbonaceous compressions. It represents an extraordinary preservation, showing a number of anatomical details not recognized in other fossil enteropneusts, in which only vague outlines have been found. The taphonomy of the closely related but often much smaller pterobranchs has been barely investigated, and little is known on the modifications introduced to the fossils during fossilization and weathering processes. Many features found in fossil graptolites can be shown to represent postmortem effects and the interaction of sedimentary, diagenetic, and metamorphic processes affecting the organic material. In the end, it may be impossible to identify a certain fossil as a pterobranch, as all characteristic features may have been lost.

Benthic graptolites may have been preserved *in situ* in the sediments of the environment in which they grew, but planktic graptolites lived in the water column. Thus, they invariably have to be interpreted as transported and deposited in environments others than the ones they lived in and therefore represent death assemblages. This fact has considerable implication for the interpretation of graptolite taphonomy, as the formative first changes happened to the colonies even before burial in the sediment.

PRESERVATION POTENTIAL

The differences in the preservation potential of the various tissues of the graptolites leads to considerable influence on the decay processes and the degree of preserved anatomical details. Pterobranchs consists of three different parts: (1) the tubaria, the housing constructions secreted by the zooids from organic material; (2) the zooids made from soft organic tissues; and (3) the stolon system of the graptolites (except for the Cephalodiscida), a highly durable strand of organic material connecting the zooids.

Maletz, Jörg. 2018. Part V, Second Revision, Chapter 5: Hemichordate taphonomy. Treatise Online 110: 1–15, 5 fig.

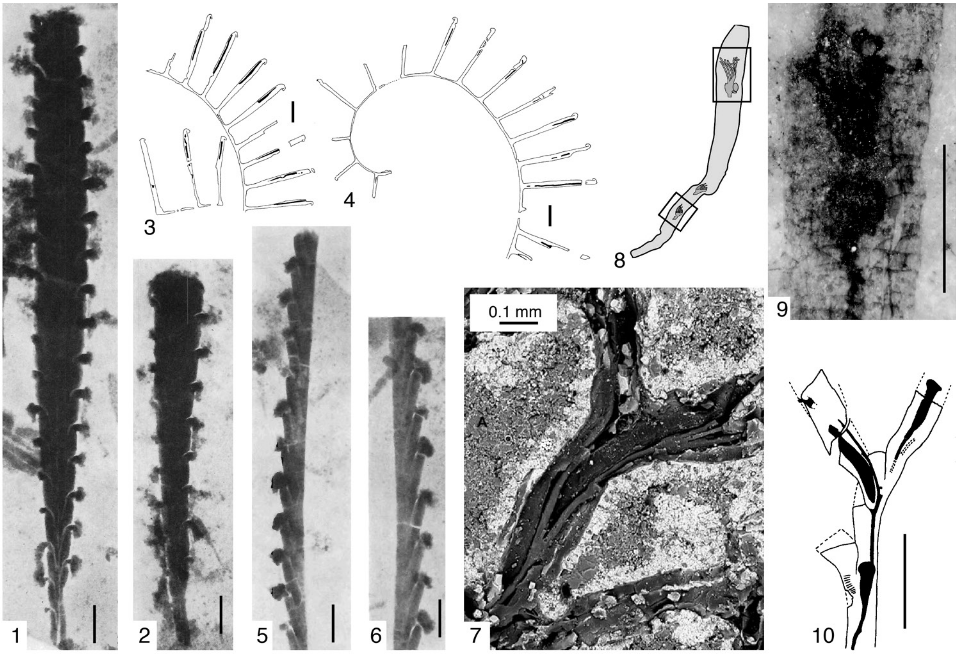

Fig. 1. Remains of fossil zooids and stolons. *1–2, Rhaphidograptus toernquisti* (Elles & Wood, 1906) showing pyritic clouds protruding from the thecal apertures (Bjerreskov, 1978, pl. 21); *3–4, Rastrites geinitzii* Törnquist, 1907, possible remains of the contractile stalk of the zooids in black (Loydell, Orr, & Kearns, 2004, fig. 3); *5–6, Pernerograptus revolutus* (Kurck, 1892), pyritic casts with pyritic clouds at the apertures (Bjerreskov, 1978, pl. 20); 7, *Desmograptus micronematodes* Spencer, 1884, relief specimen showing stolon system (Saunders & others, 2009, fig. 3); *8–9, Sphenoecium obuti* (Durman & Sennikov, 1993); *8,* drawing of thecal tube with possible remains of three zooids (Sennikov, 2016, fig. 3); 9, possible zooidal remains (Sennikov, 2016, pl. 2); *10, Psigraptus jacksoni* Rickards & Stait, 1984, fragment showing remains of zooids (Rickards & Stait, 1984, fig. 4i). Scale bars, 1 mm unless stated otherwise.

Within a few days, the graptolite zooids decay into unrecognizable remains (Briggs & others, 1995) and their fossil record is negligible. The presence of fossil zooids was claimed by Durman and Sennikov (1993) and Sennikov (2016) for the Middle Cambrian *Sphenoecium obuti* (Durman & Sennikov, 1993), showing evidence of anatomical details, such as the soft and hard stolon and the body with the arms associated with the preserved tubarium, showing fuselli (Fig. 1.8–1.9). Surprisingly, the stolon system is largely lacking in this material, even though it should be more durable (Beli, Piraino, & Cameron, 2017). Specimens of *Psigraptus* Jackson, 1967 (Rickards & Stait, 1984; Rickards, Partridge, & Banks, 1991) (Fig. 1.10) and some Silurian monograptids (Bjerreskov, 1978, 1994) may show evidence of decayed zooids through the presence of mineral accumulations inside the tubaria and as cloudy patches in front of the thecal apertures (Fig. 1.1–1.2; 1.5–1.6). Anatomical details are not found in this material. Otherwise, pterobranch zooids are known exclusively from extant species, and their anatomy is well known (see compilation in Maletz & Cameron, 2016).

The only parts of the original zooids that show a higher resistance to decay are the stolons of the graptolites as decay experiments of *Rhabdopleura* Allman in Norman, 1869 specimens indicate (Briggs & others, 1995; Beli, Piraino, & Cameron, 2017). The preservation of the resistant stolon system is known to be common in benthic graptolites, and details are available for the Dendrograptoidea, as shown in

Desmograptus micronematodes Spencer, 1884 (Saunders & others, 2009) (Fig. 1.7) and the Mastigograptidae (Bates & Urbanek, 2002). Isolated material of the stolon system of benthic taxa has been described as hydroid remains (see Mierzejewski, 1986; Maletz, 2014b), and their identification still remains difficult. Stolons in planktic taxa have not been described in detail, but Jackson (1967) and Rickards and Stait (1984) illustrated pyritized stolonal remains in *Psigraptus* (Fig. 1.10), and Hutt (1974) indicated the presence of a stolon system in *Adelograptus tenellus* (Linnarsson, 1871). Zalasiewicz and others (2013) discussed a stolon-like system in the planktic graptoloid *Dicranograptus* Hall, 1865 as an abnormal recalcitrant pectocaulus, but the material appears to represent remains of pressure shadow minerals in a poorly preserved and strongly tectonized graptolite. The described structures do not show any organic material and, thus, may not represent a stolon system. Loydell, Orr, and Kearns (2004) discussed the possible preservation of the contractile stalks (zooidal stalk of Maletz & Cameron, 2016, fig. 1) in *Rastrites geinitzii* Törnquist, 1907 (Fig. 1.3–1.4) and *Neolagarograptus*? Štorch, 1998 from Latvia. The stolon system, however, is not preserved, nor are the zooids. The remains are preserved as a two-dimensional film of organic carbon residues surrounded by an early diagenetic pyrite fill of the thecal tubes.The fusellum of the graptolite tubaria is made from an organic compound, probably collagen (Towe & Urbanek, 1972; Crowther & Rickards, 1977; Runnegar, 1986), but details on the biochemical composition are not available (Foucart & others, 1965; Florkin, 1969; Sewera, 2011). The tubaria of extant pterobranchs are light brown to completely translucent. In some cephalodiscid taxa, foreign material may be incorporated in the tubarium formation (Harmer, 1905; Harmer & Ridewood, 1913). Fossil graptolites are usually dark brown to black (Fig. 2.1–2.5), indicating some compositional modification through the fossilization processes. Sometimes, specimens are lighter brown and partly translucent, indicating their fusellar composition in shale material (Fig. 2.5), but this preservation may, in part, be due to subsequent weathering.

DECAY

The tubes of extant *Rhabdopleura* begin to show signs of decay after four days in oxic environments as actuo-paleontological data show (Beli, Piraino, & Cameron, 2017), but the tubaria remained largely unchanged within the sediments for hundreds of millions of years, as we can see from chemically isolatable specimens. These were originally regarded as representing the animals themselves, but are now understood as the housing constructions (Mitchell & others, 2013; Maletz, 2014b) formed from individual fuselli (e.g., Crowther, 1981; Andres, 1961, 1977, 1980). It is clear that the preservation of graptolite tubaria under oxic conditions is quite limited, and most fossil graptolites are preserved in dysoxic or anoxic sediments or have been entombed in the sediments and protected from the damaging effects of oxigenated organic decay.

Graptolites may be part of the marine snow and the clingfilm preservation (Jones, Zalasiewicz, & Rickards, 2002) described for *Spirograptus turriculatus* (Barrande, 1850) and may be more widely distributed, even though difficult to demonstrate. Even though organic material may be eaten by predators, this has rarely been shown for graptolites (Underwood, 1993; Loydell, Zalasiewicz & Cave, 1998). The sinking of planktic graptolite colonies may have been retarded through the decay of the zooids, leading to uplift from decay gases. Eventually, however, they started settling through the water column and the tiny zooids would have likely disappeared by the time their tubaria reached the seafloor. Once there, the tubaria would be exposed to microbial attacks and damage by burrowers and grazers. Fine hash consisting of graptolite fragments is common worldwide, indicating

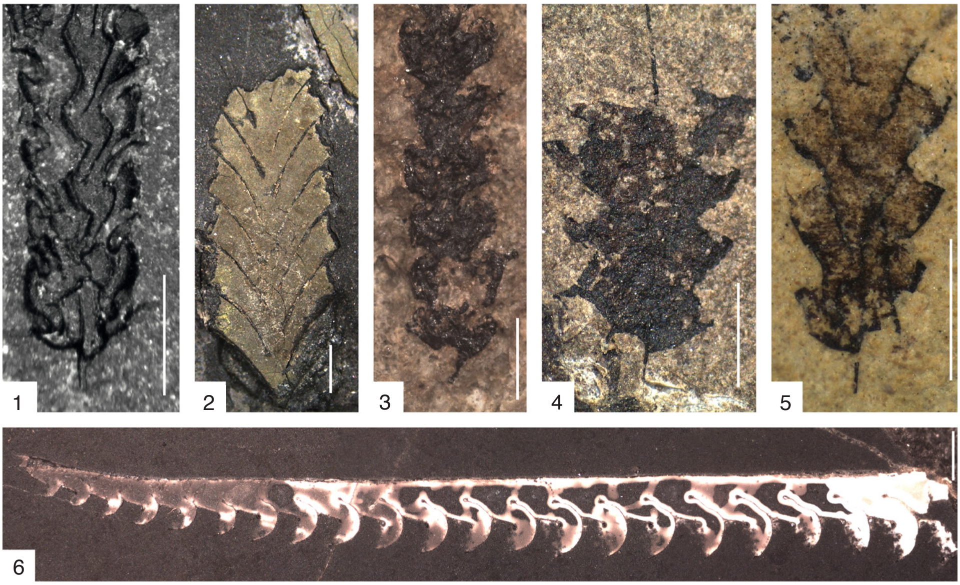

FIG. 2. Graptolite preservation. *1, Archiclimacograptus* MITCHELL, 1987 sp., full relief, Darriwilian, western Newfoundland, Canada (new); *2, Petalolithus palmaeus* (BARRANDE, 1850), LO 1116t, full relief, pyrite fill, polished section, Tomarp, Sweden (new); *3, Levisograptus sinicus* (MU & LEE, 1958), SMF XXIV 424, partial relief, Karga Village, southern Urals, Russia (new); *4, Orthograptus quadrimucronatus* (HALL, 1865), GSC 139251, flattened, L'Egaré Motel, Quebec, Canada (new); *5, Rectograptus gracilis* (ROEMER, 1861), SMF 75826, flattened, showing fuselli, Maquokea Group, Graf, Iowa, USA (new); *6, Monograptus priodon* (BRONN, 1835), SMF XXIV 401, silica coating in chert, Schnebes, Frankonian Forrest, northern Bavaria, Germany (new). All scale bars, 1 mm.

considerable destruction and fragmentation of the tubaria prior to final burial. This process may be interpreted as bioturbation and/or scavenging within unlithified sediments containing abundant graptolite specimens. Microbial destruction may even occur in organically preserved, chemically isolated material in modern fossil collections (see example in Fig. 3.3). RADZEVIČIUS, SCHOPF, and KUDRYAVTSEV (2013) described possible fossil bacteria on the tubarium surface of Silurian monograptids, forming spherical and spirally coiled structures.

There are several ways in which the decay of a graptolite tubarium can be stopped or at least slowed down. Retardation of decay may occur through early lithification of the host rock. Paleozoic limestones often bear well-preserved graptolites, which are supposedly entombed in the rock through early lithification of the lime mud, sheltered from a destructive oxic environment. Preservation in a dysoxic to anoxic environment is another way of delaying the decay of organic material. This is how most graptolites are preserved, and the often-used term, graptolite black shale, reflects this preservation. However, the common occurrence of graptolites in black shales does not indicate an environment in which graptolites flourished (COOPER & others, 2017).

DEPOSITION AND BURIAL

A number of processes can be recognized that modify graptolites before they are entombed in the sediments, showing that they have to be regarded as sediment particles in their behavior. Postmortem transport is commonly demonstrated in graptolite tubaria. Depending on the water current pattern, tubaria of planktic graptolites may either sink vertically down onto the sediment surface or experience a variable lateral displacement. Transport from shallow water regions into deep-water basinal regions appears to be common, exhibited exemplarily by the

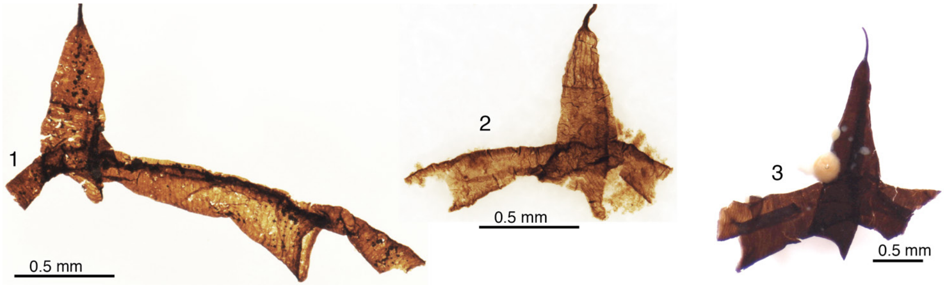

Fig. 3. Flattened graptolites from shales. *1,* Sigmagraptine indet., GSC 140110, showing fusellar construction and prosicula with longitudinal rods, Table Head Group, western Newfoundland; *2,* Sigmagraptine indet., GSC 140111, showing fusellar construction and considerable crumpling, Western Brook Pond, Cow Head Group, western Newfoundland, Canada; *3, Tetragraptus* Salter, 1863 sp., SGU 9621, specimen showing modern fungus growth, Skattungbyn, Dalarna, Sweden. All specimens flattened, chemically isolated from shales, bleached (new).

toe-of–slope environment in which the Lower to Middle Ordovician graptolites of the Cow Head Group in Newfoundland were preserved (Williams & Stevens, 1988, 1991), and in which fragmented specimens of benthic graptolites are also common.

Graptolites can be randomly distributed in a sediment pile or current aligned (Hundt, 1935; Moors, 1970; Cooper & others, 2017), showing postmortem transport. It is not clear whether premortem transport in the water column can also lead to alignment on the sediment surface, but it is unlikely in the case of planktic taxa. Current transport may, however, be a reason for the death of the colonies, in which case the alignment is only the final result of transport into unsuitable environments and subsequent death and settlement of the dead colonies. Graptolites are found in turbidites and tempestites (Hills & Thomas, 1953; Schleiger, 1968; Moors, 1969, 1970), and even in bentonite beds (Mitchell, Brussa, & Astini, 1998), indicating a possible transport as living organisms caught in water turbulences and, on occasion, trapped in volcanic ash.

Time averaging may be common in areas of low sediment accumulation rates, causing high concentrations of taxa that were not living in the same environment or at the same time in suitable environments (Cooper & others, 2017). Time-averaged faunas may also show a quite variable preservation, as specimens deposited earlier on the sediment surface may already have partly decayed before the latest specimens arrived on the seafloor and before the specimens were covered by a new layer of sediment. Time averaging is most prominent in regions with very low sediment input, often in pelagic and hemipelagic sediments, but may also be found in shelf regions with low sediment input.

Benthic graptolites may be covered by layers of sediment and preserved *in situ* (e.g., Bouček, 1957; Erdtman, 1976), but in most cases their fossil remains represent fragments transported from shallow shelf regions into deeper water environments (Maletz, 2006), where they may be found in association with numerous planktic taxa (e.g., Hall, 1865). However, quite a number of well-known planktic graptolite faunas are not associated with benthic taxa. There are barely any benthic graptolites associated with the famous Ordovician graptolite faunas of the Tøyen Shale and Elnes formations of Scandinavia (Monsen, 1937; Maletz, 1997; Maletz & Egenhoff, 2005) or the Silurian faunas of Thuringia, Germany (Schauer, 1971).

Reworking is expected to have been rare or even impossible in graptolites as the tubaria may easily break into pieces when exhumed from a sediment. Transport, thus, was restricted to recently deceased colonies and likely records a secondary depositional site. However, transport of graptolites in clasts of resistant rock types is more common. The best examples can be found in the glacial erratic boulders of Scandinavian origin in northern Germany and Poland (Roemer, 1861; Heidenhain, 1869; Kraft, 1926; Eisenack, 1951; Urbanek, 1958; Maletz, 2008, 2010; Radzevičius & others, 2010; Maletz & Schöning, 2017). Here, Ordovician and Silurian graptolites can be found in sediments deposited during the Pleistocene glaciations. A Paleozoic example of transport of graptolites in clasts is seen in the Daniel's Harbour conglomerate of western Newfoundland (Whittington & Rickards, 1969; Stenzel, Knight, & James, 1990). Reworked clasts of the Table Cove Formation are found in this conglomerate bed, bearing a graptolite fauna that is out of place and older than the conglomerate and the surrounding sediments of the American Tickle Formation. A good example of larger scale transport is the olistostromes of the allochthonous Dauphin Formation of the Hamburg succession of Pennsylvania, which have been tectonically moved twice. Boulder to kilometer-sized masses containing an early Ordovician graptolite fauna of slope origin were first transported to a Middle Ordovician trench and encased within a clastic matrix containing a Darriwilian fauna. Tectonic slices of the trench sequence were then structurally transported to the Martinsburg foreland basin during the Taconic orogeny in the Sandbian (Ganis, Williams, & Repetski, 2001; Ganis, 2005).

During transport, the graptolite tubaria may have experienced bending and breakage, especially in long and robust taxa, while slender forms remained more flexible. Eisel (1908) and Hundt (1910, 1951) already described the influence of tectonic deformation in kinked monograptid taxa, thus, indicating the possibility of bending of tubaria without breakage. Bent specimens were, however, rarely illustrated or mentioned (for an exception, see Haberfelner, 1931, pl. 1,*19b*). Fragmentation may be more common, but astonishingly large, thought to be complete specimens have been described, such as *Paratemnograptus magnificus* (Pritchard, 1892) with an estimated diameter reaching nearly one meter and an incompletely preserved specimen of the straight monograptid *Stimulograptus halli* (Barrande, 1850), showing a length of 1.45 m (Loydell & Loveridge, 2001).

POST-BURIAL MODIFICATIONS

Graptolite tubaria need to be covered within the sediment before stabilization and protection from decay can be established, as they are quite vulnerable to organic decay and destruction when exposed on the sediment surface. After they are covered by a layer of sediment, other factors begin to play a role in the preservation of these seemingly very delicate fossil remains.

Graptolites can be preserved in sediment in full relief (Fig. 2.1) or partly flattened (Fig. 2.3) through infilling with sediment or diagenetic mineral growth before the compaction, leaving the three-dimensional construction still recognizable. Specimens fully preserved in relief may show little outward detail, but slight compaction can reveal the median septum and thecal septae in axonophorans (Fig. 2.1). An early formation of carbonate concretions has prevented the compaction of graptolite colonies in many places. Most notably are the beautifully preserved Llandovery, Silurian graptolites in the Kallholn Shale of Dalarna, Sweden (Hutt, Rickards, & Skevington, 1970; Loydell, 1991; Loydell & Maletz, 2004, 2009); Arctic Canada (e.g., Lenz & Kozłowska, 2006; Lenz & Melchin, 1987; Melchin, 1998); and the glacial erratic boulders of Scandinavian origin mentioned earlier, all of which represent carbonate concretions.

The first post-burial diagenetic effects on the graptolite tubaria are related to the compaction and dewatering of the surrounding sediment, leading to flattening of the specimens. As the graptolite tubaria are made from flexible organic material, flattening within the sediment usually does not cause noticeable effects such as breakage and fractures, but certain other effects of deformation, such as shape distortion, may be noticeable (Briggs & Williams, 1981; Williams & others, 1982). Flattened graptolites are found as thin films of organic material in which only the outlines of the colonies are apparent (Fig. 2.4). Thus, several layers of organic material of the originally three-dimensional fossil (Fig. 2.1) can be superimposed so that thecal outlines, sicular shape, and other features become compressed into a relatively thin, difficult to untangle, layer. Even with IR photography or through chemical bleaching of the specimens, most details cannot be recovered (Bates, Maletz, & Zalasiewicz, 2015). Flattened specimens chemically isolated from shales may preserve their fusellar structure (Fig. 3.1), but also show considerable crumbling of the fusellum without breakage (Fig. 3.2).

Although evidence of chemical alteration of the organic material of the tubaria is problematic, it is to be expected. The dark color of most fossil material reveals an incipient alteration, at the very least. Gupta, Briggs, and Pancost (2006) indicated the presence of aliphatic polymers and lack of proteins in fossil graptolites. Various authors have supposed that the material was originally collagen (Towe & Urbanek, 1972; Bustin, Link, & Goodarzi, 1989), modified by *in situ* polymerization.

Graptolite tubaria preserved in three dimensions can be filled with various mineral material. Pyrite (Fig. 2.2) is the most common mineral infilling graptolites and can lead to beautiful golden shimmering casts when the covering fusellum is lost. Williams (1990b) described winnowed beds of three-dimensional pyritic graptolites originally formed as internal casts from the Youngsters Gulch Member of the Powers Steps Formation from Bell Island, Newfoundland, Canada. The presumed origin of the pyrite was early diagenetic, sulphide-rich conditions in a prodelta environment that also replaced associated oolites. Bjerreskov (1991) recognized incomplete infilling with geopetal orientation and pyritic stalagmites and stalactites in Silurian monograptids. The pyrite fill may be weathered to oxides of various colors and the spectacular pink to white examples of *Cymatograptus bidextro* Toro & Maletz, 2008 are a good example. Phosphatic casts are rare, but have been described for *Climacograptus putillus* (Hall, 1865) from the Elgin Member of the Maquoketa Formation at Graf, Iowa (Werner & Echols, 1958; Goldman & Bergström, 1997). Maletz and Steiner (2015) discussed the preservation of the Middle Cambrian *Sphenoecium wheelerensis* Maletz & Steiner, 2015 and noted a lack of organic material. Thus, they interpreted the remains as a replacement of the fusellum with clay minerals, which could be a secondary development due to weathering processes and not a replacement within the sediment.

A replacement of the graptolite tubaria has often been noted, but appears to be a misinterpretation in most cases. A closer look at the material usually shows a mineral infill or coating of the tubarial walls. A number of papers described silicified graptolites from Silurian chert pebbles of Germany found in various secondary deposits of glacial or glacio-fluvial origin (Hundt, 1934, 1946, 1957; Richter, 1948, 1951; Münch, 1951; Horstig, 1952). These graptolites actually show internal and external coatings of silica (Fig. 2.6) forming a thin crust around the tubarium (Greiling, 1958). Maletz (2009) described another instance of silica-coated graptolites from the Middle Ordovician of Quebec, Canada. The specimens show an irregular mass of silica around the tubaria, keeping the colonies intact when the graptolites were chemically isolated from the limestones. They were, apparently, already somewhat distorted tectonically, before the silica was formed around them. It is not known whether the specimens are also filled with silica. Silica also replaced the biomineralized shells of ostracods in the samples.

The thermal alteration of the graptolite fusellum is known in some detail though the investigation of coalification of organic material to understand the potential for oil and gas generation of graptolite-bearing rocks. It can be regarded as essentially similar in its geological behavior to cuticles of arthropods or to plant tissues. The effect of the thermal alteration is, thus, similar to the coalification of plant material and can even be compared and correlated with the Color Alteration Index for conodonts (Epstein, Epstein, & Harris, 1977; Hartkopf-Fröder & others, 2015). The material changes considerably in its optical properties (Teichmüller, 1978; Goodarzi, 1990; Hoffknecht, 1991; Inan & others, 2016; Schmidt Mumm, & Inan, 2016). Unaltered fossil graptolite material has a dark brown to black color (Fig. 2.1,3–5) that changes with increasing maturation to an intense silvery shine (Fig. 4.1) that may have been mistaken as a pyritization in the past. This is typical of many graptolite faunas of Scandinavia that were affected by regional or local contact metamorphism. The organic material of the graptolite tubaria disappears completely at a moderate to high metamorphic rank but casts may still be recognizable, such as in schists. In these cases, flattened graptolites would have been destroyed without a trace. Graptolite remains may be able to survive considerable alteration; Dieni and others (2005) described identifiable graptolites from boudins in a greenschist unit in the eastern Alps of northern Italy. The material does not show any discernible tectonic deformation. Greenschist-grade metamorphism can also be seen in the sediments yielding early Darriwilian graptolites at Bratland in the Gausdal region of Norway (Lapworth, 1906; Williams, 1984).

DEFORMATION AND RETRODEFORMATION

The morphology of most fossil groups is susceptible to shape distortion from structural deformation in the rock body in which they are found. This, of course, can affect graptolites, sometimes dramatically, and was recognized early. Ironically, the distortion of fossils can assist the structural geologist in kinematic analysis if the undeformed shape of the fossil is known for comparison. Graptolites have been frequently used in this endeavor. Conversely, kinematic analysis can assist the paleontologist in retrodeformation of deformed fossils. Techniques for these procedures have advanced from relatively simple to highly technical. Eisel (1908, p. 219) discussed the deformation of graptolites and the influence on the taxonomic identification of the material. He used a black rubber layer on which he drew the specimens and then imitated the distortion by pulling the material in various directions. Various methods have subsequently been used to understand graptolite deformation (Hills & Thomas, 1944; Jenkins, 1987; Cooper, 1970, 1990; Williams, 1990a).

A closer look at graptolite deformation shows that the effects are more severe and do not just concern the taxonomic identification of the material. The graptolite specimens are distorted with the tectonic deformation of the encasing sediments. This deformation may be dramatic as is shown by the changes in dimensions described by Maletz and others (1998) from Albania and is known from the classic locality of the Wenlock graptolites at Goni, Sardinia, Italy (Gortani, 1922). The direction of deformation can have considerable influence on the appearance of the graptolite specimens as the example of *Spirograptus turriculatus* shows (Fig. 5.2). Specimens with a wide and low cone are associated with ones showing narrow and high cones. On closer examination, the graptolite fusellum shows parallel lines of fractures (Fig. 5.1,5), indicating the tectonic deformation if the organic material is still preserved and recognizable (Mitchell, Brussa, & Maletz, 2008). Characteristic and easily recognizable tectonically deformed graptolites are preserved as pale mineral films on black shale (Fig. 5.4). In these cases, the graptolites are clearly outlined and show strong contrast to the surrounding dark sediment. These mineral films can be identified as phyllosilicate minerals growing as pressure shadow

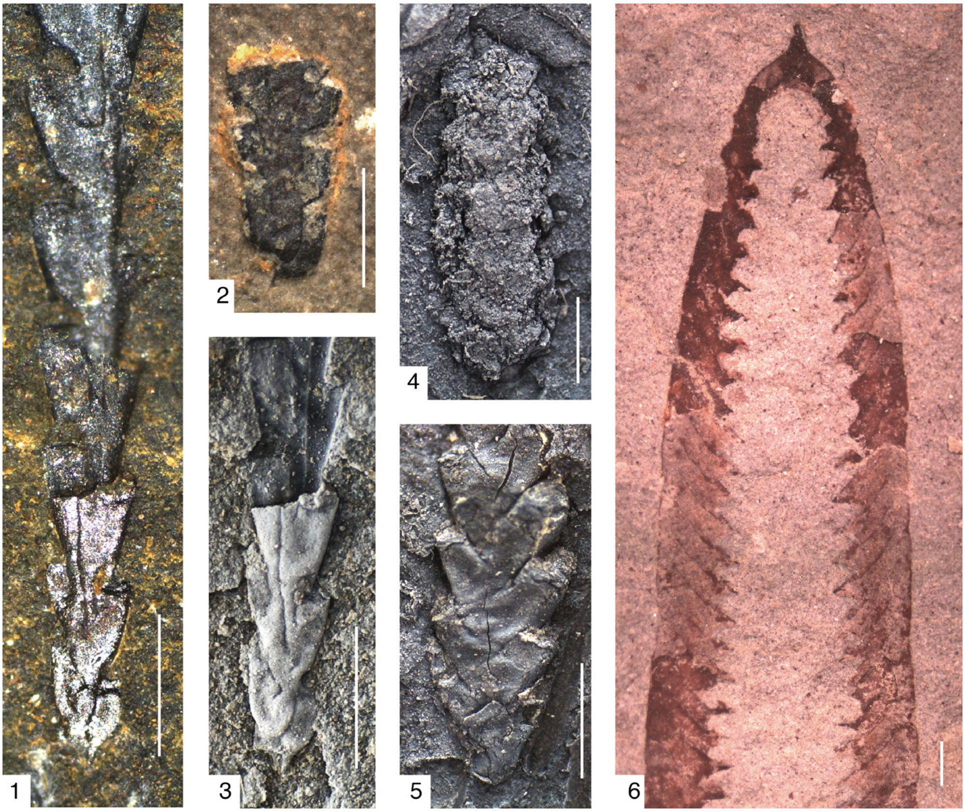

FIG. 4. Weathering. *1, 3, Pronormalograptus antiquus* (GE in GE, ZHENG, & LI, 1990), PMO 234.061, preserved in relief, Elnes Formation, Slemmestad, Norway; *1,* showing highly coalified, silvery shining fusellum; *3,* same specimen coated with ammonium chloride to highlight structure; *2, Normalograptus mohawkensis* (RUEDEMANN, 1912), GSC 139252, low relief, weathered pyritic cast with preserved dark fusellum, L'Egaré Motel, Quebec, Canada; *4–5, Pseudorthograptus cyperoides* (TÖRNQUIST, 1897), Tomarp, Scania, Sweden; *4,* LO 1294T, strongly weathered pyritic cast; 5, LO 1296t, weathered pyritic cast, surrounding fractured fusellum; *6, Didymograptus murchisoni* (BECK in MURCHISON, 1839), SMF 75827, flattened, weathered, Darriwilian, Jordan, exact locality unknown; all scale bars, 1 mm (new).

minerals around the organic remains of the graptolites (UNDERWOOD, 1992). Often the organic material of the graptolites is preserved in unweathered specimens. The mineral films can be of various colors, from whitish to yellow and orange, and light green to blue, depending of the composition of the minerals and the amount of weathering. The minerals are often loosely termed chlorite-group minerals and were regarded as replacement of the graptolites in earlier literature. RICHTER (1853) originally described them as fibrous, silvery white to greenish minerals from the Silurian of Thuringia, but GEINITZ (1852) had already termed the material talcum. GÜMBEL (1868) described the mineral as a pyrophyllite and compared it with the minerals surrounding many Carboniferous plant fossils. KOBELL (1870) described the mineral as gümbelite, but this name has rarely been used in the scientific literature.

The scanning electron microscope backscatter method (BSEM) can easily differentiate the films of pressure shadow minerals from the organic material of the graptolite fusellum (Fig. 5.5), which is difficult to see with the unaided eye (Fig. 5.6). Even

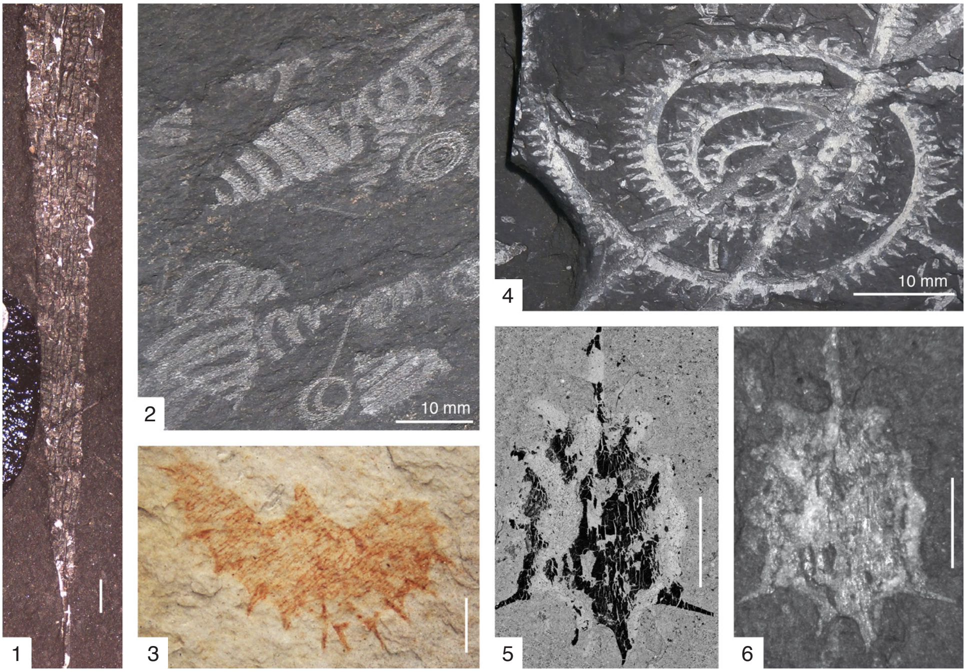

FIG. 5. Deformation and weathering. *1, Normalograptus rectangularis* (M‘Coy, 1850), SMF XXIV 350, flattened, strongly tectonically distorted, showing parallel fractures in fusellum, Ölsnitz, Voigtland, Germany; *2, Spirograptus turriculatus* (Barrande, 1850), SMF XXIV 328 (acquired through exchange from Hemmann), flattened, tectonically distorted, zone 15, locality unknown, Hemmann collection; *3, Arienigraptus angulatus* (Mu, Geh & Yin, in Mu & others, 1962), SMF 75825, flattened, tectonically distorted and weathered, Wellsford Riffle Range, east of Bendigo, Victoria, Australia; *4, Oktavites spiralis* (Geinitz, 1842), SMF PK 767, flattened, showing high amount of pressure shadow minerals (white), Grobsdorf, Thuringia, Germany; *5–6, Nanograptus phylloides* (Elles & Wood, 1908), paratype, GSE 5495; *5,* BSEM photo showing preserved fusellum in black; *6,* normal light photo, showing light color of fusellum and pressure shadow minerals in contrast to dark sediment; all scale bars, 1 mm, unless stated otherwise (new).

in deeply weathered material, the tectonic lineation or foliation may provide clear evidence of deformation of a graptolite (Fig. 5.3). In this specimen, the fusellum is not preserved and the reddish material represents iron-stained pressure shadow minerals.

WEATHERING

Weathering effects (Fig. 4–Fig. 5) have rarely attracted attention in graptolite research, even though it is obvious in many graptolite specimens. Black shale may weather to a light grey, yellow, or even whitish color, and the organic material of the graptolites in these cases show a strong contrast, while in fresh material they are barely visible. Red iron staining may also be common in specimens and on pressure shadow minerals (Fig. 4.6). Surface weathering of strata or the mineral infilling of the tubaria can degrade or destroy graptolite specimens. Pyrite weathering (Fig. 4.2) may destroy beautiful relief specimens in short time and even affect material in collections as pyrite disease (Birker & Kaylor, 1986; Newman, 1998) (Fig. 4.4–4.5). Weathering of pyritic casts may lead to the formation of reddish to yellow iron minerals or staining of the sediment surface (Fig. 4.2). Weathering is independent of tectonic deformation and both factors may be difficult to separate in seemingly well-preserved material.

ABBREVIATIONS FOR MUSEUM REPOSITORIES

GSC: Geological Survey of Canada, Ottawa, Canada

GSE: Geological Survey Museum (British Geological Survey), Keyworth, Nottingham, UK

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

PMO: Natural History Museum, Paleontological Type collections, University of Oslo, Norway

SGU: Sveriges Geologiska Undersökning, Uppsala, Sweden

SMF: Naturmuseum Senckenberg, Frankfurt am Main, Germany

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